

TESTUDO CUBENSIS AND THE
EVOLUTION OF WESTERN
HEMISPHERE TORTOISES

ERNEST WILLIAMS

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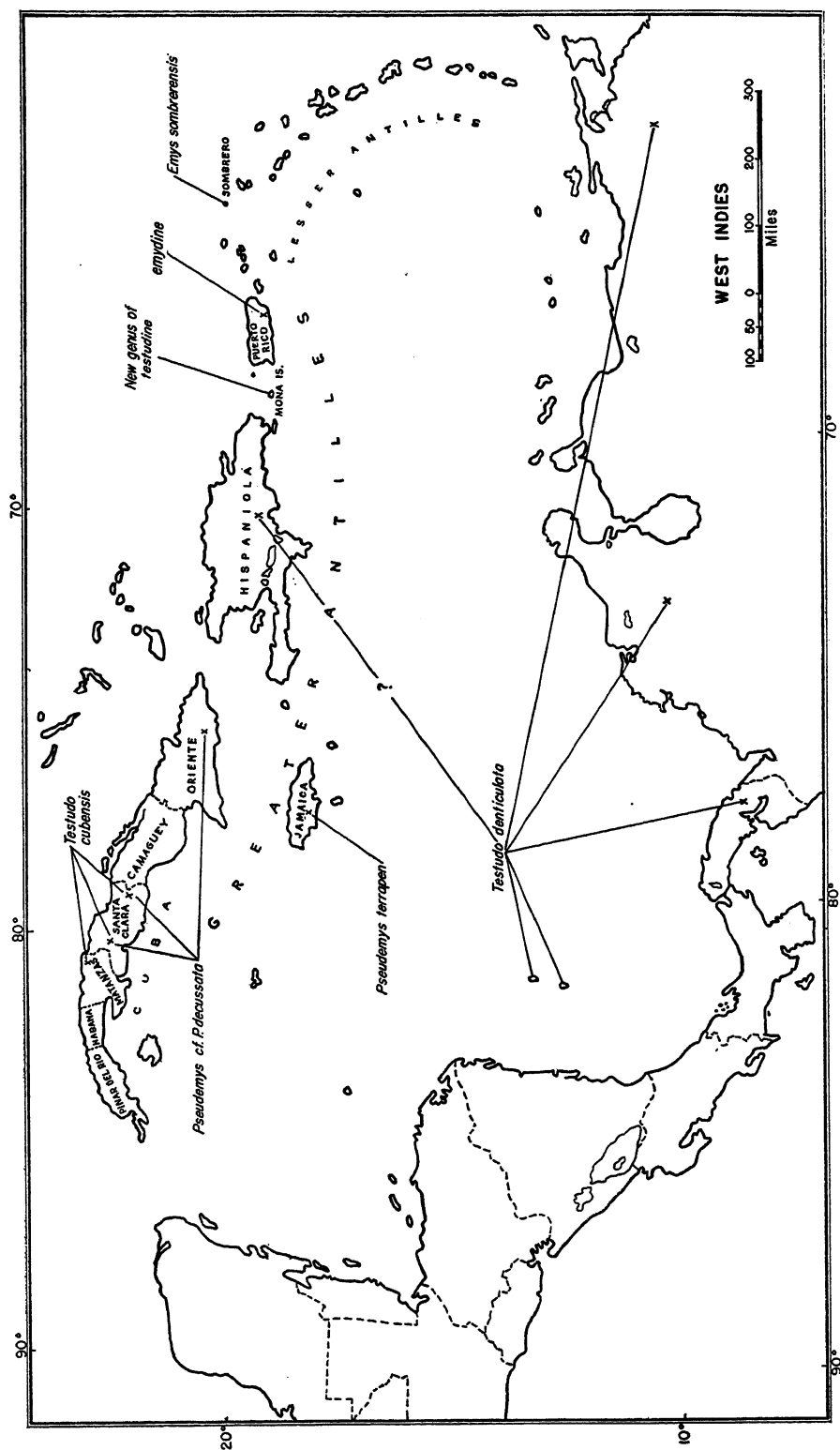


FIG. 1. Map showing localities of all fossil West Indian turtles. The range of living *Testudo deniculata* as it approaches that of †*T. cubensis* is also shown. The range of *T. deniculata* in the northern part of South America is continuous.

INTRODUCTION

IN THE MORE THAN 80 years since the description by Leidy of testudinate fossil remains from Cuba and Sombrero Island, few additions have been made to the knowledge of this West Indian fauna. During this period enough material has accumulated at the American Museum of Natural History to demonstrate that the testudinate fauna of the West Indian Pleistocene was much richer than has ever been suspected. From Cuba there is now available, in part from the same deposits that provided the ground sloths named by Matthew (1931), not only considerable material of Leidy's †*Testudo cubensis* but a number of partial shells and fragments of a †*Pseudemys* evidently related to the still

living *P. decussata*. From Jamaica a single partial shell records the existence of *Pseudemys terrapen* contemporaneously with certain Jamaican fossil mammals sometimes regarded as older than most other so-called Pleistocene West Indian mammals, while from Puerto Rico a great number of fragments give evidence of a large and thick-shelled emydine not at present generically determinable. Finally from the caves of Mona Island elements of a turtle have been collected which in limbs and cervical vertebrae closely resemble *Testudo* but from the palate and certain features of the shell must belong to an undescribed genus of uncertain relationships.

HISTORICAL BACKGROUND

Vertebrate fossils were first found in Cuba in April, 1860, in a thermal spring at the Baños de Ciego Montero by a student at the University of Havana, José de Figueroa. He brought them to Felipe Poey, who presented them on the fifteenth of September, 1861, before the Academy of Sciences at Havana. Poey sent several of the fossils to Leidy who in 1868 described †*Testudo cubensis* from a single partial pleural¹ plate found at Ciego Montero. Carlos de la Torre, who succeeded Poey in the chair of zoology at Havana, continued collecting at the Ciego Montero spring. He also devoted much time to a new locality in the Sierra de Jatibonico, a fissure discovered by a refugee Cuban patriot, Ramon Gonzalez, during the Cuban fight for liberation from Spain. In 1910 de la Torre reported some of his findings to the International Geological Congress at Stockholm.

The material collected by de la Torre was

¹ The terminology here employed endeavors to be consistent in distinguishing horny scutes from bony plates. The following are the corresponding terms for the sets of elements in the carapace:

SCUTES	PLATES
vertebral	neural
costal	pleural
marginal	peripheral
nuchal	nuchal
supracaudal	pygal

Plastral nomenclature is already consistent and unambiguous.

partly studied by him and partly entrusted to the American Museum of Natural History for more thorough research in conjunction with further exploitation of the localities. In 1911 Barnum Brown in association with de la Torre completed collections at the locality in the Sierra de Jatibonico and also obtained a large sample from Ciego Montero. In 1918 Brown completed the excavation of the Ciego Montero spring. At both localities material was gathered not only of †*T. cubensis* but also of †*Pseudemys* cf. *P. decussata*.

Three other localities in Cuba have yielded testudinate remains. A fragment of a *Pseudemys* plastron was found by H. E. Anthony in 1917 in a cave at Daiquirí, Oriente Province, and fragments of a small specimen of the same genus were collected by Barnum Brown in the Cueva de los Machos near Cienfuegos, Santa Clara Province. In a tar pit near Hato Nuevo, Matanzas Province, Roy E. Dickerson and P. J. Bermudez in 1933 found, besides some bones of domestic animals, ground sloth claws, and small rodent bones, a few plates and a femur of †*T. cubensis*. The latter fragments from a source apparently deserving of further investigation were donated to the American Museum of Natural History by Dickerson.

Leidy, in the same brief note in which he described †*T. cubensis*, erected the name †*Emys sombreroensis* for a partial plastron

found during excavations for fertilizer on tiny Sombrero Island. Leidy was uncertain whether the form was an *Emys* or a *Testudo*. The type is now lost, and the description is not determinable. The specimen was not *Emys* as the genus is now understood. That it was *Pseudemys* is not probable either; the described depth of the xiphiplastral notch suggests *Testudo* as more likely.

In 1920 a third island was added to the list of those on which fossil turtles were to be found. In that year H. E. Anthony procured a shell of *Pseudemys terrapen* from the breccia of the same cave in Jamaica in which he found †*Clidomys*, †*Spirodonomys*, †*Speoxenus*, and †*Alterodon* (Anthony, 1920a).

The abundant mammalian remains in West Indian caves reported principally by Anthony stirred considerable interest at this time. In 1926 K. P. Schmidt, discussing the modern herpetofauna (in which no turtles are included) of the small island of Mona off Puerto Rico, suggested that the numerous limestone caves on that island would probably afford much of interest. As it happened,

at the moment of publication of Schmidt's paper, Anthony was in the process of exploring the caves of Mona. The only fossil vertebrate he found, aside from a very few bones of a small mammal (†*Isolobodon*) probably of human importation, was a new and peculiar genus of tortoise.

Two years previously from Puerto Rico itself (the exact locality and circumstances of the find uncertain) still another form was added to the growing collection at the American Museum of Natural History. This form, the gift of Señor Rabell Cabrera, was represented by numerous fragments of plastron, pelvis, and of the buttress region of the carapace, but was unfortunately so incomplete as to afford no generic characters.

Of this material only †*Testudo cubensis* Leidy is described in the present paper, special emphasis being placed on the relationships of that form and on its position in the phylogeny of Western Hemisphere tortoises. It is intended to discuss the other forms in succeeding papers.

SYSTEMATIC DESCRIPTION

ORDER TESTUDINATA FAMILY TESTUDINIDAE SUBFAMILY TESTUDININAE

DEFINITION: Testudinids with never more than two phalanges per digit on fore or hind foot.

GENUS *TESTUDO* LINNÉ, 1758

GENOTYPE: *Testudo graeca* Linné, 1758.

NEW RESTRICTED DEFINITION: A genus of Testudininae world-wide in distribution, with the alveolar surface of the maxillae broad and usually with one to three rather distinct ridges, never with a ridge at the symphysis of the alveolar surfaces of the premaxillae, palatines and vomers forming a deep trough, cervical vertebrae rather slender, carapace never hinged, centrum of first dorsal vertebra not elongate.

†*Testudo cubensis* Leidy, 1868

Testudo cubensis LEIDY, 1868, Proc. Acad. Nat. Sci. Philadelphia, vol. 20, p. 179.

TYPE: Part of a first right pleural plate, Academy of Natural Sciences of Philadelphia No. 8923.

HORIZON: Pleistocene? (see below).

TYPE LOCALITY: The Chapepote spring at Baños de Ciego Montero, Santa Clara Province, Cuba.

ADDITIONAL LOCALITIES: Casimba de Jaticbonico, Santa Clara Province, Cuba; a tar pit near Hato Nuevo, Matanzas Province, Cuba.

TOPOTYPES: The American Museum of Natural History Nos. 6201, left posterior quadrant of plastron; 6202, anterior lobe of plastron; 6204, part of nuchal plate; 6209, first pleural; 6211, sixth and seventh pleurals; 6227, pygal; and numerous other fragments of carapace, plastron, and limb bones.

ADDITIONAL MATERIAL: Fragments of carapace, plastron, and limb bones from the Casimba locality in the collection of the American Museum of Natural History; fragments (Moreno collection) from the Casimba locality in the collections of the Museum of Comparative Zoölogy, Harvard College; a femur and plate fragments from the tar pit in Matanzas Province in the collections of the American Museum of Natural History.

DIAGNOSIS: A species of *Testudo* distinguished by having the borders of the vertebral and costal scutes raised into sharp-crested ridges on the plates and by having the humerus markedly compressed in the plane of the head and with a deep medial pit for the latissimus dorsi.

ADDITIONAL CHARACTERS: Size comparable to that of Galápagos species. Shell rather elongate, thin and weak in central portions of carapace and plastron. Areas underlying the marginal, gular, and anal scutes more or less thickened. Neural and pleural plates probably partly discontinuous with vacuities at the sutural junctions. Nuchal scute absent, the first marginal scutes in broad contact. Marginal scutes often, and plastral scutes mostly, with impressed borders. Posterior free margin of the carapace strongly recurved. Anterior rim moderately recurved. Free margins markedly thin, dentate. Anterior lobe of plastron flat and long. Epiplastral lip either projecting and quadrate or low and rounded. Gular scutes paired, never encroaching on the entoplastron. Pectoral scutes, so far as known, not narrowed. Posterior lobe of plastron long, with somewhat convex lateral margins. Femoral-anal boundary transverse. Anal scutes small. Anal median sulcus short. Xiphiplastral notch very shallow or wholly absent.

DISCUSSION

GEOLOGIC OCCURRENCE AND CONDITION OF THE MATERIAL

THE TYPE PLEURAL PLATE of †*T. cubensis* was obtained at the Chapepote thermal spring, one of three such springs located in a bend of the Analla River at the Baños de Ciego Montero, Santa Clara Province, 30 miles northwest of Cienfuegos, Cuba. The deposits were black mud at the bottom of a pool 10 feet deep which required much pumping to clear. The fossiliferous layers were believed by Barnum Brown to result from periodic overflows of the Analla River. Heavy rains still bring shells and river turtles into the spring (Brown, 1913). The accumulations of organic material included bones, river shells, crustaceans, trees, pine cones, nuts, and leaves.

The vertebrate fauna found is listed in table 1 (taken with only minor changes from a manuscript of Matthew). The forms so

listed are represented by dissociated bones. Barnum Brown (1919) remarks that in his two expeditions the only bones found together were a few crocodile vertebrae (1911) and a few †*Megalocnus* vertebrae (1918). The same species occurred from top to bottom of the deposits, except that the earliest layers contained the amphibian and most of the small bird, snake, and rodent bones.

The age of the deposits is difficult to estimate. The ground sloths are usually listed as Pleistocene in age (Simpson, 1945). †*Nesophontes* is regarded as "Pleistocene or Recent." †*Geocapromys columbianus*, mentioned by Matthew as occurring rarely in these deposits, is, according to Brown, at least as old as the sloth bones. The fossil crocodile described by Leidy (1868) as †*Crocodylus pristinus* from a single vertebra from these de-

TABLE 1
PLEISTOCENE AND SUB-RECENT CUBAN FAUNAS

	Ciego Montero	Casimba	Caves (Various)
EDENTATA			
Megalonychidae			
<i>Megalocnus rodens</i>	Abundant	Abundant	—
Species 2 ^a	?	Scarce	Rare
Species 3	—	Rare	—
<i>Mesocnus browni</i>	Scarce	Scarce	—
<i>torrei</i>	Rare	Common	—
<i>Miocnus antillensis</i>	—	Scarce	—
<i>Microcnus gliriformes</i>	Rare	Rare	—
RODENTIA			
Octodontidae			
<i>Capromys</i> sp.	—	—	—
<i>Geocapromys columbianus</i>	Rare	Rare	Abundant
<i>Boromys</i> sp.	—	—	Abundant
INSECTIVORA			
Nesophontidae			
<i>Nesophontes micrus</i>	Rare	—	Common
TESTUDINATA			
<i>Testudo cubensis</i>	Abundant	Abundant	—
<i>Pseudemys</i> cf. <i>P. decussata</i>	Abundant	Abundant	Present
CROCODYLIA			
<i>Crocodylus rhombifer</i>	Abundant	Abundant	—
AVES, SAURIA, SALIENTIA			

^a Names are given in Matthew's MS, but they cannot be repeated here since they would be *nomina nuda*.

^b Common in uppermost levels only, not in older deposits.

posits is now regarded (on Barbour's authority; Matthew, 1918, p. 662) as identical with still living *Crocodylus rhombifer*; the largest fossil specimens, however, much exceeded any modern specimens in size.

Probably significant is the evidence of the fossil flora. Pine cones¹ were found abundantly in the spring deposits, although at present the nearest pines are known from Pinar del Rio and Oriente Provinces, more than 150 miles to the west and east, respectively. This is certainly indicative of climatic change. Pines may have been characteristic of the colder periods of the Pleistocene. Brown regarded the deposits as early Pleistocene, and they are usually so regarded in standard geological works (Schuchert, 1935; Wood *et al.*, 1941).

It is true that Wetmore's (1928) discovery of *Gallus* among the bird remains at Ciego Montero indicates that at least the uppermost levels of the deposit are quite recent. This, however, is not remarkable, since the Chapepote spring has remained open to contamination of this sort. The bones of *Gallus* also are, as Wetmore remarks, quite different in color from the older remains.

The nature of the deposit has had important consequences for the condition of the fossils. The elements of †*T. cubensis* are as completely dissociated as those of the other animals. The largest parts found together are the anterior lobe of one plastron and the left posterior quadrant of another. All the plates of the carapace were found wholly isolated or, at most, parts of few together. No portion

of a skull nor any vertebrae were recovered. Only a few limb bones, broken and water worn, are known.

The deposits at the fissure or "casimba" in the Sierra de Jatibonico in the eastern part of Santa Clara Province are in many ways very similar to those of Ciego Montero. Here the fossils were found in a fissure, about 15 feet deep and 300 feet long, opening into a small cave. The fragments tend to be of smaller individuals than those of Ciego Montero (see below).

A few fragments of †*T. cubensis*, including a perfect femur, parts of a peripheral and of a nuchal, have been obtained from a tar pit near Hato Nuevo, Matanzas Province. As in the case of the Baños de Ciego Montero, bones of some recent (domestic) animals have been found in addition to ground sloth, tortoise, and crocodile. Fossil invertebrates taken from the tar pit were identified by Carlos de la Torre and are believed to indicate Pleistocene age for the bulk of the fauna.

Taken together, the collections from Ciego Montero, Casimba, and Hato Nuevo include fragments of individuals covering a considerable size range, but no single individual is even approximately complete. Such material is, of course, not entirely satisfactory, but it has several advantages over any single perfect shell. Both age and individual variation are indicated. A population is represented, and those characters of the species that can be determined are the more useful because they are more securely based.

CHARACTER ANALYSIS

Leidy's (1868) description of this species, based upon a single, partial, and apparently water-worn pleural plate, was as follows:

"*Testudo cubensis* n. s.

"Indicated by a portion of what I suppose to be the first costal plate of the right side. It is marked by the lateral borders of the first and second vertebral scutes and their transverse separation. At the former borders the plate is 51 lines² and along the latter sepa-

ration 16 lines. The articular border with the first vertebral plate is 30 lines; that with the second vertebral plate 14 lines. The articular border from the first vertebral plate to the lateral groove defining the first vertebral scute is convex forward and inward and 14 lines in a direct line. A strong costal process projects from the under part of the plate nearly parallel with its length. The surfaces corresponding with the vertebral scutes are somewhat depressed, and are generally everywhere nearly smooth or without markings so conspicuous as to affect the investing scutes. The greatest thickness of the bone is where it articulated with the first and second marginal plates,

¹ Mostly referable to the living species *Pinus caribaea*, in the opinion of Brother Léon who generously consented to examine them. One cone, however, may represent a new species.

² A line is one-twelfth of an inch, or a little over 2 mm.

measuring from $3\frac{1}{2}$ to $4\frac{1}{2}$ lines, and where thinnest it measures only one line.

"No living *Testudo*, I believe, at present inhabits Cuba, and the fossil probably indicates a species contemporary with the *Megalonyx*."

Leidy's type, though not so labeled, is in the possession of the Academy of Natural Sciences of Philadelphia, bearing the catalogue number 8923. It is here figured in plate 1.

Fifty years after Leidy's description the name was revived in the literature by Matthew, without, however, any formal redescription and only in preliminary reports (1918, 1919) on the Cuban fossils collected by Barnum Brown. Matthew's brief mentions were based on the much more adequate material here again reported on, and he characterized the species for the first time in a recognizable fashion. He had in preparation a manuscript describing the new material in detail. This manuscript has been at hand and of considerable service in the course of the present study; it has not been followed consistently and both additions and corrections have been made.

The character that Matthew believed isolated †*Testudo cubensis* from all other species of the genus was the fact that the margins of the horny shields were marked out on the bony plates not by the usual simple grooves but by sharp raised ridges enclosing deep median furrows (see pl. 4, figs. 2, 4). This is certainly the most striking feature of the species, and in fact the majority of the pleural and neural plates can be recognized as belonging to this species on this character alone.

This feature, however, is not unique; it is no longer possible to say, as Matthew (1919, p. 170) did, that "this alone would forbid any close relationship with any of the species I have compared." Matthew and Granger (1923) discovered the same character in †*Testudo insolitus* of the Lower Oligocene (Ardyn Obo) of Mongolia. Gilmore (1931), in redescribing †*T. insolitus*, noticed that the same peculiar feature had already been described in 1908 by O. P. Hay in †*Testudo laticuneus* of the Chadron beds of the North American Oligocene (and in †*T. quadratus* of the same age as well as in †*T. edae* of the Lower Miocene). Gilmore further pointed out that this character is known in living

tortoises; he found it in a specimen of *T. radiata* and one of *T. abingdoni* (= *T. elephantopus*¹ of this paper) at the United States National Museum (U.S.N.M. Nos. 29214 and 29269, respectively, both on exhibition).

The present author has verified the existence of this character on the pleurals and neurals of †*T. laticuneus* and †*T. insolitus* and on the nuchal of †*T. quadratus*, the types of which are in the American Museum of Natural History, and on the living species cited by Gilmore in the United States National Museum. He has seen it also on the gular median sulcus of the type of †*T. orthopygia* (Lower Pliocene of North America) in the American Museum of Natural History. It is well developed over the whole carapace of a *Gopherus polyphemus* in the Museum of Comparative Zoölogy. It is rather frequently present in *Testudo pardalis*, mostly on peripherals and posterior pleurals, and tends to be generally though feebly present in *T. denticulata* and *T. radiata*.

The rather surprisingly widespread occurrence of this character, while disposing of it as a feature isolating †*T. cubensis* from other tortoises, does not diminish its utility as a species character. It is not so much the presence of raised sulci as their degree of expression that is the peculiar mark of †*T. cubensis*. The raised sulci of other fossil and recent tortoises are feebly developed and not noticeable without close examination of the specimen. The raised sulci of †*T. cubensis*, on the contrary, are very obvious. The ridging is usually high and narrow; it varies, however, considerably and may, especially on the peripherals, be broad and shallow, fading away into grooves without ridging. In other forms, also, the raised sulci tend to be most clearly expressed on the nuchal plate or on the peripherals or on the plastron. In †*T. cubensis* the raised sulci are best marked on the neural and pleural plates, infrequently present and then, as just noted, less developed on the peripherals, absent altogether from the nuchal plate, in the two instances in which that is known, and from the plastron. Clearly the raised sulci of †*T. cubensis* show the fixation and elaboration of a character

¹ *Testudo elephantopus* is used in the sense of Rothchild (1931), Flower (1937), and Mertens (1942) to include all Galápagos "species."

frequently, but irregularly and poorly, developed in other tortoises.

The other characters of †*T. cubensis* are less striking, but in combination they make it a very well-marked species:

1. The absence of a nuchal scute, seen in †*T. cubensis*, is a character of many advanced species of *Testudo*. All the three living species assigned to the genus *Testudo* in the Western Hemisphere (all of them Neotropical) agree in this regard (*T. denticulata*, *T. chilensis*, *T. elephantopus*). Likewise †*T. praestans* and †*T. gringorum* of the South American Pliocene and Miocene, respectively, lack the nuchal (Rovereto, 1914; Simpson, 1942). In strong contrast all the species of the North American Tertiary retained this shield, as also does the modern genus *Gopherus* of North America.

2. Much emphasis was placed by Matthew (1919 and MS) on the thinness of the shell and especially on the thinning of the neural and pleural plates at their junction with one another. He believed that irregular vacuities must have existed at these sutural junctions. The thinness of the shell seems to have been a very constant character of the species and, like the large size, is a point of resemblance to Galápagos tortoises. It is not, however, as Matthew himself remarked, comparable in detail to the thinning of the shell in Galápagos tortoises and seems to have been independently acquired. Thinning of the shell and consequent fontanelles are not infrequent in testudines. The extreme of such a process is reached in *Testudo* (*Malacochersus*) *tornieri* (Proctor, 1922), but it is often carried very far in *Gopherus polyphemus*, in which only a very fragile and incomplete bony shell is sometimes preserved (Gadow, 1901; Proctor, 1922, specimen at the Chicago Natural History Museum, specimen on exhibition at the American Museum of Natural History). Giant forms, also, as can be seen not only on individuals from the Galápagos but on those from the islands of the Indian Ocean, seem to be very susceptible to weakening of the bony plates. Unfortunately the extent to which dietary deficiencies play a part in this process is not known (Loveridge, 1947).

3. In †*T. cubensis*, as in many other tortoises, the areas covered by the marginal, gular, and anal scutes are characteristically

thickened, and the amount and nature of the thickening in each of these regions vary notably with the individual or perhaps with the age and sex of the individual.

4. The shape of the pleural plates in modern *Testudo* and *Gopherus* as in certain emydines, e.g., some species of *Pseudemys*, is that of alternating wedges. †*T. cubensis* is quite typical in this respect. A number of the testudines of the North American Tertiary lacked this advanced character.

5. The shape of the neural plates, regarded as of considerable taxonomic importance by Hay and others, is not readily ascertained in †*T. cubensis*. The thinning of the neural plates at their junction with the pleural plates and with each other, combined with the fractures inevitable in fragile, dissociated, water-carried material, effectively prevents knowledge of the shape of these bones in the intact carapace. The best-preserved neural plate might reasonably be interpreted as quadrate.

6. Hay has called attention to the reduction of the rib heads in advanced testudines (for example, *T. denticulata*) and to their frequent origin in whole or part from the neural plates. In this regard, as Matthew (in MS) noticed, †*T. cubensis* is quite primitive. The rib heads are strong and arise well within the borders of the pleural plates.

7. The shape of the pygal was used by Hay to define several species of the North American Tertiary. That of †*T. cubensis*, however, is not distinctive and resembles that of many other species, fossil and recent. The supra-caudal scute was apparently undivided, as is usual in *Testudo* except in the subgenera *Manouria* and *Malacochersus* and in *Testudo hermani*, where it is divided as in emydines.

8. The recurved, thin, and dentate margin of the anterior and posterior free edges of the carapace of †*T. cubensis* impressed Matthew as quite distinct. The known fragments of these areas in †*T. cubensis* certainly show a condition quite different from the straight, blunt, smooth margin of such a form as *T. denticulata*. The condition of †*T. cubensis* is perhaps most closely approached by *T. chilensis* (specimens examined in the Museum of Comparative Zoölogy, see also the figure in Gray, 1870). The importance of this character has probably been much exaggerated. In three specimens of *Terrapene*

carolina (author's personal collection), in one case the margin is very distinctly dentate and recurved, in another the margin is recurved but only obscurely dentate, and in still another the margin is very little recurved but very clearly dentate. Other examples could be cited of the individual variability of this character.

9. The elongation of the carapace and plastron of †*T. cubensis* is a character in which it strongly resembles †*T. denticulata*. It is also a feature in which †*T. cubensis* differs from most of the species of the North American Cenozoic (except †*T. emiliae* of the Lower Miocene).

10. The depth of the xiphiplastral notch is a character much used by Hay and others to define species of the North American Cenozoic. The notch is almost always present but varies in depth. In †*T. cubensis* it is minimal to absent. In †*Testudo osborniana* (Pawnee Creek Miocene) it is nearly as much reduced. In living testudines comparable conditions exist in the genus *Kinixys* of Africa, for example, and in the giant tortoises of both the Old and New Worlds.

11. The position and direction of the anal sulcus are also generally considered to be of taxonomic importance. In †*T. cubensis* they are very characteristic, being not oblique with the inner angle of junction of the sulci of opposite sides anteriorly directed, as in the tortoises of the North American Tertiary (†*T. osborniana*, for example) and most modern *Testudo* and *Gopherus*, but oblique, with the inner angle of junction posteriorly directed. The median sulcus between the anal scutes is consequently very short in †*T. cubensis*.

12. The shape of the entoplastron has occasionally been considered of taxonomic value. In the one example in †*T. cubensis* in which it is preserved, it is pentagonal, with internal bosses, and not much broader than long. The breadth of the entoplastron is probably a more useful taxonomic character than its precise shape, but it also must be used with caution. A limited check of various emydines and testudines seems to show considerable individual variation.

13. The pectoral scute tends in many specialized testudines to be much narrowed. †*T. osborniana* is an extreme example. The

present material is fragmentary, but enough remains of the axillary region of several plastra to show that †*T. cubensis* has remained relatively primitive, with the pectorals only moderately narrowed.

14. In †*T. cubensis* the gular scutes are widely removed from the entoplastron in all the several specimens of the anterior plastral region that are available. This character has not previously received much attention; it seems, however, to be a good species character for †*T. cubensis*. Primitively the gulars extended onto the entoplastron. Except in †*T. emiliae* (Lower Miocene of South Dakota) they did so in all the species of the North American Tertiary and in †*T. crassiscutata* and in other less well known Pleistocene forms. In †*T. praestans* and †*T. gringorum* of the South American Tertiary the condition is the same, and in *T. chilensis* the gulars in the figure of Freiberg (1938, fig. 5) at least touch the entoplastron. In *T. elephantopus* the gulars similarly at least touch the entoplastron. However, there is some evidence that the character is not always constant within species. In four specimens of *Testudo denticulata* in the American Museum of Natural History the gulars in one case encroach considerably on the entoplastron, in another case they barely reach it, and in two others they are as far from the entoplastron as in †*T. cubensis*. In *Gopherus agassizii* the gulars at least quite frequently are out of contact with the entoplastron, and in this species this phenomenon seems to be correlated with a lengthening of the anterior plastral lobe. Probably it was also the lengthening of the anterior lobe of the plastron that brought about the retraction of the gulars from the entoplastron in *T. denticulata*, †*T. emiliae*, and †*T. cubensis*.

15. Epiplastral bones are the most frequently preserved, precisely identifiable elements of †*T. cubensis*. Nine epiplastra representing three growth stages are present in the material studied. This series is of some importance in the evaluation of a character upon which much reliance was placed by Hay, namely, the projection or lack of projection of the gular region of the plastron. The smaller epiplastra show considerable variation from individual to individual in the degree of projection of the gular region. The

series exhibits a complete transition from a gular region conforming completely to the general contour of the anterior plastral lobe to a gular region markedly and abruptly projecting.

Size and age are presumably not noteworthy factors. A middle-sized pair of epiplastra from the Casimba locality (M.C.Z. No. 1901) show a stage in the differentiation of the gular region only a little more advanced than the least differentiated of the smaller epiplastra. In strong contrast A.M.N.H. No. 6235 from Ciego Montero shows the gular region projecting very prominently, as does the largest specimen, A.M.N.H. No. 6202, also from Ciego Montero.

This very striking difference in the degree of gular projection within species is paralleled in modern *Gopherus*, and in that genus, as Grant (1936) and Woodbury and Hardy (1948) have noticed, is a secondary sexual character. In *Gopherus agassizii*, according to both Grant and Woodbury and Hardy, the gular projection is longer, larger, and more upturned in the males, especially as they get older. The difference may be quite extreme, as the present author has determined on a male *Gopherus agassizii* personally captured at Laguna, Arizona, and on material in the American Museum of Natural History. A series of *Gopherus berlandieri* examined in the Kansas Natural History Museum show the sexual characters of the gular region in that species. Characteristically bifurcate in both sexes in this species, the gular region in *G. berlandieri* males is longer, more sharply projecting, more deeply forked, and very much thickened. There is some individual variation in all these features, but the contrast between the sexes is almost always sharp and unmistakable.

It is possible that in †*T. cubensis* also a strongly projecting gular region is an indication that the specimen was a male. In fact, A.M.N.H. No. 6202, the element exhibiting the most prominent gular projection, perhaps should be associated with A.M.N.H. 6201, the left posterior quadrant of a plastron, which is definitely that of a male as shown by the characteristic strong concavity (the area under the anal scutes is also strongly thickened as in males of *Gopherus berlandieri* and *G. agassizii*). The two elements are certainly

from animals of the same or nearly the same size; unfortunately proof that they are from one animal is lacking, since a middle portion of the plastron that might unite them is missing.

On the other hand it may be that the differences in the form of the gular region in †*T. cubensis* are not secondary sexual characters. In a series of *T. denticulata* in the American Museum of Natural History very marked differences in the shape and especially in the thickness of the gular region are not sexual in origin; at least none of the conditions is consistently correlated with the marked plastral concavity that has been taken as a sign of the male.

If sexual difference is not involved, there is another possibility to be considered: it is conceivable that the materials from Ciego Montero and from Casimba are at least subspecifically distinct. All the referred material from Casimba is consistently smaller than the topotypical Ciego Montero †*T. cubensis*. The gular region in none of the Casimba specimens projects so much as in the two large epiplastra from Ciego Montero.

There is precedent for recognition of a taxonomic difference between materials from the two localities in Matthew's action in a parallel situation involving the ground sloth remains. Matthew (MS) erected a distinct subspecies of †*Megalocnus rodens* for the slightly differing material at the Casimba locality and also erected two full species of †*Megalocnus* for some small jaws from Casimba. One of Matthew's genera of smaller ground sloths (†*Miocnus*) is likewise known only from Casimba.

There is therefore some warrant for believing that Casimba and Ciego Montero had different faunas in the Pleistocene. It is also, of course, uncertain that the two faunas are strictly contemporaneous. It is possible therefore that distinct subspecies of †*T. cubensis* might characterize the two areas. However, an alternative explanation of the difference in the fossils at the two localities is possible: it may be that the conditions of deposition in the fissure springs at Casimba de Jatibonico have introduced a definite bias in the matter of the size of the material swept into the deposit, so that the fossils

are not a truly random sample of the populations in the area. It is this hypothesis that the author provisionally adopts. The differences in size between the Casimba and the Ciego Montero materials of †*T. cubensis* are considered to be ontogenetic, and the differences in gular prominence are interpreted as secondary sexual difference.

16. The limbs of †*T. cubensis* are stout and heavy, resembling in this regard those of †*T. osborniana* or of †*T. orthopygia* rather than those of †*T. laticuneus* or †*T. vaga* among the tortoises of the North American Tertiary. The two known humeri (both from Ciego Montero) are strongly compressed in the plane of the head; the depth of the shaft in that plane is about one and one-half times the depth in the plane at a right angle to that of the head. In *T. denticulata*, *T. elephantopus*, and the living species of *Gopherus*, as well as in the Old World species examined (*T. pardalis*, *T. elegans*), the ratio of the same two dimensions is very nearly 1:1. The femur of †*T. cubensis* from the tar pit in Matanzas Province shows the same sort and degree of compression as the humeri. The femur of the type of †*T. osborniana* (A.M.N.H. No. 5868), as Hay has already stated (1908, p. 425), exhibits the same condition.

There is another peculiarity of the humerus of †*T. cubensis*; it has a large and deep pit on the medial surface for the insertion of the latissimus dorsi. This pit occurs as an abnormality in *T. denticulata* (one specimen in three in the American Museum of Natural History) and is present in a somewhat less distinct but still plainly visible form in many Galápagos tortoises (many specimens in the American Museum of Natural History). This pit has not been seen in other tortoises.

17. A few caudal vertebrae of †*T. cubensis* are present and are typically testudine, the anterior ones being quadrangular and tending to be higher than broad, the posterior ones

equally quadrangular but much broader than high. They do not differ much from comparable vertebrae of *T. denticulata* or *T. pardalis*, probably more closely resembling the former. A specific character may be the extreme dorsoventral thickness of the neural laminae in certain of the anterior vertebrae. There is no evidence of a heavy, closely united dermal armor covering the tail as described by Hay (1908, figs. 560, 603) for †*T. osborniana* and †*T. orthopygia*, nor is there any hint of an abrupt, paddle-shaped termination to the tail with several fused vertebrae as in †*T. orthopygia* (Hay, 1908, fig. 601).

TABLE 2

SUMMARY OF THE CHARACTERS OF
†*Testudo cubensis*

Nuchal scute absent
Vertebral and costal sulci on raised ridges
Marginal and plastral sulci usually in simple grooves
Thinning of shell greatest at neural-pleural junctions and in midplastron
Areas of thickening under marginal, anal, and gular scutes
Rib heads strong, arising well within pleural borders
Shape of carapace markedly elongate
Xiphiplastral notch minimal or absent
Free carapace margins recurved, thin, and dentate
Femoral-anal sulcus transverse or posteriorly directed at its middle
Anal median sulcus very short
Pectoral scutes expanding gradually at axillae
Gular scutes never encroaching on entoplastron
Humerus short, stout, strongly compressed in plane of head, with large and deep pit for latissimus dorsi
Femur short, stout, strongly compressed in plane of head
Caudal vertebrae normally testudine except for extreme dorsoventral thickness of neural lamina of some anterior caudals which may exceed dorsoventral thickness of centrum

INTERRELATIONSHIPS OF WESTERN HEMISPHERE TESTUDINES AND
THE PHYLOGENY OF †*TESTUDO CUBENSIS*

Since the relationships of †*Testudo cubensis* are rather certainly with testudines of the Western Hemisphere, we may reasonably limit our attention to these forms. However, even with this admittedly serious limitation,

analysis of the relationships and phylogeny of †*Testudo cubensis* is a task presenting a number of difficulties and requiring an extended discussion. There are already more than 70 species of testudines assigned to eight

genera described from the Cenozoic of the New World. The larger number of these are known only from single shells or shell fragments. In only 11 species is the skull known. In some of these and in a few others limbs and limb girdles are known. Further, the types of these numerous described species are very widely scattered, so that no worker since Hay has seen even a majority of them. (In the case of a few South American species it has not been possible to locate even the original descriptions, and they are known only from citations by Ameghino and other authors.)

In combination this multiplicity of species and the inadequacy or inaccessibility of material make it inevitable that an assessment of the phyletic relationships of Western Hemisphere testudines will be even more theoretical and tentative than phyletic judgments usually are. It is felt, however, that a carefully framed set of hypotheses suggesting relationships that can be tested by those with access to the material will add something pertinent and perhaps decisive to the present mass of non-integrated detail.

MIocene TESTUDINES

It will be best to begin the analysis of Western Hemisphere testudines in the Miocene, since only for that period have any number of species been described from really good material—skulls, limbs, and quite perfect shells.

Seventeen Miocene North American forms are named in the literature, all allocated by their describers to the genus *Testudo*. In reality only three forms can be assigned with immediate certainty to the genus *Testudo*, while the one other form in which the skull is known, †*Testudo brevisterna* Loomis, 1909, is clearly better assigned on the basis of characteristic palatal ridging to the genus *Gopherus*.

The character on which this generic determination is made is worth examining. Loomis (1909, pp. 21–22) describes the condition in †*Gopherus brevisterna* thus: "The vault of the palate is very low and has a median ridge running from the basisphenoid onto the premaxillae. . . . The median ridge mentioned above as continuing onto the premaxillae separates two deep pits, one on

either side." This contrasts with Hay's (1908) description of †*Testudo osborniana*: "There is no ridge occupying the midline along the symphysis of the premaxillae; hence this species cannot be regarded as a *Gopherus*. The masticatory ridges of the right and left sides are separated by a deep longitudinal groove." The conditions here described in two fossil species are identically those used to distinguish *Gopherus* and *Testudo* in living forms.

The transformation of one type of skull into the other would seem to be relatively simple. A ridge exists on the vomer in *Testudo*; lateral maxillary ridges are also present. All of these ridges approach the borders of a premaxillary pit. To attain the †*G. brevisterna* condition all that is necessary is an extension of the vomerine ridge forward across the premaxillary pit.¹ The *Gopherus* palatal pattern is thus only a slightly specialized derivative of the typical *Testudo* condition.

The skull difference is in fact trivial, but it is of considerable antiquity and cannot be disregarded. Furthermore when the series of fossil tortoises is examined carefully enough, shell characters are found to be associated with the diagnostic skull difference. The forms of the North American Miocene can, for example, be separated into two series, one of which may be called the †*Testudo osborniana* series and the other the †*Gopherus brevisterna* series. In the first series the three forms with *Testudo*-like skulls are readily arrayed, and in the other the single form known to have a *Gopherus* palate finds its natural place. Table 3 displays the differences between the two series.

A single form of the sufficiently known tortoises of the New World Miocene (†*Testudo*

¹ The skulls of *Gopherus polyphemus* examined by the author show a further specialization: the lateral maxillary ridges do not stop short at the premaxillary boundary but continue on that bone to join the median premaxillary ridge. This character of *G. polyphemus* was long ago observed by George Baur (MS notes made available by Dr. Doris Cochran). This condition has not been seen in *Gopherus agassizii* or *G. berlandieri*, the other living species of the genus, by either Baur or the author; according to Baur it may sometimes be absent in *G. polyphemus*. It should be emphasized that the contact of maxillary and premaxillary ridges is never evident in unprepared skulls, in which the maxillae and premaxillae are still covered by a horny sheath.

TABLE 3

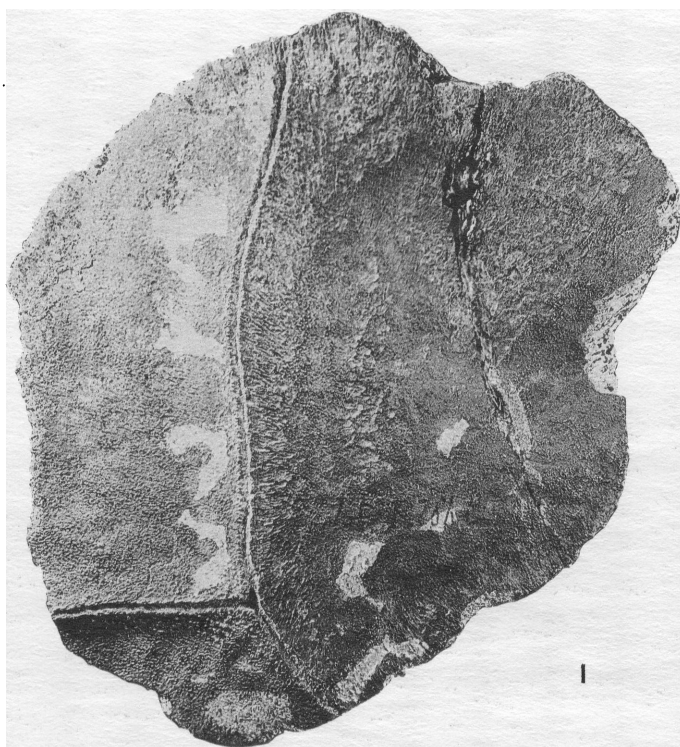
	† <i>Testudo osborniana</i> Series	† <i>Gopherus brevisterna</i> Series	† <i>Testudo gringorum</i>
Palate	One or two lateral maxillary ridges and a premaxillary pit	One lateral maxillary ridge and a median premaxillary ridge	Not known
External surface of dentary	With fine vertical ribbing	Without vertical ribbing	Not known
Nuchal scute	Much longer than wide	Nearly as wide as long	Absent
Shell shape	Tending to be high and globular	Tending to be flattened	Not high
Anterior shell margin	With flared anterolateral corners	Anterolateral corners rounded, not flared	Anterolateral corners slightly flared
Nuchal indentation	Marked	Usually absent	Slight
Fourth vertebral scute	As long as wide	Wider than long	Uncertain
Entoplastron	Wider than long	Usually longer than wide	Not wide
Pectoral scutes	In contact with entoplastron or very close, median sulcus 1/15 to 1/30 of abdominal median sulcus	Usually well separated from entoplastron, median sulcus usually about 1/5, never less than 1/10, of abdominal median sulcus	Separated from the entoplastron, median sulcus 1/5 of abdominal median sulcus
Neural plates	Fully differentiated, second and fourth octagonal, third and fifth quadrilateral	Usually less completely, or not at all, differentiated, often the fifth hexagonal or all hexagonal	Partly differentiated but first and second hexagonal
Dermal ossicles on fore and hind limbs and tail	Present and extremely developed, often compacted and suturally united	Absent or not well developed	Not known

gringorum Simpson, 1942) cannot be included in these two series. The characters of †*T. gringorum* are compared with those of the two series in table 3. The absence of the nuchal scute readily separates this form from both the †*T. osborniana* and †*G. brevisterna* series. Relationship, however, is probably closer to the †*T. osborniana* group. The narrowed nuchal of the †*T. osborniana* group, for example, could more easily lead into a condition with the nuchal absent and the first marginals in broad contact (as in †*T. gringorum*) than with the broad nuchal of the †*G. brevisterna* group. †*T. gringorum* also has traces of some of the shell specializations of the †*T. osborniana* group, and, while its skull is regrettably unknown, the species is

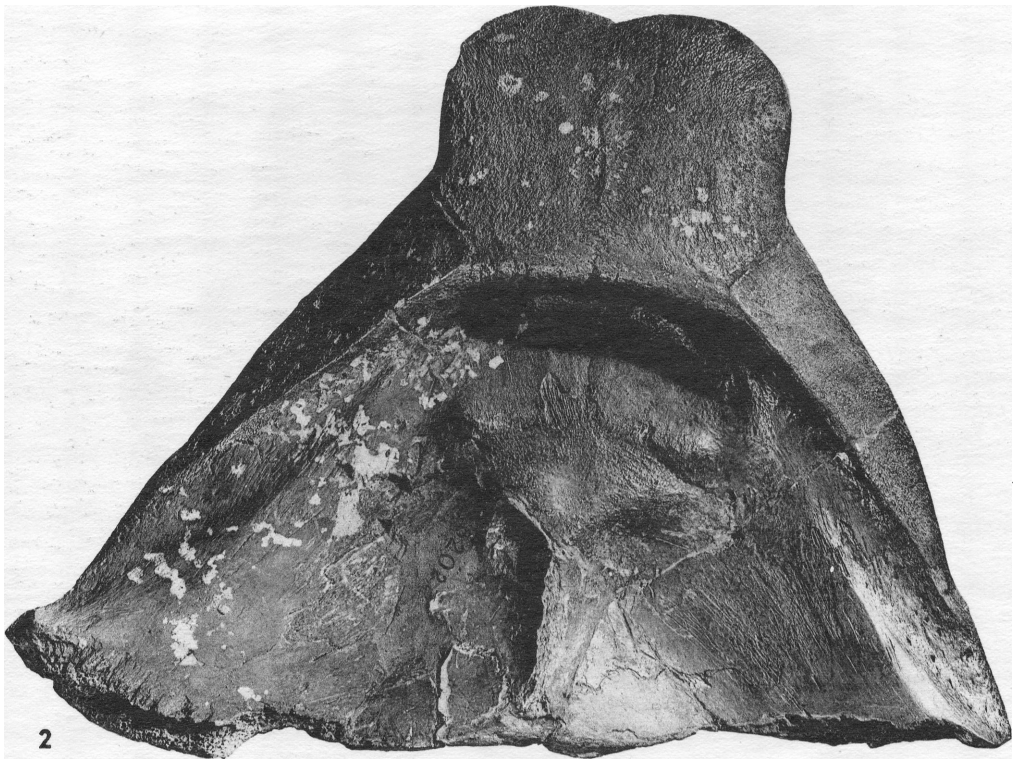
Patagonian and probably the ancestor of the modern South American species, all of which have retained the relatively primitive *Testudo* palate seen in †*T. osborniana*.

The Miocene representatives of the †*Testudo osborniana* series are †*T. osborniana*, †*T. impensa*, †*T. angusticeps*, and †*T. arenivaga*. All these show the listed characters of the series in full development.

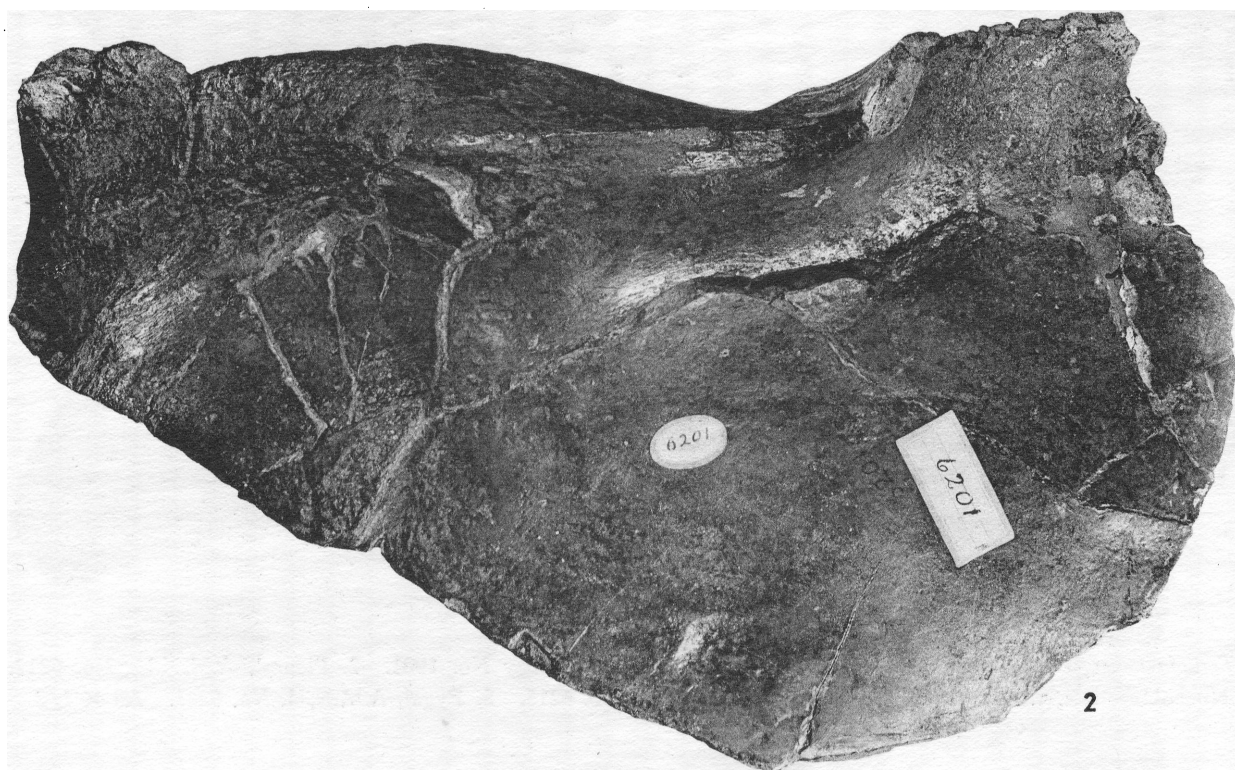
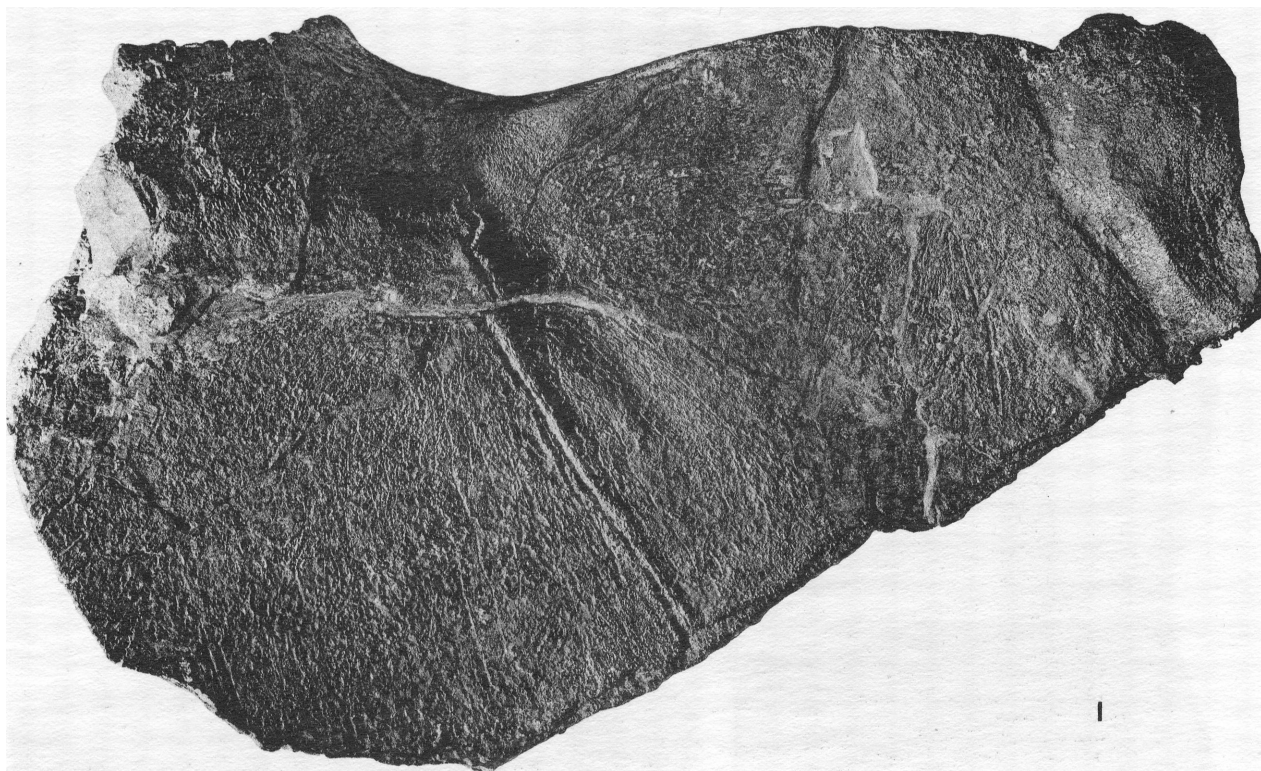
†*Gopherus brevisterna*, described from a complete skeleton, is the most adequately known representative of its group. †*G. hollandi*, †*G. edae*, †*G. pansa*, and †*G. mohavense* are known from good shells. †*G. vaga* is represented by a good plastron, limb bones and girdles and vertebrae, and fragments of the carapace. All of these are much alike



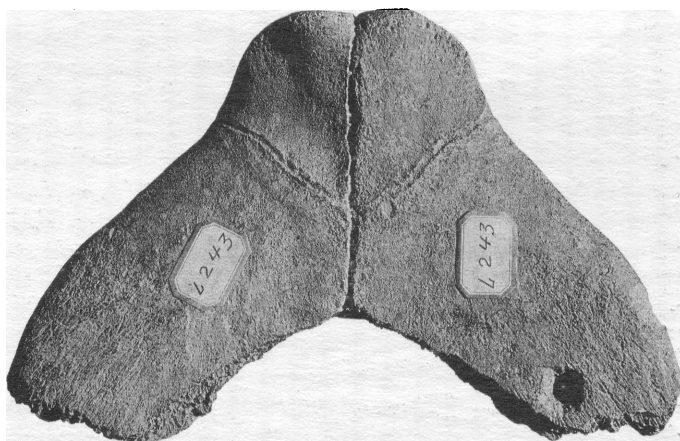
Testudo cubensis, type pleural plate, Academy of Natural Sciences of Philadelphia
No. 8923. 1. External view. 2. Internal view. $\times 1$



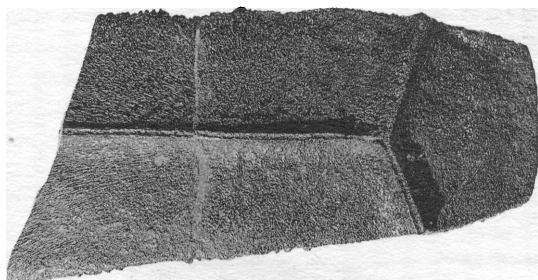
Testudo cubensis, anterior lobe of plastron, A.M.N.H. No. 6202. 1. External view. 2. Internal view. $\times 1/2$



Testudo cubensis, left posterior quadrant of plastron, A.M.N.H. No. 6201. 1. External view. 2. Internal view. $\times 1/2$



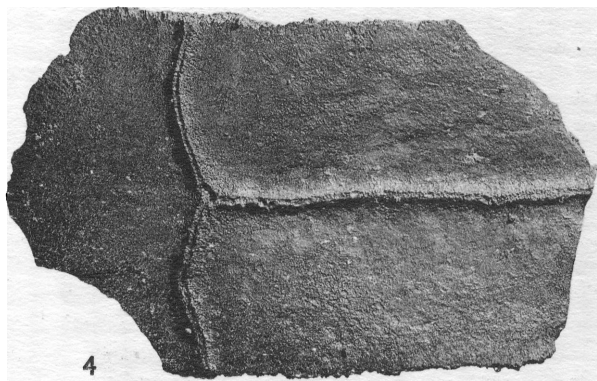
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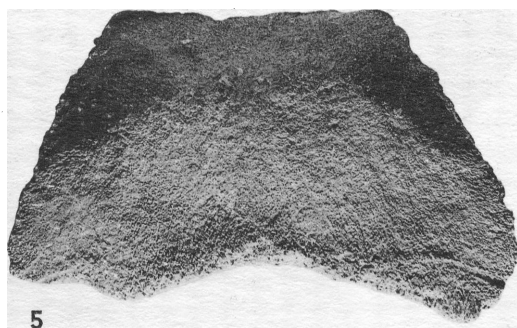
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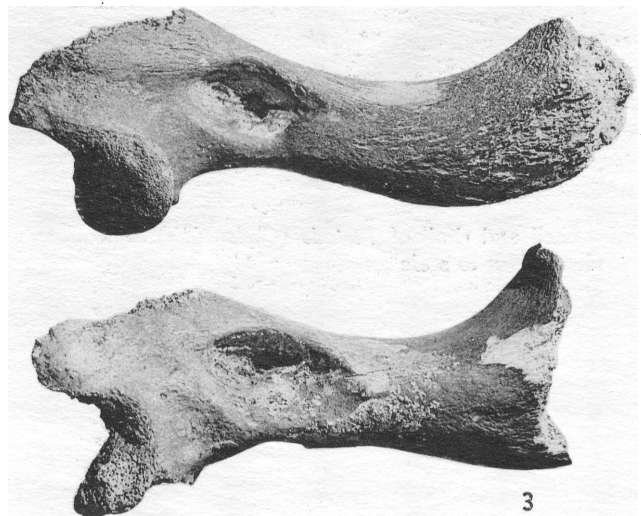
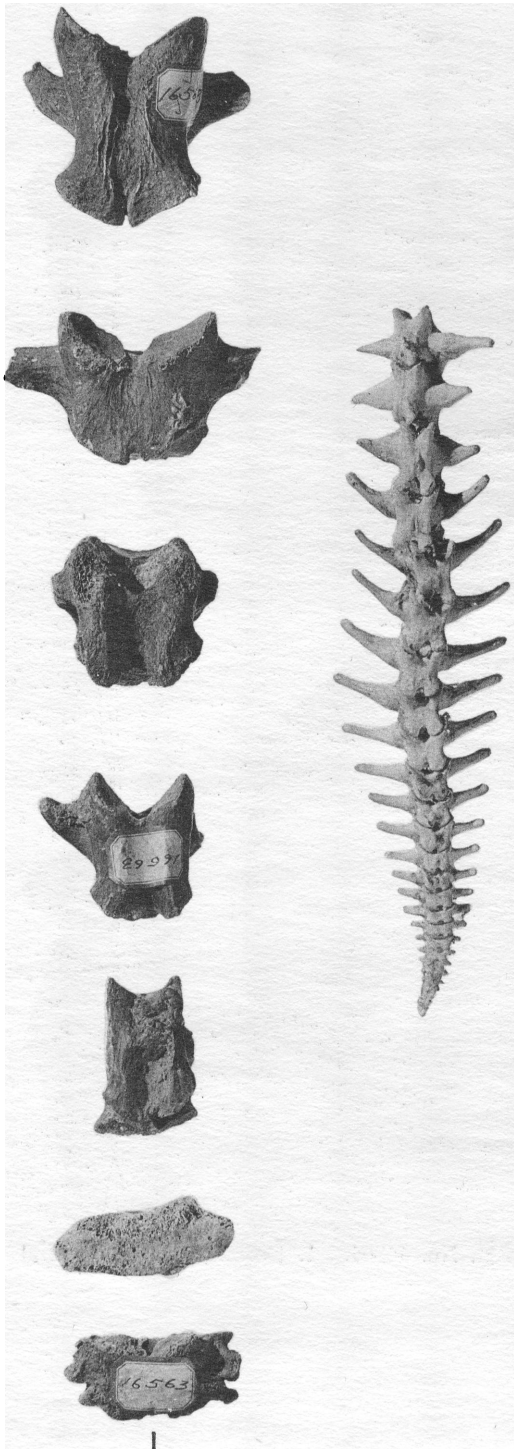


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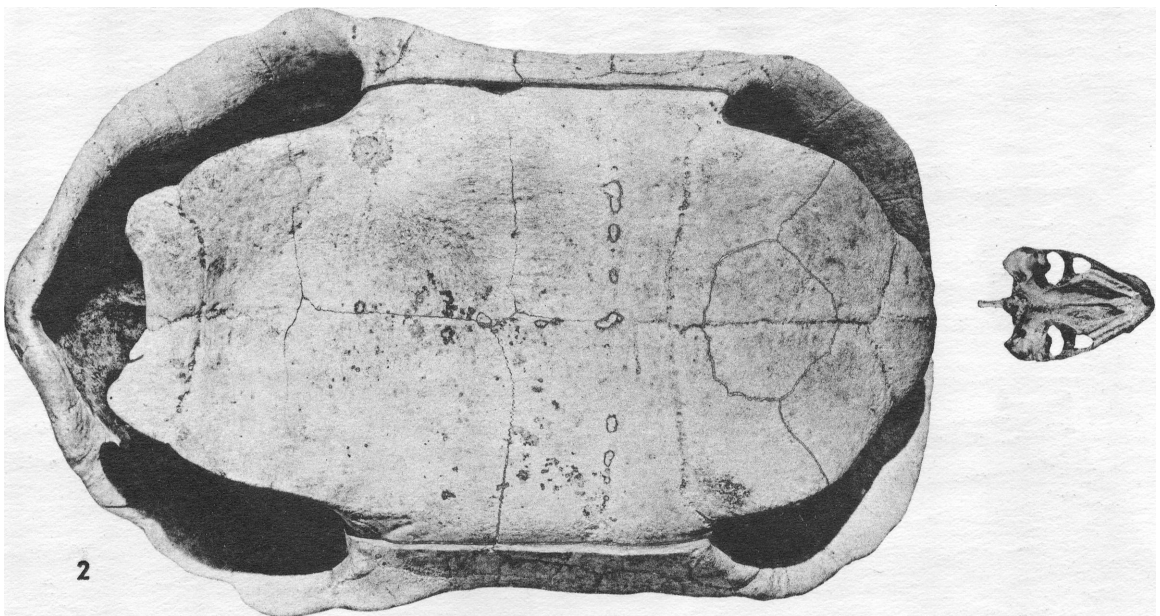
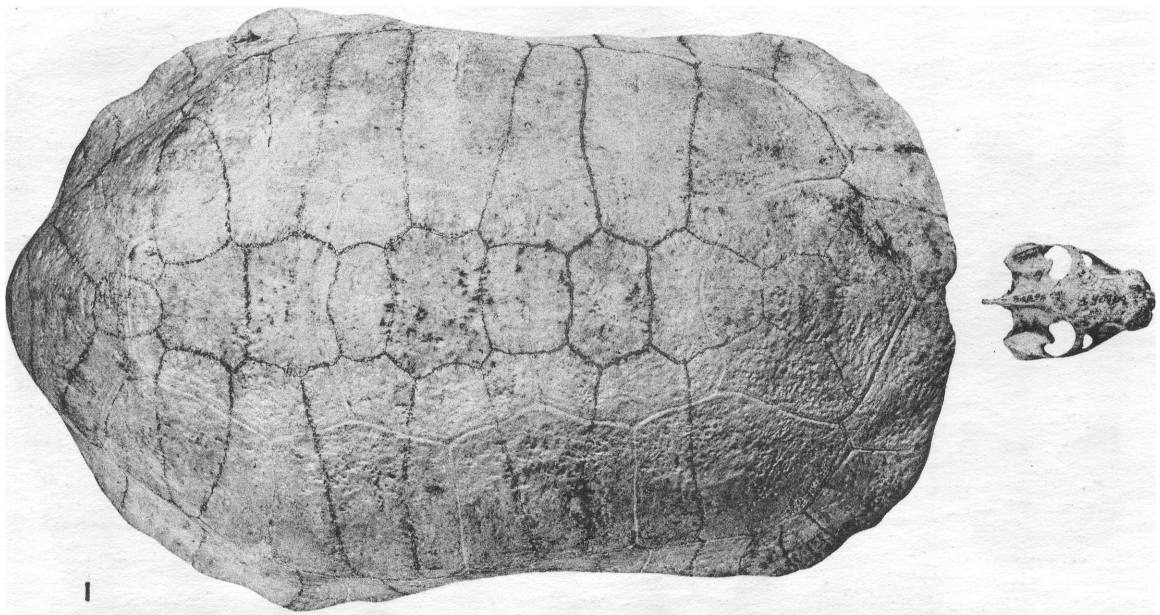


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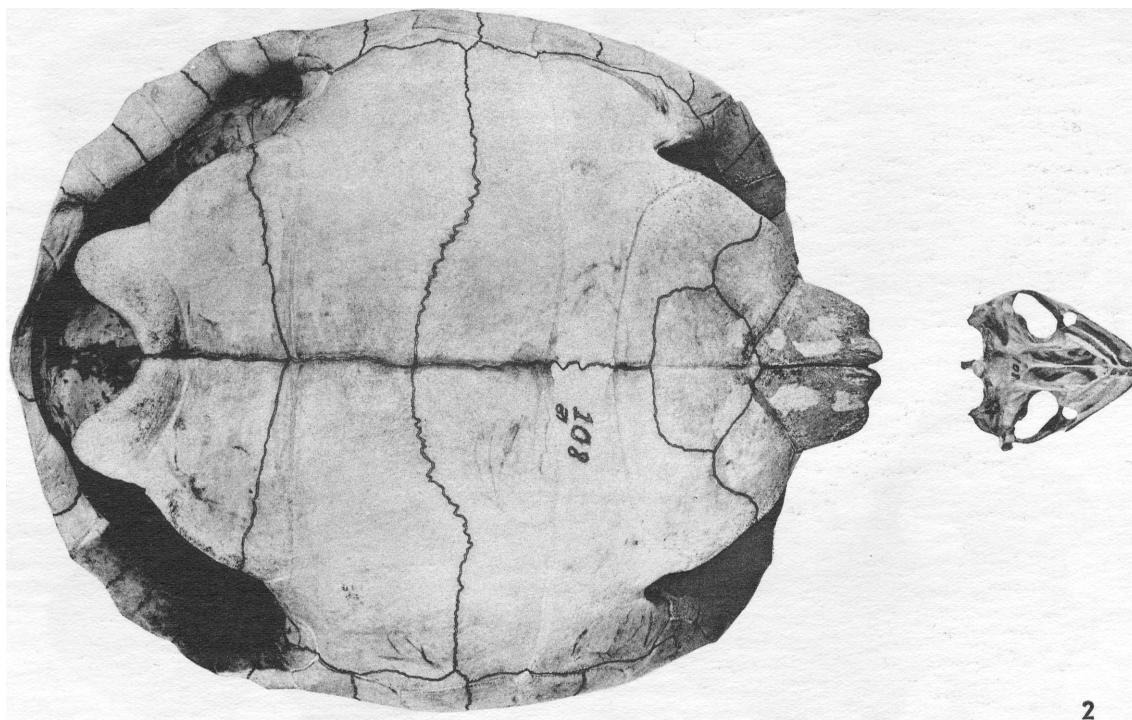
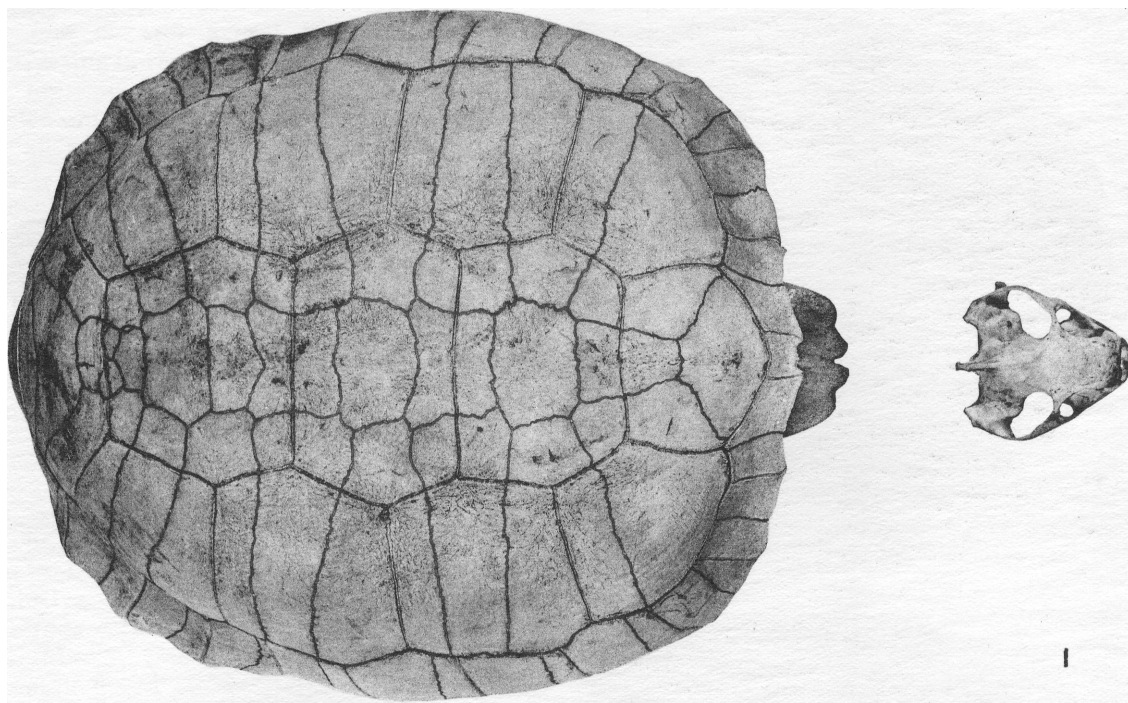
Testudo cubensis. 1. Epiplastra, Museum of Comparative Zoölogy No. 1901. 2. Pleural, A.M.N.H. No. 6212. 3. Nuchal, A.M.N.H. No. 6204. 4. Peripheral, A.M.N.H. No. 6215. 5. Pygal, A.M.N.H. No. 6227. All $\times 1/2$



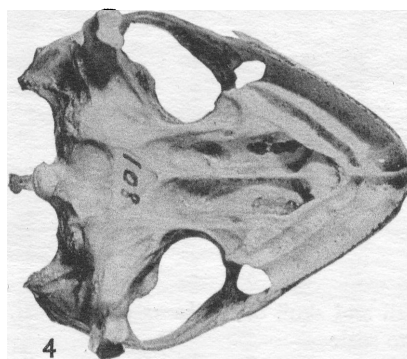
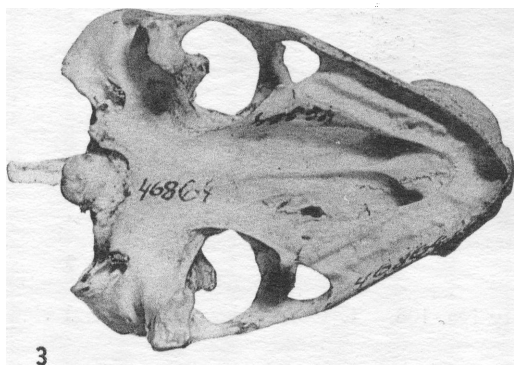
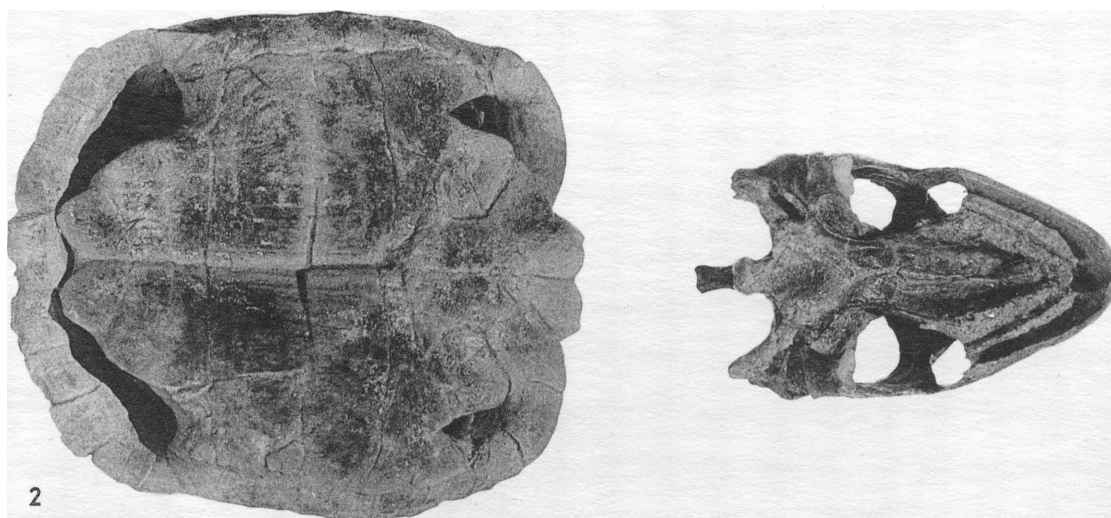
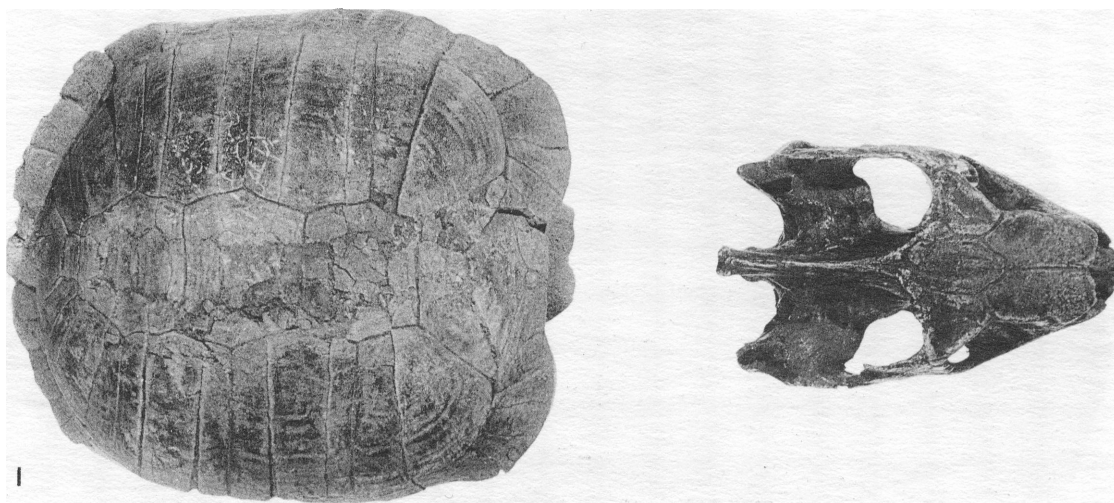
Testudo cubensis. 1. Caudal vertebrae (caudal column of *T. denticulata* at right for comparison). $\times 1/2$.
2. Femur, A.M.N.H. No. 6242. $\times 1$. 3. Humeri. $\times 1/2$



Shell and skull of *Testudo (Chelonoidis) denticulata*. A.M.N.H. No. 46864. 1. Dorsal view. 2. Ventral view. Not to scale



Shell and skull of *Gopherus polyphemus*. Cornell University No. 108. 1. Dorsal view. 2. Ventral view.
Not to scale



1. Shell and skull of *Testudo* (*Hesperotestudo*) *angusticeps* (skull of type, A.M.N.H. No. 6295; shell of young specimen, A.M.N.H. No. 6799), dorsal view. 2. The same, ventral view. Both $\times 1/2$. 3. Skull of *Testudo* (*Chelonoidis*) *denticulata*, palatal view. A.M.N.H. No. 46864. $\times 1$. 4. Skull of *Gopherus polyphemus*, palatal view. Cornell University No. 108. $\times 1$

in essentials and in particular agree in having one or two neural plates octagonal, contrasting in this respect with †*G. undabuna*, †*G. inusitata*, †*G. emiliae*, and †*G. copei* (all known only from shells) in which the neurals are all hexagonal. All the latter species are closely similar, much more like one another than like the subseries typified by †*G. brevisterna*, but they fall within the broad limits of the †*G. brevisterna* group as defined in table 3, and they are very different from the †*T. osborniana* series.

†*Testudo gringorum* stands alone. It is the only known Miocene testudine of South America and shows no close approach to the characters of any other tortoise of that period.

OLIGOCENE ANCESTORS

The two North American testudine lineages can be traced into the Oligocene. The representative in this period of the Miocene †*Testudo osborniana* series is †*Testudo brontops* Marsh, 1890. In most respects, in its strongly flared anterolateral corners to the carapace, strong nuchal indentation, narrow nuchal scute, humeropectoral sulcus encroaching slightly on the entoplastron, and fourth vertebral scute long with parallel sides, it resembles the Miocene members of its group. In one respect, however, it is more primitive: the pectoral scute is not narrowed, its median sulcus being about one-fourth that of the abdominal scute. Two octagonal neurals are present in the one described specimen of this form.

Conspicuously different from †*Testudo brontops* are the two known Oligocene representatives of the †*Gopherus brevisterna* group. These two forms, †*Gopherus praeextans* Lambe, 1913, and †*G. laticuneus* Cope, 1873, so similar that Gilmore (1946, pp. 306-307) was for a time inclined to regard them as the two sexes of one species, have round or truncate carapace borders, neither flared nor indented; the nuchal scute is broad; the humeropectoral sulcus is widely removed from the entoplastron; the pectoral scute is very broad, its median sulcus about one-half that of the abdominal, all characters quite congruent with those of their Miocene relatives. In two respects, however, these forms are somewhat different from the comparable Miocene forms: the fourth vertebral scute tends to

be long with parallel sides, and the skull in the one specimen of †*G. praeextans* in which it is known, although typical *Gopherus* in its palate, is as a whole more dolichocephalic than †*G. brevisterna* or any modern *Gopherus*. In both these respects the Oligocene forms can be regarded as more primitive.

Like †*Testudo brontops* these forms are large (420-540 mm. in carapace length), larger certainly than the average of modern *Gopherus*, but otherwise they are very similar not merely to the Miocene forms but to the living members of the genus. As the illustrations of the shell of a living form (pl. 7) demonstrate, the characters pictured by Hay (1908, figs. 509, 510, pl. 67) and Gilmore (1946, pls. 38-43) in forms from the Chadronian are reproduced with only minor change in at least some specimens of living species. The differences between †*G. laticuneus* and *G. polyphemus* appear to be less than those between *G. polyphemus* and *G. berlandieri*, although the last two are contemporaneous and separated from †*G. laticuneus* by half the span of the Cenozoic.¹ The resemblance is the more astonishing since the specific status of the living forms (*G. polyphemus*, *G. berlandieri*, *G. agassizii*) has sometimes been considered doubtful. In such circumstances doubt would appear to be cast on the validity of the numerous currently recognized fossil forms. It is the feeling of the author, however, that at present any extensive synonymizing of currently accepted names is unwarranted. Neither material nor analysis is yet adequate to determine which are the valid species, nor have the osteological characters of the modern species thus far been worked out with sufficient care to afford any yardstick by which to judge the distinctness of the fossil species or vertical subspecies or individual variants, whichever they may be.²

¹ Hay (1908, p. 403) expressly commented on the resemblance of †*G. laticuneus* to *G. polyphemus*. He drew from that resemblance no phyletic or nomenclatorial conclusions. This action is characteristic. Admirable in a descriptive sense as Hay's work was, it must be stated that, while he displayed extraordinary temerity in the erection of specific names, he displayed extraordinary timidity in inferring relationships.

² Lack of adequate osteological series and the fact that this is a subsidiary and not a primary problem for this paper have prevented the author from going into this matter more completely. Internal shell and skull characters can, it would seem from a preliminary survey,

Five shells of †*Gopherus praeextans* and five of †*G. laticuneus* have been described, enough to establish that the shapes of the neural plates are variable, but more often hexagonal, in both forms. In one specimen of †*G. praeextans* two octagonal neurals are present, in another specimen, one octagonal neural is present. In †*G. laticuneus* a single neural is octagonal in two of the five shells.

†*Testudo gringorum* has no known ancestors in the earlier Tertiary of South America, and it is suspected (Simpson, 1942, 1943) that the genus *Testudo* was a late invader of the southern continent, rafting there over a sea gap after the breaking of the Panama connection in the early Tertiary.

EOCENE PROTOTESTUDINES

The three testudine lineages we have been describing cannot be followed as such into the Eocene. The known Eocene forms are essentially prototestudine in stage of differentiation, perhaps some of them even pretestudine. †*Hadrianus corsoni* (Leidy), 1871, of the Bridger Eocene is primitive enough in its known characters to have given rise to any later Western Hemisphere testudine. Its neurals are all hexagonal; its pleurals do not show alternating broad and narrow distal ends; the nuchal scute is present and neither very broad nor very narrow; the contact of the humeropectoral sulcus with the entoplastron and the rather narrow, parallel-sided vertebrals may imply a special relation to the †*T. brontops*-†*T. osborniana* series, but even if this is true, it is not a specialization so radical that it bars relationship to the other lineages as well. Whether this species is itself the ancestor of the three later testudine lineages or not, it would seem to exemplify a grade of organization through which they all have passed. It is still not completely known; the skull has never been discovered,

be used to distinguish these species, in addition to the external features listed and evaluated by Bogert and Oliver (1942). Baur (MS) cites a number of osteological characters. L. T. Murray (MS) finds also a character of the soft anatomy to distinguish *G. berlandieri* from the other living species. According to Murray, in *G. agassizii* and *G. polyphemus* the trachea extends into the body cavity before bifurcating; in *G. berlandieri*, on the other hand, the trachea is very short, and the bronchi extend down the side of the neck for a considerable distance before reaching the body cavity.

and until the feet are found, we cannot be sure that they did not, like †*Stylomys*, so long considered a testudine, have the emydine phalangeal formula (Case, 1936). As in emydines and some living testudines, the supracaudal scute is divided.

†*Testudo uintensis* Gilmore, 1915, has more testudine characters, but its relationship to the three testudine lineages of the later Cenozoic is as problematical as that of †*H. corsoni*. Neither the nuchal scute nor the anterior carapace margin is known. The fourth vertebral scute is longer than wide. The pectoral scute is very broad, its median sulcus one-half that of the abdominal. The humeropectoral sulcus touches the entoplastron. The supracaudal scute is divided. There are two octagonal neurals, but these are the second and sixth rather than the second and fourth as in later North American forms. There are only seven neurals. The latter character in this form, known from a single shell, quite probably is a matter of individual variation.

A tenuous argument can be made for closer relationship to the †*T. brontops*-†*T. osborniana* line. A resemblance can be found in the contact of the humeropectoral sulcus with the entoplastron; this, however, may be a primitive feature. Further, if it is permissible to reason from the single shells of †*T. uintensis* and †*T. brontops* that have been so far described to populations of these species, the early occurrence of octagonal neurals may possibly be considered a diagnostic feature of a †*T. uintensis*-†*T. brontops*-†*T. osborniana* line. On the basis of our present knowledge of Oligocene and Miocene forms, the *Gopherus* phyletic group does seem to have a lower frequency of neural patterns with alternating octagonal and quadrilateral neurals, but admittedly our present knowledge of both the *Gopherus* and †*T. osborniana* sequences is seriously defective.

If early differentiation of a complex neural pattern is characteristic of a †*T. uintensis*-†*T. brontops*-†*T. osborniana* line, neither the South American forms nor *Gopherus* is likely to have been derived from †*T. uintensis*. From minor morphological approaches to the †*T. osborniana* series in †*T. gringorum* it appears possible that the South American tortoises have some not too remote relation

to that series. Such a relationship would be either at the level of †*T. uintensis* or at that of †*H. corsoni*. Since neural plate differentiation is evident in Eocene †*T. uintensis* and not in Miocene †*T. gringorum* (again reasoning from single shells to populations) it would seem more probable that the relationship is at the earlier (†*H. corsoni*) level. *Gopherus*, with fewer similarities and well-marked specializations of its own, would seem to have originated at some even earlier stage.

PLIOCENE AND PLEISTOCENE DESCENDANTS

If the three Miocene testudine series cannot be followed with confidence backward into the Eocene, they can be traced forward into the Pliocene and Pleistocene. But here also there is a difficulty, not this time arising from the primitiveness of the material but solely from the fragmentary nature of much of it. Especially in the Pleistocene there is a multiplicity of named forms too poorly represented for even generic allocation. Those forms that are known adequately cause no such difficulty and are each quite typical of their phyletic group.

Pliocene †*Testudo orthopygia* Cope and †*T. gilberti* Hay, the first very completely known, the second known from the skull only, continue the †*T. osborniana* line, manifesting the characters of typical Miocene forms.

†*Testudo sellardsi* Hay of Florida, as described by Loomis (1927), appears to carry at least one of the †*T. osborniana* specializations one point further. The nuchal scute in this form has become still narrower and smaller and is in fact retracted from the anterior margin of the shell so that the first marginal scutes meet in front of it.

†*Testudo riggsi* Hibbard, 1940, of the Kansas Pliocene, on the other hand, is not merely a *Gopherus* but, as the author can testify from personal examination of the type and additional and comparative material, one whose affinities to a living species seem determinable. In several characters rather peculiar within the genus it is similar to *Gopherus berlandieri*.¹ It has the nearly hemispherical shape, moderate nuchal in-

dentation and gular process parallel sided and deeply bifurcate so typical of the living form. It is distinguished from *G. berlandieri*, as Hibbard noticed, by the greater thickness of shell and by the lack of differentiation of the pleurals.

†*Gopherus riggsi* may, however, be a synonym or race of †*G. turgida* (Cope), 1892, from the Blanco beds of Texas. The type of †*G. turgida* in the Academy of Natural Sciences of Philadelphia resembles to a remarkable degree certain Meade County, Kansas, specimens at the Kansas Natural History Museum referred to †*G. riggsi*. †*G. turgida* and the Meade County specimens differ from the type and paratype of †*G. riggsi* from Seward County, Kansas, primarily in greater thickness of shell and an extraordinary tendency to gibbosity, especially in certain scutal areas such as the areas under the gulars and anals. In these respects and indeed in all points †*G. turgida* and the Meade County †“*riggsi*” strikingly resemble †*Testudo kalaganensis* Gilmore, 1931, from the Cenozoic of Mongolia (horizon undetermined). This set of described forms merits renewed investigation.

†*Bysmachelys canyonensis* Johnston, 1937, known from very complete material but imperfectly described by its author, is undoubtedly a *Gopherus*. It has many resemblances on the one hand to †*G. vaga* and †*G. brevisterna* and on the other to *G. polyphemus*. The extreme brachycephaly (width across quadrates 103 per cent of basal length from snout to occipital condyle), considered part of the generic definition by Johnston, is paralleled in †*G. brevisterna* (same width 100 per cent of basal length, Loomis, 1909) and in *G. polyphemus*. The size is large (805 mm. plastral length), larger than any other form definitely known to be *Gopherus*, but this is not of generic value. The very short cervical vertebrae and especially the exaggeratedly widened and lengthened postzygapophyses of the eighth cervical resemble the same elements in †*G. vaga* and *G. polyphemus*. The ridge on the distal end of the femur separating the articular surfaces for the tibia and fibula, regarded as important by Johnston, has been described by Hay (1908, p. 417) in †*G. vaga*.

Pliocene †*Testudo hayi* Sellards, in which all the neurals are still hexagonal, may be a

¹ This resemblance has already been noticed by Malcolm Smith in the Zoological Record for 1944 (section on Amphibia and Reptiles, p. 26).

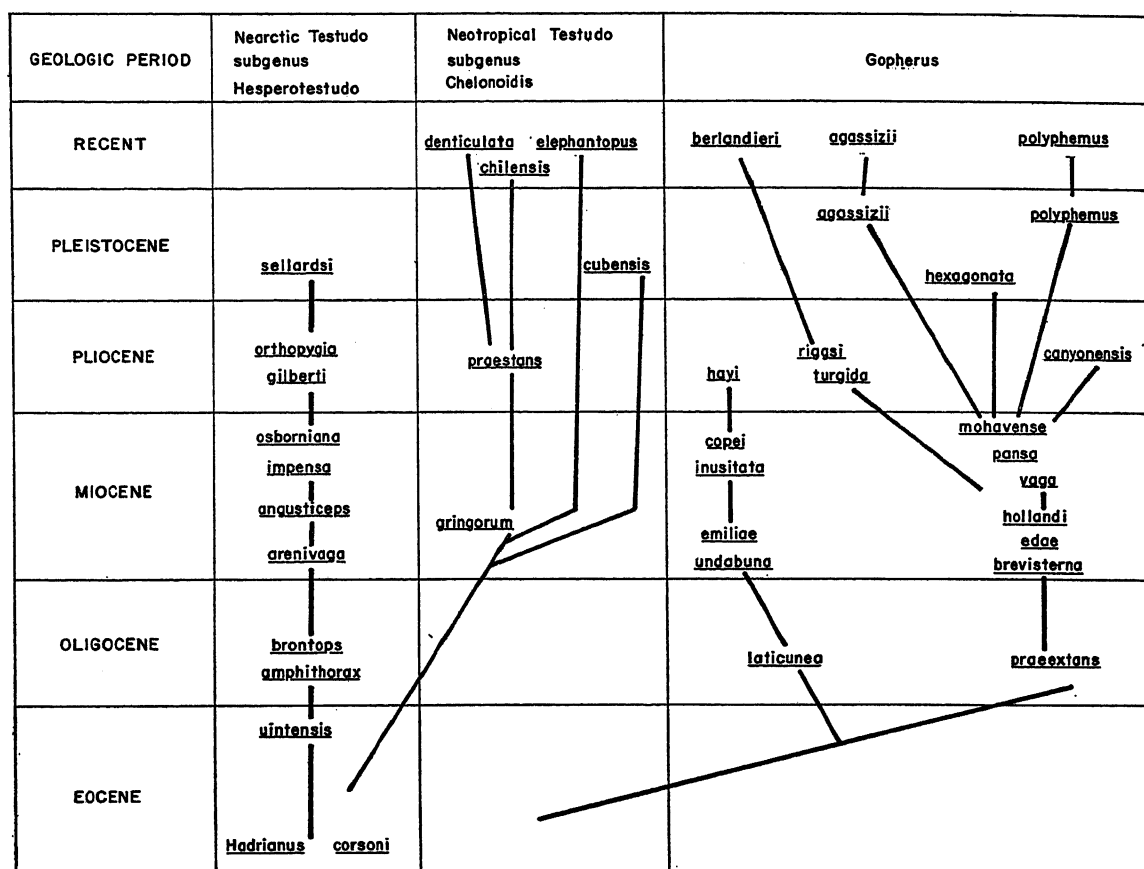


FIG. 2. Phyletic diagram of Western Hemisphere tortoises, accurate not to species but only as to group, although special relationship is indicated where there is some evidence for it. Forms of doubtful provenance are not included. The separation of *Gopherus* into two phyletic groups may or may not be real.

continuation of the Miocene †*undabuna*-†*copei* subseries of *Gopherus*. This is a very large and thick-shelled form; its relation to the thick-shelled giant forms of the Pleistocene might be suggested.

Pleistocene forms definitely referable to *Gopherus* are known but are either stated to be indistinguishable from a living species (*G. polyphemus* Hay, 1917b; *G. agassizii* L. Miller, 1942) or are doubtfully distinct (†*G. hexagonata* Cope, various fragmentary species). †*Gopherus praecedens*, if a rather complete shell in the United States National Museum identified by Gilmore be accepted as such, appears to differ little from *Gopherus polyphemus* except in larger size.

In South America †*Testudo praestans* Ro-

vereto is the Pliocene representative of †*T. gringorum*. The two forms are in fact not certainly distinct. By an unfortunate error Rovereto in his original figure mistook the femoral-anal sulcus for the hypoxiphiplastral suture, and the shortness of the xiphiplastral region which was the most important feature relied upon by Simpson (1942) in distinguishing this species from †*T. gringorum* is therefore illusory. Because †*T. praestans* Rovereto, 1914, considerably antedates †*T. gringorum* Simpson, 1942, the applicability of the latter name may be called in question. Provisionally, however, †*T. gringorum*, by far the better known form, may be retained on the hypothesis that evolution in neural pattern (the neurals are hexagonal in †*T.*

gringorum, unknown in †*T. praestans*) occurred in the Miocene-Pliocene interval. †*T. praestans* as the later form may reasonably be expected to be closer in its neural pattern to the alternating octagonal-quadrilateral pattern of its living descendants (*T. denticulata*, *T. chilensis*, *T. elephantopus*). †*T. gringorum*, as represented by the type, is also much smaller than the type of †*T. praestans*.

Pleistocene South American tortoises are undescribed or too imperfectly preserved to merit discussion. Gervais (1877) based †*T. elata* on bits of a giant tortoise from the Pleistocene of Brazil. Swinton (1928) has cited fragments of a thick-shelled form from Venezuela. Ameghino (1921, p. 708) mentions the existence of Pampean Argentine forms.

THE PHYLETIC POSITION OF †*Testudo cubensis*

The analysis has now proceeded to a point where it is possible to make some inferences concerning the position of †*T. cubensis* in the phylogeny of Western Hemisphere testudines.

All the special resemblances of †*T. cubensis* are to the South American tortoises. Like them it is southern in distribution, lacks the nuchal scute,¹ and has the first marginals in broad contact. It also resembles, as Matthew noticed, the individual South American forms in special ways, *T. denticulata* in the elongation of the shell, *T. chilensis* in the dentate margins, *T. elephantopus* in the thinning of the shell. Resemblances to North American forms are less frequent and apparently convergent.

¹ The nuchal scute is occasionally absent as a congenital variation in modern *Gopherus berlandieri*, but when this occurs, the first marginals are not in broad contact; instead the first vertebral scute attains the anterior margin of the carapace. The nuchal scute, when present in *G. berlandieri*, is much broader than long, so much so that its disappearance in the fashion just mentioned is only an extreme of this normal character. The reduction of the nuchal scute in Pleistocene †*T. sellardsi* as described by Loomis (1927) is probably a better model of the mode of suppression of the nuchal scute in †*T. cubensis* and the other Neotropical tortoises, but in †*T. sellardsi* the reduction of the nuchal scute is combined with highly specialized characters (e.g., the extremely narrowed pectoral scute) not found in the Neotropical tortoises.

Still avoiding all discussion of possible European and Asiatic affinities,² I suggest the following picture of the origin and evolution of †*T. cubensis*:

The primitive testudines of the New World were early separated into three series: (1) *Gopherus*; (2) Nearctic; and (3) Neotropical members of the genus *Testudo*. The Neotropical tortoises probably differentiated in Central America at a time when this area tended to be separate from both the northern and southern continents (Schuchert, 1935; Weeks, 1948). During this period of differentiation the nuchal scute was lost. Then, probably over a rather narrow sea gap, this progenitor of the Neotropical tortoises sent a representative eastward into the West Indies, the ancestor of †*T. cubensis*. Southward via Panama another representative went into South America, and southwestward over a much larger sea gap still another to the Galápagos Islands. Isolated in Cuba, perhaps beginning with the Miocene, †*T. cubensis* had ample time to develop its special characters.

² It is a source of regret to the author to have neglected the relation of the North American testudine fauna to that of Eurasia. To do so, however, would have been a crushing task, requiring a complete review and revision of the Eurasian (and African) testudines, fossil and recent. Especially discouraging in such a task is the absence, for the fossil forms, of any general review nearly so competent as that of Hay. The work most nearly comparable in bulk (Bergounioux, 1935) must be received with extreme caution. The identification, for example, in that work of *Kinixys* in the Miocene of France is unquestionably an error, deriving in part from a radical misconception of the definition of *Kinixys*, ascribing to it a hinge in the plastron rather than in the carapace. The works of Peyer (1942) on European †*Testudo vitodurana* and its relatives (affinities to African *T. pardalis* are apparently very justly suggested) and of Glaessner (1933) on †*T. antiqua* are, on the other hand, examples of illuminating studies of small segments of the problem.

Examples may easily be cited to show that the lack, unavoidable as it is, may not be trivial. De Stefano (1902) described a possible †*Stylomys* (†*S. botti*) from the Miocene of France, and Riabinin (1927) has founded another species, †*S. karakolensis*, on a shell from the late Oligocene or early Miocene of Siberia. The case of †*Testudo kalganensis* Gilmore (Cenozoic of Mongolia), which remarkably resembles †*G. turgida* (Cope) and the Meade County specimens referred to †*G. riggsi* (Hibbard), has already been mentioned. Such instances emphasize the impossibility of artificially limiting discussion to the forms of any one continent.

THE NOMENCLATURE OF WESTERN HEMISPHERE TESTUDINES

THE NEOTROPICAL TORTOISES

Lindholm (1929) placed the three living Neotropical species of tortoise in separate monotypic subgenera, placing *T. denticulata* in *Chelonoidis* Fitzinger, 1835, *T. chilensis* in *Pampatestudo* Lindholm, 1929, and *T. elephantopus* in *Elephantopus* Gray, 1873. He was to a certain extent justified in this procedure. These three species are very distinct forms. The skull of *T. denticulata*, for example, has certain specializations that permit its immediate recognition. The shell peculiarities of the same species are almost equally well marked. Nevertheless, adoption of Lindholm's subgeneric criteria would compel recognition of †*T. cubensis* as still another subgenus, and at least one more subgenus would be needed for the reception of the fossil South American species. Such a multiplication of names, probably all of which on these principles would be monotypic, would reduce the subgeneric category to an absurdity. It is therefore suggested that the living Neotropical tortoises and their fossil ancestors and †*T. cubensis* be united under the oldest available name, which will then be redefined as follows:

GENUS TESTUDO LINNÉ

SUBGENUS CHELONOIDIS FITZINGER, 1835

TYPE SPECIES: *Testudo denticulata* Linné.

NEW DEFINITION: A Neotropical division of the genus *Testudo* with the nuchal scute lacking, the entoplastron large, and with little or no trace of radiating pattern on the horny shields. Miocene to Recent, South America; Pleistocene, Cuba; Recent, Galápagos Islands; probably existing in Central America in the early Cenozoic.

This definition will not seem sufficiently restrictive unless it is remembered that in broadening the subgeneric concept to include a varied assemblage of forms, both fossil and recent, the number of characters that are possessed by all members of the subgenus and not also found, or not found in this combination, in other members of the genus is reduced. The group as here defined is certainly a natural group—both a geographic and a phyletic unit. It is possible, however, to raise a question of the advisability of formal nomenclatorial recognition.

Lindholm (1929) has already argued for subdivision of the genus *Testudo*. The latter is, of course, a relict of the Linnean genus and as such is much more heterogeneous than, for example, are emydine genera. The size range within the genus has been commented upon by Lindholm (1929, p. 284) as unique in the animal kingdom. Primarily, however, the argument for subgeneric separation must rest upon convenience and utility. As proposed here, the subgenus is intended to include a phyletic line recognizable as such over several geologic periods, perhaps restricted to a geographic area or major region, and not morphologically sufficiently distinct to be called a genus. It is believed that such phyletic lines can be distinguished in the tortoises, and that their formal recognition will clarify the generic picture.

Chelonoidis, as here recognized, includes, in addition to the type species *T. denticulata* (Recent of tropical South America, east of the Andes¹) the following: †*Testudo gringorum* Simpson (Patagonian = Miocene of Argentina); †*T. praestans* Rovereto (Monte Hermoso = Pliocene of Argentina); †*T. cubensis* Leidy (Ciego Montero = Pleistocene of Cuba); *T. chilensis* Gray (Recent of Argentina and Uruguay); and *T. elephantopus* Harlan (Recent of the Galápagos Islands). Additional South American forms found fossil have been named and, if valid, probably belong in this subgenus, but their status is very doubtful. †*T. gallardoi* Rovereto, 1914 (Araucanian = Pliocene of Argentina), is poorly known; its only well-defined character as given by its describer is the gibbosity of some of the neurals and pleurals. In view of the marked gibbosity of these elements in a specimen of *T. denticulata* examined in the American Museum of Natural History, it is not felt that this character by itself establishes the reality of †*T. gallardoi*. †*T. elata* Gervais, 1877 (Pampean = Pleistocene of Brazil), is a giant form known only from a fragment of the dentary, ends of two arm

¹ Also extending a short distance into Central America, in Panama, and present, perhaps feral, on several West Indian islands. A specimen caught by Hassler in the interior of Haiti (Grant and De Sola, 1934) was identified as this species.

bones, and a very small piece of the plastron; it is not at present determinable. †*T. australis* Moreno (Monte Hermoso = Pliocene of Argentina), †*T. formosa* Moreno (Monte Hermoso = Pliocene of Argentina), and †*T. paranensis* Scalabrini (Entre Rios = Pliocene of Argentina) are cited by Ameghino (1921), but unfortunately the original descriptions have not been seen. These may be *nomina nuda*.¹

THE NEARCTIC TORTOISES

The North American phyletic group of which †*Testudo osborniana* is an example is, as are the Neotropical tortoises, a geographic and phyletic unit. It deserves recognition as a new subgenus, which may be called:

HESPEROTESTUDO, NEW SUBGENUS

TYPE SPECIES: †*Testudo osborniana* Hay.

DEFINITION: A Nearctic subdivision of the genus *Testudo* with the nuchal scute narrow, the entoplastron wider than long, the pectoral scutes extremely reduced from the axilla to the midline, and the limbs and tail heavily armored with dermal ossicles. Eocene to Pleistocene, North America.

This is a highly specialized line, early differentiated, exclusively North American, and now extinct. The number of valid included species is not certain, but the named forms: †*T. uinensis* Gilmore (Uinta Eocene of Utah); †*T. brontops* Marsh (Chadronian Oligocene of South Dakota); †*T. amphithorax* Cope (Chadronian Oligocene of Colorado); †*T. ligonia* Cope (Chadronian Oligocene of Colorado); †*T. arenivaga* Hay (Arikareean Miocene of Nebraska); †*T. angusticeps* Matthew² (Hemingfordian Miocene of Nebraska); †*T. osborniana* Hay (Barstovian Miocene of Colorado); †*T. impensa* Hay (Barstovian Miocene of Montana); †*T.*

orthopygia Cope (Lower Pliocene of Kansas); †*T. gilberti* Hay (Lower Pliocene of Kansas); and †*T. sellardsi* Hay (Pleistocene of Florida) appear to be members of this subgenus.

The place of the other group of Nearctic tortoises, *Gopherus* Rafinesque, 1832, whether as genus or subgenus, is problematical. The palatal character that distinguishes this natural taxonomic unit is a minor one but one nowhere else developed within the order. Vertebral and pelvic characters also seem to distinguish this series of forms. Divergence from *Testudo*, if in fact any close relationship exists, must, it seems clear, have been very early, at a stage that would have been classed by Hay as "*Hadrianus*." It was at an evolutionary level, therefore, which included some emydine characters, e.g., a divided supra-caudal scute and perhaps even the emydine phalangeal formula. (Compare the discovery by Case, 1936, of an emydine type of foot in †*Stylomys*.) At present it appears wise to retain *Gopherus* as a genus.

Until further investigation establishes additional characters (other than merely primitive ones) the genus may be defined as follows:

GENUS GOPHERUS RAFINESQUE, 1832

TYPE SPECIES: *Testudo polyphemus* Bartram.

DEFINITION: A Nearctic genus of Testudininae distinguished by the continuation of a palatal vomerine ridge upon the premaxillaries at their symphysis; cervical vertebrae short. Oligocene to Recent, North America. Formerly widespread, now much restricted in range.

The difficulty of establishing the number of valid species in this genus has been commented upon above. The following named forms are, however, undoubted *Gopherus*: †*G. laticuneus* Cope (Chadronian Oligocene of Colorado); †*G. praextans* Lambe (Chadronian Oligocene of Wyoming); †*G. brevisterna* Loomis (Arikareean Miocene of Wyoming); †*G. undabuna* Loomis (Arikareean Miocene of Wyoming); †*G. emiliae* Hay (Arikareean Miocene of South Dakota); †*G. edae* Hay (Arikareean Miocene of Nebraska); †*G. hollandi* Hay (Arikareean Miocene of Nebraska); †*G. vaga* Hay (Barstovian Miocene of Montana); †*G. inusitata* Hay (Bar-

¹ The species named by Moreno are cited also in the Zoological Record for 1889 and in Nicholson and Lydekker (1889, p. 1111).

² Originally described by Matthew (1924) as †*T. orthopygia angusticeps* "new mutant." For the sake of consistency the name is treated as a full species here. The form is, however, certainly close to †*T. orthopygia* and may on further analysis prove to be best regarded as a synonym.

The shells contemporaneous and sympatric with †*T. angusticeps* referred by Matthew to †*orthopygia* are here provisionally regarded as †*angusticeps*.

stovian Miocene of Montana); †*G. copei* Koerner (Barstovian Miocene of Montana); †*G. pansa* Hay (Barstovian Miocene of Colorado); †*G. mohavense* Merriam (Barstovian Miocene of California); †*G. turgida* Cope (Pliocene of Texas); †*G. canyonensis* Johnston (Pliocene of Texas); †*G. campester* Hay (Pliocene of Texas); †*G. riggsi* Hibbard (Pliocene of Kansas); †*G. hayi* Sellards (Pliocene of Florida); †*G. hexagonata* Cope (Pleistocene of Texas); and the living forms *G. polyphemus* (Pleistocene of Florida, Recent of Florida and adjoining states), *G. agassizii* (Pleistocene of California, Recent of southern California, portions of Arizona, Utah, Nevada, and Sonora), and *G. berlandieri* (Recent of Texas and adjoining Mexico).

SPECIES AND GENERA INCERTAE SEDIS

A number of named Western Hemisphere testudines or supposed testudines cannot, or can only provisionally, be placed in the three phyletic groups that have been described. These names will now be considered.

GENERA

†*Stylemys* Leidy (several named species in the North American Oligocene and the John Day portion of the Miocene): This well-known genus has been considered emydine since Case's (1936) discovery of its emydine phalangeal formula. It shows, however, so many parallels to testudine structure that it probably must be conceded some fairly close relation to the common stem of all testudines. Further, when it is considered that the living genera considered testudine may have arisen independently from a †*Hadrianus* stage (a grade of organization with several emydine characters), it is necessary to inquire whether the Testudininae or even the genus *Testudo* as currently defined is not polyphyletic, that is, has arisen several times independently from forms on the basis of present definition emydine. If this possibility is substantiated, the definition of the subfamily must be put on a new basis or, alternatively, the Testudininae must be admitted to be impossible of formal separation from the Emydinae.

Attention should be called to Hay's description of the skull of †*Stylemys* (Hay, 1908, pp. 389-390). Hay believed that he had

skulls of †*S. nebrascensis* (one definitely associated with "enough of the shell to establish clearly the species") that showed the *Gopherus* ridge at the premaxillary symphysis. Hay's comparison of †*Stylemys* with *Gopherus* was contested by Case (1925) in the course of a detailed study of an undoubted †*Stylemys* skull. Case found differences in the otic region and in the extension of the pterygoids lateral to the palatines, but because the lower jaw of his specimen was tightly set in position he was unable to determine the presence or absence of the diagnostic premaxillary ridge.

Hay's comparison of †*Stylemys* and *Gopherus* was not based on skulls alone but also on limbs (1908, p. 390) and on shells. In a discussion of the two genera in 1905 he was quite explicit: "There are also various resemblances between the shells of the living [*Gopherus*] and the extinct forms [†*Stylemys*]; so that a real relationship is suggested" (Hay, 1905, p. 342).

It is certain that †*S. nebrascensis* is not directly ancestral to *Gopherus*, since two species of *Gopherus* have now been shown to coexist in the Oligocene with that species, but it is possible that †*Stylemys* and *Gopherus* are both members of a distinct group independently derived from the Emydinae, and that they are more closely related to each other than either is to *Testudo* (or †*Hadrianus*). There is, however, no uncontested evidence on this point at present.

This interesting point will not be settled until an associated shell and a skull, both completely prepared, of an undoubted †*Stylemys* are available. A number of Oligocene skulls with the *Gopherus* premaxillary ridge are now known (specimens seen in Princeton University, the Kansas Natural History Museum, and the United States National Museum). Some of these may be †*Stylemys*, but since only the skull of Gilmore's †*G. praeextans* has unquestioned association with an identified and identifiable shell, the critical point cannot now be demonstrated.

†*Cymatholcus* Clark (Eocene of Utah): This genus, erected by Clark in 1931, will probably stand in spite of the apparent vagueness of its known generic characters. It is rather specialized (and specialized in a quite in-

dividual way) for an Eocene form. If the presence of the testudine phalangeal formula is essential for allocation to subfamily, this form is not certainly a testudine, since the limbs are quite unknown. The skull also is unknown. †*Hadrianus* ? *schucherti* Hay, 1903 (Eocene of Alabama), would seem from detailed similarities in form and in the sulcal and sutural relationships of the plastral elements, as these are figured by Hay (1908), to be a member of the same genus and perhaps even conspecific with †*C. longus* Clark, 1931.

†*Bystra* Hay (Pliocene ? of Florida): This genus is founded upon a single very small (105 mm. in carapace length) shell manifesting a single aberrant character. Despite the temptation to regard this specimen as an individual variant, the name must be provisionally retained. The aberrant character, the transverse gular-humeral sulcus, is in the form exhibited here rare in tortoises. (See, however, *T. schweiggeri* in Boulenger, 1889, pl. 3.) When so rare a character is coupled with extremely small size in an animal apparently adult (Hay, 1916), it becomes necessary to withhold judgment until additional material is found. That this genus is testudine is impossible to establish, since the shell alone is known.

Hay's name †*Bystra*, 1916, is preoccupied by *Bystra* Cameron, 1902, for a genus of Hymenoptera. It must therefore be replaced, and †*Floridemys*, new name, suggested to the author by Mr. C. M. Bogert, is therefore proposed.

†*Achilemys* Hay (Bridger Eocene of Wyoming): This genus is reported on extremely fragmentary material. Its testudine affinities are more than doubtful.

†*Colossoemys* Rodrigues (Pleistocene of Brazil): This name is based on two caudal vertebrae believed to pertain to a turtle of enormous size. Its significance is very uncertain. It may be a tortoise. Rodrigues' plates have not been seen.

SPECIES

The species here listed as of uncertain position are so listed for reasons that are very different in the several cases. †*Testudo obtusa* Leidy, described from a peripheral, †*T. exornata* Lambe, described from a few costals,

and †*T. snoviana* (Cope), described from a phalanx, may never be determinable. †*T. undata* Cope, †*T. klettiana* Cope, †*T. annae* Hay, †*T. distans* Hay, †*T. equicomis* Hay, †*T. luciae*, Hay, †*T. francisi* Hay, and †*T. munda* Hay, described from almost equally uncharacteristic fragments, may possibly be validated or at least placed as to genus by further discoveries of material at the type locality or horizon. The author has seen the types of all these forms except †*T. exornata* and †*T. snoviana*, and he cannot deny their different appearance, but he considers that the evaluation of this subjective impression of a difference is impossible with material so incomplete as to be nearly beyond the hope of proper comparison.

†*Testudo crassiscutata* Leidy, †*T. niobrarenensis* Leidy, †*T. laticaudata* Cope, and †*T. lousekressmani* Wark may be determinable when more complete material is collected. †*Gopherus atacosae*, †*Testudo ocalana*, and †*T. incisa*, all of Hay, though known from fragments probably specifically indeterminate, are doubtless justifiably referred to the genus *Gopherus* on the basis of close resemblance to modern species. In the case of †*T. thomsoni* Cope and †*T. peragrans* Hay,¹ although the skulls of the type specimens are known, diagnostic features are missing or unexposed. †*T. cultratra* is known only from Cope's description, in which unfortunately the characters here believed to be significant are not mentioned. †*T. pertenuis* Cope is poorly described and badly figured, and the greater part of Cope's material seems to have been lost (Hay, 1908). †*T. ducatelli* Collins

¹ The form described and figured as this species in Schlaikjer (1935) is not properly so assigned. It is closer to †*Gopherus praexians* (Lambe) of the Brulé of Wyoming and comes from the county just south of the type locality of the latter species. The questionable form is Lower Miocene in age, however, as the associated mammalian fauna clearly shows (Schlaikjer, 1935, pp. 123-125). A close comparison of all parts of the skeleton (fortunately very complete in the Miocene form) with the appropriate elements of the United States National Museum specimens from the Brulé described by Gilmore (1946) will be necessary to decide the specific identity of the form. Quite similar cases of the extension of the same or a closely related species of land turtle from one geologic period to another are †*Stylomys nebrascensis* (Brulé Oligocene), †*S. conspecta* (John Day Miocene), †*Testudo angusticeps* (Sheep Creek Miocene), and †*T. orthopygia* (Republican River Pliocene).

and Lynn and †*T. farri* Hay are probably assignable to *Gopherus*, but in both cases some important diagnostic features are not known, and one other character is atypical for the genus. In †*T. ducatelli* the humero-pectoral sulcus encroaches on the entoplastron; in †*T. farri* the pectoral scute is narrowed, though not to the extreme of †*T. osborniana*.

The type of †*T. quadrata* Cope (A.M.N.H. No. 1149) shows the gular-humeral sulcus transverse somewhat as in the genus †*Floridemys* (= †*Bystra* Hay). The condition of the type is probably an individual variation as suggested by Gilmore (1946); it is quite different from †*Floridemys* in detail, the whole contour of the anterior plastral lobe of

the latter being more like that of an emydine than like the exaggeratedly projecting epiplastra of *T. quadrata*.

As redefined by Gilmore †*T. quadrata* is a doubtfully distinct form the precise affinities of which can be assessed only when it becomes more completely known.

Of named living forms regarded as American, only *Testudo schweiggeri* Gray, 1831, is questionable. It was regarded as a relative or variant of *Gopherus* (*G. polyphemus*) by Boulenger (1889). The nuchal scute is missing in the type and only specimen, and the relationships of the first marginal scutes resemble those of *Chelonoidis* species rather than those of such variants of *Gopherus* as lack the nuchal.

CHECK LIST OF NEW WORLD TESTUDINES AND SUPPOSED TESTUDINES

BELOW ARE LISTED the named New World testudines and those other named forms that have been considered at one time or another testudine. The forms, considerable in number, that have been named from material so fragmentary as probably to be indeterminate or of which the types are lost are marked with an asterisk. Some of these names may be validated (as was, in effect, †*T. cubensis*) by additional material from the type locality, but at present they cannot be defined, synonymized, or allocated.¹

¹ Dr. Paulo Vanzolini of the Department of Zoology, State of São Paulo, Brazil, has suggested to the author that specific names of this nature be designated *species inquirendae*. This nomenclatorial category seems to be unusual or unknown in North American taxonomy. It would, the present author believes, serve a useful purpose. Certainly names of possible but presently indemonstrable validity cannot properly be treated as of equivalent value with adequately based, well-known taxonomic categories, nor is it at all reasonable to place such names in synonymy, since this could be done only arbitrarily and doubtfully. There is evident need for a

Double asterisks indicate probable *nomina nuda*.

Geologic age is stated in each case and in many instances is revised from that of the original literature in accordance with recent standard work on the nomenclature and correlation of the North American continental Tertiary (Wood *et al.*, 1941) and Simpson's parallel correlation of the South American Tertiary (Simpson, 1947). Forms of the same age and phyletic group are perhaps synonyms or races, but determination of this point will require very close study of the types and referred material.

Because most forms were originally described as *Testudo*, most imperfectly known forms remain in that genus for the purposes of this list. Such forms are not to be considered as referred to *Hesperotestudo* (this paper).

purgatory in which such names may reside until proper disposition can be made of them.

NORTH AMERICA

EOCENE

- **Achilemys allabiata* (Cope), 1872. Wyoming: Bridger
- Cymatholcus longus* Clark, 1931. Utah: Duchesne
- schucherti* (Hay), 1899. Alabama: Jackson
- Hadrianus majusculus* Hay, 1904. New Mexico: Wasatch
- corsoni* (Leidy), 1871. Wyoming: Bridger; Utah: Uinta
- tumidus* Hay, 1904. Utah: Uinta
- robustus* Gilmore, 1915. Utah: Uinta
- utahensis* Gilmore, 1915. Utah: Uinta
- Testudo uiniensis* Gilmore, 1915. Utah: Uinta

OLIGOCENE

- Gopherus laticuneus* (Cope), 1873. Colorado: Horsetail Creek; Wyoming: Brulé; South Dakota: Chadron; Nebraska: Oreodon beds
- praeextans* (Lambe), 1913. Wyoming: Brulé
- Stylemys nebrascensis* Leidy, 1851. Nebraska: Oreodon beds; Colorado: Oreodon beds; Wyoming: Oreodon beds; North Dakota: Oreodon beds; South Dakota: Oreodon beds
- Testudo brontops* Marsh, 1890. South Dakota: Chadron
- amphithorax* Cope, 1873. Colorado: Horsetail Creek
- ligonia* Cope, 1873. Colorado: Horsetail Creek
- **cultrata* Cope, 1873. Colorado: Horsetail Creek
- **quadrata* Cope, 1884. Colorado: Horsetail Creek
- **exornata* Lambe, 1906. Saskatchewan: Cypress Hills
- **thomsoni* Hay, 1908. South Dakota: Chadron
- **peragrans* Hay, 1906. Montana: McCarty's Mountain

MIOCENE

- Gopherus brevisterna* (Loomis), 1909. Wyoming: Harrison
undabuna (Loomis), 1909. Wyoming: Harrison
emiliae (Hay), 1908. South Dakota: Rosebud
edae (Hay), 1907. Nebraska: Harrison
hollandi (Hay), 1907. Nebraska: Harrison
vaga (Hay), 1908. Montana: Deep River
inusitata (Hay), 1907. Montana: Deep River
copei (Koerner), 1940. Montana: Deep River
pansa (Hay), 1908. Colorado: Pawnee Creek
mohavense (Merriam), 1919. California: Barstow
Styemys capax Hay, 1908. Oregon: John Day
conspicua Hay, 1908. Oregon: John Day
**oregonensis* Leidy, 1871. Oregon: John Day
**calaverensis* Sinclair, 1903. California: auriferous gravels
Testudo arenivaga Hay, 1907. Nebraska: Harrison
angusticeps Matthew, 1924. Nebraska: Sheep Creek
impensa Hay, 1908. Montana: Madison Valley
osborniana Hay, 1905. Colorado: Pawnee Creek
**farri* Hay, 1908. Montana: Deep River
**ducatelli* Collins and Lynn, 1936. Maryland: Calvert
**undata* Cope, 1875. New Mexico: Santa Fe
**klettiana* Cope, 1874. New Mexico: Santa Fe

PLIOCENE

- Floridemys nanus* (Hay), 1916. Florida: phosphate mine, Holder, Citrus County
Gopherus turgida (Cope), 1892. Texas: Blanco
campester (Hay), 1908. Texas: Blanco
canyonensis (Johnston), 1937. Texas: Blanco
riggsi (Hibbard), 1944. Kansas: Seward and ?Meade counties
hayi (Sellards), 1916. Florida: Nichols phosphate mine
Testudo orthopygia (Cope), 1878. Kansas: Republican River
gilberti Hay, 1899. Kansas: Republican River
louisekressmani Wark, 1929. Florida: Nichols phosphate mine
**pertenuis* Cope, 1892. Texas: Blanco
**snoviana* Cope, 1886. Kansas: northwest part of state

PLEISTOCENE

- Gopherus agassizii* (Cooper), 1863. California: McKittrick Asphalt
polyphemus (Bartram), 1791. Florida: Vero
praecedens Hay, 1916. Florida: Vero
**ocalana* (Hay), 1916. Florida: Ocala
**incisa* (Hay), 1916. Florida: Ocala
**hexagonata* (Cope), 1903. Texas: Tule
**atacosae* Hay, 1902. Texas: Atacosa County
Testudo sellardsi Hay, 1916. Florida: Vero
crassiscutata Leidy, 1889. Florida: Peace Creek
**distans* Hay, 1916. Florida: Ocala
**luciae* Hay, 1916. Florida: Vero
**laticaudata* Cope, 1903. Texas: Tule
**annae* Hay, 1923. Texas: Brazos River
**francisi* Hay, 1923. Texas: Temple
**munda* Hay, 1920. Tennessee: Hamblen County
**equicomis* Hay, 1917. Kansas: Meade County
**obtusum* (Leidy), 1877. South Carolina: Ashley River

SOUTH AMERICA

MIOCENE

Testudo gringorum Simpson, 1942. Argentina: Patagonian

PLIOCENE

Testudo praestans Rovereto, 1914. Argentina: Monte Hermoso

**gallardoi* Rovereto, 1914. Argentina: Araucanian

***australis* Moreno, 1890? Argentina: Monte Hermoso

****formosa* Moreno, 1890? Argentina: Monte Hermoso

****paranensis* Scalabrini, 18—? Argentina: Entre Rios

PLEISTOCENE

Testudo elata Gervais, 1877. Brazil: Pampean

Testudo cubensis Leidy, 1868. Cuba: Ciego Montero

SUMMARY

1. †*Testudo cubensis* Leidy is redefined and redescribed.

2. A grouping and phylogeny of the New World testudines are attempted.

3. The species †*laticuneus* Cope, †*praeextans* Lambe, †*brevisterna* Loomis, †*vaga* Hay, †*femiliae* Hay, †*pansa* Hay, †*inusitata* Hay, †*edae* Hay, †*hollandi* Hay, †*undabuna* Loomis, †*mohavense* Merriam, †*copei* Koerner, †*turgida* Cope, †*triggsi* Hibbard, †*campester* Hay, †*hexagonata* Cope, †*ocalana* Hay, †*incisa* Hay, and †*hayi* Sellards, formerly placed in the genus *Testudo*, are here allocated to *Gopherus*. The species †*canyonensis* Johnston, placed by its author in the monotypic genus †*Bysmachelys*, is also referred to

Gopherus. †*Hadrianus ?schucherti* Hay is placed in the genus †*Cymatholcus* Clark.

4. †*Testudo cubensis* is regarded as an early offshoot of a Central American stock that also gave rise to the three living Neotropical tortoises.

5. Subgeneric separation is suggested for the Neotropical tortoises (including †*cubensis*) under the name *Chelonoidis* Fitzinger, 1835, and for the very distinct group of Nearctic tortoises typified by †*T. osborniana* under the name †*Hesperotestudo*, new subgenus.

6. The name †*Bystra* Hay, 1916, preoccupied by a genus of Hymenoptera, is replaced by †*Floridemys*, new name.

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