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INTRODUCTION

ı 1926 Dr. H. E. Anthony and Mr. G. G. oodwin, exploring the caves and phosphate ɜposits of Mona Island, between Puerto ico and Hispaniola, for fossil mammals, ob-ıined remains of a peculiar tortoise that ·oves to be a new and distinct form, the pre-se relationships of which are uncertain. This ɜw tortoise is best assigned to the genus *estudo* as broadly interpreted, but it is dif-rent enough to receive a new subgeneric ıme.[1]

The island from which the new tortoise ımes has been well described by K. P. ɜhmidt (1926), and to his paper the reader referred for information regarding the de-ils of its topography and its known verte-ate faunas. No turtles are found on it day, and only nine species of Recent rep-es.

The island is an arid limestone mass 6½ iles long and 4 miles wide, honeycombed ith caves and with sheer cliff walls on three les. It is probably the remnant of a formerly uch larger island and perhaps the relict of former land connection between Puerto ico and Hispaniola.

The greater number of fragments of the ɜw tortoise come from Lirio Cave, which has ɜen described by Anthony (MS) as a "vast ɜtwork of intercommunicating caverns . . . series of chambers which frequently lead to ı outlook on the sea and with many open-gs through the ceiling through which enter e roots of the jaguey tree."

Material in this cave was preserved in a ddish clay which immediately over the rface of most of the bones is modified into a nestone film of varying thickness but of ıiformly resistant character. The bones ɜre apparently much eroded and weathered ɜfore preservation. The few bones not vered by a limestone film are excessively oded. No elements are articulated, and veral individuals are represented. Such shell .rts as exist are in general very thin, com-etely shattered, and have nowhere sepa-rated along a suture. Land shells were en-crusted on many of the bones.

It is assumed that these tortoises fell into the cave through the fissures in the roof. Their bones then shattered, weathered, and disintegrated unless they were preserved by the formation of a lime deposit over the sur-faces.

The dissociated nature of the fragments of course raises the question of the propriety of their reference to a single form. Several indi-viduals of very different sizes are certainly represented. However, all the duplicated parts are reasonably congruent.

As with all terrestrial West Indian fossils it is difficult to establish the age of the new tortoise. In this as in most other instances the suspicion exists that the remains are barely to be considered fossil and are sub-Recent rather than Pleistocene. There are, however, few grounds for any opinion.

All the bones are fresh and unmineralized. Most of those from Lirio Cave are covered by a limestone deposit, but the few elements from other caves and phosphate deposits have the appearance of weathered fresh bone.

The associated fauna is of little assistance. Fragments of a large iguana (*Cyclura* sp.) and of the rodent †*Isolobodon portoricensis*[2] were found in the various caves and deposits but not in direct association with the turtle remains. They would not in any case imply antiquity; a species of *Cyclura* still lives on Mona, and †*Isolobodon*, though now extinct, may have survived into early post-Columbian times.

The snails encrusted on the Lirio bones have been identified by Mr. William Clench of the Museum of Comparative Zoölogy, Harvard College. Three of the four forms represented are identical with species still living on Mona. One (*Lucidella umbonata*) is known also on Puerto Rico; one is wide-spread (*Plagioptera euclasta*), being known from the Virgin Islands, Puerto Rico, His-paniola, and Cuba. One (*Chondropoma tur-nerae*) is an endemic form with its closest relative in Anguilla, St. Martin. The other

[1] In an earlier paper (Williams, 1950b) it was sug-ɜted that the form was a new genus. Reconsideration ɜr closer study of the material has altered this view, the cost, however, of broadening somewhat the inition of the genus *Testudo* given in my earlier paper.

[2] The dagger (†) is used throughout this paper to signify an extinct form.

form, a species of *Cerion*, is, in the two specimens available, one in a breccia, one encrusted on a bone, notably larger than any of the considerable series of Recent *Cerion monaense* lately described by Clench. The Mona fossils, instead, resemble in size, general shape, and sculpture †*Cerion rude* Pfeiffer, a form known only as a fossil from St. Croix in the Virgin Islands. This fact might perhaps imply some degree of antiquity for the Mona shells and the associated turtle, but Clench emphasizes that the genus *Cerion* is prolific in variation and prone to form quite local varieties and is therefore of very doubtful value as a criterion of age.

No data exist as to the depth at which the turtle fragments were found, but it is established from Anthony's notes that they were excavated and not found superficially. On the whole there seems to be no evidence for even Pleistocene age for this tortoise, and it may be another example of the relatively recent extinction of a component of the West Indian fauna.

SYSTEMATIC DESCRIPTION

FAMILY **TESTUDINIDAE**

GENUS **TESTUDO** LINNAEUS

GENOTYPE: *Testudo graeca* Linnaeus.

†**MONACHELYS**, NEW SUBGENUS

GENOTYPE: †*Testudo* (*Monachelys*) *monen-*
s, new species.

SUBGENERIC DIAGNOSIS: Differs from other
ecies of *Testudo* in having the centrum of
e first dorsal vertebra elongate and very
rrow at its middle (only one-quarter to
e-sixth as wide at its waist as it is long
m the posterior margin of the anterior co-
le to the caudal line of suture with the sec-
d dorsal centrum) and in having a shallow
late with the vomer less arched dorsally.
ze moderate. Margin of carapace not
alloped or dentate. Sulci feeble. Shell thin.
iphiplastral notch absent.

This new subgenus at present includes
ly the unique species:

†**Testudo (Monachelys) monensis,** new species

TYPE: A.M.N.H. No. 1969, a first dorsal
rtebra.

TYPE LOCALITY: Lirio Cave, Mona Island,
/est Indies.

HORIZON: ?Sub-Recent.

SPECIFIC DIAGNOSIS: With the characters
the subgenus.

MEASUREMENTS OF TYPE

ip of cotyle to caudal margin	36.3 mm.
/idth of centrum at narrowest point	6.2
Width across anterior zygapophyses	43.0
Width at posterior margin	8.6
Width of anterior cotyle	24.1

PARATYPE: A.M.N.H. No. 1935, a first dorsal vertebra, Lirio Cave, Mona.

REFERRED MATERIAL: A.M.N.H. No.1936, Lirio Cave: anterior and posterior fragments of a skull, two complete left humeri, a larger and incomplete left humerus, a right and a left glenoid facet, an ulna, a proximal end of a radius and a distal end of a radius, shaft of a scapula, distal ends of two scapulae, distal end of an acromion, broken proximal end of a femur, a complete tibia, distal end of a tibia, proximal ends of three fibulae, four ilia, a pubis, two acetabula, the second, third, fourth, and seventh cervical vertebrae, probably of one specimen, a fifth cervical vertebra of another specimen, and miscellaneous carapacial and plastral fragments.

A.M.N.H. No. 1972, "below Playa": a large ulna and tibia, a small radius, and an anterior caudal vertebra.

A.M.N.H. No. 1971, Playa Sardinera: distal end of an acromion.

ASSOCIATED FAUNA: Lirio Cave, encrusted on the bones:

Gastropoda Pulmonata

Cerion sp. (cf. *Cerion rude* Pfeiffer)
Lucidella umbonata Shuttleworth
Chondriopoma turnerae Clench
Plagioptera euclasta Shuttleworth

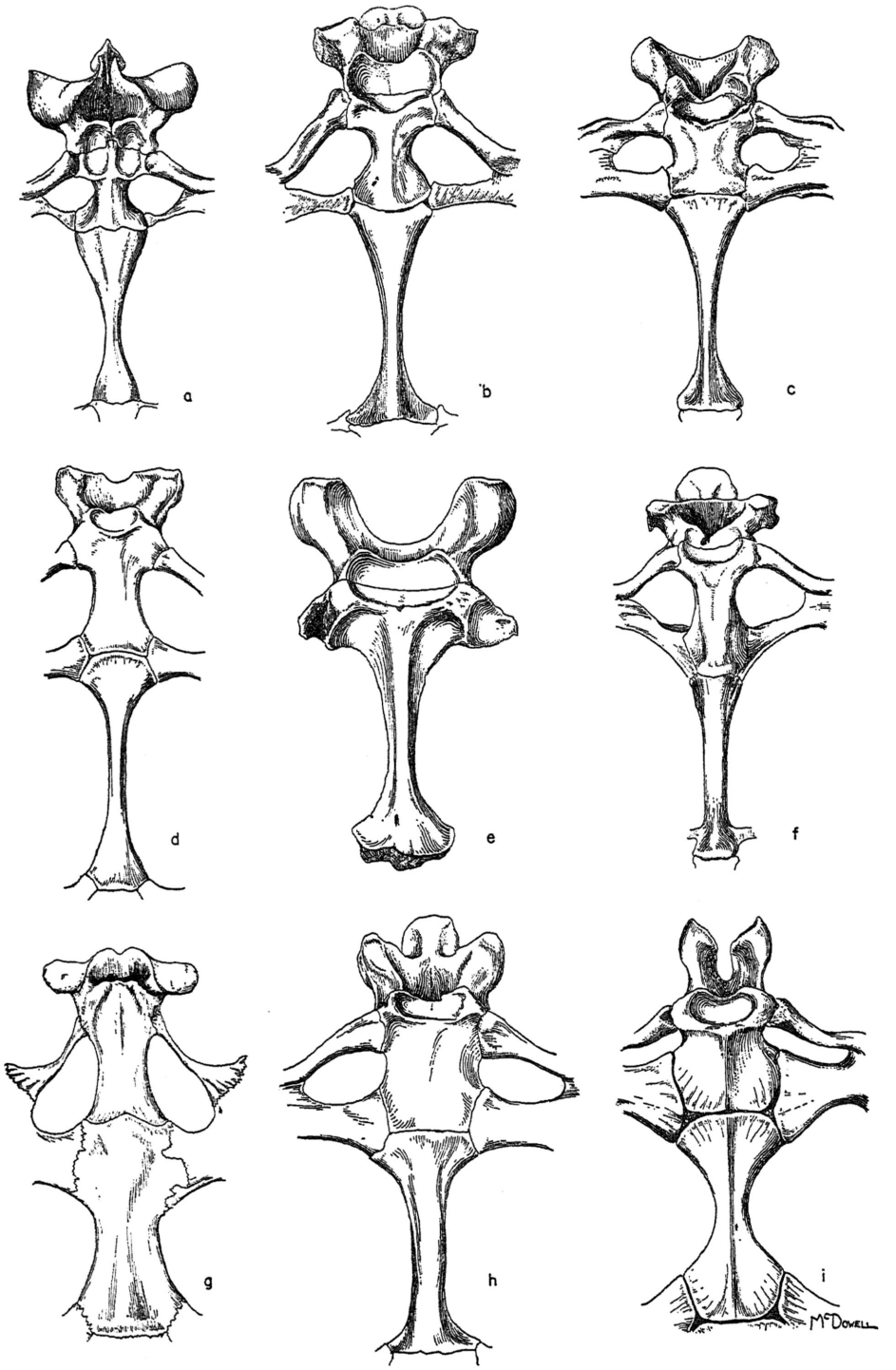


FIG. 1. First dorsal vertebrae in various turtles. A. *Gopherus polyphemus*. B. *Testudo ibera*. C. *Testudo denticulata*. D. *Geoemyda pulcherrima*. E. Type vertebra of †*Testudo* (*Monachelys*) *monensis*. F. *Kinixys belliana*. G. *Trionyx ferox*. H. *Terrapene carolina*. I. *Eretmochelys imbricata*. Not to scale.

CHARACTER ANALYSIS

ONLY A FEW of the known characters of the Mona Island tortoise are unique; most can be found in the other members of the genus *Testudo* as currently recognized, although not in the same combination.

The first dorsal vertebra is the really extraordinary feature of the animal. Extreme attenuation of the centra is usual in the posterior dorsal vertebrae of tortoises, but it is not elsewhere seen to extend to the first dorsal vertebra. On the contrary the form of the first dorsal in all other turtles tends to approximate the shortened, broadened form of the eighth cervical.

Two factors are involved in the distinctive appearance of the first dorsal vertebra in †*Testudo monensis:* (1) the thinning and elongation of the middle portion of the centrum, and (2) a lateral expansion of the anterior end of the vertebra including both the central and the zygapophysial articulations. The latter feature is general in tortoises and not greatly exaggerated in †*T. monensis.* However, it contrasts so strongly with the slenderness of the centrum that it greatly accentuates the impression made by that really unique character. This is especially true since the width across the anterior zygapophyses is greater than the total length of the attenuated centrum.

The uniquely slender first dorsal vertebra is represented by two specimens which because of their good agreement have been made type and paratype. The agreement, however, is not perfect. The larger element, the paratype, is relatively stouter than the smaller type. The length-width relationship most relied upon is 1:4 in the paratype, 1:6 in the type. But these elements resemble each other far more closely than either resembles the first dorsal vertebra of any previously known turtle. The same length-width ratio in a series of other forms ranges from 1:1.5 to 1:3. It is simpler to believe that these elements belong to variants of one species than that they represent two species of rather similar size, both of a sort previously unknown, living together on this small island.

The skull of †*T. monensis*, as reconstructed from the anterior and posterior fragments from Lirio Cave, is less remarkable than the first dorsal vertebra. It is well differentiated as compared with other New World types, but, except for an apparently shallow palate, its characters are included within the range of difference seen in *Testudo, sensu lato*, as previously known.

The two skull fragments do not join, and there is uncertainty as to the extent of the gap that should be left between them. The skull is, however, reasonably reconstructed as rather brachycephalic, with an estimated basal length of 75 mm. and a width across the quadrates of 60 mm. According to this estimate the face must have been carried at a slight angle to the horizontal, somewhat as in *Testudo impressa* from Burma.

The narial opening is partly broken, but it appears to have been quadrangular, widest dorsally, the dorsal margin rather far posterior to the ventral, which has no trace of a dorsally directed process tending to divide the opening in two. The dorsal surface of the prefrontals and frontals is very flat, without any suggestion of convexity. The premaxilla seems to have had a small notch medioventrally. Its alveolar surface has a moderately deep pit, approximately pentagonal in shape, with the apex of the pentagon directed posteriorly. No ridge crosses the pit, but on a small posterior portion of the premaxilla carried horizontally between the maxillaries there is a distinct ridge. This ridge does not continue on the adjoining dorsally arched portion of the vomer. Only small portions of the maxillaries and vomer are preserved. The alveolar surfaces of the maxillae were apparently very broad and bore two low ridges parallel to the outer edge. The edge itself was simple, without ribbing on inner or outer surfaces. The low ridges were continued anteriorly as far as the elevations bounding the premaxillary pit. The vomer does not arch dorsally abruptly but instead rather gradually, and the palate must have been rather shallow.

A shallow palate is either a primitive emydine or a secondarily specialized feature of †*T. monensis.* In all other tortoises a long, deep, palatal trough is present, roofed by the elongate vomer, which may extend back so far that it makes contact with the basisphe-

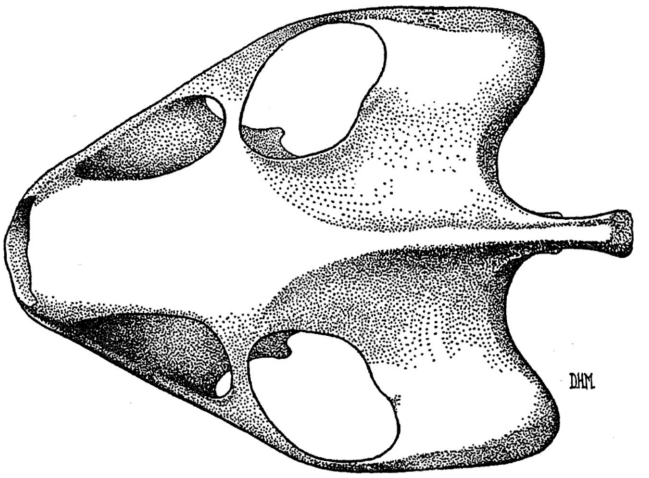


FIG. 2. †*Testudo* (*Monachelys*) *monensis*. Dorsal view of reconstructed skull. ×1.

noid. (A vomer-basisphenoid contact appears probable in †*T. monensis*, but the sutures are obscure.)

The occcipital spine is very short, only about twice as long as the condyle, including its pedicel. The spine makes a sharp angle with the plane of the skull base posteriorly; it parallels the angle that the face makes with the skull base anteriorly. The outline of the foramen magnum is rather ovoid, the flattened side ventral.

Five of the eight cervical vertebrae are known, four of them (the second, third, fourth, and seventh) probably from one specimen, the other (a fifth vertebra), from a smaller individual. All the vertebrae are very like those of other *Testudo* but more elongate than in some species. The fourth centrum is biconvex, centra 2 and 3 are opisthocoelous, the fifth is procoelous, the seventh biconcave with double articulations both cranially and caudally. The cervical central articular formula was thus what was termed N ("normal") in Williams (1950a).

The limb girdle elements that have been preserved and the long bones are in almost all respects typical of *Testudo*. The glenoid facet of the scapula seems deeper than in compared

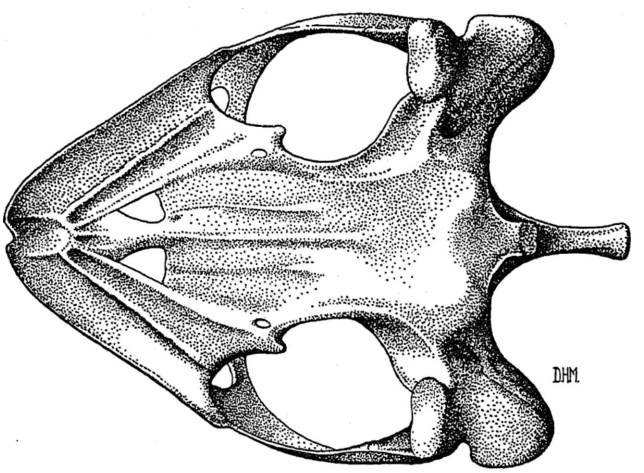
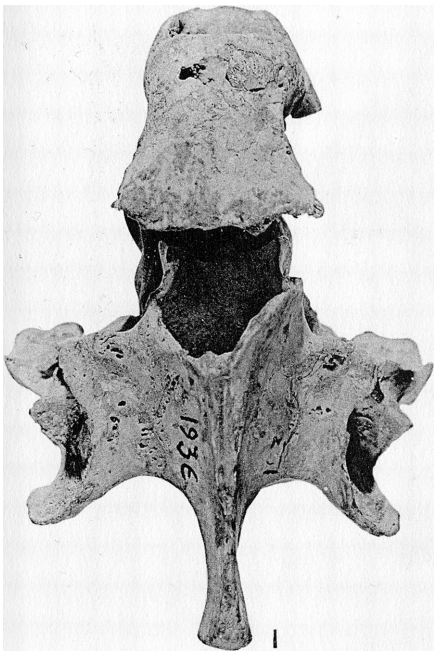
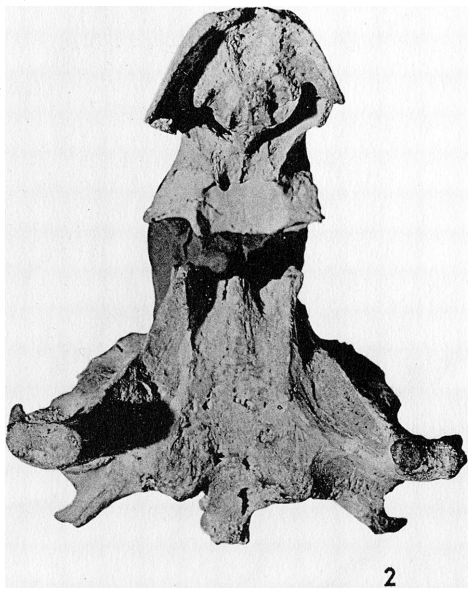
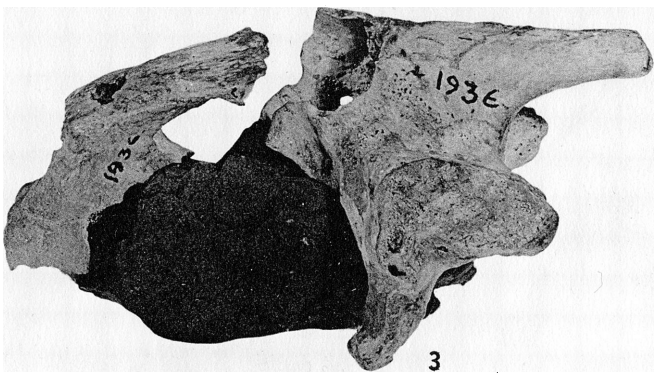
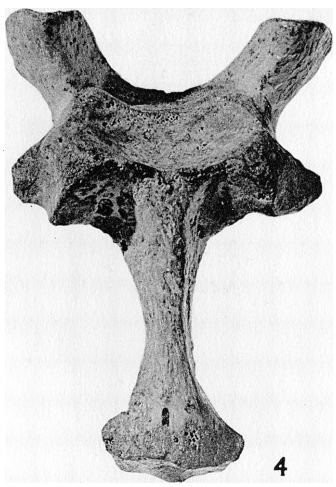


FIG. 3. †*Testudo* (*Monachelys*) *monensis*. Palatal view of reconstructed skull. ×1.

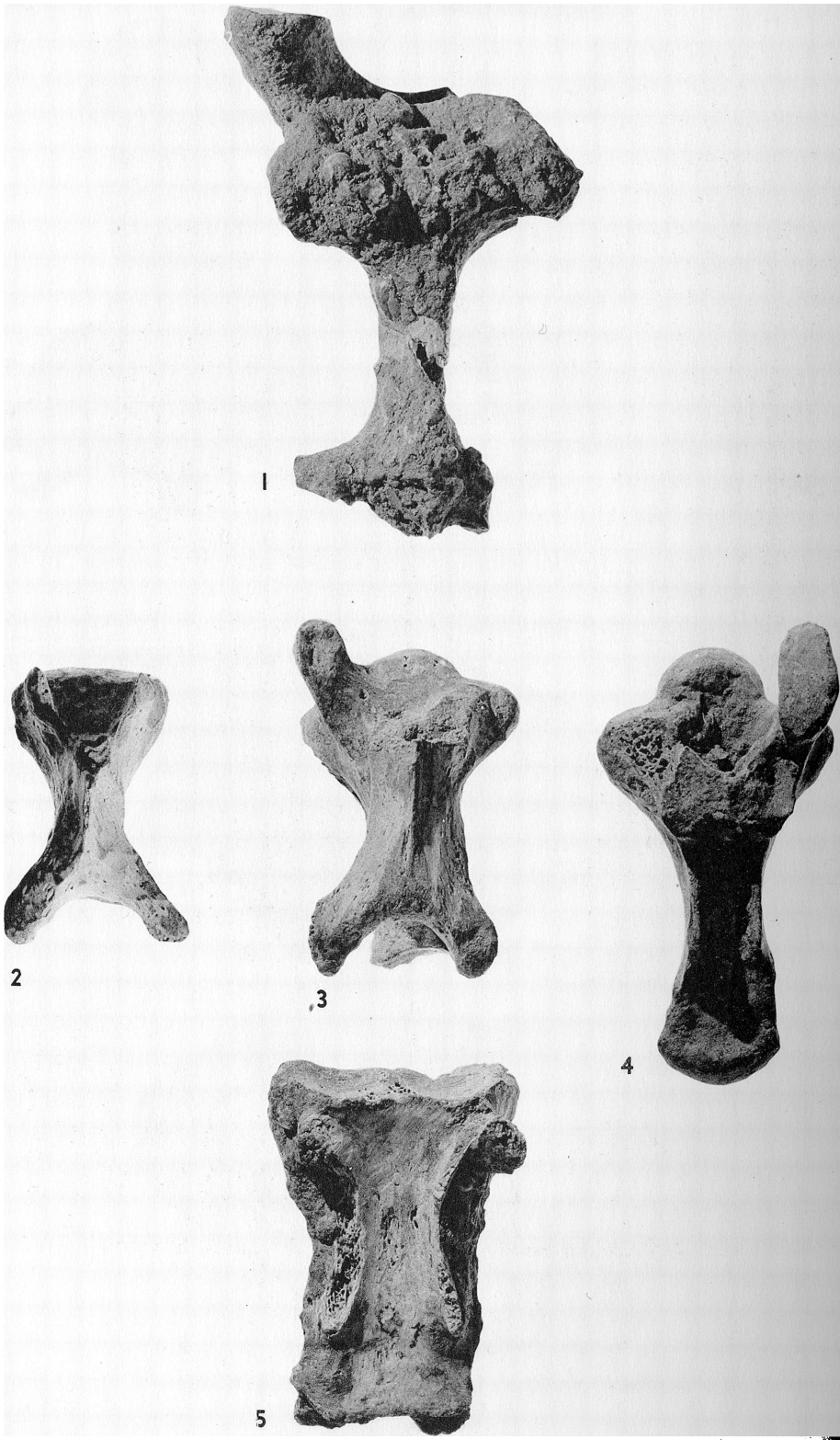




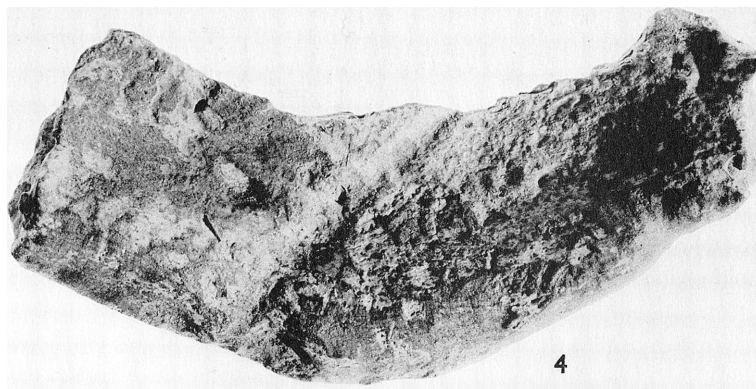




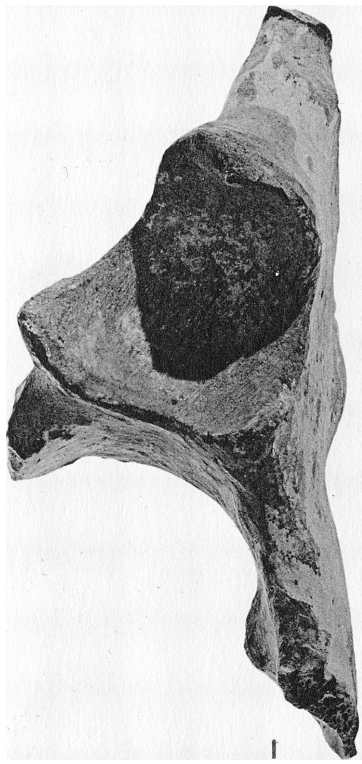
†*Testudo* (*Monachelys*) *monensis*. 1–3. A.M.N.H. No. 1936. 1. Dorsal view of skull. 2. Palatal view of skull. 3. Lateral view of skull. 4. A.M.N.H. No. 1969. Holotype, first dorsal vertebra

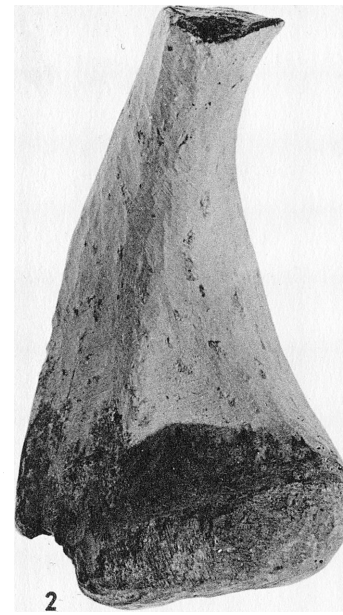


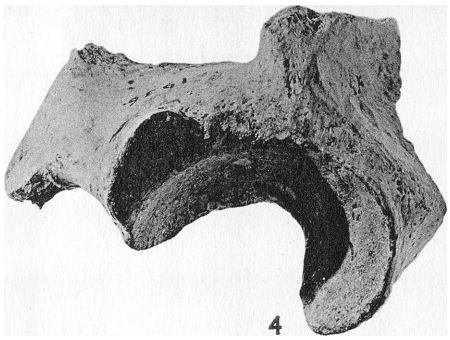
†*Testudo* (*Monachelys*) *monensis*. 1. A.M.N.H. No. 1935, paratype, first dorsal vertebra. 2–5. A.M.N.H. No. 1936. 2. Second cervical vertebra. 3. Third cervical vertebra. 4. Fourth cervical vertebra. 5. Seventh cervical vertebra

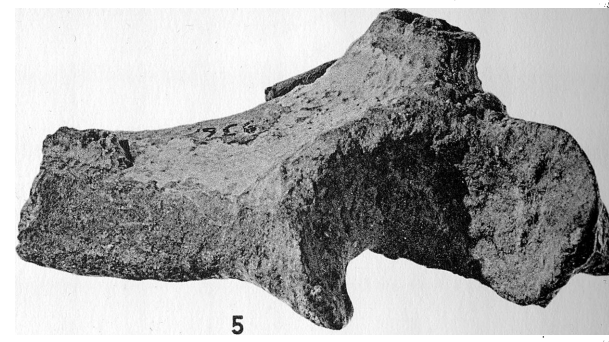


Testudo (*Monachelys*) *monensis*. A.M.N.H. No. 1936. 1. Humerus. 2. Broken humerus showing land shell crusted on articular surface. 3. Ulna. 4. Xiphiplastron









†*Testudo* (*Monachelys*) *monensis*. A.M.N.H. No. 1936. 1. Acetabular region. 2. Distal end of femur. Tibia. 4, 5. Glenoid region

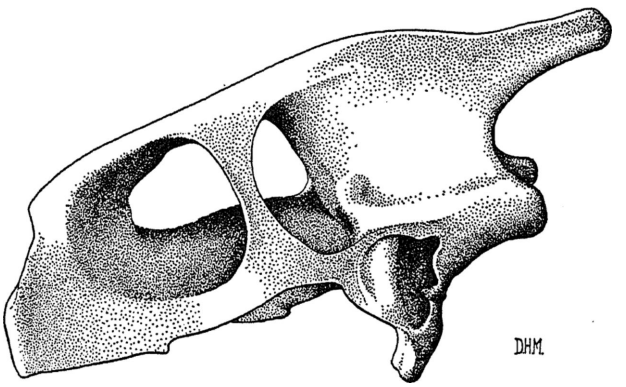


FIG. 4. †*Testudo* (*Monachelys*) *monensis*. Lateral view of reconstructed skull. ×1.

forms, and its scapular edge in particular seems to overarch the articular surface. The humeri are not especially distinctive. They lack the specializations, for example, of †*Testudo cubensis* (Williams, 1950b). The shaft is round rather than compressed, and the attachment of the latissimus dorsi is merely a roughened area and not a pit. The femur is known only from one distal end. The distal end is perhaps broader and the middle of the shaft narrower than is usual in *Testudo*. The shaft exhibits no compression. The pelvis, as far as preserved, is not distinctive. Distal limb bones are present, but those that are duplicated seem to show as great differences from one another as from the compared bones of other species.

An anterior caudal vertebra is available from the locality designated by Anthony as "below Playa." It is procoelous and presents no special characters. The neural arch is not thickened, as it is to an extraordinary degree in †*T. cubensis*.

The shell is very poorly preserved, quite badly broken, and incomplete. The bony plates were for the most part very thin; only the buttress and bridge areas and the area under the anal scutes are known to have been thickened. The sulci bounding the horny scutes seem for the most part to have been very feeble and are in fact usually not discernible. The margin of the carapace is smooth, not dentate. There is no xiphiplastral notch, and the sulcus of the anal scutes is slightly oblique antero-internally.

DISCUSSION

THE DESCRIPTION of a new subgenus of tortoise from the West Indies requires that the form be compared first with other known West Indian tortoises and then with other subgenera and genera throughout the world.

COMPARISON WITH WEST INDIAN TORTOISES

The fossil tortoises previously known from the West Indies are two:

1. †*Testudo cubensis* Leidy, the giant extinct tortoise of Cuba. This form has been redescribed (Williams, 1950b) and its affinities discussed. Known from material as fragmentary as that of †*T. monensis* but more abundant, it has been established that it is a well-differentiated species of *Chelonoidis*, the South American subgenus of *Testudo*. No skull is known, but shell, limbs, and tail vertebrae provide decisive characters for its recognition. It has been found in three localities in middle Cuba in deposits that seem surely to be of Pleistocene age.

2. The second previously recorded West Indian fossil tortoise is that of Sombrero Island. This is the form described by Leidy (1868) from the posterior part of a plastron as †*Emys sombrerensis*. It is almost certainly a member of the genus *Testudo* and provisionally may be called †*Testudo sombrerensis*.

Leidy's material, consisting of two large masses of bone breccia, was presented to him in 1859 by a Philadelphia merchant. On the basis of this material he reported the presence of abundant turtle bones on Sombrero in a paper before the Academy of Natural Sciences of Philadelphia the same year. Leidy was in fact so much impressed by the high phosphate content and many included bones of the Sombrero breccia that he proposed for this mineral a new name, osite, and regarded it "as the first instance of an extensive island formed alone of the bones of the higher animals." He did not publish a description of the turtle, however, until 1868.

In the meantime more material was collected by A. Julien who in two papers, generally neglected (as by the present author in 1950), recorded the existence of this form from fragments collected during a stay of four years on this barren rock 2½ miles long and ¾ mile wide. Julien first mentioned the existence of this tortoise in a paper on the geology of Sombrero in 1867, a year prior to Leidy's description of †*Emys sombrerensis*. Julien had submitted his fragments to Jeffries Wyman for study in 1864 and had received a report in 1865, but owing to a fire that injured his manuscript he did not publish Wyman's observations in full until 1878.

Julien had limb bones, parts of limb girdles, and carapacial fragments of a large land form. Several sizes of elements were involved, and Wyman suggested the existence of "at least three species"; this suggestion would no longer be seriously considered without very strong evidence.

Julien's materials were apparently too fragmentary to be very helpful in defining the Sombrero form. In his transcript of Wyman's report only statements regarding two of the fragments are quoted as possibly significant:

"Fragment 1: Left humerus of a large turtle: the ends are gone and the shaft alone is preserved; it is 6 inches in length and at the smallest part has a diameter of 2.07 inches from before backwards and of 1.57 inches from side to side. Admitting that the usual proportions existed, the whole length would have been about 12 inches. . . .

"Fragment 17a: An irregular cast of part of the interior of the carapace and plastron, the walls of the latter being broken but portions of them still adhering. Three of the median bony dermal plates, the largest 2.25 inches in diameter. These plates have neither ridge nor tuberosity on the median line, though there are slight projections over the heads of the ribs resembling those of very old specimens of *E. serpentina* [*Chelydra serpentina*]. The plastron is indistinctly seen, but enough remains to show that its union with the carapace was by a broad surface and not by a narrow one, as in the marine and some of the freshwater species."

Leidy's description adds details concerning the plastron of the Sombrero form. I quote in full:

"*Emys sombrerensis*, n.s.

"The bones of an extinct species of turtle are not unfrequently found in the so-called Sombrero guano, Sombrerite or Ossite [*sic*],

a material rich in phosphate of lime, largely mined in the island of Sombrero, W. I. and used in the preparation of fertilizer for agricultural purposes. In a mass of this material presented to the museum of the Academy (see Proc. 1859, 111) the posterior part of the plastron of a species of Emys or perhaps Testudo is perceived for which the above name is proposed. The specimen consists of both xiphisternals and the greater proportion of both hyposternals, articulated in natural juxtaposition. Other fragments of the plastron and carapace, together with a portion of the thigh bone are also contained in the mass. The specimen indicates the sternum to have approximated a foot in length; and the breadth at the lateral sutures of the hyposternals has been about 7½ inches. The under surface of the sternum is flat and smooth; and laterally it curves but slightly upward. The posterior sternal notch is two-thirds as deep as the width, and almost forms an equilateral triangle. The posterolateral border from the inguinal notch to the rounded triangular ends of the xiphisternals is bow-like, or presents two concavities with an intervening convexity. The caudal scutes are small, reaching slightly beyond the bottom of the sternal notch. The femoral scutes are on a level with the inguinal notches. Estimated length of the hyposternals in the median suture 35 lines; breadth 45 lines. Length of the xiphisternals in median suture 17 lines; greatest length about middle 25 lines; breadth along anterior suture 28 lines. Length of caudal scutes internally 13 lines; externally 10 lines. Length of femoral scute internally 25 lines. The bones present about the ordinary proportion of thickness observed in emydes."

Neither the type of †*Emys sombrerensis* nor most of Julien's material can now be found.[1] In any event all his material together seems unlikely to have been sufficient to characterize this form in adequate fashion, although the published descriptions are sufficient to show differences from the other known West Indian tortoises, †*T. monensis* and †*T. cubensis*.

[1] Through the efforts of Dr. Karl F. Koopman and the courtesy of Dr. Marshall Kay I have been enabled to examine the few fragments of the Julien collection that are retained in the Department of Geology, Columbia University. No diagnostic elements are preserved.

It is not known whether any more scraps of this animal were collected or can still be collected. At one time, as Julien states (1878, p. 30) much more might have been obtained: ". . . fossil specimens of these turtles, mostly fragmentary, have been found in many of the northern excavations upon Sombrero, since they were first worked in 1856 and perhaps are still, as its exploitation has been continued by an English company for many years past. They occur altogether in the guano veins which intersect the limestone beds to an unknown depth beneath the sea level and which are certainly but insertions from an ancient surface bed of rock guano, overlying but long since entirely denuded along with the crown of the key. In 1860–61, just before my arrival, enormous quantities of a guano breccia were taken out from the largest of the northern quarries, which was largely made up of these fragments probably to the amount of hundreds of tons!"

Living tortoises have been reported on most of the West Indian islands, but no authenticated case of endemic living land forms is known. A "*Testudo denticulata*" was collected by Hassler in central Barahona, Hispaniola (cited by Grant and De Sola, 1934), but the specimen, which was in the possession of the American Museum of Natural History, has now been lost. There is considerable probability that it was a human importation, though not necessarily a recent one. Dr. C. G. Aguayo (oral communication) has described the existence of a number of colonies of feral North American turtles in Cuba at the present time. The earliest natural histories of the West Indies mention the frequent importation of South American tortoises. It is therefore altogether likely that colonies of feral tortoises may have become established. *T. denticulata* on Providencia (specimens examined by the writer) are believed by E. R. Dunn (Dunn and Saxe, 1950) to have been imported by man.

Nevertheless the existence of an undoubted native species of the subgenus *Chelonoidis* on Cuba in the Pleistocene (a form close to *T. denticulata* and probably in the living state easily confused with it) does raise the question of possible error in identification of reported West Indian tortoises.

It is worth attention that no certain rec-

TABLE 1

COMPARISON OF CHARACTERS OF †*Testudo cubensis*, †*Testudo sombrerensis*, AND †*Testudo monensis*

†*Testudo* (*Chelonoidis*) *cubensis*	†*Testudo* (*Monachelys*) *monensis*	†*Testudo* (?Subgenus) *sombrerensis*
Size large	Size moderate	Size large
Shell except margins and areas under the gular and anal scutes extremely thin	Shell except margins and areas under anal scutes extremely thin. Gular region not known	Unknown
Margin recurved and dentate	Margin not recurved, entire	Unknown
Sulci on raised ridges	Sulci indistinct, scarcely apparent	Unknown
Anal sulcus transverse	Anal sulcus oblique antero-internally	Unknown
Xiphiplastral notch very reduced	Xiphiplastral notch absent	Xiphiplastral notch well marked
Humerus with a deep pit for the latissimus dorsi	Humerus with pit for the latissimus dorsi faintly indicated	Unknown
Humerus and femur flattened at middle in plane of head; ratio of diameters at middle approximately 1.5:1	Humerus and femur with nearly round section at middle; ratio of diameters approximately 1:1	Humerus somewhat flattened at middle; ratio of diameters approximately 1.3:1
Caudal vertebrae with tremendously thickened neural arch roof which may be thicker than the centrum	Caudal vertebrae with neural arch roof much thinner than centrum	Unknown

ords of living or fossil endemic tortoises (not even uncertain records for fossil ones) exist for two of the largest islands of the Greater Antilles, and in fact those between which Mona lies: Hispaniola and Puerto Rico. This is the more extraordinary in view of the fact that Mona is believed by many to be a fragment of a former connection between the two larger islands (Schmidt, 1926; Schuchert, 1935).

Fossil deposits are known on both Puerto Rico and Hispaniola. They are extensive and important. Many fossil mammals have been found in them but no tortoises. In both islands (but especially in Hispaniola) the deposits are suspected of being very late in time, extending upward into the period of man's occupancy. It is possible that on all the islands the tortoises became extinct before man arrived; even on Cuba there is no present evidence of the contemporaneity of man and the giant tortoise as there is of the contemporaneity of man and the sloths (Aguayo, 1950, pp. 123–124). Whatever the explanation, the record as it stands is completely anomalous with three quite distinct species known from widely separated points in the northern Antillean island chain, two from very small islands.

COMPARISON WITH THE OTHER TORTOISES OF THE WORLD

It would be desirable, but at this time it is not possible, to place the new subgenus within a revised classification and phylogeny of the tortoises of the world. At the moment it must suffice to list with very little comment the genera and subgenera of tortoises, Recent and fossil, that have so far been described, giving their known occurrences, indicating synonymies where evident, and grouping and arranging to the extent that is possible at present.

The list that follows is a compilation of names, each of which (excluding the stated synonymies) corresponds in my opinion to a biological entity, whether that entity should be called genus, subgenus, or species group. This list is not to be taken as a formal or final taxonomic arrangement. In it generic and subgeneric names are frankly used to call attention to more or less distinct groups of species; final decision on the rank of these groups is reserved.

I do not list all species that might be or have been assigned to the various genera and subgenera. To allocate all the fossil tortoises that have been described is an impossible task; some are indeterminable, some are synonyms, and most will require careful restudy to be placed correctly. Even with living tortoises the number of named forms in certain groups is surely excessive. I have therefore listed consistently only type species (including the types of synonyms) and representative fossil species, if these exist. For genera or subgenera containing only a few species I have listed all those currently recognized. The more unwieldy groups (most in need of revision) I have indicated by ending the list of included species with the phrase "and others."

GROUP 1: THE GENUS *Testudo*[1]

Genus *Testudo* Linnaeus, 1758; Eocene to Recent, world wide
- TYPE: *Testudo graeca* Linnaeus
- Subgenus †*Hadrianus* Cope, 1872; Eocene of North America
  - TYPE: †*Testudo corsoni* Leidy
  - INCLUDED SPECIES: †*Testudo corsoni*, †*T. majusculus*, and others
- Subgenus *Asterochelys* Gray, 1873; Eocene of Africa, Pleistocene and Recent of Madagascar, Aldabra, and Seychelles
  - TYPE: *Testudo radiata* Shaw
  - SYNONYM: *Megalochelys* Fitzinger, 1843. Type: *Testudo gigantea* Schweigger. Preoccupied by †*Megalochelys* Falconer and Cautley, 1837
  - INCLUDED SPECIES: *Testudo radiata*, †*T. grandidieri*, †*T. ammon*, *T. gigantea*
- Subgenus *Manouria* Gray, 1854; Recent of Asia
  - TYPE: *Manouria fusca* Gray = *Testudo emys* Schlegel
  - SYNONYMS: *Teleopus* LeConte, 1854. Type: *Teleopus luxatus* LeConte = *Testudo emys* Schlegel
  - *Scapia* Gray, 1869. Type: *Scapia falconeri* Gray = *Testudo emys* Schlegel
  - INCLUDED SPECIES: *Testudo emys*, *T. impressa*
- Subgenus †*Hesperotestudo* Williams, 1950; Eocene to Pleistocene of North America
  - TYPE: †*Testudo osborniana* Hay
  - ?SYNONYM: †*Eupachemys* Leidy, 1877. Type: †*Eupachemys obtusus* Leidy (based on a single marginal)
  - INCLUDED SPECIES: †*Testudo osborniana*, †*T. brontops*, †*T. orthopygia*, and others
- Subgenus *Indotestudo* Lindholm, 1929; Recent of Asia and the East Indies
  - TYPE: *Testudo elongata* Blyth
  - INCLUDED SPECIES: *Testudo elongata*, *T. travancorica*, *T. forsteni*
- Subgenus *Chelonoidis* Fitzinger, 1835; Miocene to Recent of South America
  - TYPE: *Testudo boiei* Wagler = *T. denticulata* Linnaeus
  - ?SYNONYM: †*Testudinites* Weiss, 1830. Type: †*Testudinites sellowii* Weiss (based on fragments)
  - SYNONYMS: *Gopher* Gray, 1870. Type: *Testudo chilensis* Gray
  - *Elephantopus* Gray, 1873. Type: *Testudo planiceps* Gray = *T. elephantopus* Harlan
  - *Pampatestudo* Lindholm, 1929. Type: *Testudo chilensis* Gray
  - INCLUDED SPECIES: *Testudo denticulata*, *T. chilensis* *T. elephantopus*, †*T. gringorum*, and others
- Subgenus *Geochelone* Fitzinger, 1835; Miocene of Europe to Recent of Asia, Africa
  - TYPE: *Testudo stellata* Schweigger = *T. elegans* Schoepff
  - SYNONYMS: *Centrochelys* Gray, 1872. Type: *Testudo sulcata* Miller
  - *Stigmochelys* Gray, 1873. Type: *Testudo pardalis* Bell
  - *Megachersine* Hewitt, 1931. Type: *Testudo pardalis* Bell
  - INCLUDED SPECIES: *Testudo elegans*, *T. platynota*, *T. pardalis*, *T. sulcata*, †*T. bolivari*, and others
- Subgenus †*Megalochelys* Falconer and Cautley, 1837; Pleistocene of Asia and Mauritius
  - TYPE: †*Megalochelys sivalensis* Falconer and Cautley
  - SYNONYM: †*Colossochelys* Falconer, 1844. Type: †*Colossochelys atlas* Falconer = †*Megalochelys sivalensis* Falconer and Cautley
  - INCLUDED SPECIES: †*Testudo sivalensis*, †*T. gadowi*
- Subgenus *Cylindraspis* Fitzinger, 1835; Recent of Rodriguez and Mauritius
  - TYPE: *Testudo vosmaeri* Schoepff
  - INCLUDED SPECIES: *Testudo vosmaeri*, *T. indica*
- Subgenus *Acinixys* Siebenrock, 1903; Recent of Madagascar

[1] Complete references for the original publication of most names can be found in Lindholm (1929) for most recent forms, or in Hay (1908) and Williams (1950b) for many fossil types; references for the remaining names can be found in the bibliography of this paper.

TYPE: *Testudo planicauda* Grandidier
INCLUDED SPECIES: *Testudo planicauda*

Subgenus †*Monachelys* Williams, new subgenus; ?Pleistocene of West Indies
TYPE: †*Testudo monensis* Williams, new species
INCLUDED SPECIES: †*Testudo monensis*

Subgenus *Psammobates* Fitzinger, 1835; Recent of Africa
TYPE: *Testudo geometrica* Linnaeus
INCLUDED SPECIES: *Testudo geometrica*, *T. oculifera*, *T. tentoria*, and others

Subgenus *Testudo* Linnaeus, 1758; Miocene of Europe to Recent of Europe, Asia, Africa
TYPE: *Testudo graeca* Linnaeus
SYNONYMS: *Chersine* Merrem, 1820. Type: *Testudo graeca* Linnaeus
Chersus Wagler, 1830. Type: *Testudo graeca* Linnaeus
Chersinella Gray, 1870. Type: *Testudo graeca* Linnaeus
Testudinella Gray, 1870. Type: *Testudo horsfieldi* Gray
Peltastes Gray, 1869. Type: *Testudo graeca* Linnaeus
Peltonia Gray, 1872. Type: *Testudo graeca* Linnaeus
Medaestia Wussow, 1916. Type: *Testudo graeca* Linnaeus
INCLUDED SPECIES: *Testudo graeca*, *T. horsfieldi*, †*T. antigua*, and others

Subgenus *Malacochoersus* Lindholm, 1929; Recent of Africa
TYPE: *Testudo tornieri* Siebenrock
INCLUDED SPECIES: *Testudo tornieri*

GROUP 2: THE ETHIOPIAN ENDEMIC GENERA

Genus *Homopus* Dumeril and Bibron, 1835; Recent of Africa
Type: *Testudo areolata* Thurnberg
SYNONYMS: *Chersobius* Fitzinger, 1835. Type: *Testudo signata* Walbaum
Pseudomopus Hewitt, 1931. Type: *Testudo signata* Walbaum
INCLUDED SPECIES: *Homopus areolata*, *H. signata*, and others

Genus *Chersina* Gray, 1831; Recent of Africa
TYPE: *Testudo angulata* Schweigger
SYNONYMS: *Goniochersus* Lindholm, 1929. Type: *Testudo angulata* Schweigger
Neotestudo Hewitt, 1931. Type: *Testudo angulata* Schweigger
INCLUDED SPECIES: *Chersina angulata*

Genus *Bellemys* Williams, 1950; Recent of Madagascar
TYPE: *Pyxis arachnoides* Bell
SYNONYM: *Pyxis* Bell, 1827 (Trans. Linnean Soc. London, vol. 15, p. 395). Type: *Pyxis arachnoides* Bell. Preoccupied by *Pyxis* Chemnitz (*in* Martini and Chemnitz, 1784, Neues systematisches Conchylien-Cabinet, vol. 7, p. 301)
INCLUDED SPECIES: *Bellemys arachnoides*

Genus *Kinixys* Bell, 1827; Recent of Africa
TYPE: *Kinixys castanea* Bell = *Testudo erosa* Schweigger
SYNONYM: *Cinothorax* Fitzinger, 1835. Type: *Kinixys belliana* Gray
INCLUDED SPECIES: *Kinixys erosa*, *K. homeana*, *K. belliana*

GROUP 3: THE GENERA *Gopherus* AND †*Stylemys*

Genus *Gopherus* Rafinesque, 1832; Oligocene to Recent of North America, Tertiary of Asia
TYPE: *Testudo polyphemus* Bartram
SYNONYMS: *Xerobates* Agassiz, 1857. Type: *Xerobates carolinus* Agassiz = *Testudo polyphemus* Bartram
†*Bysmachelys* Johnston, 1937. Type: †*Bysmachelys canyonensis* Johnston
INCLUDED SPECIES: *Gopherus polyphemus*, *G. berlandieri*, *G. agassizii*, †*G. laticunia*, †*G. canyonensis*, and others

Genus †*Stylemys* Leidy, 1851; Oligocene to Miocene of North America, ?Tertiary of Asia, Europe
TYPE: †*Stylemys nebrascensis* Leidy
INCLUDED SPECIES: †*Stylemys nebrascensis* and others

GROUP 4: GENERA OF UNCERTAIN POSITION

Genus †*Achilemys* HAY, 1908; EOCENE OF NORTH AMERICA
TYPE: †*Hadrianus allabiatus* Cope
INCLUDED SPECIES: †*Achilemys allabiatus*

Genus †*Cheirogaster* Bergounioux, 1935; Eocene of Europe
TYPE: †*Cheirogaster maurini* Bergounioux
INCLUDED SPECIES: †*Cheirogaster maurini*

Genus †*Colossoemys* Rodrigues, 1892; Pleistocene of South America
TYPE: †*Colossoemys macrococcygeana* Rodrigues
INCLUDED SPECIES: †*Colossoemys macrococcygeana*

Genus †*Cymatholcus* Clark, 1931; Eocene of North America
TYPE: †*Cymatholcus longus* Clark
INCLUDED SPECIES: †*Cymatholcus longus*, †*C. schucherti*

Genus †*Floridemys* Williams, 1950; ?Pliocene of North America
TYPE: †*Bystra nanus* Hay

INCLUDED SPECIES: †*Floridemys nanus*

Genus †*Sinohadrianus* Ping, 1929; Eocene of Asia
TYPE: †*Sinohadrianus sechuanensis* Ping
INCLUDED SPECIES: †*Sinohadrianus sechuanensis*

Group 1 above is the genus *Testudo* itself. The inclusion of †*Hadrianus* and *Acinixys* and the removal of *Gopherus* and *Chersina* are the only major changes, except nomenclatural ones, from the generic concept as it was left by Lindholm (1929). The genus as here recognized is probably, but by no means certainly, a monophyletic assemblage. The inclusion of †*Hadrianus* is, I believe, required to insure even a modest probability that it is monophyletic. I feel certain that several of the subgenera listed here have no common ancestor except a form with at least as many emydine characters as †*Hadrianus*.

I list the subgenera in approximate order of divergence from the primitive condition, taking †*Hadrianus* as primitive in shell characters and assuming that a ridged maxilla is primitively characteristic of the skull. *Melacochoersus* and †*Megalochelys*[1] may perhaps deserve removal from the genus when further studied. *Psammobates* and *Testudo, sensu stricto*, are regarded as specialized dwarf forms in which the alveolar ridging of the maxilla is obsolescent.

Whether group 2, the Ethiopian endemics, is an assemblage in anything except a geographic sense is doubtful. The listed forms have some characters in common suggestive of real relationship: alveolar surface of the maxilla without a median ridge, neurals usually not differentiated as in *Testudo* (except in *Pyxis*), anterior marginals much enlarged (except in *Homopus*).[2] I have here taken *Chersina* out of *Testudo* and placed *Acinixys* in that genus largely on the key feature of the presence or absence of ridging on the maxilla; the validity of this action is debatable. It is possible that all these forms may be merely African derivatives of a primitive *Testudo* stock, but it is equally possible that they may be of wholly independent phylogeny, paralleling *Testudo* in habitus but originating from a *Homopus*-like ancestor.

In regard to group 3, I have recently been able to make certain observations that clarify the picture. A skull found inside a fragmentary †*Stylemys* shell (M.C.Z. No. 1530) establishes the existence of a ridge like that of *Gopherus* on the alveolar surface of the premaxilla in that genus and confirms a relationship suggested by Hay (1908) and regarded as doubtful by Case (1925). Since Case has proved that †*Stylemys* has the emydine phalangeal formula (except for this consideration †*Stylemys* might well be considered a synonym or subgenus of *Gopherus*), the antiquity and independence of the *Gopherus* line seem now securely established.

Most of the fossil forms of the *Gopherus* series are American, as are all the living representatives, but †*Stylemys* has been described from the Tertiary of Asia and Europe, and some of Gilmore's (1931) Mongolian fossils may belong in this series (e.g., †"*Testudo insolitus*") as †"*Testudo kalganensis*" certainly does.

By the courtesy of Mr. Roy Reinhardt of the Pan Handle Plains Museum I have been privileged to examine the palate of †"*Bysmachelys canyonensis*" Johnston, and I can now confirm my earlier judgment based on Johnston's (1937) incomplete description of the shell and skeleton that †*Bysmachelys* is indeed a synonym of *Gopherus* and is in fact a form most closely related to *Gopherus polyphemus* although a gigantic and distinct species. As in *G. polyphemus* the lateral maxillary ridges are extended medially to meet the median premaxillary ridge.

The inclusion of †*Stylemys* in the Testudininae, apparently made necessary by its close relationship to *Gopherus*, introduces a new element of doubt as to the distinctness of

[1] †*Megalochelys* Falconer and Cautley, 1837, with type †*M. sivalensis* (withdrawn by the authors in favor of †*Colossochelys*), preoccupies *Megalochelys* Fitzinger, 1845 (type *Testudo gigantea*). Technically this leaves the Aldabra tortoises, for which *T. gigantea* is the oldest name, without subgeneric allocation. Since, however, †*T. ammon* of the Fayum Eocene of Egypt and *T. radiata* (and †*T. grandidieri*) of Madagascar seem to differ in no notable characters from the Aldabra tortoises, I take advantage of the nomenclatural situation to unite all these forms under *Asterochelys* Gray (type *Testudo radiata*).

[2] No characters except distribution and the unridged maxilla are known to characterize this group, but the occurrence of so many forms in this one region, otherwise very distinct, with even one striking anatomical peculiarity in common has led me provisionally to separate this group.

that subfamily. It disposes of the one character of the tortoises, the phalangeal formula, that seemed most surely diagnostic. I do not at this time formally unite the Emydinae and Testudininae because to do so would be to take action on the basis of only a cursory and inadequate survey of the groups in question and would deprive us also of a term for an assemblage which is at least a natural habitus grouping.

Group 4 is merely a collection of genera that, because of the inadequacy of the material or the description, are impossible to place. A very few comments will suffice.

†*Achilemys* Hay: The few fragments on which this name is based doubtfully deserve taxonomic recognition and certainly do not permit even a guess concerning its affinities.

†*Cheirogaster* Bergounioux: This genus was founded on a perfect shell. If correctly described, it is certainly a distinct genus, since it is said to lack an entoplastron and have the gular scutes in contact with the pectorals. Unhappily it is not possible to have any confidence in the accuracy of the description, and discussion of this form must await reëxamination of the type.

†*Colossoemys* Rodrigues: The elements on which this generic name was erected were two very large procoelous vertebrae considered to be caudals, a bone considered to be the pubis of the left side, and a plastral fragment. Of these, after examining Rodrigues' plates, I regard only the indeterminable plastral fragment as turtle.

†*Cymatholcus* Clark: To this genus I have referred, in addition to the type species (*C. longus*), a species described by Hay as "*Hadrianus? schucherti.*" The shell is peculiar and the skull is unknown. Relationship to †*Stylemys* suggested by Clark (1931) is as probable as any other hypothesis.

†*Floridemys* Williams (=*Bystra* Hay preoccupied): This is a remarkable dwarf form known only from the shell. Its affinities cannot at present be determined.

†*Sinohadrianus* Ping: This name records a single imperfect shell of Eocene age which displays almost no distinctive characters. If it is a tortoise it is as primitive as, or more primitive than, †*Hadrianus*.

In this list of tortoise genera and subgenera †*Monachelys* falls inevitably in group 1. On palatal characters alone it is sharply set off from the *Gopherus* group and from the Ethiopian endemics, while in this regard, except for the apparent shallowness of the palate, it fits very well within the genus *Testudo*. However, it can be confused with no other form in which the skull is known. The first dorsal vertebra is very distinctive, and the few known characters of the shell indicate considerable specialization. Its relationships do not appear to be at all close to any known form, and it may well be a representative of an ancient independent line within the genus *Testudo*, deriving ultimately, no doubt, from a *Hadrianus*-like form.

With its phylogeny so obscure, discussion of the zoogeography of †*Testudo* (*Monachelys*) *monensis* would be without point. The discovery of this form, however, serves again to remind us that much remains to be learned about West Indian faunas.

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