

## *Scaptochelys*: Generic Revision and Evolution of Gopher Tortoises

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Comparative morphologic studies of the modern and fossil gopher tortoises of North America have led to the documentation of two species complexes. These species groups are judged sufficiently distinct so as to warrant formal generic separation. Accordingly, the genus *Gopherus* is restricted to an assemblage of highly specialized tortoises ranging from the early Middle Miocene (Hemingfordian) to Recent times. *Gopherus polyphemus* (=type species) and *G. flavomarginatus* are the living representatives. A new genus, *Scaptochelys*, is proposed for the more generalized gopher tortoises ranging in age from Middle Oligocene (Orellan) to Recent. *Scaptochelys agassizii* (=type species) and *S. berlandieri* are the surviving members of this genus.

*Gopherus* is characterized by a suite of morphological features which distinguish it from *Scaptochelys* and all other known testudinids. These include: 1) a hypertrophied inner ear containing a massive saccular otolith; 2) short, robust cervical vertebrae with enlarged, closely joined pre- and postzygapophyses; 3) a specialized, interlocking joint between cervical 8 and the first dorsal vertebra; 4) attachment of the first dorsal vertebra to a distinct, bony strut on the nuchal plate; 5) a modified manus typified by enlarged, spatulate ungual phalanges, 3 to 4 subradial carpal bones, a restricted mesocarpal joint and true unguligrade stance. *Scaptochelys* exhibits none of these derived characters. In the development of its otolithic ear, *Gopherus* appears to be unique among tetrapods.

Structural specialization of the cranium and neck in *Gopherus* are functionally related to burrowing. Members of this genus appear to use the head and neck to brace or stabilize the trunk while digging with the forelimbs. Burrowing in *Scaptochelys* presumably does not involve comparable "head-bracing" behavior. Unlike *Gopherus*, the skull and neck of *Scaptochelys* show no modification for withstanding large mechanical stresses. The unique otolithic ears of *Gopherus* most probably function as high-gain seismometers for the detection of weak ground vibrations.

The homologies of the chelonian carpus and those of land tortoises in particular are reevaluated utilizing newly acquired data from Eocene and Oligocene testudinids. The primitive carpal arrangement of turtles is similar to that of certain stem reptiles (i.e. Permian captorhinids). Homologies established by previous workers for the carpus of gopher tortoises are shown to be incorrect. The carpus of *Gopherus* is structurally adapted for digging in friable soils whereas that of *Scaptochelys* is more suited to overland travel and burrow excavation in resistant soils.

Paleontologic evidence points to an Early Miocene (Arikarean) origin of *Gopherus* in the Great Plains region of North America. At least three environmental factors may have contributed to the origin of the genus by favoring increased fossorial ability. These factors are: 1) climatic cooling; 2) increased aridity and seasonality of rainfall; 3) the widespread development of sandy soils.

THE gopher tortoises of North America are widely recognized as a distinct, closely related testudinid assemblage characterized by their fossorial habits. At present, the four living species and numerous fossil relatives are collected under a single generic heading, *Gopherus*

(Auffenberg, 1962, 1966, 1974, 1976; Auffenberg and Milstead, 1965; Brattstrom, 1961; Legler and Webb, 1961; Loveridge and Williams, 1957; Williams, 1950b, 1952). Despite some ill-founded arguments to the contrary (e.g. Grant, 1960; Wermuth and Mertens, 1961),

there is now considerable evidence that the genus *Gopherus* embodies two separate species complexes. Auffenberg (1966, 1976), in particular, has demonstrated numerous osteological features by which the modern species may be divided into an *agassizii* group (i.e., *G. agassizii*, *G. berlandieri*) and a *polyphemus* group (*G. polyphemus*, *G. flavomarginatus*). The two species groups are, according to Auffenberg (1976), distinct by the Early Pleistocene.

My own comparative morphological and functional investigations of fossil and Recent gopher tortoises support the existence of two species complexes (Bramble, 1971, in press). Indeed, these studies have shown structural and functional divergence between the groups to be far more profound than the published literature would indicate. The *agassizii* and *polyphemus* groups are, in fact, demonstrably separate, distinct lineages since at least the early-Middle Miocene (Bramble, 1971). Tortoises of the *polyphemus* group have become highly specialized for a fossorial existence. Attendant structural adaptations immediately set the lineage apart—not only from other gopher tortoises, but all other chelonians and, in certain respects, from all known tetrapods.

A generic revision of gopher tortoises is overdue. So radically different is the *polyphemus* group, that it surely warrants a separate generic standing within the Testudinidae. Accordingly, in this paper I recommend a new genus, *Scaptochelys*, be erected for gopher tortoises of the *agassizii* group. In the pages that follow I have outlined some of the major structural distinctions between *Scaptochelys* and the restricted genus, *Gopherus*. Brief discussions on the potential functional or adaptive significance of these character states is also provided, but a more rigorous functional analysis will be the topic of a separate paper. Also included in this paper are comments on the skeletal homologies of the chelonian carpus as well as possible historical influences on the evolutionary patterns of gopher tortoises.

#### MATERIALS

The comparative morphologic data upon which this study is based comes from an extensive body of Recent and fossil osteological materials belonging to the following institutions and the personal collection of the author. Listings of individual specimens examined are available upon request. R and F are used to indicate

whether the specimens examined were Recent or fossil. Abbreviations in parentheses indicate specific collections whose specimens are cited in the text or figures of this article. American Museum of Natural History (F, R); Arizona State University, Department of Zoology (F); Bureau of Economic Geology, University of Texas (F); California Academy of Sciences (R); Carnegie Museum (CM) (F); Field Museum of Natural History (F, R); Florida State Museum (R); Natural History Museum of Los Angeles County (F, R); National Museum of Natural History, (USNM) (F); Museum of Comparative Zoology (MCZ) (F, R); Museum of Northern Arizona (F); Museum of Paleontology, University of California, Berkeley (UCMP) (F, R); Museum of Vertebrate Zoology (MVZ) (R); Plains Pamphlet Historical Museum, Canyon, Texas (F); San Diego State University, Department of Zoology (Collection of Richard Etheridge) (RE) (R); South Dakota School of Mines and Technology, Rapid City (F); University of California, Riverside, Department of Geology (F); University of Colorado, Museum of Natural History (F); University of Kansas, Natural History Museum (KUP) (F); University of Oregon, Museum of Natural History (F, R); Texas Natural History Collection (R); University of Utah, Department of Biology (UU) (R); Yale Peabody Museum (F); osteological collection of the author (DMB).

#### SYSTEMATICS

Formal definitions of the genera *Scaptochelys* and *Gopherus* are given below together with their known geologic ranges and included species. Species synonymies are listed on the basis of original descriptions only. Auffenberg (1974) has provided a more extensive listing of past usages and generic assignments for fossil species. Also indicated are those fossil taxa which have either been described as gopher tortoises or are assigned to the genus *Gopherus* by Auffenberg (1974) but which, in my opinion, are neither *Gopherus* nor *Scaptochelys*.

#### *Scaptochelys*, new genus

*Etymology*.—Greek, *scaptos*, digger + *chelys*, tortoise.

*Type species*.—*Xerobates agassizii*.

*Geologic range*.—Middle Oligocene (Orellan) to Recent.

*Included species.*—*Scaptochelys agassizii* (Pleistocene, Recent); *S. berlandieri* (= *Gopherus auffenbergi*) (Pleistocene, Recent); *S. laticuneia* (= *Testudo praeextans*) (Oligocene); *S. mohavense* (= *Gopherus depressus*; *Testudo milleri*) (Miocene); additional undescribed fossil species.

*Definition.*—Gopher tortoises with the following combinations of features: cranium relatively dolicocephalic; inner ear chambers not inflated; sacculus containing a small otolithic mass; cervical vertebrae not appreciably shortened, pre- and postzygapophyses not enlarged, widely separated; cervical 8 without elongated postzygapophyses; first dorsal vertebra with small zygapophyses and neural arch suturally united with neural plate 1; manus with two subradial bones (carpal 1, medial centrale); ungual phalanges not greatly enlarged or spatulate; mesocarpal joint well-developed; manus digitigrade.

*Gopherus* Rafinesque, 1832

*Synonyms.*—*Bysmachelys*, *Xerobates*.

*Type species.*—*Testudo polyphemus*.

*Geologic range.*—Middle Miocene (Hemingfordian) to Recent.

*Included species.*—*Gopherus brevisterna* (Miocene); *G. canyonensis* (= *Testudo pertenuis*) (Pleistocene); *G. edae* (= *Testudo hollandi*) (Miocene); *G. flavo-marginatus* (= *Gopherus huecoensis*) (Pleistocene, Recent); *G. hexagonata* (= *Testudo laticaudata*) (Pleistocene); *G. pansa* (Miocene); *G. polyphemus* (= *Testudo atascosae*) (Pleistocene, Recent); *G. praecedens* (Pleistocene); *G. vaga* (Miocene); additional undescribed fossil species.

*Definition.*—Gopher tortoises with the following combination of features: cranium relatively brachycephalic; inner ear chambers hypertrophied; sacculus containing a massive otolithic structure; cervical vertebrae short, pre- and postzygapophyses enlarged and drawn together, especially so on cervicals 6 and 7; postzygapophyses of cervical 8 elongated, separated by a deep, slot-like notch; first dorsal vertebra with expanded zygapophyses, neural arch extended anteriorly and suturally joined to strut on nuchal plate; manus with three or four subradial bones (carpal 1, 2, medial centrale, frequently metacarpal 1); ungual phalanges en-

larged, spatulate; mesocarpal joint restricted or eliminated; manus sub- to fully unguligrade.

The following fossil species have been referred to *Gopherus* by Auffenberg (1974) and certain earlier workers (e.g., Williams, 1950b, 1952). But on present evidence these appear not to be gopher tortoises. I have indicated in parentheses the probable generic assignments of these taxa. *Gopherus copei* (= *Stylemys*) (Miocene); *G. dehiscus* (= *Geochelone*) (Miocene); *G. emiliae* (= *Stylemys*) (Miocene); *G. neglectus* (= *Stylemys*) (Oligocene); *G. undabuna* (= *Stylemys*) (Miocene).

#### CRANIAL MORPHOLOGY

The skull of *Scaptochelys* has proportions similar to that of other testudinids, e.g. *Geochelone*, *Testudo*, but the cranium of *Gopherus* is decidedly brachycephalic (Legler, 1959; Bramble, 1971; Auffenberg, 1976). Most of the relative increase in skull width in *Gopherus* occurs in the otic region. Investigations show that broadening of the head in this genus is the result of marked hypertrophy of the inner ear, particularly the saccular chamber (Bramble, 1971, in press). Externally, modification of the inner ear is reflected in the broad dorsal exposure of the prootic and opisthotic bones (Fig. 1B). These same bones have limited exposure in *Scaptochelys* (Fig. 1A), and the prootic is often nearly obliterated in dorsal view by an overlapping parietal bone just as in *Testudo* (Loveridge and Williams, 1957). Internally, the inner ear of *Gopherus* is unlike that of *Scaptochelys* and all other tetrapods. The sacculus contains an enormous otolithic mass. Relative to head size, the otolith of *G. polyphemus* is comparable to the largest otoliths reported in teleost fishes. In *G. flavo-marginatus* the otolith is relatively smaller but, nonetheless, still huge by any tetrapod standard. A very much smaller, but well-formed saccular otolith is present in *Scaptochelys* (Bramble, in press).

In other details of auditory structure *Gopherus* continues to be set apart from *Scaptochelys* and all other testudinids. Thus, the saccular macula of *Gopherus* is modified to support the heavy otolith. The enlarged macula is reinforced internally by hyaline cartilage and also contains bundles of smooth muscle (Bramble, in press). This is so far the only known instance of muscular tissue within the vertebrate inner ear. Two longitudinal tracts of hair cells lie on the macular surface rather than a single tract

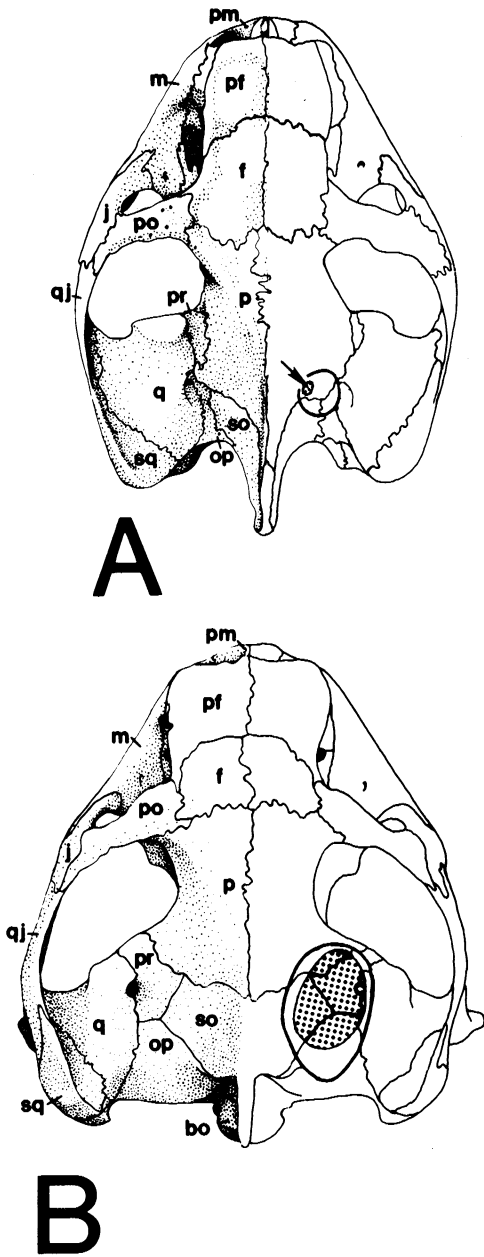


Fig. 1. Dorsal views of adult crania of *Scaptochelys agassizii* (MVZ 55512) (A) and *Gopherus polyphemus* (DMB 1020) (B). Margins of the inner ear chamber are indicated on the right by heavy outline; saccular otolith is stippled and marked by the tip of the arrow in *Scaptochelys*. Abbreviations for cranial bones: f = frontal; j = jugal; m = maxillary; op = opisthotic; p = parietal; pm = premaxillary; po = postorbital; pr = prootic; prf = prefrontal; qj = quadratojugal; soc = supraoccipital; sq = squamosal.

as is seen in *Scaptochelys*, *Geochelone* and *Testudo*. Hypertrophy of the inner ear has also led to relative reduction of the middle ear chambers in *Gopherus* (Bramble, 1971, in press). Other secondary modifications of the middle ear include a substantial expansion of the stapedial footplate together with concurrent reduction in the size of the tympanic membrane and extra-stapedial plate. Representative surface area ratios of extrastapes to stapedial footplate are approximately 3:1 and 8:1 respectively for *G. polyphemus* and *G. flavomarginatus* as compared to 28:1 in *S. agassizii*. The relative proportions of the middle ear chambers and stapedial footplate of *Scaptochelys* appear to be comparable with that of other land tortoises.

**Function.**—Behavioral and biomechanical considerations suggest that at least two factors may be responsible for cranial specialization in *Gopherus*. The inflated, otolithic ears most probably function as extremely sensitive vibration detectors, or seismometers (Bramble, in press). Presumably, these unique sensory mechanisms permit *Gopherus* to detect weak, low-frequency ground motion produced by the footfalls of heavy-bodied mammals, such as ungulates. The evolution of seismic ears in *Gopherus* may represent a major adaptation allowing these tortoises to coexist with a diverse and plentiful ungulate fauna in the Great Plains and Central Mexican Plateau throughout the later Cenozoic. The otolithic ears of *Scaptochelys* are probably also utilized as ground vibration detectors. However, the relative small size of the otolithic masses and the organization of the macular hair cells would imply that they are far less sensitive than those of *Gopherus*.

A second factor which may account for the distinctive shape of the cranium in *Gopherus* is its use in burrowing. My observations of digging behavior in captive *G. polyphemus* show that the head and neck are used to brace the body against torques produced when the forelimb encounters soil resistance during the digging stroke (Fig. 2). The broad, blunt rostrum and compact head of *Gopherus* (cf. Fig. 3A, B; 3C, D) may be better able to absorb and redistribute mechanical loads resulting from its use in digging. Broadening of the occipital region in *Gopherus* increases both the area of attachment and the mechanical advantage of neck musculature used to stabilize the cranio-cervical joint (Fig. 3A, C). Blunt snouts and expanded occiputs are characteristic structural features of those fos-



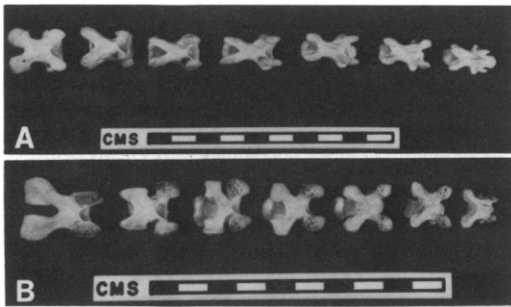


Fig. 4. Dorsal views of cervical vertebrae 2–8 in *Scaptochelys agassizii* (MVZ 55512) (A) and *Gopherus polyphemus* (RE 104) (B). Note the relatively massive zygapophyses of *Gopherus* as well as the close approximation of these articular processes in C6 and C7. See text for discussion.

and 7 are further specialized in having the pre- and postzygapophyses drawn closely together. In some *G. polyphemus*, these articular processes may actually be united at their bases. The 8th cervical is also unique in *Gopherus* in that the posterior zygapophyses are exaggerated in length and separated by a narrow, slot-like interzygapophyseal notch.

A highly specialized first dorsal vertebra also distinguishes *Gopherus* from all other testudinids. In *Scaptochelys* and other land tortoises the first dorsal carries small prezygapophyses, the central articular surface faces anteroventrally and its neural arch is attached principally to the underside of the first neural plate (Fig. 5A). However, in *Gopherus* the zygapophyses are greatly enlarged, curved structures with extensive articular surfaces. The central articular facet is unusually deep; it is oriented almost directly downward (Fig. 5B). Frequently this socket is distinctly biconcave, a reflection of the unusual biconvex centrum which is found on the 8th cervical of Recent *Gopherus polyphemus* (Williams, 1950b) and *G. flavomarginatus* (Legler, 1959). The same central configuration is also exhibited by Miocene *G. pansa* (KUVP 65693) and the giant Pleistocene form, *G. canyonensis* (UCMP 63746). By far the most striking structural modification of the first dorsal vertebra of *Gopherus* is its mode of attachment to the carapace. The neural arch is enlarged and extends anteriorly beneath the nuchal plate where it is firmly sutured to a distinct strut developed on the lower surface of this bone.

**Function.**—More certainly than the cranium, the peculiar design features of the vertebrae of *Gopherus*

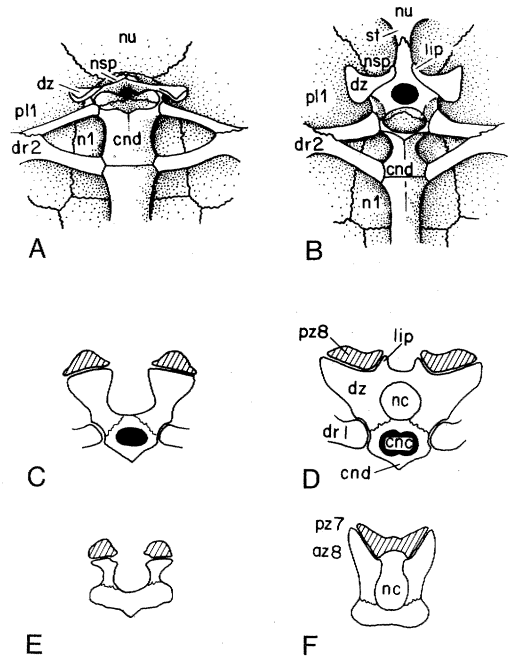


Fig. 5. Ventral views of first dorsal vertebra and adjacent carapacial bones in *Scaptochelys berlandieri* (A) and *Gopherus polyphemus* (B). Semistylized cross sections through the articulated first dorsal vertebra and C8 of *S. agassizii* (C) and *G. polyphemus* (D); same through articulated C8 and C7 of *S. agassizii* (E) and *G. polyphemus* (F). Note that vertebral articulations of *Gopherus* are designed to resist lateral bending, shear and long-axis torsion while those of *Scaptochelys* are not. Refer also to Fig. 4 and 6. Abbreviations: az = anterior zygapophysis; cnc = cervical centrum; cnd = centrum of first dorsal; dr = dorsal rib; dz = zygapophysis of dorsal vertebra; lip = medial lip; n = neural plate; nc = neural canal; nsp = neural spine; nu = nuchal plate; pl = pleural plate; pz = posterior zygapophysis; st = strut on nuchal plate. Figures not to scale.

are explicable as mechanical adjustments to "head-bracing." Use of the head as a buttress while digging imposes a complex mosaic of stresses upon the neck and its union with the shell. Chief among these stresses are long-axis torsion, bending and compression (Fig. 2, 3). As Fig. 6 illustrates, the modified cervicals of *Gopherus* permit the posterior region of the neck to be telescoped in the hyperflexed position and interlocked when under load. Such a vertebral configuration greatly improves the ability of the neck to sustain and transfer mechanical forces between the head and trunk. Because the anterior and posterior regions of the cervical col-

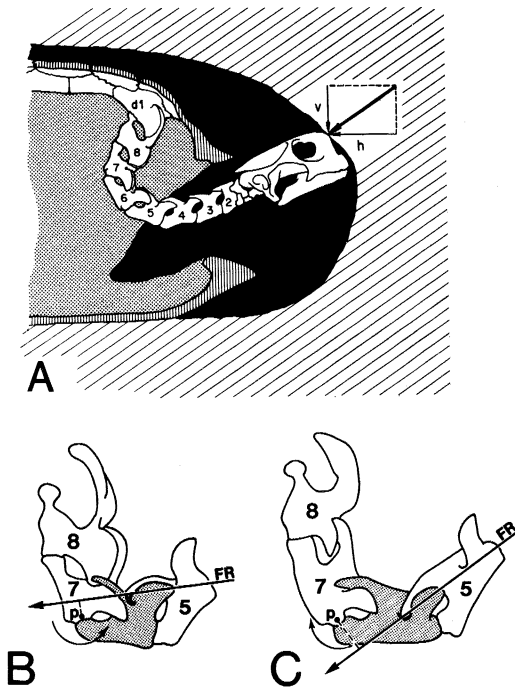


Fig. 6. A) Depiction of the skeletal relationships of cranium, neck and shell during "head-bracing." The neck consists of two functional units, 1) anterior vertebrae (1-5), and, 2) posterior vertebrae (7 and 8) lying in different planes. Cervical 6 is transitional between the units but structurally and functionally more a member of the posterior unit. In lateral view, resistance forces from the soil (heavy arrow) will impose both vertical (v) and horizontal (h) components on the skull. Lower figures contrast mechanical consequences of vertebral structure in B) *Gopherus polyphemus* and C) *Scaptochelys agassizii*. In *Gopherus* hyperextension of posterior cervicals brings about a stable interlocking of the enlarged zygapophyses. Modified C6 (stippled) allows C5 and C7 to closely approximate each other. A mechanical force (FR) passed rearward between C5 and 7 produces a moment (arrow) about the joint (p) between C6 and C7. The moment only strengthens the neck by forcing C6 and C7 together. In *Scaptochelys* cervical hyperextension weakens neck by causing small zygapophyses to overshoot. Shape of C6 causes force FR to force open joint between C6 and C7.

umn lie in different planes, the effective transfer of forces between these units is particularly critical. Cervical 6 is the transition element and it is the most modified of the cervical series. The nearly fused pre- and postzygapophyses of this bone is a key feature of the cervical interlocking mechanism. In *G. polyphemus* the spe-

cialized 6th cervical allows cervical 5 to nearly or actually contact the 7th cervical (Fig. 6B).

Large stresses will also accrue at the cervico-dorsal joint from head-buttrussing behavior. Indeed, if the head and neck are viewed as a cantilevered beam fixed to the shell and loaded at the end (Fig. 2), then maximum lateral bending forces will exist at the cervico-dorsal articulation. These forces are resisted in large measure by a special interlocking feature of the vertebrae comprising the joint. The central articulation between C8 and the first dorsal is an especially deep, ball-and-socket union. Further, the medial edges of the prezygapophyseal surfaces of the dorsal vertebra form dorsally directed lips which lock securely into the postzygapophyseal "slot" of the last cervical (Fig. 5D). The result is an extremely stable connection between neck and trunk and one in which the last cervical is constrained to run on a rail formed by the zygapophyses of the first dorsal vertebra. Accordingly, cervical motion at the joint is restricted to simple extension and retraction. In *Scaptochelys* and other testudinids no such guide mechanism is present and significant lateral excursion of cervical 8 on the shell is possible (Fig. 5C). Restriction of lateral bending at the base of the neck in *Gopherus* appears to be compensated for by exceptional lateral mobility in the anterior half of the neck.

Further stability at the base of the neck in *Gopherus* derives from the interlocking joint between cervicals 7 and 8 (Fig. 5F). Here the hypertrophied zygapophyses are aligned so as to buttress against torsion, lateral bending and shear forces. The same joint in *Scaptochelys* provides little or no passive check against such forces (Fig. 5E). Moreover, hyperextension of the posterior cervicals in this genus does not result in improved stability of the intervertebral articulations (Fig. 6C). Rather, stability actually declines since the small zygapophyses of *Scaptochelys* tend to overshoot one another and are, thereby, partly dislocated.

#### CARPAL MORPHOLOGY

In 1966 Auffenberg reviewed the structure and homologies of the testudinid carpus; he has since supplied additional information on the carpus of Recent gopher tortoises (Auffenberg, 1976). However, on the basis of a large sample of Recent materials available to me, I have been unable to confirm many of his conclusions. Moreover, these same conclusions are contra-

dicted by several excellent carpi of fossil gopher tortoises. On these grounds I conclude that the homologies and bone relationships established by Auffenberg (1966, 1976) are largely incorrect. It therefore seems advisable to briefly review the probable homologies of the chelonian carpus and their application to the manus of gopher tortoises.

Auffenberg (1966) correctly pointed out that chelonian carpal homologies have not been established beyond all doubt. However, the situation seems not as difficult as it might at first appear and I believe the homologies suggested by Romer (1956) to be well founded. The major difficulty has been in the correct identification of the radiale and centralia (Romer, 1956; Walker, 1973). A small cartilage block occurs between the distal articular surface of the radius and the first carpal in most juvenile testudinids and emydids. This same element is frequently ossified in aquatic pleurodiran (e.g., *Pelusios*, *Elseya*; Fig. 7B) and cryptodiran (e.g., *Chelydra*, *Staurotypus*) turtles. This bone (Auffenberg's mediale 1; 1966) is most probably a small, medially displaced radiale (Fig. 7C). Thus, the element which has largely assumed the topographic position of the radiale in emydids and testudinids is equivalent to the medial centrale of the primitive reptilian carpus. This bone commonly fuses with its smaller neighbor, the lateral centrale lying beneath the intermedium. Even when unfused, as in immature turtles, the two centralia are often united by a bridge of cartilage and connective tissue and, hence, act as a single functional unit. A close association between the centralia is maintained in emydids and testudinids. Assuming the validity of the homologies advocated here, the primitive chelonian carpus (Fig. 7B) is remarkably like that of the small, Lower Permian stem reptiles (captorhinids) recently described by Holmes (1977) (Fig. 7A).

It is now possible to reconstruct with some confidence the primitive carpal arrangement for a testudinid. This reconstruction, illustrated in Fig. 7D, is based upon: 1) well-preserved carpi associated with a Late Eocene tortoise (Fig. 8A, B) collected in the Uinta Formation of Utah; 2) several articulated carpi of Middle Oligocene *Scaptochelys laticunea* (Fig. 8C, D); 3) two partial manus of the Early Eocene tortoise, *Hadrianus majusculus* (CM 1313; UCMP 124341). *Hadrianus majusculus* is the oldest recognized testudinid. The Eocene Uinta tortoise (UCMP 94710) provides the earliest complete testudinid carpus

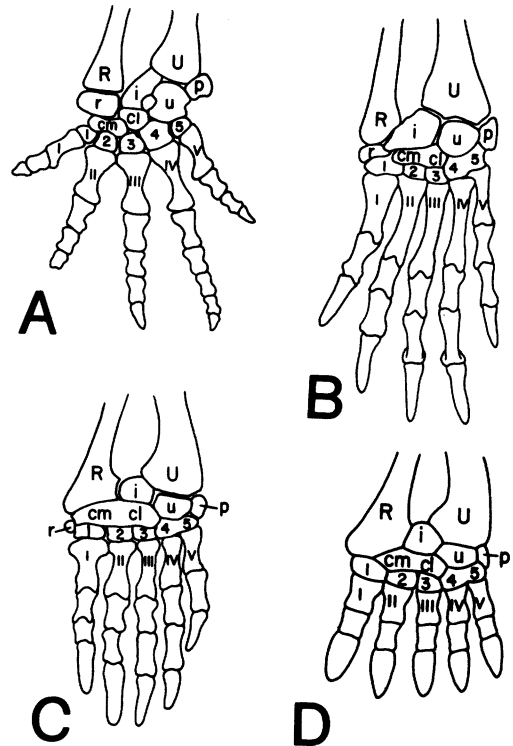


Fig. 7. Comparison of carpal structure in A) a primitive stem reptile (Permian captorhinid; after Holmes, 1977), B) a primitive pleurodiran turtle (*Elseya dentata*) (UU 17097), C) a typical, aquatic emydid (*Chrysemys scripta*) and D) a hypothetical ancestral testudinid. Notice the basic similarity in carpal organization between the stem reptile and *Elseya*. Also note the reduced radiale (r) of *Chrysemys* as compared to *Elseya* and the absence of this ossification in the primitive land tortoise. See text. Figures not to scale. Abbreviations: R, radius; U, ulna; cl, lateral centrale; cm, medial centrale; i, intermedium; p, pisiform; r, radiale; u, ulnare; 1-5, distal carpals, I-V, metacarpals.

yet available. The species is referable to that originally described by Gilmore (1915) as *Testudo uintensis*. In more recent years this tortoise has been variously regarded as either *Geochelone* ( Loveridge and Williams, 1957) or *Stylomyx* (Auffenberg, 1974). Additional materials show conclusively that "*Testudo*" *uintensis* is an early representative of the gopher tortoise lineage and probably sufficiently distinct from *Scaptochelys* to warrant a separate generic allocation (Bramble, 1971).

When compared with the carpus of a typical emydid (Fig. 7C), the hypothetical ancestral



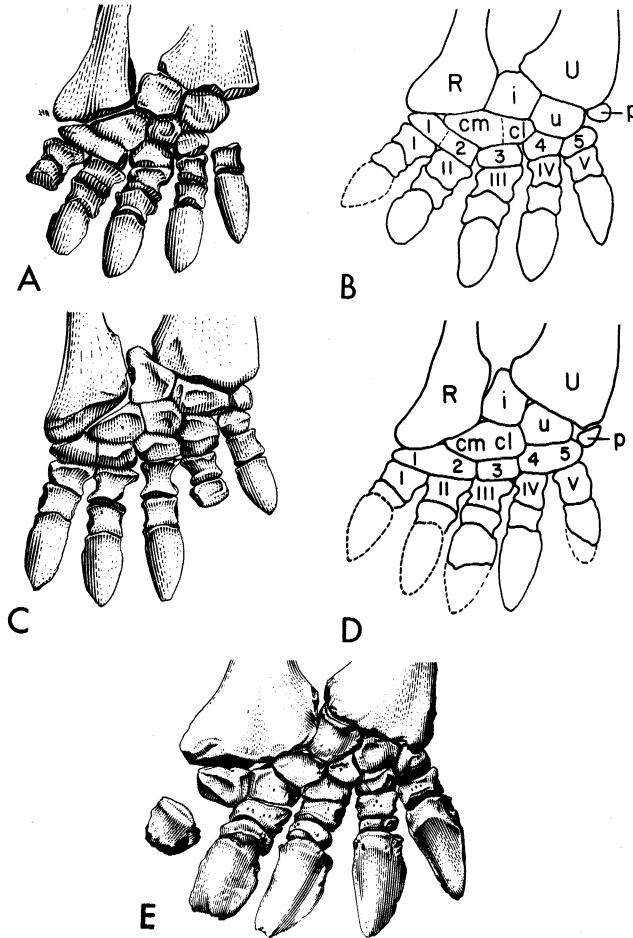


Fig. 8. Comparison of the manus in selected fossil gopher tortoises. A) right manus (UCMP 94710, reversed) of the Late Eocene tortoise "*Testudo*" *uintensis* Gilmore from Utah. B) composite reconstruction of same utilizing both forefeet of the specimen. C) right manus (USNM 15854, reversed) of subadult *Scaptochelys laticuneus* from the Middle Oligocene of Wyoming. D) left manus (UCMP 94708) of adult *S. laticuneus* from Middle Oligocene of Colorado. E) left manus (missing metacarpal and proximal phalanx of digit I) (UCMP 63746) of adult *Gopherus canyonensis* from Early Pleistocene of Texas. Note large pisiform in the Eocene and Oligocene gopher tortoises as well as the fusion of the centralia and carpals 1 + 2, 4 + 5. Refer also to Fig. 9, 10. Abbreviations as in Fig. 7.

manus of testudinids (Fig. 7D) differs only in the absence of an ossified radiale, a reduced phalangeal formula (=2-2-2-2-2), and the contact between carpal 1 and the radius. There were certainly two or, less probably, three intracarpal fusions: (1) medial + lateral centrale; (2) carpals 4 + 5; (3) carpals 1 + 2. The first two fusions are regularly present in emydids and many other aquatic groups. They are also present in adult Eocene gopher tortoises and Oligocene *Scaptochelys* (Fig. 8B, D). Carpals 4 and 5 and

the two centralia are likewise fused in adult *Hadrianus majusculus*.

Available fossils of Eocene *Hadrianus* indicate that carpals 1 and 2 are unfused in adults—a condition observed in emydid turtles. However, the first two carpals co-ossify in the known Eocene gopher tortoises (i.e., "*Testudo*" *uintensis*) as well as in all adult *Scaptochelys* and *Gopherus* except *G. polyphemus* and its Pleistocene relative, *G. canyonensis* (Fig. 8). Elsewhere among North American tortoises, carpals 1 and 2 are

unfused in the primitive genus *Stylemys* (Auffenberg, 1961, 1966; Bramble, 1971) and apparently also in *Geochelone* (*Hesperotestudo*) (Bramble, 1971). Carpals 1 and 2 are likewise separate elements in Old World *Geochelone emys* and *G. impressa* (Auffenberg, 1966). Auffenberg (1974) places these species in the subgenus *Manouria* and considers them to be the most primitive surviving land tortoises. He has further suggested that *Hadrianus* is a synonym of *Manouria* (Auffenberg, 1971, 1974). However, inasmuch as the assignment of *Hadrianus* to *Manouria* appears to rest mainly on shared primitive characters (Hutchison, 1980), Auffenberg's recommendation has not been followed here.

The unfused condition of carpals 1 and 2 is here interpreted as the primitive condition for testudinids. It follows, therefore, that the fused condition typical of gopher tortoises is a derived character state acquired early in their history. The presence of a similar fusion in some Neotropical *Geochelone* (*Chelonoidis*) as well as certain species of *Testudo* and the genera *Kinixys* and *Pyxis* (Auffenberg, 1966) most probably indicates the independent acquisition of this character one or more times during the evolution of land tortoises.

As Fig. 9 indicates, the morphology and homologies of the gopher tortoise carpus as presented in this study are plainly at odds with those given elsewhere by Auffenberg (1966, 1976). Specifically, I have found no evidence, fossil or Recent, to support the following conditions which Auffenberg (1966) reported as normal for adult gopher tortoises: 1) fusion of the metacarpals to the penultimate phalanges (*Scaptochelys*, *Gopherus*); 2) two phalanges in all digits (*Scaptochelys*, *Gopherus*); 3) contact between carpal 4 and the intermedium, thereby excluding mediale 3 (=lateral centrale) from the ulnare (*Scaptochelys*, *Gopherus*); 4) fusion of carpal 5 with the ulnare (*Scaptochelys* only); 5) the presence of a distinct proximal centrale (*Gopherus* only). Most of Auffenberg's interpretations (1966, 1976) stemmed ultimately from the mistaken conclusion that the metacarpals and adjacent phalanges fuse in adult gopher tortoises. All gopher tortoises, including the known Eocene species (Fig. 8A), normally have 2 phalanges in digits 1 through 4; in digit 5 the ungual phalanx articulates directly with the metacarpal. Accordingly, the characteristic phalangeal formula of gopher tortoises is reduced to 2-2-2-2-1. This feature alone is suffi-

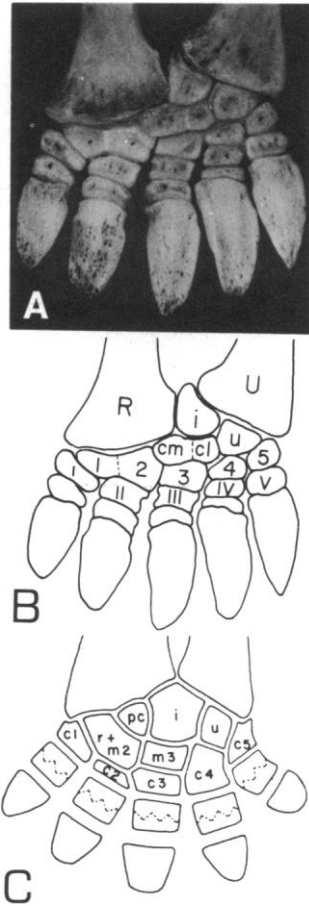


Fig. 9. A) right manus of adult *Gopherus flavomarginatus* (MCZ R157842); B) carpal homologies according to present study; C) carpal structure and homologies according to Auffenberg (1966, 1976). See text for discussion. Abbreviations for Fig. 9B are as in Fig. 7. Those for Fig. 9C are: r = radiale; pc = proximal centrale; i = intermedium; u = ulnare; m2, m3 = medialia; C1–C5 = distal carpals. Metacarpals and proximal phalanges are depicted as fused.

cient to distinguish the group from all other New World testudinids, including *Stylemys* (Auffenberg, 1961), a genus long considered to be the close phyletic associate or sister group of *Gopherus* (sensu lato) (Auffenberg, 1963, 1964; Loveridge and Williams, 1957; Williams, 1950b, 1952).

Central to Auffenberg's (1966) interpretation of the primitive chelonian carpus was the presumed presence of a separate, distinct proximal centrale in *Gopherus*. This carpal element is otherwise unreported in reptiles but was present

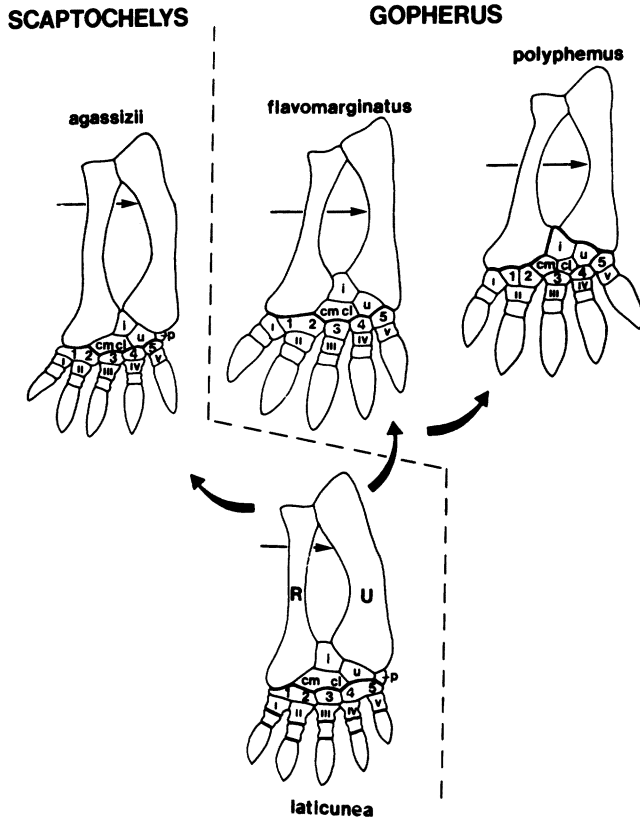


Fig. 10. Morphologic and presumed phylogenetic trends in structure of forearm and manus of gopher tortoises. Modern *Scaptochelys* and *Gopherus* are compared to the primitive Oligocene species, *S. laticunea*. Arrow indicates insertion of the biceps tendon. Heavy lines are mobile joint planes. Figures not to scale.

in the manus of early amphibians. Auffenberg (1966: Fig. 1) believed that the primitive testudinid carpus had a well-formed, separate proximal centrale articulating with the radius between the intermedium and a large ossified radiale. In typical testudinids and emydids Auffenberg suggested that the proximal centrale and radiale are incorporated into a larger composite element together with one or both of the regular centralia (=medial and lateral). However, it is now evident that the presumed "proximal centrale" of *Gopherus* is actually the reduced medial centrale (Fig. 8, 9). This element continues to be co-ossified with the lateral centrale in all adult gopher tortoises except *Gopherus polyphemus* (Fig. 10) and its giant Pleistocene relative, *G. canyonensis* (Fig. 8E).

Fig. 10 shows a comparison of the forelimbs of adult modern *Scaptochelys* and *Gopherus* with that of the more primitive condition found in Oligocene *Scaptochelys*. The relatively larger size

of the manus in *Gopherus* is clearly evident. Two morphological trends account for the evolution of an enlarged manus in *Gopherus*: 1) elongation and widening the ungual phalanges; 2) lateral migration of the subulnar and subradial carpals. Thus, in *Gopherus*, carpals 1, 2 and 5 all have well established articulations with the antibrachium. Additionally, metacarpal 1 often contacts the inner edge of the radius as well. In contrast to *Gopherus*, there are only 2 subradial elements in *Scaptochelys*—carpal 1 and the medial centrale. This appears to be the primitive and typical testudinid arrangement. The appearance of additional subradial elements in *Gopherus* is accompanied by relative widening of the distal articular surface of the radius together with a substantial reduction in the size of the medial centrale.

**Function.**—The forearm skeleton of *Gopherus* exhibits several important fossorial modifica-

tions. Relative shortening and broadening of the hand as well as the great enlargement of the unguals are primary digging adaptations. Widening of the manus provides additional surface area while shortening increases its structural stability and enhances the mechanical advantage of the flexor muscles of the hand and forearm. The digging stroke of gopher tortoises combines flexion of the forearm and manus with retraction of the humerus (Bramble, 1971). Stability of the hand in *Gopherus* is augmented by the shape of the bones themselves. The flat articular faces of the bones permit greater compaction of the carpus. In turn, this prevents individual bones from moving on each other and thereby increases resistance to torsional forces. Compaction of the carpus also results in reduction of the mesocarpal joint; this contributes to the rigidity of the shovel-like manus. In *G. polyphemus* the mesocarpal joint is effectively absent; flexion and extension is restricted to the brachiocarpal or wrist joint (Fig. 10). Limited mesocarpal mobility is maintained in *G. flavomarginatus* (Fig. 10). Due to restriction of the mesocarpal joint, *Gopherus* are truly unguigrade (Auffenberg, 1966).

Externally, the manus of *G. polyphemus* is well designed for digging. It is relatively very broad, short, and bears large, flat nails. The palmar surface is soft, flexible and overlain by very small scales. When the hand is flexed, the palm is flat or slightly concave to provide an effective paddle-like scoop. The edges of the spatulate nails are close together in *G. polyphemus* and in *G. flavomarginatus* to restrict the slippage of soil between them. Externally, as well as internally, the manus of *Gopherus* is best suited for burrowing in sandy, friable soils. *G. polyphemus* inhabits the sandy, well-drained soils over its range (Carr, 1952; Auffenberg, 1969; Ernst and Barbour, 1972), while *G. flavomarginatus* is apparently restricted to sandy areas along the margins of dried lakes (Legler and Webb, 1961). Recent analyses of the soils associated with the burrowing and nesting activities of *G. flavomarginatus* show these substrates to consist of 50–70% sand and fine gravel and only 20–25% silt and clay particles (D. Morafka, pers. comm.).

The manus of Recent *Scaptochelys* is far less specialized for digging than *Gopherus*. It is relatively smaller and possesses round, widely spaced nails. The palmar surface is covered by a tough, inflexible dermis capped by large scales. The palm remains decidedly convex even when the manus is fully flexed. A well-formed me-

socarpal joint persists in all *Scaptochelys*; the hand is, therefore, effectively digitigrade. Proximally within the carpus, the medial centrale remains large and thereby excludes carpal 2 from the radius. Carpal 5 does not have a functional articulation with the ulna, even in cases where the pisiform fails to ossify (Fig. 10).

Both living species of *Scaptochelys* inhabit arid regions where indurated and often rocky soils predominate. *S. agassizii* constructs both individual and communal burrows (Woodbury and Hardy, 1948) whereas *S. berlandieri*, formerly thought not to construct a burrow (True, 1882; Bogert and Oliver, 1945; Carr, 1952), is now known to dig short ones in areas where the ground is sandy (Auffenberg and Weaver, 1969). *Scaptochelys* is nomadic compared to *Gopherus*, most of whose surface activities are limited to established feeding trails within a hundred feet or so of its burrow. The activity range of male *G. polyphemus* may be significantly extended in the breeding season and in this species there is generally an inverse relationship between activity range and the density of herbaceous ground cover (Auffenberg and Iverson, 1979). *S. berlandieri* may wander over 400 meters a day from its temporary, over-night pallet (Auffenberg and Weaver, 1969). The manus of *Scaptochelys* appears to represent a compromise between a structure adapted for prolonged locomotion over rough terrain and digging holes in resistant ground. Many *Scaptochelys* burrows represent rodent holes (Auffenberg, 1969), which the tortoises have gradually enlarged by scratching away the sides with their strong nails. The rounded palmar region in this genus is due to a thick pad of dense connective tissue which cushions the hand in walking. This pad is poorly developed or absent in *Gopherus* (Auffenberg, 1966).

The radius and ulna show a few, though less obvious, fossorial modifications. Both bones tend to be more powerfully built in *Gopherus* than in *Scaptochelys*. The distal ends are transversely expanded with extensive articular surfaces. An important specialization in *Gopherus* is that the major proximal bones of the carpus are seated in sockets developed on these articular surfaces (Fig. 11B, D) and the entire brachio-carpal joint is enclosed in a tough joint capsule and bounded anteriorly and posteriorly by strong ligaments. The apparently unique ball-and-socket arrangement of the wrist joint in *Gopherus* better enables it to withstand the compressional and shear forces developed in digging than the

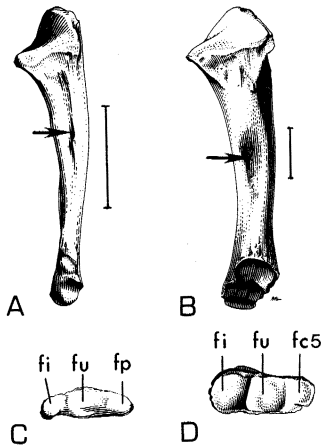


Fig. 11. A), medial view of right ulna (reversed) of *S. laticuneus* (USNM 15854) and B), left ulna of *G. canyonensis* (UCMP 63746). C) and D) are views of the distal articular surfaces of the same ulnae. Arrow indicates biceps scar. Abbreviations: fc5 = facet for carpal 5; fi = intermedium facet; fpi = pisiform facet; fu = ulnare facet. See also Fig. 8, 10. Scale = 2.5 cm.

flat or convex joint surfaces of *Scaptochelys* (Fig. 11A, C) and non-burrowing testudinids. In Recent *Gopherus*, particularly *G. flavomarginatus*, a flange from the radius partially overlaps the anterior surface of the intermedium. The flange may help to prevent the intermedium from being dislocated anteriorly when the hand encounters strong resistance. The main flexor muscles of the forearm (*M. pronator teres*, flexor carpi radialis, biceps profundus) are large and insert well down on the radius and ulna to provide greater mechanical advantage. The biceps is the most important flexor. This muscle, as well as the other principal digging muscles, is much less developed in *Scaptochelys* than in *Gopherus*, and has, as a rule, a shorter lever arm (Fig. 11A, B). The biceps profundus typically inserts near the proximal end of the ulna in *Scaptochelys*, but at about the middle of the bone in *Gopherus* (Fig. 10, 11).

#### DISCUSSION

The data assembled here demonstrate just how distinct, structurally and functionally, the two species groups of gopher tortoises actually are. Both exhibit structural modification for digging but in *Gopherus* the commitment to a fossorial existence is clearly greater. Evidence for this is wholesale in the construction of the

head, neck and anterior limbs, as well as elsewhere in the body. In several respects *Gopherus* is unique among testudinids. Indeed, the distinctions between *Gopherus* and *Scaptochelys*, as defined here, generally exceed those which distinguish many (perhaps most) other genera of land tortoises (e.g., *Testudo* vs. *Geochelone*; Loveridge and Williams, 1957; Auffenberg, 1974). For these reasons *Gopherus* and *Scaptochelys* deserve separate generic ranking.

The differentiation of *Gopherus* and *Scaptochelys* can be related to separate biogeographic and environmental histories (Bramble, 1971). Nearly all of the Tertiary history of *Gopherus* is centered in the western Great Plains and the contiguous Central Mexican Plateau (Bramble, in press). The projected origin of *Gopherus* in the Early Miocene appears to be more or less coincident with three important changes in midcontinental environments. These are: 1) a general cooling trend during the Late Oligocene and Early Miocene; 2) increased aridity and resultant lowered equibility; 3) the extensive development of sandy, well-drained soils. All three factors would favor greater efficiency in burrowing. Declining environmental temperatures during this interval are indicated by numerous paleobotanical indicators (Dorf, 1964; Wolfe and Hopkins, 1967; Wolfe, 1971). Evidence for increased aridity comes from both sedimentary profiles and changes in the relative abundance of aquatic reptiles (crocodiles and turtles) and fish (Bramble and Hutchison, 1971, 1980; Hutchison, 1982). It is remarkable, in fact, that almost no aquatic reptiles are known to occur in Early Miocene (Arikarean) deposits in the midcontinent although they are common, if not abundant, in both older and younger sediments in the region. This evidence suggests an absence or at least scarcity of permanent bodies of water and very possibly seasonal aridity.

Sandy sediments first became widespread in the Great Plains during the Early Miocene. This may have been a particularly critical event in the origin of *Gopherus*. The reason is that the peculiar digging strategy of *Gopherus* (i.e., head buttressing) would appear to be mechanically feasible only in friable soils that offer relatively little resistance to the burrowing action of the forelimbs. It is significant that virtually all Tertiary *Gopherus* remains are found in sand-rich deposits (Bramble, 1971). Seemingly, then, the coincidence of modern *Gopherus* with sandy soils is not fortuitous. Rather, it is the extension of

a primary association established at, and perhaps largely responsible for, the very inception of the lineage.

Although the present range of *Scaptochelys* does include areas of sandy substrates, the Tertiary record of this genus indicates no special relationship to soils of this type. Most Tertiary *Scaptochelys* derive from clay-rich facies. Such fine grained sediments imply hard, compact parent soils that would not be suitable to the burrowing tactics employed by *Gopherus*. Increased aridity and overall environmental perturbation associated with the later Pleistocene and Holocene may ultimately have favored the more generalized locomotor capabilities of *Scaptochelys* over those of the more specialized, substratum-dependent *Gopherus*.

A detailed analysis of the biogeographic history of gopher tortoises is to be presented elsewhere. Nonetheless, a few comments regarding the past distribution of gopher tortoises may help to place their evolution in historical perspective.

Pleistocene environmental changes clearly resulted in major disruption of what appears to have been the relatively stable distributions of gopher tortoises during Miocene and Pliocene times (Auffenberg, 1962, 1969; Auffenberg and Milstead, 1965; Bramble, 1971; Brattstrom, 1961; Moodie and Van Devender, 1979; Van Devender et al., 1976). For example, Late Pleistocene and Holocene *S. agassizii* in the northern Chihuahuan Desert of New Mexico and extreme western Texas are well east of the present range of this species (Brattstrom, 1961; Van Devender et al., 1976). Later Tertiary (Miocene) and earlier Pleistocene deposits in this same region as well as the adjacent southern Great Plains contain the abundant remains of *Gopherus*. In no instance, however, have these deposits produced fossil *Scaptochelys* (Bramble, 1971). Conversely, beds of equivalent age in southern California and neighboring areas of Mexico (Baja California; coastal Sonora) commonly contain *Scaptochelys* but, so far, no trace of *Gopherus*.

The existing fossil record, therefore, would seem to imply that from approximately the early Middle Miocene (Hemingfordian) to at least the Early Pleistocene (Blancan) the two genera of gopher tortoises were very probably allopatric. The subsequent rapid and profound alterations of range experienced by these tortoises during the later Pleistocene could have resulted in temporary, local sympatry as has been re-

cently suggested by Moodie and Van Devender (1979). At the moment, however, direct evidence of sympatry between *Scaptochelys* and *Gopherus* is virtually nonexistent. The single likely example is the apparent joint occurrence of *S. auffenbergi* (= *berlandieri*) and *G. flavomarginatus* in medial Pleistocene beds near Aguascalientes, Mexico (Mooser, 1972; Auffenberg, 1974). Nonetheless, even in this case, exact information on the stratigraphic relationships of the two tortoises is not yet available.

On the other hand, recent discoveries of Pleistocene *G. flavomarginatus* from several localities in southern Arizona (e.g., Phoenix, El Mirage, Safford, Ajo) (Bramble, 1971; T. R. Van Devender, pers. comm.) place this characteristically Chihuahuan Desert species (Morafka, 1977) some 1,000 km northwest of its present range and well within the current Sonoran Desert distribution of *S. agassizii*. It is significant that although fossils of *G. flavomarginatus* are extremely abundant at some Arizona localities (e.g., near Phoenix), no *Scaptochelys* material has yet been recovered from these sites. The historical evidence at hand, then, would tend to support the notion that allopatry, first established in the Miocene, continued to characterize the geographical distributions of *Scaptochelys* and *Gopherus* during the Pleistocene. Consonant with this view is the prediction that eastward extensions of the range of *Scaptochelys* during the Pleistocene would have been concurrent with, or preceded by, extirpation of *Gopherus* from the areas involved. Certainly the fossil record of gopher tortoises is potentially adequate to test this hypothesis as well as competing points of view.

#### ACKNOWLEDGMENTS

This paper represents, in part, work originally submitted as a doctoral dissertation at the University of California, Berkeley. I wish to thank the members of my thesis committee, Joseph T. Gregory, David B. Wake and Milton Hildebrand for their encouragement and advice. J. Howard Hutchison has kindly reviewed the present manuscript. I also extend my sincere thanks to the curators of the many collections of fossil and Recent materials upon which this study so heavily depended. The stipple illustrations of Fig. 1 were drawn by David Cook and the line drawings of Fig. 8 and 11 are the work of Augusta Lucas. Other illustrations are by the author. I also wish to acknowledge

Maurine Vaughan for her efforts in the completion of the manuscript.

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Aug. 1981.

*Copeia*, 1982(4), pp. 867–890

## Revision of the South American Skate Genus *Sympterygia* (Elasmobranchii: Rajiformes)

JOHN D. MCEACHRAN

Comparison of the holotypes and only known specimens of *Psammobatis asper*, *P. breviceaudatus*, *P. caudispina*, *P. chilcae* and *P. maculatus* with each other and with 31 similar specimens from the same area, Ecuador to northern Chile, failed to reveal more variation than could be explained by sexual dimorphism and intraspecific variation, indicating that all species should be synonymized with the oldest available name, *P. breviceaudatus*. *P. breviceaudatus* and *P. lima* share a number of apomorphies with *Sympterygia acuta* and *S. bonapartei* but only pleiomorphies with the other species of *Psammobatis*, *P. bergi*, *P. extenta* and *P. scobina*. Thus *P. breviceaudatus* and *P. lima* are reallocated to *Sympterygia*. The four species of *Sympterygia* are redescribed and a key is given for their identification. A phylogenetic analysis indicates that *S. breviceaudata* is the sister group of the other *Sympterygia* species and that *S. lima* is the sister group of *S. bonapartei* and *S. acuta*.

**D**ESPITE recent widespread interest in the systematics and phylogeny of skates (Rajiformes) (Ishiyama, 1958, 1967; Stehmann, 1970, 1976a; Hulley, 1970, 1972a, 1973; McEachran and Compagno, 1979, 1982), the apparently unique skate fauna of temperate South America has been little studied. The endemic genera *Sympterygia* Müller and Henle and *Psammobatis* Günther are important elements of the fauna. However, the species composition, validity and interrelationships of these taxa remain largely uncertain. Müller and Henle (1841) distinguished *Sympterygia* from other skate genera by the presence of pectoral fins which meet at the tip of the snout, and pelvic fins with only slightly concave outer (posterior) margins. Günther (1870) distinguished *Psammobatis* by a circular disc, pectoral fins which meet in front

of the snout, tube-like posterior narial lobes and deeply incised pelvic fins. No extensive modern comparisons have been made between the genera but Bigelow and Schroeder (1948, 1953) suggested that *Psammobatis* and *Sympterygia* may intergrade in the shape of the posterior margins of the pelvic fins, hence may not be distinct from one another. Menni (1972b) described the clasper structure of representatives of the two genera (*S. acuta*, *S. bonapartei*, *P. extenta* and *P. scobina*) but did not comment on the relative distinctiveness of the two genera.

The species composition of *Sympterygia* has remained rather stable (consisting of *S. acuta* Garman and *S. bonapartei* Müller and Henle), while that of *Psammobatis* has varied considerably. Norman (1937) in his revision of the latter genus recognized five species: *P. breviceaudatus*