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A New Fossil Tortoise from the Texas Miocene, With Remarks on the Probable Geologic History of Tortoises in Eastern U.S.

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TEXAS MEMORIAL MUSEUM, THE UNIVERSITY OF TEXAS

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W. W. Newcomb, Jr.
Director

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A New Fossil Tortoise from the Texas Miocene, with Remarks on the Probable Geologic History of Tortoises in Eastern U.S.[1]

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A complete shell of a fossil tortoise in the collection of The University of Texas—Bureau of Economic Geology, from the Miocene Oakville formation of the Texas Coastal Plain, represents an undescribed and distinctive species. It is referred to the genus *Geochelone* on the basis of a narrow nuchal scute, first suprapygal embracing the second, and with the median length of the hypoplastral greater than that of the hyoplastral.

Geochelone williamsi new species[2]

Holotype.—A complete shell of an adult male tortoise, University of Texas —Bureau Economic Geology, 31084–11; collected by Dr. John A. Wilson in 1949.

Type Locality and Horizon.—Garvin Gully, 2 mi. north of Navasota, Grimes County, Texas, Garvin Gully local fauna, Lower Oakville member, Oakville formation, Arikareean, Early Miocene.

Diagnosis.—A species of *Geochelone* (subgenus uncertain), apparently most closely related to *G. ducatelli* from the Miocene Calvert formation of Maryland. It is distinct from *G. ducatelli* in the following characters: a rhomboidal, instead of a pentagonal entoplastron; epiplastral projection not truncated, not sculptured, nor swollen ventrally; carapace and plastron more elongate; xiphiplastral notch deeper.

Description of Type.—A complete shell of an adult male land tortoise, slightly displaced dorsally and crushed laterally (Figs. 1, 2). Pertinent measurements are provided in Table 1.

Carapace smooth, without deep growth rings, only moderately broad, slightly truncated anteriorly, rounded posteriorly, with the free peripheral borders not emarginated, and without any recurving or flaring; vetebral region of the carapace forming a smooth arc when viewed from the side, slightly more sloping anteriorly; no keel on the bridge, though this area is linearly swollen; plastron just even with the anterior edge of the carapace

[1] Sponsored in part by NSF G–17613 and G–23562.

[2] Named for Ernest E. Williams, Museum of Comparative Zoology, Harvard College, in recognition of his contributions to our knowledge concerning both fossil and Recent land tortoises.

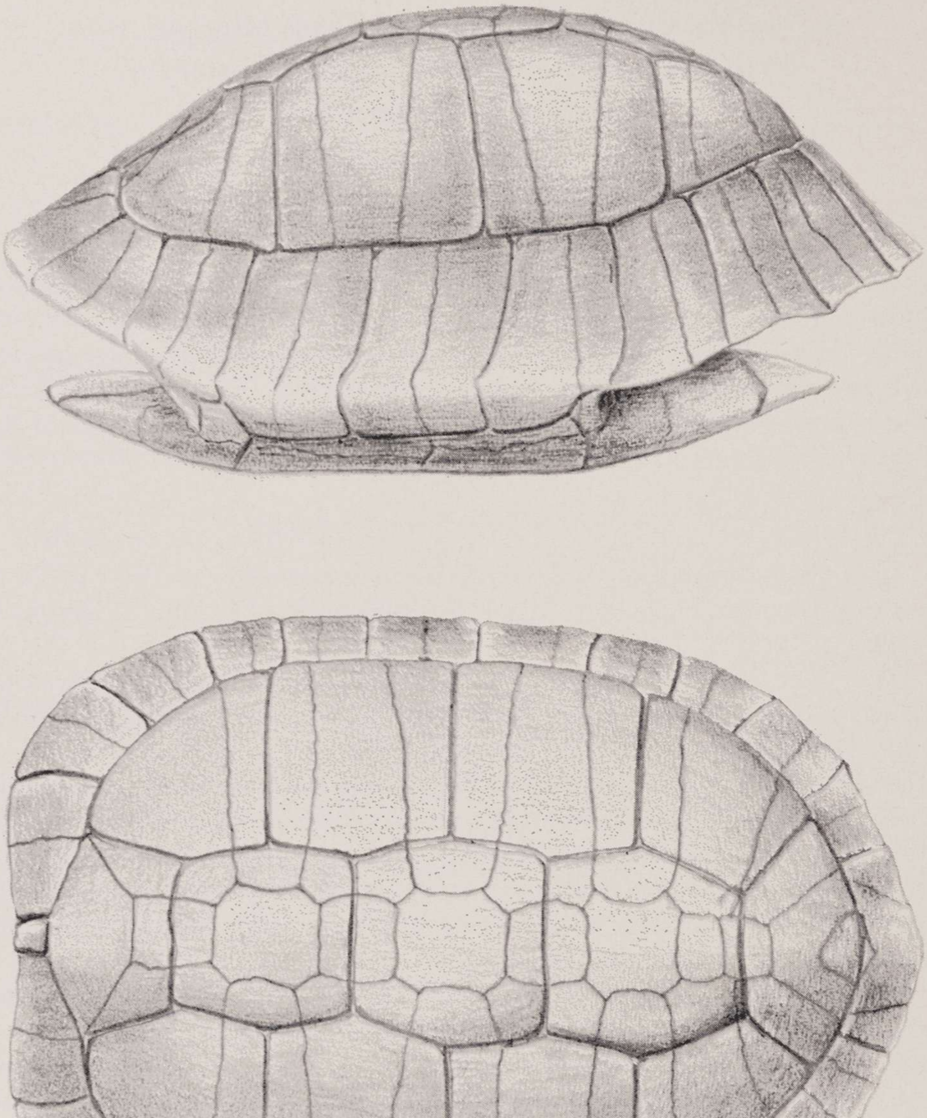

Fig. 1. Carapace of *Geochelone williamsi* new species, Holotype, University of Texas—Bureau Economic Geology 31084–11, Lower Miocene, Arikareean, Grimes County, Texas; close to *G. ducatelli* (Collins and Lynn), Calvert Miocene, Maryland. Top: lateral view. Bottom: dorsal view.

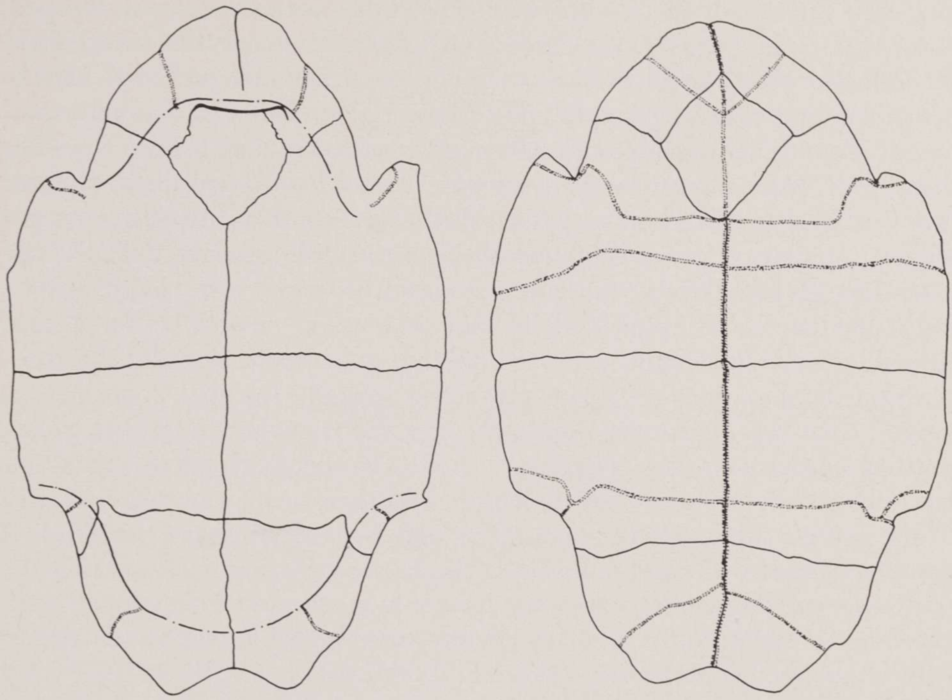

Fig. 2. Plastron of *Geochelone williamsi* new species, Holotype, University of Texas—Bureau Economic Geology 31084–11, Lower Miocene, Arikareean, Grimes County, Texas. Left: internal view. Right: ventral view.

TABLE 1

Measurements (in mm) of the type of *Geochelone williamsi* new species

carapace length	334.0	bridge length	144.5
plastral length	313.0	entoplastron length	64.0
gular length	54.0	entoplastron width	62.5
humeral length	49.0	hyoplastron length	67.0
pectoral length	20.5	hypoplastron length	78.0
abdominal length	108.0	xiphiplastron length	59.5
femoral length	36.0	1st suprapygal length	55.0
anal length	40.0	anterior width 1st suprapygal	19.5
xiphiplastral notch length	10.5	posterior width 1st suprapygal	73.5
xiphiplastral notch width	38.0	2nd suprapygal length	32.5
xiphiplastral external height	32.0	2nd suprapygal width	42.5
greatest thickness epiplastral lip	29.0	nuchal scute width	13.0
epiplastral lip length	48.0	nuchal scute length	21.0
anterior lobe length	76.5	2nd vertebral length	66.0
posterior lobe length	92.0	2nd vertebral width	65.0

and with the tips of the xiphiplastral projections not extending to the posterior carapaceal border. Free borders of peripherals acute; first, third, fifth, seventh and eighth neurals subrectangular, second, fourth and sixth clearly octagonal; first suprapygal embracing a low, diamond-shaped, second suprapygal; pleurals only moderately alternately narrower and broader at their distal ends. Nuchal scute longer than wide; costal scutes low, almost square; first vertebral scute as long as wide, third not wider than the others, fourth longest; epiplastral projection thickened, and slightly concave dorsally, not extending greatly beyond the anterior plastral margin, edge acute, with a slight median notch epiplastral lip long, extending posteriorly for a considerable distance, deeply excavated behind; gular scute entering the entoplastron; humero-pectoral sulcus extending laterally for about one half its length, then turning forward abruptly in a sharp angle, continuing to the plastral border in a very gentle arc; abdomino-pectoral sulcus extending laterally for slightly over half its length, and then turning postero-laterally to the bridge; abdomino-femoral sulcus and hypo-xiphiplastral articulation not superimposed, former anterior to the latter; both inguinal and axillary scutes present, large and simple, the former in moderately long contact with the femoral scute, and visible in ventral view; hypoplastron considerably longer than the hyoplastron; posterior lobe moderate in length, its outer edge with a distinct angle just anterior to the outer end of the femoro-anal sulcus, and a broad notch at this point; femoral and anal scutes normal; xiphiplastron broadly notched posteriorly with the tips broadly divergent; ventral surface of the epi- and xiphiplastron without distinctive sculpturing; posterior portion of the hypoplastron and most of the xiphiplastron slightly concave.

Comparisons.—Most of the other Miocene species of *Geochelone* with which *G. williamsi* is to be compared can be placed in the subgenus *Hesperotestudo.* Miocene members of this subgenus include *G. osborniana, impensa, angusticeps,* and *inusitata.* This group is very distinct from that to which *williamsi* belongs. *G. vaga* and *G. farri* are both species with rugose shells that may belong to the *Hesperotestudo* line. *G. klettiana* and *G. undata* are large tortoises from New Mexico, represented by only the pygal areas. It is doubtful if these species can ever be properly diagnosed. The specimen on which the name *Geochelone undabuna* is based is probably aberrant, and the name may be a synonym of *G. primavae.* The latter is quite distinct from *G. williamsi* in possessing all hexagonal neurals. *G. niobrarensis* and *G. tedwhitei* seem to belong to the subgenus *Caudochelys*; both differ from *G. williamsi* in the shape of a number of different parts of the plastron and carapace. The shape of the anterior projection of the plastron, shape of the entoplastron, and the distance between the humeral and abdominal sulci in *G. arenivaga* are all quite different from those in *williamsi. Testudo copei* from the Deep River Miocene belongs to the genus *Gopherus* because it has a nuchal scute which is wider than long.

The species most closely related to *G. williamsi* is clearly *Geochelone* *ducatelli* of the Maryland Calvert formation. Both forms are characterized by (in combination) slender rib heads, the great extent of the gular and pectoral scutes on the inner, anterior surface of the plastron, and a proportionately thick posterior lobe at its base. Fortunately, the types of both species are adult males, of about the same size. Although the carapace of *ducatelli* is not complete, in every character which can be compared these two species approach each other more closely than either approaches any other North American fossil tortoise described so far.

In summary, the major distinguishing features of the two species are:

G. williamsi	*G. ducatelli*
Entoplastron essentially rhomboidal.	Entoplastron essentially pentagonal.
Entoplastral projection not truncated, not sculptured, not swollen ventrally, very thick.	Entoplastral projection truncated, slightly sculptured, and swollen ventrally, thinner.
Carapace and plastron more elongate.	Carapace and plastron less elongate.
Xiphiplastral notch deeper (anal scute/anal notch = 3.81).	Xiphiplastral notch shallower (anal scute/anal notch = 0.95).
Dorsal and ventral edges of pleurals more differentiated (dorsal pleural 3/ventral pleural 3–2.00).	Dorsal and ventral edges of pleurals less differentiated (dorsal pleural 3/ventral pleural 3 = 1.52).
Anal scute longer (femoral scute/anal scute = 0.90).	Anal scute shorter (femoral scute/anal scute = 2.35).
Epiplastral lip thicker (length lip/thickness lip = 1.66).	Epiplastral lip thinner (length lip/thickness lip – 2.37).

DISCUSSION

At least two species groups of land tortoises are known to have existed in eastern North America during the Miocene. One of these groups is now known to have been represented by two species in this area. These are *Geochelone williamsi* and *G. ducatelli*. The relationships of this group to other fossil or Recent species groups of *Geochelone* remain unknown. The second species group in the Miocene of eastern North America is represented by *Geochelone tedwhitei*. This species is a member of the extinct subgenus *Caudochelys* (Auffenberg, 1963), which had a long fossil history, extending from the Oligocene to the Late Pleistocene of North America.

It is only after the Early Miocene that additional tortoise taxa appear in eastern North America. These include the subgenus *Hesperotestudo* (Auffenberg, 1962) and the genus *Gopherus*.

The available data suggest that the subgenus *Hesperotestudo* first successfully invaded eastern United States during the Late Miocene or Early Pliocene, and that it was probably restricted to the southern part of this geographic area from this time to the Late Pleistocene, when it became extinct.

The genus *Gopherus* also invaded eastern North America from the present

Central Plains area, but at an even later time. In the Southeast the earliest known forms occur in the Pleistocene of Florida. Furthermore, the eastern species represents only one of several phyletic lines known to have occurred in western United States at the same time.

As far as tortoise evolution in North America is concerned, several basic working hypotheses are suggested:

1. Almost all the major phyletic lines within the North American tortoise genera or subgenera evolved in central and/or western North America. Only one species group (*G. williamsi* and *G. ducatelli*) may have evolved in eastern North America, probably in the Late Oligocene.
2. Of the three fairly well known and widely distributed tortoise groups in western North America during the Miocene (*Gopherus, Hesperotestudo* and *Caudochelys*), only one (*Gopherus*) failed to reach eastern United States by the end of the Pliocene. In all three groups diversification within eastern United States seems negligible. Furthermore, the successful immigrant species represent only a small part of the total phyletic diversification found in western United States during the same time periods.

The relationships, or indeed even the validity of *Floridemys nanus*—an unusual, diminutive form from the Pliocene of Florida—remain uncertain. The peculiar arrangement of the gular-pectoral sulcus (transverse, and not crossing the entoplastron) may be an example of a variant, unfortunately present in the only individual of this species known. The remainder of the specimen bears a considerable similarity to some of the species of *Stylemys* from the John Day beds of Oregon. If related to *Stylemys*, then *Floridemys* is probably a Pliocene zoogeographic counterpart of the amphisbaenid genus *Rhineura*, of which extinct species are known from the Oligocene of Colorado, whereas the only living species is restricted to Florida. The peculiar snake genus *Stilosoma* (Pliocene to Recent of Florida) may eventually be found to fit the same chronogeographic pattern.

The discoveries of fossil tortoises during the past two decades in the far West, the northern and central plains states, and southeastern United States have greatly extended our knowledge of the history of these interesting vertebrates. Conclusions of a preliminary and general nature regarding the phylogeny and paleogeography of tortoises are now possible. This contribution, as well as those of Hibbard (1960) and Brattstrom (1961) are examples. Nevertheless, data are still lacking from certain geographic areas important to such considerations. Northeastern United States is an example, since there are no terrestrial deposits of Tertiary age in this area that contain fossil tortoises. As a result, our knowledge of the history of fossil tortoises in eastern United States is based on remains that have been found only in the Southeast.

Another important area for which there are very few paleozoogeographic data is that encompassing Arizona, New Mexico and all of Mexico. This is a critical region in tortoise evolution in view of its role as a potential source area for new taxa, an area traversed by both east-west and north-south highways of dispersal, and (at least as far as Mexico is concerned) a presumably important tortoise refugium (as it is for *Gopherus* at the present time).

SUMMARY AND CONCLUSIONS

1. A new species of land tortoise, *Geochelone williamsi,* is described from the Lower Miocene Oakville formation of the Texas Coastal Plain.

2. With *G. ducatelli* of the Maryland Miocene it seems to form a small species group confined to southeastern United States. Together they may be part of the Miocene equivalent of an Austroriparian fauna; probably ultimately derived from the *Caudochelys* phyletic line, which is more characteristic of western United States during this same geologic period.

3. Throughout the Tertiary there were several eastward migrations of tortoise groups. The earliest of these migrations was effected by the subgenus *Hadrianus,* a primitive group that apparently reached southeastern United States in the Early or Middle Eocene.

   According to the available data the second major eastward migration from western United States was effected by the subgenus *Caudochelys,* whose earliest southeastern records are from the Lower Miocene of Florida. By this same time, a typically (?) eastern group, including both *williamsi* and *ducatelli,* had already evolved in eastern United States, presumably from a pre-Miocene ancestral form that moved eastward during the Oligocene. No Oligocene tortoises are known from eastern United States.

4. During the Miocene there were a number of distinct phyletic lines of tortoises in western North America that either never reached eastern North America, or did so only after the Miocene. One of the groups which apparently never reached eastern United States was the genus *Stylemys* (unless *Floridemys nanus* was derived from *Stylemys*). A distinct group present in the Miocene of central and western North America, but that did not reach eastern North America until a later date, is the subgenus *Hesperotestudo* of the genus *Geochelone.* By the Miocene, *Hesperotestudo* had already broken into a number of species groups. Two of these reached Florida in the Pliocene. The Orthopygia series is represented by *G. hayi,* and the Turgida series by an undescribed species. The genus *Gopherus,* with a long fossil history and considerable diversification in western North America, did not reach the eastern half of the continent until the Middle Pliocene.

5. The unique eastern United States genus *Floridemys* may be related to *Stylemys.* If so, it is a relict Pliocene form with essentially the same chronogeographical pattern as the genus *Rhineura.*

6. During the Pleistocene there were three groups of tortoises in eastern United States: *Caudochelys, Hesperotestudo,* and *Gopherus.* The presumed typically eastern groups found in this area during both Miocene and Pliocene times had already disappeared. Both *Caudochelys* and *Hesperotestudo* became extinct

over most of North America during the Wisconsin.[3] The genus *Gopherus* is still found in southeastern United States.

7. The peninsula of Florida is often regarded as both a center of speciation and a refugium for more northern or western animal groups. However, it does not seem to be particularly important in either as far as tortoise evolution is concerned. The only major tortoise evolutionary lines that may have evolved in Florida are those represented by *G. williamsi* and/or *G. ducatelli,* and *Floridemys nanus.* As far as is known, no tortoise group existed in Florida for any longer period of time than the same group did in western United States (unless *Floridemys* is a synonym of *Stylemys*). Though several major evolutionary lines are known to have extended their ranges to southeastern United States, the migrations were apparently accomplished only long after these same groups had already made their appearance in western United States.

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[3] *Geochelone* (*Hesperotestudo*) *wilsoni* is known from post-Pleistocene deposits of southeastern Oklahoma (C^{14} date of 10,000 B.P. fide Staughter–pers. comm., 1962). Specimen examined by the author.

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