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CHECKLIST OF FOSSIL LAND TORTOISES (TESTUDINIDAE)

WALTER AUFFENBERG[1]

SYNOPSIS: This checklist is based on the main literature pertaining to fossil tortoises and an examination of many important specimens in museums in North and South America, Europe, and India.[2] Zoogeography and evolutionary trends are outlined and briefly discussed. Of 318 species originally described as fossil land tortoises, 22 are removed from the family and placed elsewhere, 9 are considered nomina nuda, 13 are based on material unidentifiable at the species level. Two primary homonyms are suppressed: *Gopherus depressus* and *Hadrianus robustus*, here renamed *Gopherus brattstromi* and *Geochelone gilmorei* respectively. Many species formerly placed in *Testudo* (sensu latu) are reallocated to other genera.

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INTRODUCTION

More than 200 species of fossil and Recent turtles are now assigned to the family comprising the land tortoises. The fossil species are listed in the following pages together with the named forms that were at one time or another considered tortoises. The considerable number of fossil forms named from material too fragmentary to be determinable have been placed in a separate category. Such placement serves a useful purpose in that names of possible, but presently questionable, validity cannot be treated as having equivalent value with adequately based taxonomic categories. Nor can such names be placed in synonymy, as this action would be only arbitrary and doubtful.

In almost all of even the better known fossil tortoises, the skull remains unknown. In only a few are the limbs and girdles known. Type specimens are widely scattered in collections, and no worker has ever seen a majority of both the fossil and Recent forms.

This multiplicity of species and the inadequacy or inaccessibility of the fossil material make the assessment of phyletic relationships even more theoretical and tentative than in most other checklists, but it is felt a complete set of named forms, arranged to suggest relationships that can be tested, will add something pertinent and perhaps decisive to the present mass of nonintegrated detail. Accordingly the following is submitted with a full understanding of its transitory status, because even with its shortcomings the time seems right for such a summary. It is hoped that its availability will stimulate contributions, particularly in the fossil forms that otherwise might not be forthcoming for many years.

Methods and Definitions

My primary objective has been to list those species of fossil turtles that are now, or have sometime in the past been considered as belonging to the family Testudinidae. I have followed no particular rule for including inadequately known fossil species in this family. In many cases the final criterion was similarity of shape or ornamentation of various osteological elements between these and known testudinids.

All extant Recent genera are included for convenience. Extant species are listed only if they have also been reported as prehistoric fossils.

To make this checklist more useful, the particular set of ground rules to which I have adhered must be stated:

(1) Use of parentheses: The International Rules of Zoological Nomenclature are clear on this point (Article 23) and have been followed throughout. The rule states that parentheses are to be used only to indicate the changes prescribed, not indiscriminately to indicate any change of combination.

(2) The synonymy includes a reference to the original description or use of each name. These are usually listed chronologically.

(3) The nature and location of type specimens, as well as type localities and horizons, are cited for each species wherever possible.

(4) Both geographic and geologic ranges are provided for each taxon. In many instances geologic age is revised from that of the original work in accordance with more recent standard references on the nomenclature and correlation of continental fossiliferous deposits.

(5) Our knowledge of fossil tortoises is actually quite meager, so it is impossible to place each taxon in a definite phyletic position at this time. The arrangement of all genera, subgenera, and species is alphabetic rather than phyletic.

(6) The large number of species listed (206) may lead some to believe that I have recognized an unduly large proportion of species names. In general I have preserved names for many presently questionable forms until there is some proof that they represent variant or aberrant individuals. I have taken certain liberties in synonymyzing Tertiary forms from both Europe and Asia. For the names of Recent forms I follow mainly Williams (1952) and Loveridge and Williams (1957). The question of subspecific relationship for the fossil populations is impossible to determine on the basis of intergradation, and therefore morphological similarity remains the sole criterion on which my judgments are based.

A wide possible range in degree of distinctness usually occurs between the genera, subgenera, or species of fossil and Recent forms. The number and kinds of differ-

ences between fossil species of a single genus that can be accepted as commensurate with the definition must vary with the investigator, the trend of the times, and the nature of the specific group being studied. As the criteria for recognizing full species in fossils are not yet standardized, it is impossible to be absolutely consistent in the definition of both fossil and Recent genera, subgenera, or species.

(7) Every extinct taxon is preceded by the symbol †.

(8) The present interpretation of the homonym rule requires that the names of two tortoises are affected as follows:

A. *Gopherus †depressus* Brattstrom (1961), Miocene of California.
Testudo depressa Guerin-Meneville (1828) (=*Gopherus polyphemus*), Recent of southeastern United States.
Gopherus †depressus Brattstrom is here renamed *Gopherus †brattstromi* in honor of its discoverer.

B. *Hadrianus †robustus* Gilmore (1915), Uinta Eocene, Utah (=*Geochelone* [*Hadrianus*] *†robusta*).
Testudo †robusta Leith-Adams (1877), Pleistocene Malta (=*Geochelone* [*?Geochelone*] *†robusta*).
Hadrianus †robustus Gilmore is here renamed *Geochelone †gilmorei* in honor of its discoverer.

(9) Species groupings and subgeneric categories of tortoises rest on fairly secure bases; above this uncertainties increase. Placing almost all of these groups in the genus *Testudo,* as is most often done, does not in my opinion reflect the apparent fact that the homogeneity of tortoises is due to similar trends in several phyletic lines. Therefore the classification of Williams (1952) and Loveridge and Williams (1957), rather than the more recent but conservative treatment of Wermuth and Mertens (1961), is followed.

(10) Under most generic and species accounts a section headed "Remarks" includes literature citations to important publications as well as comments on presumed relationships. No attempt has been made to include every reference to fossil tortoises—only those that seem most important for purposes of this checklist.

(11) Genera not represented by fossils are briefly diagnosed with pertinent remarks appended.

(12) To bring this work to completion no publications were included that appeared after 1 January 1972.

Zoogeography and Ecology

The family Emydidae probably has the widest distribution of all the nonmarine turtle families. The family Testudinidae (the true tortoises) has a more restricted distributional pattern. It is here regarded as being represented by at least 16 genera, 10 of which are still living. Of the extant genera 5 are Ethiopian endemics (*Psammobates, Malachochersus, Chersine, Kinixys,* and *Homopus*), 2 are confined to Madagascar (*Acinixys* and *Pyxis*), 1 is widely distributed throughout the southern Palearctic (*Testudo*), and 1 is restricted to the southern Nearctic (*Gopherus*). The remaining genus, *Geochelone,* is the largest, being represented at least within historic times by about 19 species. It is distributed throughout much of Africa south of the Sahara, Madagascar, several smaller islands in the western Indian Ocean, extreme southeastern Asia, including some of the East Indian islands, extreme southern Central America, most of South America east of the Andes, some of the Leeward Islands in the

West Indies, and the Galapagos Islands. Although never native to Australia or Melanesia, waif dispersal across marine barriers is common (Williams 1950a, 1952; Simpson 1942, 1943).

The living tortoises are for the most part subtropical to tropical in distribution, being most common in subhumid to arid grasslands and savanna habitats, though there are a few mesic tropical forest forms.[1] During the Tertiary their ranges extended throughout what are now temperate latitudes (Brattstrom 1961; Hibbard 1960; Auffenberg and Milstead 1965) (Fig. 1). This is believed due to a high degree of climatic equability, enabling tropical and temperate biotas to intermingle (Axelrod 1967). As the climate became cooler, the distribution of tortoises was obviously affected (Hibbard 1960; Brattstrom 1961). Quaternary tortoises in the middle and northern latitudes were subjected to at least four major periods of colder climate, often more moist. Drier, warmer climates characterized parts of the three interglacial ages. Each of the glacial and interglacial periods may have been cooler than the preceding corresponding periods. Though the evidence is meager, tortoises seem to have expanded northward during each interglacial. More important, the northern range limit of tortoises with each successive interglacial was farther southward. Though the range was smaller during glacial periods, it seems to have become more restricted with each succeeding advance, but none of these changes were severe enough to bring about major tortoise extinctions. During and after the last glacial, severe drought and cold in the northern latitudes played important complementary roles in extinction of large tortoises. Unlike their large contemporaries, smaller species of tortoises survived these major temperature changes by retreating into a burrow. It is inconceivable on mechanical grounds alone that the extinct giant tortoises of the Pleistocene tunneled. Few living testudinids of any size burrow in the earth. Those that are known to do so (*Gopherus* and some species of *Testudo*) continue to inhabit the higher latitudes.

Not all tortoise extinction can be explained solely on late Quaternary climatic changes. For example it does not fully explain the extinction of truly gigantic land species in tropical continental areas. Within historic times such giant species have lived only on islands without large predators. This has led some workers to suggest that gigantism in tortoises occurs only in the absence of predation, but this is not so. Each of the

[1] Few really complete ecological studies of tortoises are available. The more important ones are: Beck 1903; Fryer 1911; Miller 1932, 1955; Hediger 1935; Bogert and Cowles 1947; Woodbury and Hardy 1946; Guibe 1950, 1954; Cherchi *et al.* 1958; Cernov 1959; Eibel-Eibesfeldt 1959; Khozatsky 1959; Medem 1960, 1962; Honegger 1964; Obst and Meusel 1965; Carpenter 1966; Hutchison *et al.* 1966; Schmidt-Nielson and Bentley 1966; Grubb 1967; Stoddart and Wright 1967; Frazier 1968; Auffenberg 1969; Auffenberg and Weaver 1969.

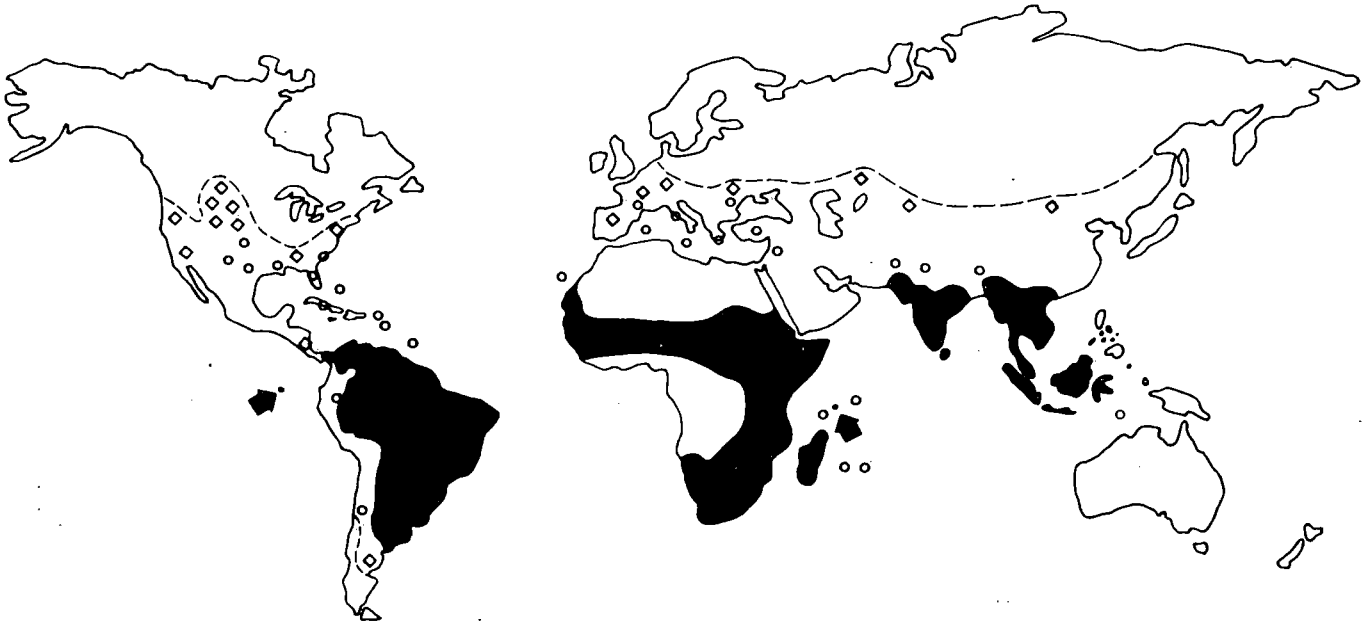

FIGURE 1.—Distribution of land tortoises of the genus *Geochelone*, showing reduction of range with time. Diamonds, northern and southern limits in Oligocene-Miocene. Circles, Pliocene-Pleistocene limits. Solid black and arrows, Recent.

extant elephantine tortoises is represented by gigantic continental relatives. Large carnivores existed in these same continental areas from the Eocene to the Recent[1] alongside several dominant groups of these gigantic tortoises. In fact the presence of such carnivores may have been partly responsible for the gigantism witnessed in several phyletic lines.

The extinction of giant land tortoises in all parts of the world probably cannot be explained by a single theory. Man may have played a role in it, though only near the culmination of a series of climatic changes that had already greatly reduced the ranges of the giant species of many different animals (Webb 1969). Man's repeated visits to those Pacific and Indian Ocean islands formerly harboring innumerable individuals of gigantic land tortoises has certainly caused near or complete extinction in several species. It is also true that in several continental areas the disappearance of some tortoise species can be roughly correlated with the presence of early man. Two important facts not often mentioned bear on this problem: (1) some very small species of land tortoises also became extinct at the same time, and (2) the distribution of land tortoises has been continuously restricted since the Miocene. The extinction of the small species cannot be considered part of the general extinction of large land animals in temperate latitudes that characterized the end of the Pleistocene. The pre-Pleistocene extinction of tortoise species was entirely climate-activated. Near the end of the Pleistocene and during the Early Recent man undoubtedly played a contributory role through habitat modification, as well as through direct predation on relict populations.

The only described extinct tortoise genera considered valid in this contribution are *Floridemys, Cheirogastor, Kansuchelys, Sinohadrianus,* and *Stylemys.* Others are either synonyms of presently recognized tortoise genera or subgenera or are not testudinids.

Evolution, Phylogeny, and Trends

Extinct species of land tortoises are known from deposits of Middle Eocene to Recent geologic age. Undoubtedly Paleocene and perhaps even Upper Cretaceous members of the family will eventually be found. These prototestudinids will be intermediate between the earliest known tortoises of the Eocene and primitive members of the Emydidae.

In Eocene deposits of both North America and Africa and the earliest Oligocene of North America, Asia, and western Europe all the known

[1] Lydekker's view that the gigantic tortoises became extinct in all continental areas at the close of the Pliocene is now known to be incorrect. Their presence in the Pleistocene is well documented in North and South America, as well as in Asia, where many gigantic Middle and Late Pleistocene species are known.

representatives of the family were in an evolutionary stage represented by the extant *Geochelone emys* of Southeast Asia. They were large, low shelled, plantigrade, nomadic, frugivorous tortoises living in mesic tropical evergreen forests. Much of the evolutionary history of tortoises reflects adaptations to grazing in semiarid, subtropical grassland and thorn forest. The change in habits and ecology is reflected in several major morphologic evolutionary trends (Hay 1908, Williams 1950a, 1950b, Loveridge and Williams 1957).[1]

1) The high, convex shell of almost all extant testudinids is evolved from one that was low and similar to that in *Chrysemys*. The depressed shell of a few Recent species of tortoises is probably a specialization related to shelter utilization. Two reasons have been suggested for the major trend in changing shell shape: 1) carnivorous land animals cannot span the greater convexity of a domed shell with their jaws as readily as a more flattened shell, and 2) the vaulted shell provides greater space for the lungs. Several workers (Koch 1934, *et al.*) have shown that the capacity of the lungs of testudinids is somewhat greater than that of equal sized emydids (except *Terrapene*, which has a life style similar to that of testudinids).

2) In emydids the neurals are usually hexagonal, with the broader end directed anteriorly. The earlier species of tortoises also exhibit this condition, though in occasional individuals the second neural is octagonal (sometimes a rare variant in other families of turtles[1]). Among later fossil testudinids a high degree of neural differentiation is the rule, usually an alternation of octagonal and tetragonal elements at least anteriorly. In some fossil and Recent species the hexagonal neurals have the broad end directed posteriorly. This is a specialized condition (Fig. 2). Some extant tortoises retain the emydid condition, except that few neurals may be tetragonal as in *Homopus*.

3) Considerable modification has taken place in the pleurals during the evolution of tortoises. In almost all other turtles the proximal and distal ends of the second through the sixth pleurals are nearly the same width. In almost all testudinid species the proximal ends of the second, fourth, and sixth pleurals are much narrower than the proximal ends of

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[1] For anatomy of turtles, including tortoises, see Bojanus 1821, Jackson 1837, Parker 1868, Gray 1873c, 1873d, 1873e, Furbinger 1874, Rutimeyer 1874, Zittel 1887-90, Hoffman 1890, Bauer 1891, Bruhl 1896, Siebenrock 1897, 1898, 1899, 1909, Wieland 1900, Sieglbauer 1909, Williston 1925, Beer 1926, Nopsca 1926a, 1931, Ruckes 1929a, 1929b, Bolk *et al.* 1931-8, Thompson 1932, Versluys 1936, Kuhn 1937, Schepers 1938, 1939, 1948, Zangerl 1939, Walls 1942, Romer 1945, 1956, Walker 1947, Schumacher 1954, 1955, George and Shah 1955a, 1955b, 1959a, 1959b, Golby and Gamble 1957, Parsons 1959, Williams 1959, McDowell 1961, Shah and Patel 1964, Zug 1966, Pawley 1968.

[1] Shell anomalies are discussed by Meyer 1867, Parker 1901, Coker 1910, Lynn 1937, Grant 1946, Lynn and Ullrich 1950, Mlynarski 1956, Zangerl and Johnson 1957, Staesche 1961, and others.

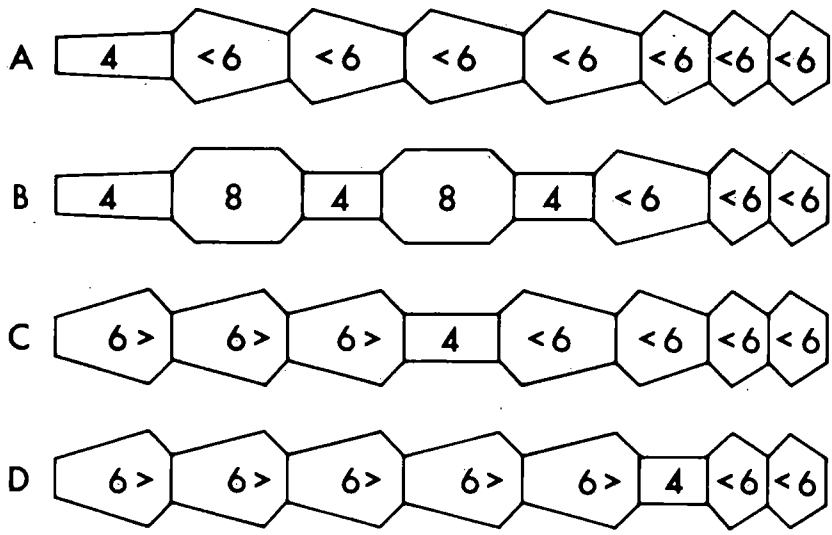


FIGURE 2.—Generalized neural formula of a pond turtle (A) and land tortoises (B-D). A. *Chrysemys concinna*. B. *Geochelone †osborniana*. C. *Geochelone †corsoni*. D. *Kinixys erosa*.

the adjacent elements. In those pleurals that are narrower proximally, they are expanded distally. Thus the pleural bones appear to be dovetailed with one another (Fig. 3), producing a very rigid dome. The mechanical advantages of this system have been discussed by Bienz (1895). These modifications are generally more conspicuous in later fossil species within each group. That this differentiation has been evolved independently in several tortoise genera is suggested by the fact that the modification takes place early in the fossil record of some genera and later in others.

4) In most turtles the position of the rib shows distinctly on the internal surface of each pleural bone, and the rib heads are broad and thick. The rib heads join their respective centra at the anterior ends of the latter, and the anterior ribs come into contact with the next anterior centrum as well. In extant tortoises the ribs are only faintly indicated on the pleurals, and the rib heads are usually greatly reduced. Early fossil types tend to have large ribs. Thus there is a gradual reduction in rib head size with time.

The distal ends of the ribs of tortoises are also reduced when compared with the emydid condition. In most turtles the distal rib ends project beyond the ends of the pleural bones, and the projected ends are usually received in pits in the dorsal edge of the peripherals. In most extant testudinids the rib ends have all but disappeared, and in adults a

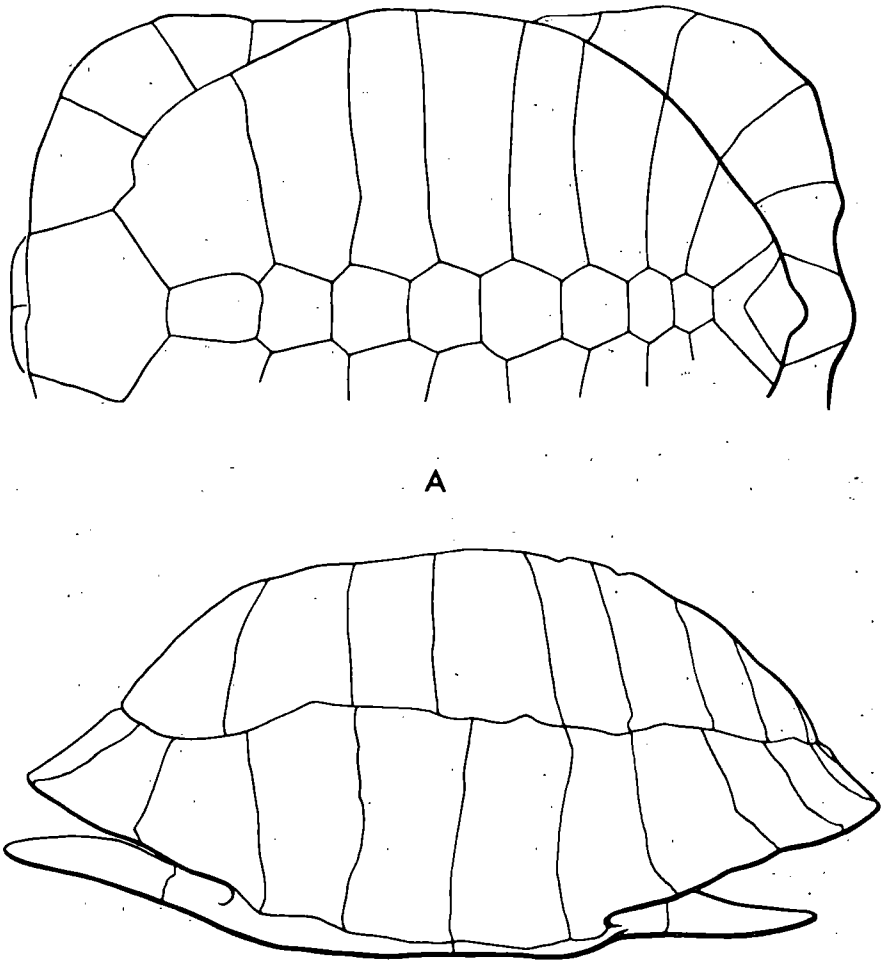
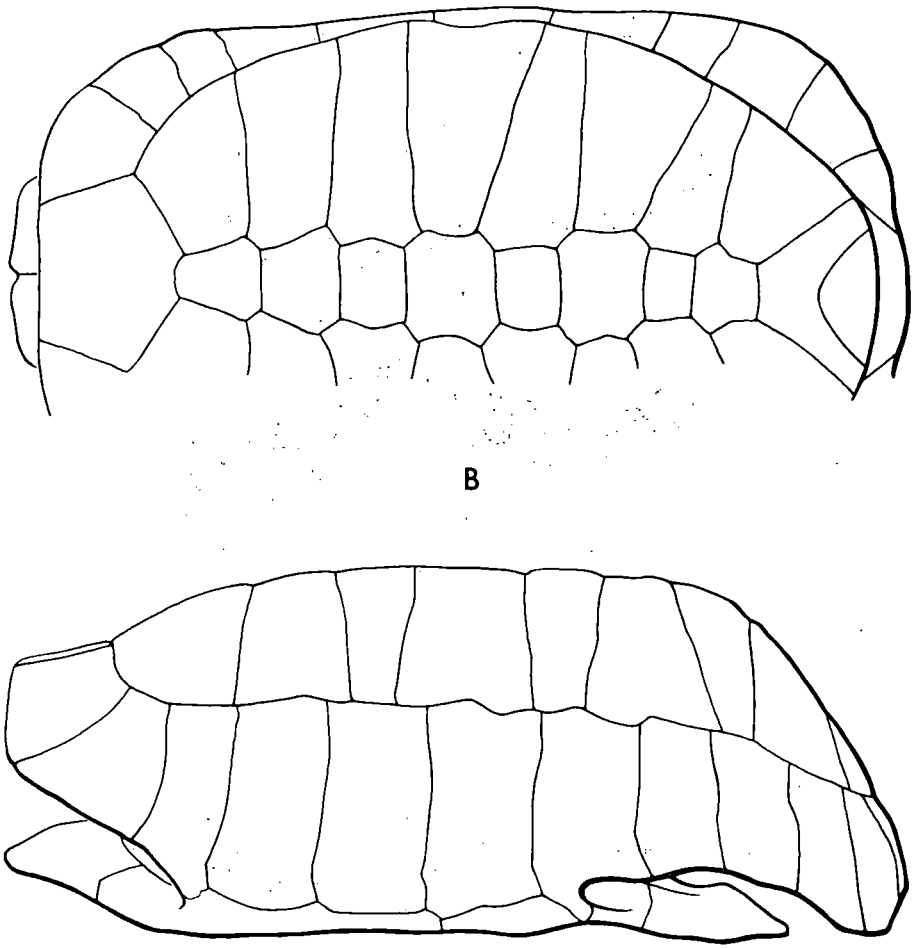


FIGURE 3.—Pleural differentiation as related to the neural formula. Alternately wide and narrow pleurals appear in the mid-Tertiary with the development of octagonal

process of the peripheral rises and enters a notch on the edge of the pleural (Fig. 4). The rib ends enter the peripherals only in juveniles. In early fossil tortoises the emydid character is often retained until the individual is almost full grown (Auffenberg 1964d).

5) In most specialized tortoises the epiplastra are thickened for some distance on either side of the midline and on the dorsal surface. At the posterior border of the thickening the elevation drops off suddenly to the level of the entoplastron. The ledge thus formed is more or less deeply excavated at its base. This excavation and the thickened epiplastra are not found in the more primitive members of the group (*Stylemys, Homo-*



neurals. A. *Stylemys* †*amphithorax*, Early Oligocene, Colorado, U.S.A. B. *Geochelone* †*hesterna*, late Miocene, Colombia, South America.

pus, etc., Fig. 5). When present, the thickened epiplastra usually project beyond the general curve of the crest of the anterior lobe. This extension forms the epiplastral lip, which takes several forms in various species and furnishes valuable specific characters.

6) At the anterior end of the bridge the hyoplastron of each side sends a process dorsally and anteriorly that articulates with the first pleural bone. The hypoplastron also sends up an inguinal buttress, which usually articulates with the anterior half of the lower border of the sixth pleural. In *Stylemys* it articulates at the juncture of the fifth and sixth pleural, as it does in the Emydidae. Thus it seems evident that in land

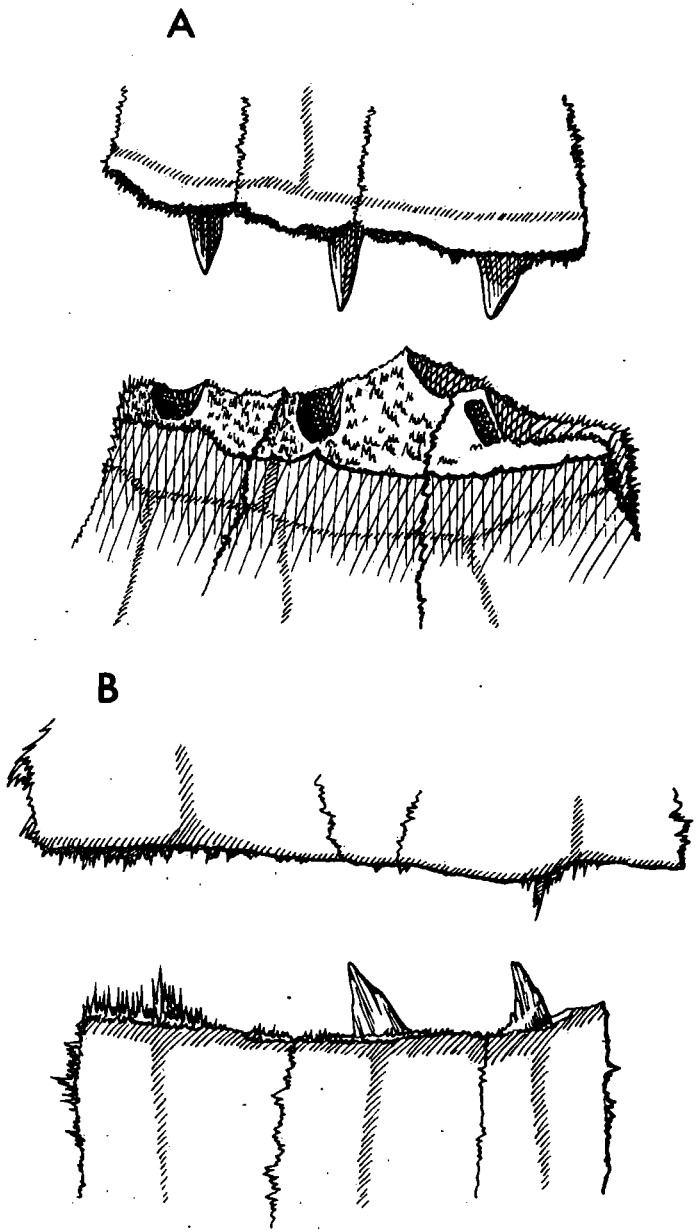


FIGURE 4.—The primitive pleural rib and peripheral pit articulation of the carapace of pond turtles (A, *Chrysemys scripta*) is modified in most land tortoise groups by the mid-Tertiary. The pits are generally absent and often replaced by dorsally directed processes (B, *Gopherus polyphemus*). The distal end of the pleural ribs are usually weakly developed, or absent.

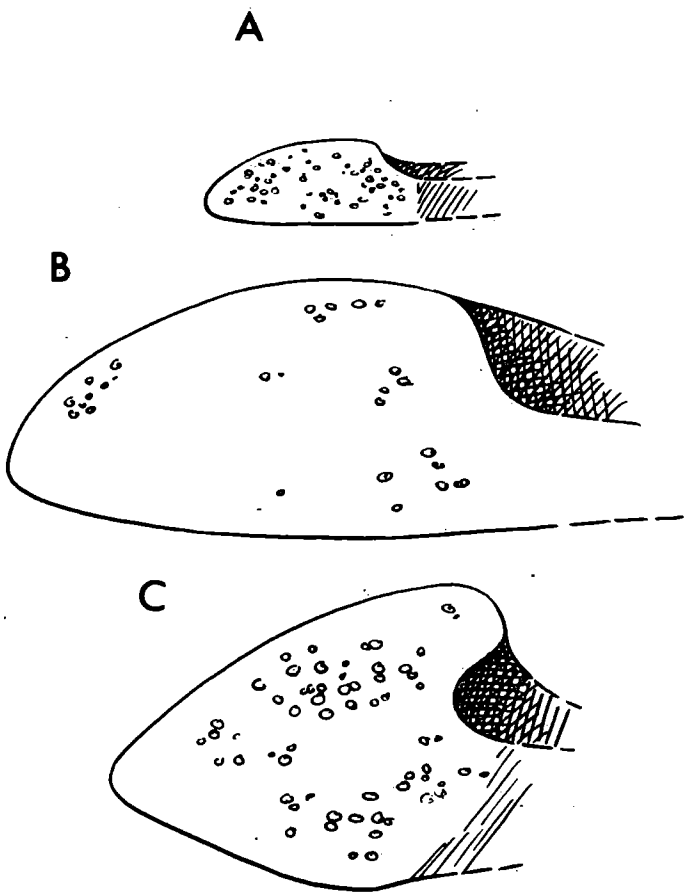


FIGURE 5.—Median longitudinal section of the epiplastron. A. *Chrysemys scripta* Pleistocene (Emydidae). B. *Stylemys †amphithorax*, Oligocene (Testudinidae). C. *Geochelone †crassiscutata*, Pleistocene (Testudinidae).

tortoises the articulation tends to be pushed posteriorly with the increased length of the bridge. The result has apparently been to diminish the posterior opening of the shell.

7) The shoulder girdle of land tortoises appears to have been modified from that of the Emydidae in two respects: the coracoid is greatly expanded at its medial border, and the procoracoid process makes an obtuse angle with the body of the scapula. In all Emydidae where the condition is known, the coracoid is only slightly expanded, and the procoracoid process makes an acute angle with the body of the bone (Fig. 6).

8) The humerus of the Testudinidae is modified from that of the

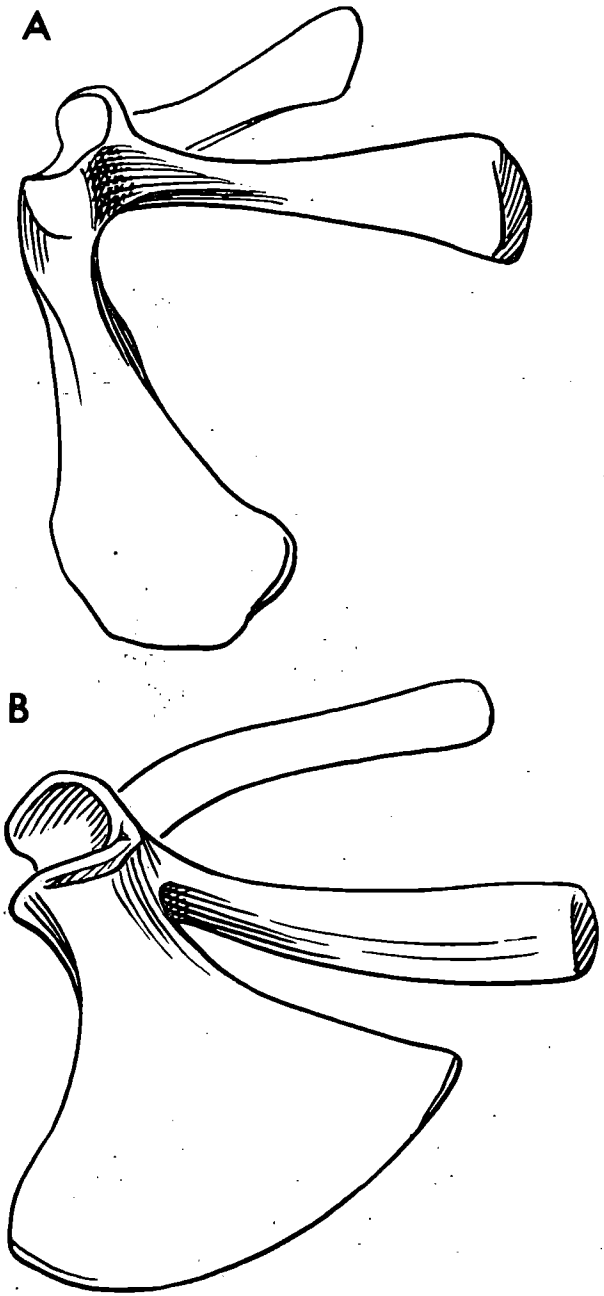


FIGURE 6.—Shoulder girdle of an emydid, *Chrysemys terrapin* (A), and a testudinid, *Geochelone chilensis* (B), showing the expanded coracoid of the latter.

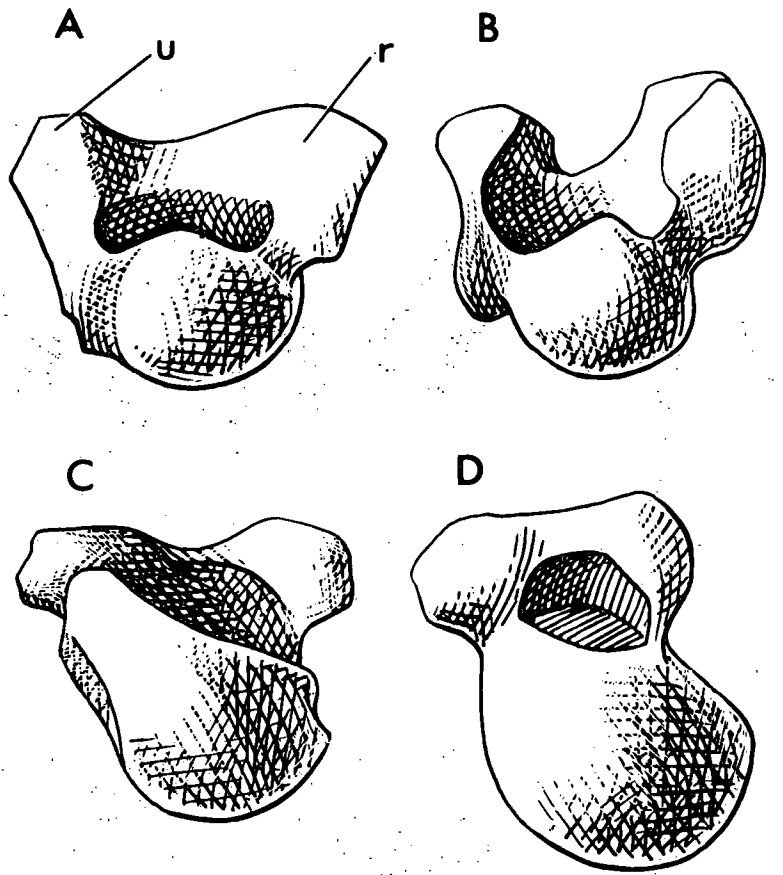


FIGURE 7.—Proximal views of humeri (A,B) and femora (C,D) of an emydid, *Chrysemys terrapin* (A,C) and a testudinid, *Geochelone chilensis* (B,D). u = ulna process, r = radial process of humerus.

Emydidae by having both the radial and ulnar processes twisted ventrally, with the included angle small (Fig. 7).

9) Most species of testudinids have five digits on each forelimb, occasionally only four. The hind foot often has only four digits. No digit has more than two phalanges (Fig. 8), emydids have three. The front foot of *Gopherus* is unguligrade, the most primitive members tend to be plantigrade, and advanced members digitigrade.

10) Major trends in the carpus include fusion of subradial elements, more distal and proximal subulnar elements, and lateral migration of both subulnar and subradial elements accompanying fusion of the medialia (Fig. 9) (Auffenberg 1966b).

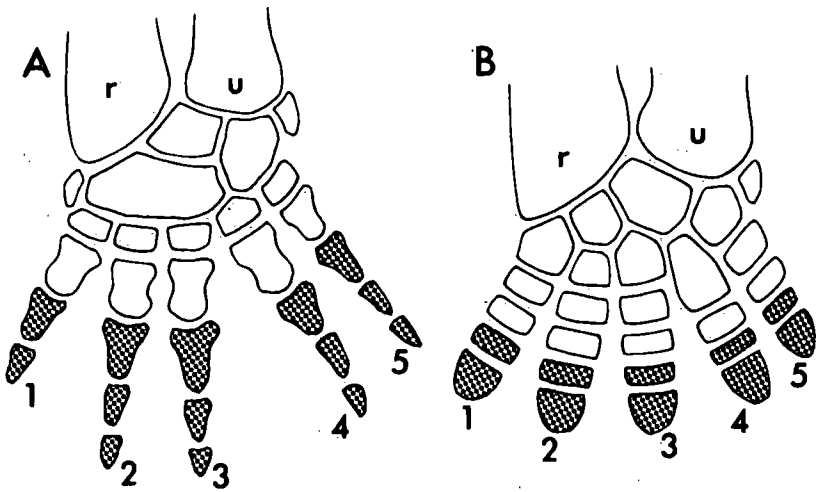


FIGURE 8.—Generalized manus of an emydid, *Chrysemys terrapin* (A), and a testudinid, *Gopherus polyphemus* (B). r = radius, u = ulna. Shaded portions are the phalanges.

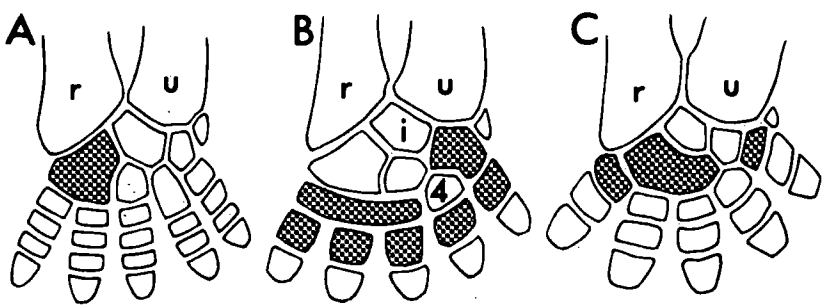


FIGURE 9.—Major trends in evolution of the tortoise carpus. A, fusion of subradial elements. B, fusion of distal and proximal subulnar elements, subradial carpals and phalanges, as well as the failure of carpal 4 to contact the intermedium (i). C, lateral migration of subulnar and subradial elements as well as fusion of medialia. r = radius, u = ulna.

11) The pelvis is constructed on the plan found in the Emydidae.

12) The femur of advanced tortoises is distinguished from that of the Emydidae by a ridge-like union of the two trochanters. Between this ridge and the head of the femur there is usually a pit of some depth (Fig. 7).

13) The most striking differences between the skulls of the Testudinidae and those of the Emydidae are found in the excavation of the former's palate and in the closure of the stapedial notch (Fig. 10). The

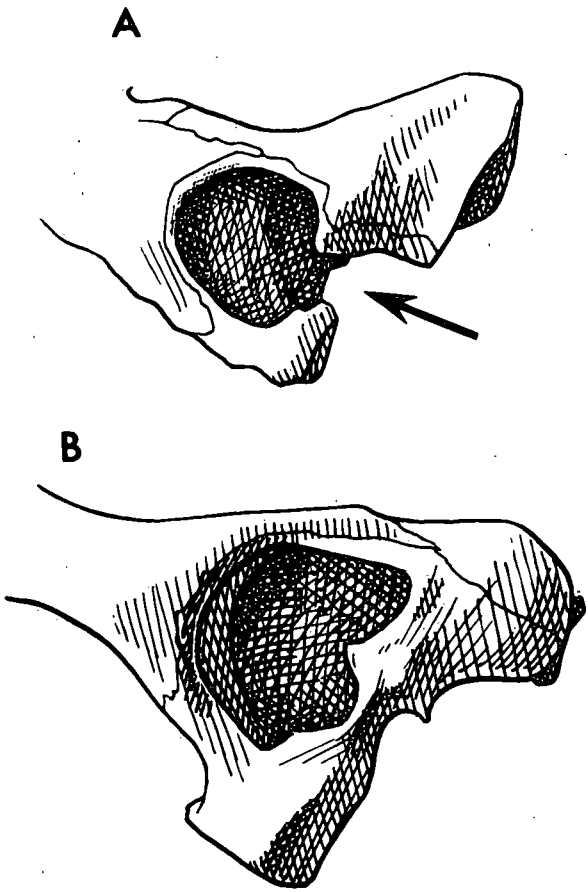


FIGURE. 10.—The stapedial notch (arrow) is usually open in emydid turtles (A, *Chrysemys terrapin*) and closed in testudinids (B, *Geochelone chilensis*).

palate rises high above the level of the crushing surfaces of the upper jaws, and the vault thus formed is carried back between the quadrates. The skulls of most of the earlier fossil tortoises remain unknown.

The division of the family Testudinidae into generic groups is difficult for a number of reasons: (1) the groups comprising the family are closely related, and much parallel evolution has occurred, (2) it is difficult to distinguish between those characters that are merely convergent and those that may indicate natural divisions, (3) they display various combinations of primitive characters, (4) advanced characters in the several lines have developed quite independently, and (5) the geologic time at which these advanced characters arose differs in various groups.

The land tortoises undoubtedly arose from primitive emydids, probably toward the close of the Late Cretaceous. The primitive forms were probably already well distributed in the Paleocene, but we have no proof of this. By the Middle Eocene they are already found in all the continental areas except Australia and South America. The view of Hay (1908) that North America is probably the ancestral home of the family is not followed here, mainly because tortoises almost as old are now known from other parts of the world. A considerable degree of evolutionary differentiation is indicated even in the earliest members of the family, suggesting a long, completely unknown prefossil history in which any continent (other than Australia) might eventually prove to be the ancestral home.

The most primitive fossil and living testudinids approach the Emydidae in the following characters:

1) Interval between ventral processes of the prefrontals only moderately widened
2) Temporal arcade strong
3) Prootic well exposed
4) Quadrate not enclosing stapes
5) Anterior neurals hexagonal (wide end forward)
6) Suprapygal one, anterior to vertebral-subracaudal sulcus
7) Entoplastron anterior to humeropectoral sulcus
8) No greatly thickened epiplastral projection, and no excavation at its base
9) Carapace not doomed, flattened
10) Rib ends fit into peripheral pits
11) At least prefrontal and frontal scales present
12) Scales on forelimb numerous, not greatly enlarged
13) Femoral tubercles present
14) No tail claw
15) Neither carapace nor plastron hinged
16) Nuchal scute present
17) Vertebrals not greatly convex
18) Carapacial keels weak
19) Supracaudal scute divided
20) Submarginal scute absent
21) Gular scutes paired
22) Anal notch moderate

The most primitive tortoise group is the subgenus *Manouria* (formerly *Hadrianus*), genus *Geochelone*. Most of the other groups probably evolved from this group (Fig. 10). Extant members of the group are restricted to mesic evergreen forests of southeastern Asia, also the habitat of the early Tertiary forms. Since that time the major evolutionary changes in both morphology and behavior in tortoises have been intimately associated with the development of xeric plant communities and spreading temperate conditions throughout the world.

Those living testudinids that have been designated 'gigantic' tortoises all belong to the genus *Geochelone*. Several extinct genera attained large size, which recurs in many groups. Some gigantic forms, living and

extinct, evolved from small species, and some diminutive types evolved from much larger ones.

Taxa Incorrectly Placed in the Testudinidae[1]

Testudo †*munda* Hay 1920. Pleistocene of Tennessee, U.S.A. (=*Terrapene carolina*, see Auffenberg 1963).

Testudo †*promarginata* Reinach 1900. Lower Miocene of Frankfort a.m., Germany. (=*Ptychogaster* †*francofurtanus*, in part, and *T. antiqua*, in part, see Glaessner 1935).

Testudo †*fejervaryi* Szalai 1930. Aquitanian of Salgotarjan, Hungary. (=*Ptychogaster* †*fejervaryi*, see Glaessner 1933).

Testudo †*eurysternum* Gervais (ex-Pomel) 1836. Lower Miocene of France. (=*Ptychogaster* †*eurysternum*, see Bräm 1951).

†*Archaeochelys pougeti* Bergounioux 1938b. (anything organic?).

†*Colossoemys macrococcygeana* Rodrigues 1892. Miocene of Peru. (=Triassic ammonodont, see Huene 1944).

Testudo †*laurea* Forster and Becker 1888. (=*Ptychogaster* †*laurae*, see Glaessner 1933).

Testudo †*stricklandi* Phillips 1871. (=*Protochelys* †*stricklandi*, see Lydekker 1889a).

Testudo †*calarea* Fritsch 1893. Upper part of the Lower Miocene of Eger, Bohemia, Germany. (=*Ptychogaster* †*calarea*, see Glaessner 1933).

Testudo †*leithii* Sukheswala 1947. Eocene of India. (=*Hydraspis leithii* [Carter] Mukerjee 1949; [=*Carteremys leithii* Williams 1953a]).

"*Testudo*" †*plana* Koenig 1825. (=*Puppigerus*? *crassicostatus* Owen 1841).

Testudo †*anyangensis* Ping 1930. Archeologically associated in South China. (=*Pseudocadia* †*anyangensis*, see Lindholm 1931 and Auffenberg 1962a).

Testudo †*minuta* Fraas 1870 (part). Miocene of Steinheim, Germany. (=*Clemmys* †*steinheimensis* Staesche 1931).

Cinixys †*couzieri* Bergounioux 1935. Oligocene of France. (=*Ptychogaster* †*couzieri*).

Emys †*gaudini* Pictet and Humbert 1856. (=*Kinixys* [*Ptychogaster*] †*gaudini* Portis 1882 [=*Ptychogaster* †*gaudini*]).

"*Testudo*" †*elaverensis* Bravard 1858. (=*Clemmys* †*bravardi*).

Testudo †*lamoni* (part) Gervais 1859. (=*Clemmys* †*vidali*).

Hadrianus †*allabiatus* Cope 1872c. (=*Achilemys* †*allabiata* Hay 1908 =?Emydidae).

Although Kuhn (1964) lists *Testudo pseudovindobonensis* as appearing on p. 126 of Szalai (1934), he is actually referring to *Trionyx pseudovindobonensis* Szalai (p. 134). Kuhn also lists *Testudo dumeriliana* Lartet (1851), which should read *Emys dumeriliana* Lartet. His listing of *Testudo pliopedemontana* probably falls in the same category. However I have not seen the paper in which this reference was supposedly made (Sacco 1889).

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[1]Wermuth (1956) discusses the very broad 18th Century use of the generic term "Testudo" for nontestudinid turtles. Names involved are *Testudo boddaerta* (=*Trionyx cartilaginosis*), *Testudo brevi-caudata* (=*Terrapene c. carolina*), *Testudo caouana* (=*Caretta caretta*), *Testudo caroliniana* (=*Terrapene carolina*), *Testudo dorsata* (=*Geoemyda punctularia*), *Testudo fimbria* (=*Chelus fimbriatus*), *Testudo flava* (=*Emys blandingi*), *Testudo granulosa* (=*Trionyx punctatus*), *Testudo marina vulgaris* (=*Chelonia mydas*), *Testudo meteagris* (=*Emys blandingi*), *Testudo membranacea* (=?*Trionyx cartilaginosus*), *Testudo mydas minor* (=*Lepidochelys o. kempi*), *Testudo nasicornis* (=*Caretta caretta*), *Testudo planitia* (=*Macroclemys temminki*), *Testudo punctata* (=*Emys orbicularis*), *Testudo rubicunda* (=*Pelomedusa subrufa*), *Testudo rugosa* (=*Chelonia m. japonica*), *Testudo semimembranacea* (=*Trionyx sinensis*), *Testudo serpentina* (=*Chelydra serpentina*), *Testudo striata* (=*Trionyx cartilaginosus* and *T. triunguis* part), *Testudo verrucosa* (=*Geoemyda punctularia*), *Testudo viridi-squamosa* (=*Lepidochelys o. kempi*).

NOMINA NUDA AND UNIDENTIFIABLE MATERIAL

The following list includes those names I consider lacking a proper diagnosis. Names in parentheses indicate authors who have previously taken the same position.

Testudo †*minuta* Bravard 1844. (Szalai 1934).
Testudo †*media* Bravard 1844. (Staesche 1931).
Testudo †*aralensis* Khozatsky 1945.
(*Testudo*) †*houzei* Dollo 1912. Only the species name was used originally and later assumed to be *Testudo* by Bergounioux (1933b).
Testudo †*nurpurensis* Meyer 1865. (Kuhn 1964).
Testudo †*australis* Moreno 1889. (Williams 1950a).
Testudo †*risgoviensis* Fraas 1870. (provisional name).
Testudo †*formosa* Moreno 1889. (Williams 1950a).
Testudo †*paranensis* Scalabrini 1884.

Names based on material here considered unidentifiable at the species level include the following forms. Authors who have previously suggested such actions are in parentheses.

?*Testudo* †*nerandi* Gray 1831a.
Testudo †*cuvieri* Fitzinger 1835, (= *Testudo radiata fossilis* Meyer 1832; = *Testudo radiata* Pictet 1845).
Machrochelys †*mira* Meyer 1858, (= *Testudo* [*Macrochelys*] *mira* Zittel 1889).
Stylemys †*oregonensis* Leidy 1871c. (= *Testudo* †*oregonensis* Leidy 1873; = ?*Stylemys* †*nebrascensis* Cope 1885).
Testudo †*frizaciana* Lartet 1851 (= *Stylemys* †*frizaciana* Auffenberg 1964d) (Pictet 1853).
Testudo †*despotti* Szalai 1934. (Kuhn 1964).
Testudo †*hungarica* Szalai 1934.
Testudo †*lambrechti* Szalai 1934.
Testudo †*strandi* Szalai 1936. (Mlynarski 1966a).
Testudo †*gigas* Bravard 1844.
Testudo †*lemanensis* Bravard 1844. (Riabinin 1926).
Testudo †*racmecskeensis* Szalai 1932 (Ms. name), 1934. (Glaessner 1935).
Testudo †*pygmaea* Lartet 1851, (= *Stylemys* †*pygmaea* Auffenberg 1964d) (Maack 1869).

SYSTEMATICS

Class REPTILIA Laurent 1768, p. 23.
Order TESTUDINATA Shaw 1802, p. 5.
Suborder CRYPTODIRA Cope (part) 1870, p. 123.
Family TESTUDINIDAE Gray 1825, p. 210.

DEFINITION.—Cryptodiran turtles with no more than two phalanges in the digits of either front or hind feet; carapace usually high-arched; stapes always enclosed by quadrate; surangular developed on outer surface of jaw; splenial absent; dorsal rib heads tending to be vestigial; pubis joins ischium on same side below fenestra.

Genus *Acinixys* Siebenrock

Testudo Grandidier 1867, p. 233 (part).
Pyxis Boulenger 1889, p. 145 (part).
Acinixys Siebenrock 1903b, p. 244-6, pl. 33-34.

GENOTYPE.—*Acinixys planicauda* (Grandidier).

DEFINITION.—A monotypic Ethiopian genus, restricted to the Malagasy Republic and characterized by contours of the rounded anal scales, which are not divided by a median notch.

GEOLOGIC RANGE.—No fossils known.

GEOGRAPHIC RANGE.—Malagasy Republic.

REMARKS.—Unfortunately a poorly known genus deserving considerable study and attention.

Genus *Chersina* Gray

Testudo Thunberg 1795, p. 3 (part).
Chersine Merrem 1820, p. 38 (not of Linnaeus).
Chersina Gray 1831a, p. 7, 14 (not of Humphreys).
Goniochersus Lindholm 1929, p. 285.
Neotestudo Hewitt 1931, p. 504.

GENOTYPE.—*Testudo angulata* Schweigger (=*Chersina angulata* [Schweigger]) by monotypy.

DEFINITION.—A monotypic endemic Ethiopian tortoise characterized by having no hinges on either the carapace or plastron and a single gular scute on a strongly-projecting and greatly thickened epiplastral projection.

GEOLOGIC RANGE.—No fossils known.

GEOGRAPHIC RANGE.—Cape of Good Hope Province, South Africa.

REMARKS.—Rarity of double gulars in this species (Cairncross 1958, Archer 1961) may be of importance in future finds of fossil relatives.

Genus *Geochelone* Fitzinger

Chersine Merrem 1820, p. 29 (part).
Testudinites Weiss 1830, p. 293.
Geochelone Fitzinger 1835, p. 111.
Megalochelys Falconer and Cautley 1837, p. 358 (part).
Colossochelys Falconer and Cautley 1844, p. 54.
Geoemyda Cantor 1847, p. 2 (part).
Teleopus Le Conte 1854, p. 187 (*T. luxatus*).
Manouria Gray 1854, p. 134.
Emys Milne-Edwards *In* Grandidier (part) 1868, p. 1167.
Scapia Gray 1869, p. 169 (*S. falconeri*).
Stylemys Cope 1870, p. 124 (part).
Peltastes Gray 1870b, p. 655 (part).
Gopher Gray 1870a, p. 190.
Testudo Leidy 1871a, p. 154 (part).
Centrochelys Gray 1872a, p. 5 (*T. sulcata* Miller, by monotypy).
Hadrianus Cope 1872a, p. 2 (part).
Stigmochelys Gray 1873a, p. 5 (*T. pardalis* Bell, by monotypy).
Elephantopus Gray 1873b, p. 724 (part).
Eupachemys Leidy 1877, p. 7 (nomen nudum).
Homopus Boettger 1893, p. 8 (part).

Pampatestudo Lindholm 1929, p. 285 (part).
Megachersine Hewitt 1931, p. 257 (*T. pardalis* Bell, by original designation).
Gopherus Williams 1950a, p. 30 (part).

GENOTYPE.—*Testudo stellata* Schweigger (=*T. elegans* Schoepff).

DEFINITION.—An almost cosmopolitan tortoise genus with triturating surface of maxilla strongly ridged; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina small, concealed in ventral view; prootic typically well exposed dorsally and anteriorly; quadrate usually enclosing stapes; subangular subequal in height to prearticular; neck with second, third or fourth centrum biconvex.

Carapace never hinged; typically the anterior neurals alternately octagonal and quadrilateral; outer side of third costal scute about as long as, or longer than that of the fourth; no submarginal scute; two suprapygals, the anterior larger, bifurcating posteriorly to embrace the smaller posterior elements, which (in post-Eocene forms) is crossed near its middle by the sulcus between the fifth vertebral and the supracaudal.

Plastron not hinged; gular region more or less thickened and produced; gulars single or paired, longer than broad.

GEOLOGIC RANGE.—Eocene to Pleistocene of North America, Eocene to Pliocene of Europe, Oligocene to Recent of Asia, Oligocene and Miocene of Africa, Miocene to Recent of South America, and Pleistocene to Recent of the West Indies and a number of islands in the Indian Ocean.

GEOGRAPHIC RANGE.—Galapagos Islands, South America, West Indies, Africa, Malagasy Republic, islands of the Indian Ocean, Southern Asia, East Indies, and Ceylon.

REMARKS.—A combination of primitive and advanced characters is common in species of this genus. This large tropical, nearly cosmopolitan genus contains the large extant mainland and insular tortoises as well as all the extinct giant tortoises. It is divided into the following 13 subgenera.

Subgenus *Aldabrachelys* Loveridge and Williams

Aldabrachelys Loveridge and Williams 1954, p. 225 (as subgenus).
Testudo Schweigger 1812, p. 327.
Emys Milne-Edwards *In* Grandidier 1868, p. 1167.

TYPE SPECIES.—*Testudo gigantea* Schweigger.

DEFINITION.— A subdivision of the genus *Geochelone* known only from the Aldabra Islands and the Malagasy Republic. The nuchal scute is present or absent; first dorsal vertebra short; gular scutes paired but not divergent; entoplastron not crossed by the humero-pectoral sulcus; external nares higher than wide; quadrate enclosing stapes or not.

GEOLOGIC RANGE.—Pleistocene (of Malagasy Republic) to Recent.

GEOGRAPHIC RANGE.—Aldabra Islands, Seychelles Archipelago, and Malagasy Republic, but probably more widely distributed in the past (Agalega, Assumption, Amirante, Astove, Alphonse, Africa, Providence, St. Pierre, Farquhar, Cosmoledo, Gloriosa, and possibly even Chagos Islands [Rothschild 1915, Fryer 1911]).

REMARKS.—For the best monographic treatment of the extant species (*G. elephantina*), see Rothschild (1915). The several fossil specimens from Europe referred to this group under *Testudo elephantina* of Dumeril and Bibron (Pictet 1845, Pomel 1846, Maack 1869, and Bergounioux 1938a) obviously belong to the subgenus *Geochelone*. *Testudo* †*gigantea* Bravard 1844 (not of Schweigger) is a nomen nudum. Only one species, *G. gigantea* Schweigger 1812, is extant. It is confined to the Aldabra Islands, Seychelles Archipelago, and in the Indian Ocean. For skeletal morphology see Günther (1877a, 1877b) and Loveridge and Williams (1957). At least three species and one subspecies are extinct.

Geochelone (?*Aldabrachelys*) †*abrupta* (Vaillant)

Testudo abrupta Milne-Edwards *In* Grandidier 1868, p. 1161 (nomen nudum).
Testudo abrupta Vaillant 1885b, p. 874.
Testudo grandidier Boulenger 1894, p. 305 (part).

TYPE.—Museum of Natural History (Paris); carapace and limb bones.

TYPE LOCALITY AND HORIZON.—Amboulitsate in central part of the Malagasy Republic; Late Pleistocene.

GEOLOGIC RANGE.—Pleistocene only (?).

GEOGRAPHIC RANGE.—Central Malagasy Republic.

REMARKS.—The subgeneric affinities of this species are not clear.

Geochelone (*Aldabrachelys*) *gigantea* †*gouffei* (Rothschild)

Testudo gouffei Rothschild 1906, p. 753 (?Farquhar Island).

TYPE.—Tring Museum; a mounted adult specimen.

TYPE LOCALITY.—?Farquhar Island, Seychelles Archipelago, Indian Ocean.

GEOLOGIC RANGE.—Recent, but now extinct.

GEOGRAPHIC RANGE.—Known from a single specimen of uncertain origin.

REMARKS.—The type appears to be a unique form. Skeletal morphology of the extant subspecies is discussed by Günther (1877a, 1877b).

Geochelone (*Aldabrachelys*) †*sumeirei* (Sauzier)

Testudo sumeirei Sauzier 1893, p. 7 (Mauritius?, in error).
Geochelone (*Aldabrachelys*) *sumeirei* Loveridge and Williams 1957, p. 225.

TYPE.—Tring Museum; a mounted adult.

TYPE LOCALITY.—Seychelles Islands?

GEOLOGIC RANGE.—Recent, but now extinct.

GEOGRAPHIC RANGE.—Seychelles Archipelago?, Indian Ocean.

REMARKS.—A note on the type states that it is one of five specimens taken from the Seychelles to Mauritius by Chevalier Marion de Fresne in 1766 as a gift for the Port Louis Garrison. This is the famous "Marion's" tortoise, which died accidentally after 152 years in captivity.

Geochelone (*Aldabrachelys*) †*grandidieri* (Vaillant)

Emys gigantea Milne-Edwards *In* Grandidier 1868, p. 1165 (not of Schweigger preoccupied).
Testudo grandidieri Vaillant 1885b, p. 874.
Testudo gigantea Boulenger 1892, p. 581 (part).

TYPE.—Museum of Natural History (Paris); parts of shell.

TYPE LOCALITY AND HORIZON.—Northern Malagasy Republic; late Pleistocene and/or Recent.

GEOLOGIC RANGE.—Late Pleistocene and ?Recent.

GEOGRAPHIC RANGE.—Northern Malagasy Republic.

REFERENCES.—Skeleton: Boulenger 1894, Auffenberg 1966b.

Subgenus *Asterochelys* Gray

Asterochelys Gray 1873a, p. 4.
Testudo Vaillant 1885a, p. 440.
Geochelone Loveridge and Williams 1957, p. 342.

TYPE SPECIES.—*Testudo yniphora* Vaillant (=*Geochelone* [*Asterochelys*] *yniphora* [Vaillant]).

DEFINITION.—A subgenus of the genus *Geochelone* known only by two living species from the Malagasy Republic. Characterized by presence of a nuchal scute, gulars single or double, and external nares not expanded vertically.

GEOLOGIC RANGE.—No fossils known.

GEOGRAPHIC RANGE.—Malagasy Republic.

REMARKS.—The two presently recognized extant populations (*G. radiata* and *G. yniphora*) are probably conspecific. For skeletal morphology see William 1950b, Vaillant 1905, Siebenrock 1897.

Subgenus †*Caudochelys* Auffenberg

Caudochelys Auffenberg 1963, p. 69 (as subgenus).

TYPE SPECIES.—*Testudo crassiscutata* Leidy (=*Geochelone* [*Caudochelys*] *crassiscutata* [Leidy]).

DEFINITION.—Extinct Nearctic subdivision of genus *Geochelone* with

narrow nuchal scute; entoplastron about as wide as long; pectoral scutes reduced along midline; limbs and tail heavily armored with dermal ossicles; above tail, ossicles never fuse to form supracaudal buckler; caudal vertebrae normal, not compressed or fused, without greatly elongated transverse processes.

GEOLOGIC RANGE.—Miocene to end of Pleistocene.

GEOGRAPHIC RANGE.—Central and eastern North America.

REMARKS.—Mlynarski (1969a, p. 87) mistakenly confuses this subgenus with the subgenus *Hesperotestudo*. *Caudochelys* is presently considered as being comprised of at least nine extinct species.

Geochelone (*Caudochelys*) †*annae* (Hay)

Testudo crassiscutata ? Hay 1916b, p. 11, pls. 1-3 (part).
Testudo annae Hay 1923, p. 114.
Geochelone annae Auffenberg 1963, p. 94.

TYPE.—Dr. Mark Francis collection, Texas A & M Univ.; right epiplastron, anterior part of carapace.

TYPE LOCALITY AND HORIZON.—Brazos River at Pittbridge, Burleson County, Texas, U.S.A.; Aftonian faunal age; Early Pleistocene.

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Texas, U.S.A.

REMARKS.—This probably is a synonym of *G. crassiscutata*.

Geochelone (?*Caudochelys*) †*brontops* (Marsh)

Testudo brontops Marsh 1890, p. 179, pl. 8.
Geochelone brontops Auffenberg 1963, p. 87.

TYPE.—Yale Peabody Museum; a shell.

TYPE LOCALITY AND HORIZON.—S. E. corner of Pennington County, South Dakota, U.S.A.; "Titanother beds" of Indian Creek, Chadronian faunal age, Early Oligocene.

GEOLOGIC RANGE.—Early Oligocene.

GEOGRAPHIC RANGE.—South Dakota, U.S.A.

Geochelone (*Caudochelys*) †*crassiscutata* (Leidy)

Eupachemys obtusa Leidy 1877, p. 232.
Eupachemys rugosus Leidy 1889, p. 29 (error).
Testudo crassiscutata Leidy 1889, p. 31.
Testudo obtusa Hay 1908, p. 458.
Testudo ocalana Hay 1916a, p. 45.
Testudo distans Hay, 1916a, p. 48.
Testudo sellardsi Hay 1916a, p. 49.
Testudo luciae Hay 1916a, p. 52.
Gopherus ocalana Williams 1950a, p. 30.
Geochelone distans Ray 1957, p. 126.

Geochelone luciae Ray 1957, p. 126.
Geochelone sellardsi Ray 1957, p. 126.
Geochelone (*Caudochelys*) *crassiscutata* Auffenberg 1963, p. 70.

TYPE.—U.S. National Museum; parts of plastron, femur and tibia.

TYPE LOCALITY AND HORIZON.—Shoals of Peach Creek, near Arcadia, DeSoto County, Florida, U.S.A.; Rancholabrean mammalian faunal age, Late Pleistocene.

GEOLOGIC RANGE.—Middle to Late Pleistocene.

GEOGRAPHIC RANGE.—Florida, north to South Carolina (Auffenberg 1963), west to at least eastern Texas, U.S.A. (Holman 1969).

REMARKS.—For best description see Loomis (1927) and Auffenberg (1963). Probably much more widely distributed than present records indicate.

Geochelone (*Caudochelys*) †*ducatelli* (Collins and Lynn)

Testudo ducatelli Collins and Lynn 1936, p. 166, pls. 3-4.
Testudo ducateli Kuhn 1964, p. 116 (typographical error).
Geochelone ducatelli Auffenberg 1964a, p. 3.

TYPE.—U.S. National Museum; plastron and parts of a carapace.

TYPE LOCALITY AND HORIZON.—3.4 miles south old Chesapeake Beach RR Station, Maryland, U.S.A.; Zone 10, Calvert Formation, Barstovian faunal age, late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Closely related to the Texas Miocene *Geochelone williamsi* (Auffenberg 1964a).

Geochelone (?*Caudochelys*) †*francisi* (Hay)

Testudo francisi Hay 1923, p. 116, pl. 8.

TYPE.—Dr. Mark Francis collection, Texas A & M Univ.; an epiplastron.

TYPE LOCALITY AND HORIZON.—Temple, Bell County, Texas, U.S.A.; referred to Aftonian faunal age, Early Pleistocene by Hay (1923).

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—This species is probably close to *G. crassiscutata.*

Geochelone (*Caudochelys*) †*hayi* (Sellards)

Testudo hayi Sellards 1916, p. 235, fig. 7, 9.
Testudo louisekressmani Wark 1929, p. 401.
Gopherus hayi Williams 1950a, p. 30.
Geochelone (*Caudochelys*) *hayi* Auffenberg 1963, p. 78.
Geochelone louisekressmani Auffenberg 1963, p. 79.

TYPE.—U.S. National Museum; a partial shell.

TYPE LOCALITY AND HORIZON.—Near Nichols, Polk County, Florida, U.S.A.; Bone Valley Gravel Formation, Hemphillian faunal age, Middle Pliocene.

GEOLOGIC RANGE.—Middle Pliocene.

GEOGRAPHIC RANGE.—Central to northern Florida.

REMARKS.—Close and perhaps ancestral to the Blancan *G. campester.*

Geochelone (?*Caudochelys*) †*milleri* (Brattstrom)

Testudo milleri Brattstrom 1961, p. 546, figs. 5-6.

TYPE.—Univ. of California Museum of Paleontology; a partial shell.

TYPE LOCALITY AND HORIZON.—Barstow syncline, Mojave Desert, San Bernardino County, California, U.S.A.; Barstow beds, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Southern California, U.S.A.

REMARKS.—According to Brattstrom (1961) it is close to *Geochelone tedwhitei,* but this is not certain.

Geochelone (*Caudochelys*) †*tedwhitei* (Williams)

Testudo tedwhitei Williams 1953b, p. 537, figs. 1-3.
Geochelone (*Caudochelys*) *tedwhitei* Auffenberg 1963, p. 80.

TYPE.—Museum of Comparative Zoology; a complete plastron.

TYPE LOCALITY AND HORIZON.—Thomas Farm, Gilchrist County, Florida, U.S.A.; Hawthorne Formation, Hemingfordian faunal age, Middle Miocene.

GEOLOGIC RANGE.—Middle Miocene.

GEOGRAPHIC RANGE.—Now known from several localities in northern Florida, U.S.A.

Geochelone (*Caudochelys*) †*williamsi* Auffenberg

Geochelone williamsi Auffenberg 1964a, p. 3, figs. 1-2.

TYPE.—Holotype, Univ. of Texas—Bureau of Economic Geology; a complete shell.

TYPE LOCALITY AND HORIZON.—Garvin Gully, 2 mi. north of Navasota, Grimes County, Texas, U.S.A.; Garvin Gully local fauna, lower Oakville Member, Oakville Formation, Arikareean faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Presumably close to *G. ducatelli* (Auffenberg 1964a).

Subgenus *Chelonoidis* Fitzinger

Testudinites Weiss 1830, p. 293.
Chelonoidis Fitzinger 1856, p. 112.
Gopher Gray 1870a, p. 190.
Elephantopus Gray 1873b, p. 724 (part).
Pampatestudo Lindholm 1929, p. 285 (part).

TYPE SPECIES.—*Testudo denticulata* Linnaeus (=*Geochelone* [*Chelonoidis*] *denticulata* [Linnaeus]).

DEFINITION.—A Neotropical division of the genus *Geochelone* without a nuchal scute, entoplastron large, and horny shields with little or no trace of radiating pattern.

GEOLOGIC RANGE.—Miocene to Recent.

GEOGRAPHIC RANGE.—Recent of southeastern Panama, south over most of South America east of the Andes to south central Argentina, the Galapagos Islands, and a number of islands in the Caribbean Sea.

REMARKS.—For best description see Williams (1950a). The subgenus is comprised of four extant and six extinct species. The extant species are *Geochelone denticulata, G. carbonaria, G. elephantopus*, and *G. chilensis*, of which only *G. chilensis* is known as a fossil.

REFERENCES.—Skeleton: Gray 1855, Fritsch 1871, Günther 1875, 1877a, 1896, Jeude 1896, Siebenrock 1897, Heller 1903, Ruckes 1937, Williams 1950a, Zangerl 1957, Auffenberg 1966b, 1971. Zoogeography: Bauer 1889, Simpson 1943, Auffenberg 1971.

Geochelone (*Chelonoidis*) *chilensis* (Gray)

Testudo sulcata Dumeril and Bibron 1835, p. 74 (part).
Testudo sulcata d'Orbigny 1847, p. 6 (not of Gmelin).
Testudo (*Gopher*) *chilensis* Gray 1870a, p. 190 (Chile, in error).
Testudo argentina Sclater 1870, p. 471 (substitute name for *T. chilensis* Gray 1870a).
Geochelone chilensis Williams 1960, p. 10.

TYPE.—British Museum (Natural History); two mounted specimens.

TYPE LOCALITY.—Near Mendoza, Argentina.

GEOLOGIC RANGE.—Certain fossils from Pleistocene deposits in Argentina are assignable to this species (Auffenberg 1971).

GEOGRAPHIC RANGE.—Southwestern Bolivia, Western Paraguay, and Western Argentina south to near 40° latitude.

REFERENCES.—Skeleton: Auffenberg 1966b, 1971.

Geochelone (*Chelonoidis*) †*cubensis* (Leidy)

Testudo cubensis Leidy 1868, p. 179.
Geochelone cubensis Auffenberg 1967, p. 37.

TYPE.—Philadelphia Academy of Natural Sciences; part of a first right pleural.

TYPE LOCALITY AND HORIZON.—Chapepote Springs, Banas de Ciego Montero, Las Villas Province (=Santa Clara Province), Cuba; Late (?) Pleistocene.

GEOLOGIC RANGE.—Late Pleistocene.

GEOGRAPHIC RANGE.—Brazil.

REMARKS.—Incorrectly stated as Pliocene by a few earlier workers.

Geochelone (*Chelonoidis*) †*elata* (Gervais)

Testudo elata Gervais 1877, p. 283, pl. 7.

TYPE.—Museum of Natural History (Paris); fragments of dentary, limbs, and plastron.

TYPE LOCALITY AND HORIZON.—"Lower region, Amazonian basin," Brazil; Pampean faunal age, Late Pleistocene.

GEOLOGIC RANGE.—Known only from Late (?) Pleistocene deposits.

GEOGRAPHIC RANGE.—Central to eastern Cuba.

REMARKS.—See Williams (1952) for best description.
A giant species, probably a synonym of *G. sellowi.*

Geochelone (?*Chelonoidis*) †*gallardoi* (Roverto)

Testudo gallardoi Roverto 1914, p. 115.
Testudo praestans Roverto 1914, p. 176.

TYPE.—Museo Nacional Historie Naturele (Buenos Aires); a fairly complete shell.

TYPE LOCALITY AND HORIZON.—Catamarca, Argentina; Araucanian faunal age.

GEOLOGIC RANGE.—Late Pliocene.

GEOGRAPHIC RANGE.—Argentina.

REMARKS.—Study of the type specimens of both *gallardoi* and *praestans* has convinced me they are conspecific.

Geochelone (*Chelonoidis*) †*gringorum* (Simpson)

Testudo gringorum Simpson 1942, p. 1, figs. 1-2.

TYPE.—American Museum of Natural History; a plastron and most of a carapace.

TYPE LOCALITY AND HORIZON.—South side of Chubut Valley, between Gaiman and Dolavon, Chubut Territory, Argentina; High in Patagonian section overlying the Angosturas laminated beds, Miocene (probably Early Miocene, according to Simpson 1942).

GEOLOGIC RANGE.—Miocene (Early?).

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Ancestral to *Geochelone chilensis* (Auffenberg 1971).

Geochelone (*Chelonoidis*) *hesterna* Auffenberg

Geochelone hesterna Auffenberg 1971, p. 106.

TYPE.—Univ. of California Museum of Paleontology; a complete shell and partial skeleton.

TYPE LOCALITY AND HORIZON.—3 km northeast of Villavieja, Huila, Colombia, South America; Hondo group, Cerbatana gravels and clays, La Venta fauna, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Intermediate between *G. carbonaria* and *G. denticulata*, though closer to the latter (Auffenberg 1971).

Geochelone (*Chelonoidis*) †*sellowi* (Weiss)

Testudinites sellovii Weiss 1830, p. 293.
Testudo sellovii Giebel 1847, p. 53.
Testudo sellowi Couto 1948, p. 1, pl. 1.

TYPE.—Museum of Humbolt Univ. (Berlin); 8 pieces of carapace and plastron.

TYPE LOCALITY AND HORIZON.—Rio Quequay, Paysandu, Uruguay; Pleistocene.

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Briefly redescribed by Couto (1948), who also republished some of Weiss' original plates.

Geochelone (*Chelonoidis*) †*sombrerensis* (Leidy)

Emys sombrerensis Leidy 1868, p. 180.
Testudo sombrerensis Williams 1952, p. 552.
Geochelone sombrerensis Auffenberg 1967, p. 35.

TYPE.—Academy of Natural Sciences (Philadelphia) (Lost ?).

TYPE LOCALITY AND HORIZON.—Sombrero Guano, Sombrero Island, West Indies; ? Late Pleistocene.

GEOLOGIC RANGE.—Late Pleistocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—For the most recent description and comparisons see Auffenberg (1967).

Subgenus †*Cylindraspis* Fitzinger

Cylindraspis Fitzinger 1835, p. 112.

TYPE SPECIES.—*Testudo indica vosmaeri* Shaw (=*Geochelone* [*Cylindraspis*] *vosmaeri* [Shaw]).

DEFINITION.—An extinct subgenus of the genus *Geochelone* represented by four species restricted to the islands of the Mascarene group in the Indian Ocean. They are characterized by the absence of a nuchal scute, undivided supracaudal, and single gular.

GEOLOGIC RANGE.—Late Pleistocene to Recent, now extinct.

GEOGRAPHIC RANGE.—Rodriguez, Reunion, and Mauritius Islands, Indian Ocean.

REMARKS.—A very poorly known group deserving study with a modern systematic approach. Günther (1877a) gives a very good resume of the skeletal characters of many of the named forms.

Geochelone (*Cylindraspis*) †*indica* (Schneider)

Testudo indica Schneider 1784, p. 355.
Testudo indica perraultii Shaw 1802, p. 25.
Chersine retusa Merrem 1820, p. 29.
Testudo perraultii Dumeril and Bibron 1835, p. 126.

TYPE.—Location unknown to author; shell.

TYPE LOCALITY.—Reunion Islands, Mascarene Group, Indian Ocean.

GEOLOGIC RANGE.—Recent, now extinct.

GEOGRAPHIC RANGE.—Reunion Islands, Indian Ocean.

Geochelone (*Cylindraspis*) †*grayi* (Dumeril and Bibron)

Testudo graii Dumeril and Bibron 1835, p. 155.
Testudo inepta Günther 1873, p. 397 (Mauritius).
Testudo triserrata Günther 1873, p. 397 (Mauritius).
Testudo grayi Günther 1877a, p. 43.
Testudo leptocnemis Günther 1877a, p. 47 (Mauritius).
Testudo microtympanum Boulenger 1890c, p. 4 (Mauritius?).
Testudo sauzieri Gadow 1894, p. 315 (Mauritius).

TYPE.—Museum of Natural History (Paris); a shell.

TYPE LOCALITY.—Unknown, presumably Mauritius Island, Indian Ocean (Günther 1877a).

GEOLOGIC RANGE.—Late Pleistocene to early 19th Century.

GEOGRAPHIC RANGE.—Mauritius Island.

REMARKS.—All the named Mauritius forms are here placed in the same species. Günther (1877a) provides an excellent resume of the skeleton. The data available show that all insular tortoise populations are more variable than those of the mainland. This greater variation has led to considerable taxonomic confusion regarding tortoise populations in the Mascarene, Aldabra, and Galapagos Islands.

Geochelone (*Cylindraspis*) †*peltastes* (Dumeril and Bibron)

Testudo peltastes Dumeril and Bibron 1835, p. 138.
Testudo vosmaeri Fitzinger 1826, p. 1 (part).

TYPE.—Museum of Natural History (Paris); dried specimen, less head and tail.

TYPE LOCALITY.—Rodriguez Island, Mascarene Group, Indian Ocean.

GEOLOGIC RANGE.—Recent, now extinct.

GEOGRAPHIC RANGE.—Rodriguez Island, Indian Ocean.

REMARKS.—Günther (1877a) and Boulenger (1890c) considered the specimens of *peltastes* to be the young of *vosmaeri*. The presence of an adult female *peltastes* and Rothschild's (1915, p. 441) insistence on the ankylosis of the small shells in the British Museum leads me to recognize *G. peltastes* as a distinct species for the present.

Geochelone (*Cylindraspis*) †*vosmaeri* (Shaw)

Testudo indica Schoepff 1792, p. 103. (part).
Testudo indica vosmaeri Shaw 1802, p. 27.
Testudo vosmaeri Fitzinger 1826, p. 44.
Testudo rodericensis Günther 1873, p. 397 (preliminary note).
Testudo boutonii Günther 1875, p. 43.
Testudo commersoni Vaillant 1889, p. 134.

TYPE.—British Museum (Natural History); shells, skull, and bones.

TYPE LOCALITY.—Rodriguez Island, Mascarene Group, Indian Ocean.

GEOLOGIC RANGE.—Recent, now extinct.

GEOGRAPHIC RANGE.—Rodriguez Island, Indian Ocean.

REFERENCES.—Skeleton: Haddon 1879.

Subgenus †*Cymatholcus* Clark

Cymatholcus Clark 1932, p. 132.

GENOTYPE.—*Cymatholcus longus* Clark 1932.

TYPE LOCALITY AND HORIZON.—Hoot Owl Canyon, 15 mi. southwest Vernal, Uinta County, Utah, U.S.A.; Duchesnean faunal age, Late Eocene.

DEFINITION.—An extinct North American subgenus of *Geochelone* that derives its name from its characteristically strong looped sulcus between the marginal and plastral scutes; shell longer and higher in proportion to width than other tortoises; lip conforming to contours of anterior lobe of plastron, bridge short, posterior lobe long.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Utah and Alabama, U.S.A.

REMARKS.—Certainly close to the subgenus *Hadrianus* of *Geochelone*, but considerably more specialized. Placed as subgenus of *Geochelone* by Auffenberg (1971).

Geochelone (*Cymatholcus*) †*longus* Clark

Cymatholcus longus Clark 1932, p. 132.

TYPE.—Carnegie Museum; a complete shell and parts of the skeleton.

TYPE LOCALITY AND HORIZON.—Hoot Owl Canyon, 15 mi. southwest Vernal, Uinta County, Utah, U.S.A.; Duchesnean faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Eastern Utah.

Geochelone (*Cymatholcus*) †*schucherti* (Hay)

Hadrianus schucherti Hay 1902b, p. 22, pls. 4-5.
?*Hadrianus schucherti* Hay 1908, p. 382.
Cymatholcus schucherti Williams 1950a, p. 30.

TYPE.—U. S. National Museum; a shell.

TYPE LOCALITY AND HORIZON.—Near the Cocoa Post Office, Choctaw County, Alabama, U.S.A.; Duchesnean faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Western Alabama, U.S.A.

REMARKS.—Williams (1950a) placed *schucherti* in the genus *Cymatholcus* on the basis of similarities in the details of form and the sulcal relationships of the plastral elements. He suggested *schucherti* may even be conspecific with *longus*.

Subgenus *Geochelone* Fitzinger

Geochelone Fitzinger 1835, p. 108, 112, 122, (as a subgenus) (*T. stellata* Schweigger [=*T. elegans* Schoepff]).
Centrochelys Gray 1872a, p. 5 (*T. sulcata* Miller).
Stigmochelys Gray 1873a, p. 5 (*T. pardalis* Bell).
Megachersine Hewitt 1931, p. 257 (*T. pardalis* Bell).

TYPE SPECIES.—*Testudo elegans* Schoepff (=*Geochelone* [*Geochelone*] *elegans* [Schoepff]).

DEFINITION.—An Old World subdivision of the genus *Geochelone* in which the external nares are not higher than wide; nuchal scute absent (except in *platynota*); first dorsal vertebra short; supracaudal scute undivided; gulars paired but not divergent; entoplastron not crossed by humeropectoral sulcus.

GEOLOGIC RANGE.—Tertiary of Europe.

GEOGRAPHIC RANGE.—Africa, Ceylon, India, and Burma.

REMARKS.—The giant fossil tortoises of Malta, Menorca, and Tenerife probably belong to this subgenus. Though it is widely distributed at present, it had an even greater range in the past. It contains four living species, *G. pardalis, G. sulcata, G. elegans,* and *G. platynota.* Skeletal references to these forms are Siebenrock 1900, Deraniyagala 1930, 1939, Williams 1950b, Auffenberg 1966b. Fifteen extinct species are known.

Geochelone (*Geochelone*) †*amberiacensis* (Deperet)

Testudo amberiacensis Deperet 1894, p. 717, pl. 24.

TYPE.—The Faculty of Science (Lyons); an entoplastron and nuchal bone.

TYPE LOCALITY AND HORIZON.—Ambérieu, Bresse, Ain Department, France; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—A poorly defined species without a nuchal scute. According to Szalai (1934) it is similar to *Testudo kalksburgensis*, but this is probably in error as it seems to be a member of the genus *Geochelone*.

Geochelone (*Geochelone*) †*ammon* (Andrews)

Testudo ammon Andrews and Beadnell 1903, p. 5 (nomen nudum).
Testudo ammon Andrews 1904, p. 529.

TYPE.—Geological Museum (Cairo); a complete shell.

TYPE LOCALITY AND HORIZON.—North of Birket-el-Qurun, Fayum, United Arab Republic; Bartonian faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—For best description, see Andrews (1906).

Geochelone (*Geochelone*) †*beadnelli* (Andrews)

Testudo beadnelli Andrews 1906, p. 285, fig. 91.

TYPE.—Geological Museum (Cairo); a complete shell.

TYPE LOCALITY AND HORIZON.—North of Birket-el-Qurun, Fayum, United Arab Republic; Bartonian faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Probably conspecific with *G. ammon*.

Geochelone (*Geochelone*) †*bolivari* (Hernandez-Pacheco)

Testudo sp. Hernandez-Pacheco 1917, p. 197.
Testudo bolivari Hernandez-Pacheco 1921, p. 329, 2 figs.
Testudo richardi Bergounioux 1938a, p. 62 (part).

TYPE.—Museo Nacional de Ciencias Naturales (Madrid); an incomplete shell.

TYPE LOCALITY AND HORIZON.—Alcala de Henares, Palencia, Spain; Miocene.

GEOLOGIC RANGE.—Miocene to ?Pliocene.

GEOGRAPHIC RANGE.—Spain.

REMARKS.—It seems doubtful that all the specimens figured by Royo y Gomez (1935, fig. 5) as *bolivari* are the same species. Bergounioux (1938a) refers some to *Testudo richardi*. Peyer (1942) suggests that *G. bolivari* may be subspecifically related to *G. vitodurana* Biedermann. The best description is by Royo y Gomez (1935).

Geochelone (*Geochelone*) †*burchardi* (Ahl)

Testudo burchardi Ahl 1926, p. 575, fig. 1.
Testudo buchardi Szalai 1933, p. 156 (typographical error).

TYPE.—Zoological Museum, Univ. of Berlin; a femur and humerus.

TYPE LOCALITY AND HORIZON.—South part of Tenerife, Canary Islands, Atlantic Ocean; Pleistocene volcanic tuff.

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Type locality.

Geochelone (*Geochelone*) †*crassa* (Andrews)

Testudo crassa Andrews 1914, p. 181.
Testudo crassa Szalai 1938, p. 162.

TYPE.—British Museum (Natural History); pieces of the shell.

TYPE LOCALITY AND HORIZON.—Bed 31, Kachuku near Karungu, Kenya, Africa; Burdigalian faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—A very large tortoise unquestionably belonging in the genus *Geochelone*.

Geochelone (*Geochelone*) †*grandis* (Macarovici and Vancea)

Testudo grandis Macarovici and Vancea 1960, p. 381.

TYPE.—Private collection of N. Macarovici, Malusteni, Romania; fragments of the carapace and plastron.

TYPE LOCALITY AND HORIZON.—Malusteni, Moldavia, Romania; Astian faunal zone, Late Pliocene.

GEOLOGIC RANGE.—Late Pliocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Believed closely related to *Testudo syrmiensis* by Simionesco (1930), but this is certainly incorrect.

Geochelone (?*Geochelone*) †*gymnesica* (Bate)

Testudo gymnesicus Bate 1914, p. 102, figs. 1-2.

TYPE.—British Museum (Natural History); portions of limbs.

TYPE LOCALITY AND HORIZON.—Minorca Island; Late (?) Pleistocene.

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Probably related to the Pleistocene forms of Malta and Africa, and here included within the subgenus *Geochelone* on the basis of that supposition.

Geochelone (*Geochelone*) †*isis* (Andrews)

Testudo isis Andrews 1906, p. 286, fig. 72.

TYPE.—Geological Museum (Cairo); an imperfect shell.

TYPE LOCALITY AND HORIZON.—North of Birket-el-Qurun, Fayum, United Arab Republic; Bartonian faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Relationships not clear.

Geochelone (*Geochelone*) †*meshetica* (Gabunya and Chkikvadze)

Testudo meschetica Gabunya and Chkikvadze 1960, p. 189, figs. 1-4.
Geochelone meschetica Chkikvadze 1970a, p. 59.

TYPE.—Geological collections, Academy of Sciences (Georgia SSR); partial shell.

TYPE LOCALITY AND HORIZON.—Near Benar, Adigenski District, Georgia, SSR; Middle or Late Oligocene.

GEOLOGIC RANGE.—Middle or Late Oligocene.

GEOGRAPHIC RANGE.—Georgia SSR.

REMARKS.—Close to *G. ammon*, according to Gabunya and Chkikvadze (1960).

Geochelone (?*Geochelone*) †*namaquensis* (Stromer)

Testudo namaquensis Stromer *in* Kaiser 1926, p. 139.

TYPE.—Berlin Museum of Zoology; a complete plastron.

TYPE LOCALITY AND HORIZON.—Namib, Namaqualand, South-west Africa; Burdigalian faunal age, Middle Miocene.

GEOLOGIC RANGE.—Middle Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Probably close to the extant *Geochelone pardalis*.

Geochelone (*Geochelone*) *pardalis* (Bell)

Testudo pardalis Bell 1828, p. 420.
Testudo biguttata Cuvier 1836, p. 10 (nomen nudum).

Testudo bipunctata Gray 1831a, p. 12 (erroneously attributed to Cuvier MS).
Testudo armata Boil (MS) (listed as synonym by Gray 1931a, p. 4 (nomen nudum).
Testudo pardalis Gray 1831a, p. 12.
Geochelone pardalis Fitzinger 1835, p. 211.
Testudo sulcata Smets 1885, p. 8.
Homopus signatus Boettger 1893, p. 8 (part).
Testudo calcarata Vaillant 1904, p. 186 (part).
Megachersine pardalis Hewitt 1933, p. 257.
Testudo pardalis babcocki Loveridge 1935, p. 4.
Testudo pardalis pardalis Loveridge 1935, p. 4.
Geochelone pardalis Hewitt 1937, p. 789.
Testudo pardalis pardalis Mertens 1937, p. 5.
Geochelone pardalis babcocki Loveridge and Williams 1957, p. 235.
Geochelone pardalis pardalis Loveridge and Williams 1957, p. 251.

TYPE.—British Museum (Natural History)?; a preserved adult.

TYPE LOCALITY.—Mt. Debasien, Karamojo, Uganda, Africa.

GEOLOGIC RANGE.—The species is reported from Early Pleistocene (Lehmann 1957) and Middle Pleistocene (Broadley 1962) to Recent of Africa.

GEOGRAPHIC RANGE.—*G. p. babcocki* ranges from Sudan and Ethopia south to Natal, west through Cape of Good Hope Province to South-west Africa, where it meets the typical form, *Geochelone pardalis pardalis.*

REMARKS.—For the most recent monographic treatment see Loveridge and Williams (1957). Two extant subspecies are recognized.

Geochelone (*Geochelone*) *perpiniana* †*leberonensis* (Deperet)

Testudo leberonensis Deperet 1890, p. 915.
Testudo luberonensis Joleaud 1906, p. 360 (typographical error).
Testudo perpiniana var. *leberonensis* Bergounioux 1936a, p. 28.

TYPE.—Museum of Natural History (Paris); part of carapace.

TYPE LOCALITY AND HORIZON.—Mount Leberon, west of Cucuron, France; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene only? (see remarks below).

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Peyer (1942) considered *leberonensis* very close to, and perhaps a synonym of *Geochelone perpiniana,* here treated as a separate subspecies.

Geochelone (*Geochelone*) *perpiniana* †*perpiniana* (Deperet)

Testudo perpiniana Deperet 1885, p. 214, pl. 4.

TYPE.—Museum of Perpignon (Southern France); slightly damaged specimen.

TYPE LOCALITY AND HORIZON.—Near Perpignon, France; Plaisancian faunal age, Late Pliocene.

GEOLOGIC RANGE.—Late Pliocene only? (see remarks below).

GEOGRAPHIC RANGE.—France only? (see remarks below).

REMARKS.—*G. perpiniana, G. picteti, G. bolivari,* and *G. vitodurana* all seem very close to the *pardalis-sulcata* group, and for this reason they are all placed in the same subgenus. For the best description of *G. perpiniana* see Deperet and Donnezan (1887, 1893-5). Lydekker (1889b) placed *G. perpiniana* close to *Geochelone atlas.* Arambourg and Piveteau (1929) described a skull referred to this subspecies.

Geochelone (*Geochelone*) †*picteti* (Biedermann)

Testudo picteti Biedermann 1863, p. 18, pls. 2, 2a.

TYPE.—Winterthur Museum (Switzerland); an almost complete shell.

TYPE LOCALITY AND HORIZON.—Near Winterthur, Switzerland; Upper fresh water marls of Veltheim, Vindobonian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene only? (see remarks below).

GEOGRAPHIC RANGE.—Switzerland only?

REMARKS.—Roger (1902) suggested this species may be a synonym of *G. vitodurana.*

Geochelone (?*Geochelone*) †*pyrenaica* (Deperet and Donnezan)

Testudo pyrenaica Deperet 1885, p. 216 (preliminary notice).
Testudo pyrenaica Deperet and Donnezan 1893-5, p. 155, pl. 16.

TYPE.—Museum of Natural History (Paris); a shell.

TYPE LOCALITY AND HORIZON.—Serrat Vaquar, Roussillon, France; Astian Faunal age, Late Pliocene.

GEOLOGIC RANGE.—Pliocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Placed in the genus *Geochelone,* subgenus *Geochelone,* on the basis of the absence of a nuchal scute. Szalai (1934) considered it close to *Testudo amiatae* and *Testudo marmorum* (of Gaudry), but this is obviously incorrect.

Geochelone (?*Geochelone*) †*richardi* (Bergounioux)

Testudo richardi Bergounioux 1938a, p. 271.

TYPE.—Geologic Museum, Seminario Conciliar de Barcelone; a poorly preserved shell.

TYPE LOCALITY AND HORIZON.—Terrega, Lerida Province, Catalonia Region, Spain; Oligocene.

GEOLOGIC RANGE.—Oligocene.

GEOGRAPHIC RANGE.—Catalonia Region, Spain.

REMARKS.—Bergounioux (1938a) believed this species to be close to *Testudo castrensis.*

Geochelone (?*Geochelone*) †*robusta* (Leith-Adams)

Testudo robusta Leith-Adams 1877, p. 178, pls. 5-6 (not *robustus* of Gilmore).
Testudo spratti Leith-Adams 1877, p. 186 (Maghlak, Malta).
Testudo robustissima Tagliaferro 1914, p. 77 (Corradino, Malta).

TYPE.—British Museum (Natural History); two vertebrae and parts of the appendicular skeleton, including a tibia.

TYPE LOCALITY AND HORIZON.—Zebbug Cave, Malta; Middle Pleistocene.

GEOLOGIC RANGE.—Middle Pleistocene.

GEOGRAPHIC RANGE.—Ta Xolca, Corradino Hill, Maghlak, Ghar Dalam, and Zebbug Caves, Malta.

REMARKS.—A poorly defined species. *Geochelone robustissima* and *G. spratti* are placed here because they differ only in size. This action had apparently been suggested by C. Gatto during the discussion following the oral presentation by Tagliaferro (1914:79). Bones referrable to all three species are known to occur in the same caves and in the same deposits within them.

Geochelone (?*Geochelone*) †*turgae* (Kuznetzov)

Testudo turgae Kuznetzov 1958, p. 66, figs. 1-2.
Testudo turmae Kuhn 1964, p. 32 (typographical error).

TYPE.—Location unknown to author; plastral fragments.

TYPE LOCALITY AND HORIZON.—Turgai depression, Kazakhstan, USSR; Miocene.

GEOLOGIC RANGE.—Miocene.

GEOGRAPHIC RANGE.—Kazakhstan, USSR.

REMARKS.—Here placed in the genus and subgenus *Geochelone* solely on the basis of its rather large size. Additional material is needed to determine its status and relationships.

Geochelone (*Geochelone*) †*vitodurana* (Biedermann)

Testudo vitodurana Biedermann 1863, p. 13, pls. 1, 1a, 3.

TYPE.—Winterthur Museum (Switzerland); an almost complete shell.

TYPE LOCALITY AND HORIZON.—Near Winterthur, Switzerland; Upper fresh water bed of Veltheim, Vindobonian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Switzerland and France.

REMARKS.—For best description see Peyer (1942), who also sug-

gested that *G. vitodurana* may be only subspecifically distinct from *G. bolivari.*

Subgenus †*Hesperotestudo* Williams

Hesperotestudo Williams 1950a, p. 25 (as subgenus).

TYPE SPECIES.—*Testudo osborniana* Hay (=*Geochelone* [*Hesperotestudo*] *osborniana* [Hay]).

DEFINITION.—An extinct Palearctic subdivision of the genus *Geochelone* with narrow nuchal and pectoral scutes, limbs heavily armored, with fused dermal ossicles forming a caudal buckler, supported by elongated transverse processes of the caudal vertebrae.

GEOLOGIC RANGE.—(?)Eocene to Pleistocene of North America and "Tertiary" of Asia.

GEOGRAPHIC RANGE.—Nearctic and Palearctic.

REMARKS.—For most inclusive subgeneric description see Auffenberg (1963).

Geochelone (*Hesperotestudo*) †*alleni* Auffenberg

Geochelone alleni Auffenberg 1966a, p. 877.

TYPE.—Florida State Museum; shell of adult female.

TYPE LOCALITY AND HORIZON.—McGehee Farm, Newberry, Alachua County, Florida, U.S.A.; Hemphillian faunal age, Middle Pliocene.

GEOLOGIC RANGE.—Middle Pliocene.

GEOGRAPHIC RANGE.—Several localities in central Florida, U.S.A.

REMARKS.—Auffenberg (1966a) considered it close to, and perhaps ancestral to *G. incisa.*

Geochelone (*Hesperotestudo*) †*arenivaga* Hay

Testudo arenivaga Hay 1907, p. 16, figs. 6-8.
Geochelone arenivaga Auffenberg 1963, p. 93.

TYPE.—Carnegie Museum; pygal and one peripheral.

TYPE LOCALITY AND HORIZON.—2 mi. N. Agate Springs, Sioux County, Nebraska, U.S.A.; lower Harrison beds, Arikareen faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Western Nebraska, U.S.A.

REMARKS.—Loomis (1909) described a skull, plastron, and limb elements.

Geochelone (*Hesperotestudo*) †*campester* (Hay)

Testudo campester Hay 1903, p. 627 (nomen nudum).

Testudo campester Hay 1908, p. 455, figs. 610-613.
Gopherus campester Williams 1950a, p. 30.
Testudo rexroadensis Oelrich 1952, p. 301 (Rexroad fm., Kansas).
Geochelone rexroadensis Auffenberg 1963, p. 93.

TYPE.—American Museum of Natural History; a nearly complete plastron and parts of the carapace.

TYPE LOCALITY AND HORIZON.—Near Mt. Blanco, Crosby County, Texas, U.S.A.; Lower Blanco beds, Early Blancan faunal age, Late Pliocene.

GEOLOGIC RANGE.—Late Pliocene to early Pleistocene (see Holman 1969).

GEOGRAPHIC RANGE.—Northwestern Texas to southwestern Kansas, U.S.A.

REMARKS.—Auffenberg (MS) considers *Geochelone* (*Hesperotestudo*) *rexroadensis* a synonym of *campester* and closely related to *G. orthopygia.*

Geochelone (*Hesperotestudo*) †*equicomes* (Hay)

Testudo equicomes Hay 1917b, p. 41, pls. 1 and 3.
Geochelone equicomes Auffenberg 1962c, p. 630.

TYPE.—U. S. National Museum; an epiplastron.

TYPE LOCALITY AND HORIZON.—Cragin Quarry, Meade County, Kansas, U.S.A.; Kingsdown Formation, Rancholabrean faunal age, Sangamon Interglacial, Pleistocene.

GEOLOGIC RANGE.—(Sangamon) Late Pleistocene.

GEOGRAPHIC RANGE.—Kansas, U.S.A.

REMARKS.—Close to *Geochelone* (*Hesperotestudo*) *turgida* (see Auffenberg 1962c, 1963).

Geochelone (?*Hesperotestudo*) †*exornata* (Lambe)

Testudo exornata Lambe 1906, p. 187, pl. 3, figs. 1-3.
Geochelone exornata Auffenberg 1962c, p. 635.

TYPE.—Geological Survey of Canada; fragmentary pleural bones.

TYPE LOCALITY AND HORIZON.—Bone Coulee, Cypress Hills, Assiniboia, Saskatchewan Province, Canada; Chadronian faunal age, Early Oligocene.

GEOLOGIC RANGE.—Early Oligocene.

GEOGRAPHIC RANGE.—Saskatchewan, Canada.

REMARKS.—The thick and strongly sculptured nature of the type material suggests that the species is close to the *Geochelone turgida* line. Very poorly defined.

Geochelone (*Hesperotestudo*) †*farri* (Hay)

Testudo farri Hay 1908, p. 318, pl. 69.
Geochelone farri Auffenberg 1963, p. 94.

TYPE.—Princeton University; a shell.

TYPE LOCALITY AND HORIZON.—Smith River Valley, Montana, U.S.A.; Deep River Formation, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Montana, U.S.A.

REMARKS.—Close to *G. tedwhitei* according to Williams (1953b).

Geochelone (*Hesperotestudo*) †*gilberti* (Hay)

Xerobates undata Gilbert 1898, p. 143, figs. 1-4.
Testudo gilberti Hay 1899b, p. 349.
Geochelone gilberti Auffenberg 1963, p. 94.

TYPE.—Univ. of Kansas; a complete skull and lower jaw.

TYPE LOCALITY AND HORIZON.—Phillips County, Kansas, U.S.A.; Loup Fork, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Western Kansas, U.S.A.

REMARKS.—Probably a synonym of *Geochelone osborniana*. In the *G. thompsoni—G. angusticeps—G. osborniana—G. orthopygia* evolutionary line according to Matthew (1924).

Geochelone (*Hesperotestudo*) †*impensa* (Hay)

Testudo impensa Hay 1908, p. 431, pls. 76, 77.
Testudo immensa Riabinin 1915, p. 10 (typographical error).
Geochelone impensa Auffenberg 1963, p. 88.

TYPE.—American Museum of Natural History; a shell and most of skeleton.

TYPE LOCALITY AND HORIZON.—Near the mouth of the Madison River, Broadwater County, Montana, U.S.A.; Madison Valley Formation, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Montana, U.S.A.

REMARKS.—May be a synonym of *Geochelone osborniana*.

Geochelone (*Hesperotestudo*) †*incisa* (Hay)

Testudo incisa Hay 1916a, p. 46, pl. 3.
Gopherus incisa Williams 1950a, p. 30.
Geochelone (*Hesperotestudo*) *incisa* Auffenberg 1963, p. 82.

TYPE.—U. S. National Museum; a xiphiplastron.

TYPE LOCALITY AND HORIZON.—Ocala Lime Company Quarry, near Ocala, Marion County, Florida, U.S.A.; (?) Sangamon Interglacial, Pleistocene.

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Florida, U.S.A.

REMARKS.—In *Geochelone* (*Hesperotestudo*) *turgida* evolutionary line (Auffenberg 1962c, 1963).

Geochelone (*Hesperotestudo*) †*inusitata* (Hay)

Testudo inusitata Hay 1907, p. 18.
Testudo innistata Szalai 1930, p. 354 (typographical error).
Gopherus inusitata Williams 1950a, p. 30.
Geochelone inusitata Auffenberg 1964a, p. 6.

TYPE.—Carnegie Museum; left side of shell.

TYPE LOCALITY AND HORIZON.—Near Canyon Ferry, Broadwater County, Montana, U.S.A.; Deep River Formation, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Montana, U.S.A.

REMARKS.—Has only hexagonal neurals, but with a prominent epiplastral lip. Probably a synonym of *G. osborniana.*

Geochelone (*Hesperotestudo*) †*johnstoni* Auffenberg

Testudo rugosa Johnston p. 47 (manuscript name).
Geochelone johnstoni Auffenberg 1962c, p. 627.

TYPE.—Panhandle Plains Historic Museum (Canyon, Texas); a shell.

TYPE LOCALITY AND HORIZON.—Bed 4, Cita Canyon, Tule County, Texas, U.S.A.; Late Blancan faunal age, Early Pleistocene.

GEOLOGIC RANGE.—Early Pleistocene.

GEOGRAPHIC RANGE.—Western Texas, U.S.A.

REMARKS.—In the *Geochelone turgida* evolutionary line (Auffenberg 1962c, 1963).

Geochelone (*Hesperotestudo*) †*kalganensis* (Gilmore)

Testudo kalganensis Gilmore 1931, p. 247, pl. 9.
Gopherus kalganensis Williams 1950a, p. 22-23.
Geochelone kalganensis Auffenberg 1962a, p. 633.

TYPE.—American Museum of Natural History; partial shell.

TYPE LOCALITY AND HORIZON.—Kalgan area, Changchiaklou Hopeh Province, China; Tertiary.

GEOLOGIC RANGE.—Tertiary, probably Pliocene or Pleistocene.

GEOGRAPHIC RANGE.—North China.

REMARKS.—Probably in the *Geochelone turgida* evolutionary line (Auffenberg 1962c, 1963).

Geochelone (*Hesperotestudo*) †*klettiana* (Cope)

Testudo klettiana Cope 1875, p. 75.
Geochelone klettiana Auffenberg 1963, p. 94.

TYPE.—U. S. National Museum; a pygal.

TYPE LOCALITY AND HORIZON.—North of Santa Fe, New Mexico, U.S.A.; "Loup Fork" Santa Fe series, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Probably a synonym of *Geochelone osborniana.*

Geochelone (*Hesperotestudo*) †*niobrarensis* (Leidy)

Testudo (*Stylemys*) *niobrarensis* Leidy 1858, p. 29.
Stylemys niobrarensis Cope 1870, p. 124.
Testudo niobrarensis Leidy 1873, p. 340.

TYPE.—U. S. National Museum; epiplastron and part of entoplastron.

TYPE LOCALITY AND HORIZON.—"Niobrara River," Nebraska, U.S.A.; (=Minnechaduza fauna?, Green 1956), Clarendonian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Pliocene.

GEOGRAPHIC RANGE.—Southern South Dakota and northern Nebraska, U.S.A.

REMARKS.—For best description, based on a more complete specimen from Wolf Creek Fauna, Ogallala Formation, Late Clarendonian faunal age, see Green (1956). Earlier references of this species to the Pleistocene are in error.

Geoechelone (*Hesperotestudo*) *orthopygia* †*angusticeps* (Matthew)

Testudo angusticeps Matthew 1924, p. 207 (in error).
Testudo orthopygia angusticeps Matthew 1924, p. 210.
Geochelone angusticeps Auffenberg 1963, p. 89.

TYPE.—American Museum of Natural History; complete skull and greater part of shell, doubtfully associated.

TYPE LOCALITY AND HORIZON.—Sheep Creek Quarry, Stonehouse Draw, Sioux County, Nebraska, U.S.A.; Lower Sheep Creek beds, Late Hemingfordian faunal age, Middle Miocene.

GEOLOGIC RANGE.—Middle Miocene.

GEOGRAPHIC RANGE.—Nebraska, U. S. A.

REMARKS.—Perhaps close to the *Geochelone osborniana* evolutionary line. Matthew (1924) places it in the *G. thompsoni—G. obsorniana —G. gilberti—G. orthopygia* line.

Geochelone (*Hesperotestudo*) *orthopygia* †*orthopygia* (Cope)

Xerobates orthopygius Cope 1878, p. 393.
Xerobates cyclopygius Cope 1878, p. 394 ("Miocene," Loup Fork, Kansas).
Caryoderma snoviana Cope 1866, p. 1044 ("Miocene," Loup Fork, Kansas).
Testudo undata? Williston 1898, p. 132.
Testudo orthopygia Hay 1899b, p. 349.
Testudo cyclopygia Hay 1899b, p. 349.
Testudo snoviana Hay 1902a, p. 451.
Geochelone orthopygia Williams 1950a, p. 30.

TYPE.—American Museum of Natural History; skull, jaw, plastron, parts of carapace, and limb elements.

TYPE LOCALITY AND HORIZON.—Decatur County, Kansas, U.S.A.; Republican River Formation, Clarendonian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Pliocene.

GEOGRAPHIC RANGE.—Western Kansas and eastern Colorado, U.S.A.

REMARKS.—Close to *Geochelone* (*Hesperotestudo*) *campester*. In the *G. thompsoni—G. angusticeps—G. osborniana—G. gilberti* line, according to Matthew (1924). For best description of skeletons see Hay (1908).

Geochelone (*Hesperotestudo*) †*osborniana* (Hay)

Testudo osborniana Hay 1904b, p. 503.
Geochelone osborniana Williams 1950a, p. 30.

TYPE.—American Museum of Natural History; a complete shell, skull, and post cranial skeleton.

TYPE LOCALITY AND HORIZON.—Pawnee Creek, north of Sterling, Weld County, Colorado, U.S.A.; Pawnee Creek Formation, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Northeastern Colorado, U.S.A.

REMARKS.—Probably includes *Geochelone impensa* and *Geochelone klettiana*. In *G. thompsoni—G. angusticeps—G. orthopygia—G. gilberti* evolutionary line (Matthew 1924).

Geochelone (*Hesperotestudo*) †*primaeva* (Oelrich)

Testudo primaeva Oelrich 1950, p. 44.

TYPE.—Univ. of Michigan Museum of Paleontology; shell and a few girdle and limb elements.

TYPE LOCALITY AND HORIZON.—Locality 8, west side Sweetwater Creek, about 2 miles southwest Belmont Park Ranch House, N.E. 1/4 Sec. 32, T8S, R5W, Madison County, Montana, U.S.A.; Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Relationship not clear.

Geochelone (*Hesperotestudo*) †*riggsi* (Hibbard)

Testudo riggsi Hibbard 1944, p. 72, fig. 1.
Gopherus riggsi Hibbard and Riggs 1949, p. 834.
Testudo turgida Oelrich 1957, p. 228 (part).
Geochelone riggsi Auffenberg 1962c, p. 628.

TYPE.—Univ. of Kansas; a shell.

TYPE LOCALITY AND HORIZON.—Seward County, Kansas, U.S.A.; Rexroad Formation, Saw Rock Canyon fauna, Early Blancan faunal age, Late Pliocene.

GEOLOGIC RANGE.—Late Pliocene.

GEOGRAPHIC RANGE.—Southwestern Kansas, and western Oklahoma, U.S.A.

REMARKS.—In *Geochelone turgida* evolutionary line (Auffenberg 1962c, 1963).

Geochelone (*Hesperotestudo*) †*turgida* (Cope)

Emys turgida Cope 1870, p. 125.
Testudo turgida Cope 1892a, p. 127.
Gopherus turgida Williams 1950a, p. 30.
Geochelone turgida Auffenberg 1962c, p. 628.

TYPE.—Academy of Natural Sciences (Philadelphia); a partial shell.

TYPE LOCALITY AND HORIZON.—Three miles N. Dockum, near Esquella, Dickens County, Texas, U.S.A.; Ogallala Formation, Hemphillian faunal age, Middle Pliocene ("Blanco Beds" in error by Cope 1892b).

GEOLOGIC RANGE.—Middle Pliocene.

GEOGRAPHIC RANGE.—Oklahoma, Kansas, and Texas, U.S.A.

REMARKS.—An early member of the *G. turgida* evolutionary line (Auffenberg 1962c). For a good description and discussion of this species see Oelrich (1957). Wilson (1950) stated that the type may be at the University of Texas, though Oelrich (1957) located it in Philadelphia.

Geochelone (*Hesperotestudo*) †*undata* (Cope)

Testudo undata Cope 1875, p. 995 (p. 74 in sep.).
Geochelone undata Auffenberg 1963, p. 94.

TYPE.—U. S. National Museum; pygal and seven peripherals.

TYPE LOCALITY AND HORIZON.—Santa Fe Basin, near Santa Fe, New Mexico, U.S.A.; Santa Fe series, probably Clarendonian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Central New Mexico, U.S.A.

REMARKS.—Closely related to *Geochelone orthopygia.*

Geochelone (*Hesperotestudo*) †*vaga* (Hay)

Testudo vaga Hay 1908, p. 414, pl. 19.
Gopherus vaga Williams 1950a, p. 30.
Geochelone vaga Auffenberg 1964a, p. 6.

TYPE.—American Museum of Natural History; apparently parts of three individuals.

TYPE LOCALITY AND HORIZON.—Near Laramie Peak, Wyoming, U.S.A.; Deep River Formation, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Central Wyoming, U.S.A.

REMARKS.—Relationships not clear.

Geochelone (*Hesperotestudo*) †*wilsoni* (Milstead)

Testudo wilsoni Milstead 1956, p. 168.
Geochelone wilsoni Auffenberg 1962c, p. 630.

TYPE.—Texas Memorial Museum; a complete shell.

TYPE LOCALITY AND HORIZON.—Friesenhahn Cave, Bexar County, Texas, U.S.A.; Rancholabrean faunal age, Wisconsin, Pleistocene.

GEOLOGIC RANGE.—Wisconsin Pleistocene to Early Recent.

GEOGRAPHIC RANGE.—Eastern Oklahoma and Central Texas to New Mexico, U.S.A.

REMARKS.—Last known member of the important *Geochelone turgida* evolutionary line (Auffenberg 1962c, 1963).

Subgenus *Indotestudo* Lindholm

Testudo Schlegel and Müller 1840, p. 30 (part).
Indotestudo Lindholm 1929, p. 285 (as subgenus).

TYPE SPECIES.—*Testudo elongata* Blyth (=*Geochelone* [*Indotestudo*] *elongata* [Blyth]).

DEFINITION.—An Asiatic subgenus of the genus *Geochelone* with a low shell and no radiating pattern; nuchal may be either present or not, entoplastron usually crossed by the humeropectoral sulcus.

GEOLOGIC RANGE.—Eocene to Recent.

GEOGRAPHIC RANGE.—Asia and the East Indies.

REMARKS.—A relatively primitive, tropical mesic forest group comprised of at least three extant and two extinct species. The extant populations are possibly all conspecific on the basis of broad overlap of characters, as indicated by Smith (1931) and others. The living species are *elongata, travancorica,* and *forsteni.*

REFERENCES.—Skeleton: Gray 1870c; Auffenberg 1966b.

Geochelone (?*Indotestudo*) †*kaiseni* (Gilmore)

Testudo kaiseni Gilmore 1931, p. 236, pl. 6.
Geochelone kaiseni Loveridge and Williams 1957, p. 224.
Geochelone kaisini Mlynarski 1968, p. 96 (typographical error).

TYPE.—American Museum of Natural History; a shell.

TYPE LOCALITY AND HORIZON.—Ardyn Obo Basin, Chinese Postroad, Mongolian Republic; Ardyn Obo Formation, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Mongolian Republic.

REMARKS.—May be close to, or included in *Testudo antiqua* group according to Glaessner (1935), but this is not certain according to Mlynarski (1955b). Mlynarski (1968) believes it has no close relatives.

Geochelone (?*Indotestudo*) †*nana* (Gilmore)

Testudo nanus Gilmore 1931, p. 241, pl. 7.
Geochelone nana Loveridge and Williams 1957, p. 224.

TYPE.—American Museum of Natural History; complete shell.

TYPE LOCALITY AND HORIZON.—East Mesa, Twin Oboes, Shara Murun Region, Inner Mongolia; ?Ulan Gochu Formation, Early Oligocene.

GEOLOGIC RANGE.—Early Oligocene.

GEOGRAPHIC RANGE.—Inner Mongolia.

REMARKS.—Several peculiar morphologic features of this species suggest that its present subgeneric allocation may be incorrect.

Subgenus *Manouria* Gray

Testudo Schlegel and Müller 1840, p. 37 (part).
Geoemyda Cantor 1847, p. 2 (part).
Manouria Gray 1852, p. 133.
Teleopus LeConte 1854, p. 187 (Type *T. luxatus*).
Scapia Gray 1869, p. 169 (Type S. *falconeri*).
Emys Maack 1869, p. 278 (part).
Testudo Leidy 1871a, p. 154 (part).
Hadrianus Cope 1872a, p. 2.

TYPE SPECIES.—*Testudo emys* Schlegel and Müller (=*Geochelone* [*Manouria*] *emys* [Schlegel and Müller]).

DEFINITION.—A rather primitive Holarctic and Oriental subgenus of the genus *Geochelone*, characterized by a long narrow skull with many emydid characters, a somewhat depressed shell with a nuchal scute, divided supracaudal, narrowed pectorals (wider in some fossil species), and a tendency to well developed flat epiplastral projections that are often truncated and notched anteriorly on either side of the median line.

GEOLOGIC RANGE.—Eocene to Recent.

GEOGRAPHIC RANGE.—Extant species restricted to southeastern Asia. Fossil distribution, Holarctic.

REMARKS.—A very primitive tropical mesic forest group, ancestral to several subgenera and genera (Auffenberg 1971). It contains two extant (*G. impressa* and *G. emys*) and seven extinct species. See additional comments under *Kansuchelys*. *Hadrianus* was originally considered a genus, then a subgenus of *Testudo* (Williams 1953b), then of *Geochelone* (Loveridge and Williams 1957), then as a synonym of *Manouria* (Auffenberg 1971).

Geochelone (*Manouria*) †*corsoni* (Leidy)

Testudo corsoni Leidy 1871a, p. 154.
Emys carteri Leidy 1871b, p. 372.
Testudo hadriana Cope 1872b, p. 5.
Testudo hadrianus Cope 1872d, p. 463.
Hadrianus octonaria Cope 1872b, p. 36.
Hadrianus corsoni Cope 1872b (1873), p. 36.
Hadrianus quadratus Cope 1872a, p. 468.
Hadrianus octonarius Cope 1872b, p. 3.

TYPE.—Academy of Natural Sciences (Philadelphia); the anterior part of a plastron.

TYPE LOCALITY AND HORIZON.—15 mi. S.E. Fort Bridger, Bridger Basin, Wyoming, U.S.A.; Uinta Formation, Uintan faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Wyoming, U.S.A.

Geochelone (*Manouria*) *emys* Schlegel and Müller)

Testudo emys Schlegel and Müller 1840, *In* Temminck, p. 34 (Sumatra) (see REMARKS).
Geoemyda spinosa Cantor 1847, p. 2 (part).
Testudo emydoides Dumeril and Dumeril 1851 (substitute name for *T. emys* Schlegel and Müller).
Testudo phayrei Blyth 1863, p. 639.
Manouria fusca Gray 1852, p. 134 (Singapore).
Teleopus luxatus LeConte 1854, p. 187 (Java).
Manouria luxata Strauch 1862, p. 25.
Manouria emys Günther 1864, p. 10.

Testudo (*Scapia*) *falconeri* Gray 1869, p. 169 (India?).
Scapia gigantea Gray 1872b, p. 8.
Manuria emys Lydekker 1889b, p. 209 (Pliocene specimen) (typographical error).

TYPE.—Leiden Museum; a mounted adult.

TYPE LOCALITY.—Sumatra.

GEOLOGIC RANGE.—Pliocene of the Siwaliks (Lydekker 1889b) to the Recent.

GEOGRAPHIC RANGE.—Assam, Burma, Thailand, Malay Peninsula, Sumatra, and Borneo.

REMARKS.—The publication dates of Temminck's works range from 1839-1844, but the number containing the description of *T. emys* was issued in 1840. The plastron of *Geochelone emys* reported from the Shang dynasty ruins of Anyang, China (Wu 1943) is undoubtedly the result of importation during occupation of the site. The species is very closely related to *Geochelone impressa* (Smith 1922, 1930). Lydekker (1889b) suggested *Geochelone punjabiensis* may be close to *G. emys*.

REFERENCES.—Gray 1855, 1870c, Boulenger 1889, Jeude 1896, Williams 1950b, Auffenberg 1966b.

Geochelone (*Manouria*) †*eocaenica* (Hummel)

Testudo eocaenica Hummel 1935, p. 463, pls. 2, 3.
Testudo eocenica Kuhn 1964, p. 117 (typographical error).

TYPE.—Geological-Paleontological Museum, Univ. of Halle; a shell, limbs, and skull.

TYPE LOCALITY AND HORIZON.—Geisel Valley, Bavaria, Germany; Auversian faunal age, Middle Eocene.

GEOLOGIC RANGE.—Middle Eocene.

GEOGRAPHIC RANGE.—Germany.

REMARKS.—The relationships are somewhat uncertain, but I agree with Hummel (1935) and Zimmermann-Rollius (1966) that it is close to *G. emys*.

Geochelone (*Manouria*) †*gilmorei* (new substitute name)

Hadrianus robustus Gilmore 1915, p. 146, pl. 25 (preoccupied by *Testudo robusta* Leith-Adams [1877], here placed in *Geochelone* [?*Geochelone*]).

TYPE.—Carnegie Museum; anterior half of plastron.

TYPE LOCALITY AND HORIZON.—Near Kennedy's Hole, Uinta Basin, Uinta County, Utah, U.S.A.; Horizon C, Uinta Formation, Uintan faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Utah, U.S.A.

REMARKS.—*Geochelone gilmorei* is a new combination due to the arrangement suggested here that *H. robustus* Gilmore and *T. robusta* Leith-Adams belong to the genus *Geochelone*.

Geochelone (?*Manouria*) †*insolitus* (Matthew and Granger)

Testudo insolitus Matthew and Granger 1923, p. 5.
Testudo demissa Gilmore 1931, p. 232, figs. 11-15, pls. 5, 8 (Eocene, Outer Mongolia).
Testudo insolita Glaessner 1933, p. 282.
Geochelone insolitus Mlynarski 1968, p. 87, figs. 1-6.

TYPE.—American Museum of Natural History; parts of carapace and a left hypoplastron.

TYPE LOCALITY AND HORIZON.—Promontory Bluff, Mongolian Republic; Ardyn Obo Formation, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Mongolian Republic.

REMARKS.—Was thought to belong to the *antiqua-graeca* group (Glaessner 1933, Mlynarski 1955b), but later redescribed and placed in *Geochelone* by Mlynarski (1968). Here tentatively placed in the subgenus *Manouria*.

Geochelone (?*Manouria*) †*margae* (Hooijer)

?*Testudo margae* Hooijer 1948, p. 1169, p. 1.
Testudo margae Hooijer 1954, p. 486.

TYPE.—Netherlands Museum of Natural History (Leiden); a right scapula.

TYPE LOCALITY AND HORIZON.—Desa Beru, Tjabenge (Sopeng District) about 100 km. N.E. of Makasar, South Celebes, Indonesia; Pleistocene.

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—A large species of tortoise, presumed by Hooijer (1954) to be related to some of the Upper Siwalik species, though this is uncertain.

Geochelone (*Manouria*) †*majuscula* (Hay)

(?) *Hadrianus corsoni* Cope 1874, p. 36 (part).
Hadrianus majusculus Hay 1904a, p. 271, pl. 15.

TYPE.—Yale Peabody Museum; a shell.

TYPE LOCALITY AND HORIZON.—Near Gallina, Rio Arriba County, New Mexico, U.S.A.; Wasatchian faunal age, Early Eocene.

GEOLOGIC RANGE.—Early Eocene.

GEOGRAPHIC RANGE.—New Mexico, U.S.A.

REMARKS.—The oldest known species of land tortoise. The ending of the species name has been changed to correspond with the feminine gender of *Geochelone*.

Geochelone (*Manouria*) *obailiensis* Chkikvadze

Hadrianus obailinsis Chkikvadze 1970b, 751, fig. 3 (typographical error).

TYPE.—Georgian Academy of Sciences (Tbilisi); plastron.

TYPE LOCALITY AND HORIZON.—Georgian SSR, eastern Kazakhstan, Zaisan Valley; Eocene, Obayla Formation.

GEOLOGIC RANGE.—Eocene.

GEOGRAPHIC RANGE.—Georgian SSR.

REMARKS.—Tentatively placed in the subgenus *Manouria* on the basis of shell shape.

Geochelone (?*Manouria*) †*punjabiensis* (Lydekker)

Testudo punjabiensis Lydekker 1889b, p. 87.

TYPE.—Indian Museum; right and left epiplastra.

TYPE LOCALITY AND HORIZON.—Siwalik Hills, Punjab, India; Pliocene (?).

GEOLOGIC RANGE.—Pliocene (?).

GEOGRAPHIC RANGE.—Punjab, India.

REMARKS.—Lydekker (1889b) suggests it may be close to *G. emys*.

Geochelone (*Manouria*) †*tumida* (Hay)

Hadrianus tumidus Hay 1908, p. 380.

TYPE.—American Museum of Natural History; a partial plastron and peripherals.

TYPE LOCALITY AND HORIZON.—Utah, U.S.A.; Uinta Formation, Uintan faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Utah, U.S.A.

REMARKS.—The ending of the species name has been changed to correspond with the feminine gender *Geochelone*.

Geochelone (*Manouria*) †*utahensis* (Gilmore)

Hadrianus utahensis Gilmore 1915, p. 148.

TYPE.—Carnegie Museum; plastron and bridge.

TYPE LOCALITY AND HORIZON.—South of Kennedy's Hole, Uinta

County, Utah, U.S.A.; Horizon B or C, Uinta Formation, Uintan Faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Utah, U.S.A.

Subgenus †*Megalochelys* Falconer and Cautley

Megalochelys Falconer and Cautley 1837, p. 358.
Colossochelys Falconer and Cautley 1844, p. 54.
Testudo Lydekker 1880, p. 20 (part).

TYPE SPECIES.—*Colossochelys atlas* Falconer and Cautley (=*Geochelone* [*Megalochelys*] *atlas* [Falconer and Cautley]).

DEFINITION.—An Old World subdivision of the genus *Geochelone* in which the included species are large, thick-shelled tortoises with swollen areas on the peripherals, nuchal scute absent, two gular scutes, epiplastron strongly bifurcated anteriorly, and no narrowed pectorals.

GEOLOGIC RANGE.—Pleistocene and perhaps Recent.

GEOGRAPHIC RANGE.—Southeast Asia, East Indies, Mauritius Island, Mascarene Group, Indian Ocean.

REMARKS.—An extinct, but specialized small group of large to giant tortoises.

Geochelone (*Megalochelys*) †*atlas* (Falconer and Cautley)

Megalochelys sivalensis Falconer and Cautley 1837, p. 358 (subsequently withdrawn).
Colossochelys atlas Falconer and Cautley 1844, p. 54.
Colossochelys (*Megalochelys*) *atlas* Maack 1869, p. 223.
Testudo (*Colossochelys*) *atlas* Lydekker 1880, p. 20.
Testudo (*Megalochelys*) *atlas* Lydekker 1889b, p. 209.
Testudo atlas Brown 1931, p. 183.
?*Testudo margae* Hooijer 1948, p. 1169, fig. 1 (Pleistocene, Celebes).
Testudo margae Hooijer 1954, p. 486.

TYPE.—British Museum (Natural History); an epiplastron.

TYPE LOCALITY AND HORIZON.—Siwalik Hills, Punjab, India; Siwalik Beds, Manchhar Series, Boulder-Conglomerate, Early Pleistocene.

GEOLOGIC RANGE.—Early to Late Pleistocene.

GEOGRAPHIC RANGE.—Punjab, India, Upper Burma, Java, Celebes, and Timor.

REMARKS.—According to Lydekker (1889b) *G. atlas* is close to *G. perpiniana*. The 12-foot composite reconstruction of the type and associated specimens by Falconer is incorrect; it should be closer to 6 feet (Lydekker 1889b). For latest discussion, see Hooijer (1971).

Geochelone (?*Megalochelys*) †*cautleyi* (Lydekker)

Cautleya annuliger Theobald 1879, p. 186 (nomen nudum).

Testudo cautleyi Lydekker 1889a, p. 86.
Testudo cauthley Riabinin 1915, p. 12 (typographical error).

TYPE.—British Museum (Natural History); an epiplastron.

TYPE LOCALITY AND HORIZON.—Siwalik Hills, near Nila, Potwar, Punjab, India; Upper Siwalik beds, Potwar Silts, Middle Pleistocene?

GEOLOGIC RANGE.—Middle Pleistocene.

GEOGRAPHIC RANGE.—Punjab, India.

REMARKS.—*Geochelone* (?*Megalochelys*) *cautleyi* is smaller than *G. atlas* and generally believed not the same species on the basis of the available epiplastron. The differences are conceivably sexually correlated.

Geochelone (*Megalochelys*) †*gadowi* (Van Denburgh)

Testudo guentheri Gadow 1894, p. 320 (invalid name, not of Baur 1889, proposed for *T. sumeirei;* Sauzier [part]).
Testudo gadowi Van Denburgh 1914, p. 257.

TYPE.—Museum of Zoology, Cambridge University; anterior part of plastron.

TYPE LOCALITY AND HORIZON.—Mare aux Songes, Mauritius Island, Mascarene Group, Indian Ocean; Late Pleistocene or Early Recent.

GEOLOGIC RANGE.—Pleistocene and/or Recent.

GEOGRAPHIC RANGE.—Mauritius Island.

Subgenus †*Monachelys* Williams

Monachelys Williams 1952, p. 547 (as subgenus).

TYPE SPECIES.—*Testudo* (*Monachelys*) *monensis* Williams (=*Geochelone* [*Monachelys*] *monensis* [Williams]).

DEFINITION.—A Nearctic subdivision of the genus *Geochelone* in which the majority of the characters are as in the subgenus *Chelonoidis,* except that the centrum of the first dorsal vertebra is very elongate and the xiphiplastral notch is absent.

GEOLOGIC RANGE.—Known only from the Late (?) Pleistocene.

GEOGRAPHIC RANGE.—Mona Island, West Indies.

REMARKS.—The relationships of this monotypic subgenus are not clear, but it is believed to be close to *Chelonoidis.*

Geochelone (*Monachelys*) †*monensis* (Williams)

Testudo (*Monachelys*) *monensis* Williams 1952, p. 547, pls. 44-47.

TYPE.—American Museum of Natural History; skull, parts of shell, and partial skeleton.

TYPE LOCALITY AND HORIZON.—Lirio Cave, Mona Island, West Indies; Late Pleistocene.

GEOLOGIC RANGE.—Late Pleistocene.

GEOGRAPHIC RANGE.—Mona Island, West Indies.

Subgenera Inquirendae

The following species belong to the genus *Geochelone,* but their subgeneric placement is not clear.

Geochelone †bessarabica (Riabinin)

Testudo bessarabica Riabinin 1915, p. 6, pls. 1, 3, 4.

TYPE.—Geology Museum, Academy of Sciences (Leningrad); partial shell.

TYPE LOCALITY AND HORIZON.—Tarakliya, Bender District, Bessarabia Province (Cahul), Southern Moldavian S.S.R.; Meotian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Central Bessarabia, Moldavian S.S.R., and Moldavia, Romania.

REMARKS.—The best description of the shell is that by Macarovici (1930) from near the type locality. According to Riabinin (1915) it has close affinities to *Geochelone punjabiensis* and *G. emys.* Glaessner (1933) states that it is not in the *antiqua-graeca* phyletic line. Mlynarski (1969b) correctly places it in *Geochelone.*

?Geochelone †chaileoti (Bergounioux)

Testudo chaileoti Bergounioux 1935, p. 93, pl. 5.
Testudo chailloti Kuhn 1964, p. 114 (typographical error).

TYPE.—Museum of Natural History (Montauban, France); a shell.

TYPE LOCALITY AND HORIZON.—Dieupentale, Tarn et Garonne Dept., France; Stampian faunal age, Middle Oligocene.

GEOLOGIC RANGE.—Middle Oligocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Presumably close to *Testudo catalaunica* and *T. pyrenaica* according to Bergounioux (1935). The absence of a nuchal scute indicates very clearly that this species belongs to *Geochelone.*

Geochelone †costaricensis (Segura)

Testudo costaricensis Segura 1944, p. 9-29.
Geochelone costaricensis Loveridge and Williams 1957, p. 224.

TYPE.—National Museum of Costa Rica; an almost complete shell.

TYPE LOCALITY AND HORIZON.—Milla 52, Peralta District, Costa Rica; Late Oligocene or Early Miocene.

GEOLOGIC RANGE.—Late Oligocene or Early Miocene.

GEOGRAPHIC RANGE.—Costa Rica.

REMARKS.—According to Segura (1944) it is close to *Stylemys amphithorax* but Auffenberg (1971) suggests it is close to *Indotestudo* and *Chelonoidis*.

?*Geochelone* †*cultrata* (Cope)

Testudo cultratus Cope 1873a, p. 6.
Testudo cultrata Hay 1902a, p. 451.
Geochelone cultrata Auffenberg 1963, p. 94.

TYPE.—U.S. National Museum; partial epiplastron.

TYPE LOCALITY AND HORIZON.—Head of Horse Tail Creek, Weld County, Colorado, U.S.A.; White River Series, Chadronian faunal age, Early Oligocene.

GEOLOGIC RANGE.—Early Oligocene.

GEOGRAPHIC RANGE.—Northeastern Colorado, U.S.A.

?*Geochelone* †*larteti* Pictet

Testudo gigantea Lartet 1851, p. 38 (preoccupied, not of Bravard).
Testudo larteti Pictet 1853, p. 444 (substitute name for *T. gigantea* Lartet).
Testudo larteti Lydekker 1889a, p. 90.

TYPE.—Location unknown to author; part of the shell.

TYPE LOCALITY AND HORIZON.—Sansan, Gers Department, France; Vindobonian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Sansan, France.

REMARKS.—A giant tortoise, probably referable to the genus *Geochelone*.

?*Geochelone* †*oskarkuhni* Mlynarski

Geochelone oskarkuhni Mlynarski 1968, p. 91, figs. 6-8, pl. 9.

TYPE.—Palaeozoological Institute, Polish Academy of Sciences (Warsaw); a plastron and posterior portion of carapace.

TYPE LOCALITY AND HORIZON.—Alta Teli, Dzereg Valley, Western Mongolia; Pliocene.

GEOLOGIC RANGE.—Pliocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—I agree with Mlynarski (1968) and others that the entire

question of relationships among the Asiatic Pliocene fossil tortoises needs critical review. Until this is done the allocation of this species to *Geochelone* will remain in doubt.

?*Geochelone* †*peragrans* (Hay)

Testudo peragrans Hay 1907, p. 15.
Geochelone peragrans Auffenberg 1963, p. 94.

TYPE.—Carnegie Museum; skull and shell.

TYPE LOCALITY AND HORIZON.—South of McCartney Mountain and Big Hole River, north of Dillon, Montana, U.S.A.; (?)Oligocene.

GEOLOGIC RANGE.—(?)Oligocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—The relationships of this species are unknown.

?*Geochelone* †*phosphoritarum* (Bergounioux)

Testudo phosphoritarum Bergounioux 1935, p. 85, pl. 14.

TYPE.—Toulouse Natural History Museum; partial carapace.

TYPE LOCALITY AND HORIZON.—Quercy Region, France; Phosphorites de Quercy, Oligocene.

GEOLOGIC RANGE.—Oligocene.

GEOGRAPHICAL RANGE.—Quercy Region, France.

REMARKS.—Close to *Testudo gigas* Bravard (nomen nudum) according to Bergounioux (1935).

?*Geochelone* †*quadrata* (Cope)

Testudo quadratus Cope 1885, p. 762, pl. 61.
Testudo quadrata Hay 1902a, p. 451.
Geochelone quadrata Auffenberg 1963, p. 94.

TYPE.—American Museum of Natural History; and epiplastral projection.

TYPE LOCALITY AND HORIZON.—Head of Horse Tail Creek, Weld County, Colorado, U.S.A.; White River Formation, Chadronian faunal age, Early Oligocene.

GEOLOGIC RANGE.—Early Oligocene.

GEOGRAPHIC RANGE.—Southeastern Wyoming and northeastern Colorado, U.S.A.

REMARKS.—The relationships of this species are unknown.

?*Geochelone* †*schafferi* (Szalai)

Testudo schafferi Szalai 1933, p. 154 (not *Ptychogaster schafferi* Glaessner).

TYPE.—Vienna Museum of Natural History; a skull and femur.

TYPE LOCALITY AND HORIZON.—Samos, Greece; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Samos, Greece.

REMARKS.—A large tortoise, probably in the genus *Geochelone*, subgenus *Geochelone*. Bachmayer (1967) described additional material from Pikermi.

?*Geochelone* †*sloanei* (Lydekker)

Testudo sloanei Lydekker 1889a, p. 89.

TYPE.—British Museum (Natural History); a shell.

TYPE LOCALITY AND HORIZON.—"Tertiary of Turkey."

GEOLOGIC RANGE.—Tertiary, probably early Pliocene.

GEOGRAPHIC RANGE.—Turkey.

REMARKS.—Closely related to *Geochelone radiata* or *G. pardalis* according to Lydekker (1889a) though certain of its features suggest it may be close to *Testudo*.

?*Geochelone* †*tarakliensis* Riabinin

Testudo tarakliensis Riabinin 1915, p. 12.
Testudo tarabliensis Kuhn 1964, p. 134 (typographical error).

TYPE.—Geology Museum of the Academy of Sciences; carapace.

TYPE LOCALITY AND HORIZON.—Tarakliya, Bessarabia Province, Moldavian S.S.R.; Meotian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Bessarabia, Moldavian S.S.R.

REMARKS.—Affinities not clear. Not in the *antiqua-graeca* phyletic line according to Glaessner (1933) and Mlynarski (1955a). Absence of a nuchal scute suggests it belongs to the genus *Geochelone*.

Geochelone †*thompsoni* (Hay)

Testudo thompsoni Hay 1908, p. 400, pl. 66.
Geochelone thompsoni Auffenberg 1963, p. 94.

TYPE.—American Museum of Natural History; a skull and part of plastron, cervical vertebrae and parts of foreleg.

TYPE LOCALITY AND HORIZON.—Corral Draw, Ziebach County, South Dakota, U.S.A.; Lower Oreodon beds, Orellan faunal age, Middle Oligocene.

GEOLOGIC RANGE.—Middle Oligocene.

GEOGRAPHIC RANGE.—Western South Dakota.

REMARKS.—Though the exact relationships of this species remain unknown, it is apparently in the phyletic line with *Geochelone o. angusticeps, G. osborniana, G. gilberti,* and *G. orthopygia,* according to Matthew (1924).

?*Geochelone* †*ulanensis* (Gilmore)

Testudo ulanensis Gilmore 1931, p. 245.
Geochelone ulanensis Mlynarski 1968, p. 96.
Hadrianus ulanensis Chkikvadze 1970b, p. 71.

TYPE.—American Museum of Natural History; part of plastron and carapace.

TYPE LOCALITY AND HORIZON.—North Mesa, Shara Murun Region, Inner Mongolia, China; Ulan Shireh Formation, Ludian faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHICAL RANGE.—Shara Murun Region, Inner Mongolia, China.

REMARKS.—Affinities not clear but certainly not in the *antiquagraeca* phyletic line according to Glassner (1933). The material is very fragmentary and detailed comparison is impossible. Chkikvadse (1907b) places it in *Hadrianus,* but he does not state on what basis he does so.

?*Geochelone* †*yunnanensis* (Yeh)

Testudo yunnaneensis Yeh 1963a, p. 47, figs. 27-29, pls. XVI, XVII.
Testudo lunanensis Yeh 1963a, p. 50, pl. XIII (Lower Oligocene, China).

TYPE.—Institute of Paleontology and Paleoanthropology (Peking); fragmentary plastron.

TYPE LOCALITY AND HORIZON.—Wa-yao-chung, Ta-i-ma, Lunan. Yunnan, China; Lower Oligocene.

GEOLOGIC RANGE.—Lower Oligocene.

GEOGRAPHIC RANGE.—Type locality only.

REMARKS.—*Testudo lunanensis* Yeh is placed in the synonomy of *T. yunnanensis* Yeh because of morphological similarity. Both are provisionally placed in the genus *Geochelone* on the basis of their large size.

Genus *Gopherus* Rafinesque

Testudo Bartram 1791, p. 18.
Gopherus Rafinesque 1832, p. 64.
Xerobates Agassiz 1857, p. 446.
Bysmachelys Johnston 1937, p. 439.

GENOTYPE.—*Testudo polyphemus* Daudin (=*Gopherus polyphemus* [Daudin]).

DEFINITION.—Nearctic genus of tortoises with short cervical verte-

brae; median premaxillary ridge; flattened forelimbs adapted for digging; nuchal scute usually as wide as long; hyoplastron usually longer than hypoplastron; fourth vertebral scute usually wider than long.

GEOLOGIC RANGE.—Oligocene to Recent.

GEOGRAPHIC RANGE.—As a fossil almost all of the Nearctic region south of Canada and south throughout northern Mexico to the State of Aguascalientes. Recent range much smaller.

REMARKS.—For best generic description see Williams (1950a). Recognition of this genus in the Tertiary of Asia by Williams (1952) was based on (1) a presumed close relationship between *turgida* and *kalganensis* (probably correct), and (2) reference of *turgida* to the genus *Gopherus* (certainly incorrect). For further discussion see Oelrich (1957) and Auffenberg (1962c). Four extant species are recognized: *G. agassizii, G. berlandieri, G. flavomarginatus,* and *G. polyphemus.*

REFERENCES.—Zoogeography. Blair 1958, Brattstrom 1961. Morphology. Skeleton: Williams 1950b, Auffenberg 1964b, 1966b, in press; Skull: Williams 1950a, Auffenberg in press.

Gopherus agassizii (Cooper)

Xerobates agassizii Cooper 1863, p. 120.
Testudo agassizii Boulenger 1889, p. 156.
Gopherus agassizii Stejneger 1893, p. 161.
Gopherus polyphemus agassizii Mertens and Wermuth 1955, p. 351.

TYPE.—California State Geological Survey; 3 young specimens.

TYPE LOCALITY.—Near Fort Mojave, California, U.S.A.

GEOLOGIC RANGE.—Known from the Pleistocene of California (Miller 1942, Brattstrom 1953, 1958), and the Post-Pleistocene of Nevada (Brattstrom 1954).

GEOGRAPHIC RANGE.—Southwestern United States (extreme southwestern Utah, southern Nevada, western Arizona, extreme northwestern Baja California, southeastern California), and all of Sonora, Mexico to extreme northern Sinaloa.

REMARKS.—Mertens (1956) records hybrids between this species and *G. berlandieri* in captivity. Most closely related to *G. berlandieri* (Auffenberg in press).

Gopherus †*atascosae* (Hay)

Testudo atascosae Hay 1902c, p. 383.
Gopherus atascosae Hay 1924, p. 247.

TYPE.—Academy of Natural Sciences (Philadelphia); parts of a plastron.

TYPE LOCALITY AND HORIZON.—Atascosa County, Texas, U.S.A.; probably Middle Pleistocene.

GEOLOGIC RANGE.—(?) Middle Pleistocene.

GEOGRAPHIC RANGE.—Central Texas, U.S.A.

REMARKS.—In 1908 Hay thought the type may have been taken from Miocene beds, but he established its true origin in 1930. Closely related to *Gopherus polyphemus* and perhaps conspecific with it.

Gopherus †brattstromi (new substitute name)

Gopherus depressus Brattstrom 1961, p. 548 (Preoccupied by *Testudo depressa* Guerin-Meneville [1829], here placed in *Gopherus polyphemus*).

TYPE.—California Institute of Technology; a nearly entire shell.

TYPE LOCALITY AND HORIZON.—Tehachapi Mountains, Kern County, California, U.S.A.; Bopesta Formation, Cache Peak fauna, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Southeastern California, U.S.A.

REMARKS.—Close to *G. mohavetus* and *G. pansa*, according to Brattstrom (1961).

Gopherus †brevisternus (Loomis)

Testudo brevisterna Loomis 1909, p. 21.
Gopherus brevisterna Williams 1950a, p. 19.

TYPE.—Amherst College; most of the entire skeleton.

TYPE LOCALITY AND HORIZON.—Muddy Creek, Laramie County, Wyoming, U.S.A.; Upper Harrison beds, Arikareean faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Eastern Wyoming, U.S.A.

REMARKS.—The ending of the species name has been changed to correspond with the masculine gender of *Gopherus*.

Gopherus †canyonensis (Johnston)

Bysmachelys canyonensis Johnston 1937, p. 440.
Gopherus canyonensis Williams 1950a, p. 21.

TYPE.—Panhandle Historic Plains Museum (Canyon, Texas); a plastron and skeleton (plastron now lost).

TYPE LOCALITY AND HORIZON.—North Cita Canyon, Sec. 164, block 6, Randall County, Texas, U.S.A.; Cita Canyon beds, Late Blancan faunal age, Early Pleistocene.

GEOLOGIC RANGE.—Early Pleistocene.

GEOGRAPHIC RANGE.—Northwestern Texas and beds of similar age as far west as southern Arizona, U.S.A.

REMARKS.—Close to *G. pertenuis*. Close to *G. polyphemus* according to Williams (1952).

Gopherus †copei (Koerner)

Testudo copei Koerner 1940, p. 838.
Gopherus copei Williams 1950a, p. 30.

TYPE.—Yale Peabody Museum; a shell.

TYPE LOCALITY AND HORIZON.—Sec. 14, R10N, T5E, Meagher County, Montana, U.S.A.; Deep River Formation, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Close to *G. emiliae*, according to Koerner (1940), and probably conspecific with it.

Gopherus †dehiscus Des Lauriers

Gopherus dehiscus Des Lauriers 1965, p. 1.

TYPE.—Los Angeles County Museum; internal cast of entire shell, except anterior lip of carapace.

TYPE LOCALITY AND HORIZON.—Cajon Pass, W. end of Cajon Valley, NW-1/4 Sec. 1, N.E.-1/4 Sec. 2, T3N, R7W, SBB and M. San Antonio Quad. 1/2 mile S.W. of Hwy. to Big Pines Recreation Area, San Bernadino County, California, U.S.A.; Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Occurred sympatrically with the type of *Geochelone milleri* (Brattstrom).

Gopherus †edae (Hay)

Testudo edae Hay 1907, p. 19.
Gopherus edae Williams 1950a, p. 30.

TYPE.—Carnegie Museum; most of a carapace and plastron.

TYPE LOCALITY AND HORIZON.—Near Running Water Creek, Sioux County, Nebraska, U.S.A.; Harrison Formation, Arikareean faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Western Nebraska, U.S.A.

REMARKS.—Probably close to *G. hollandi*. The best description is by Hay (1908).

Gopherus †emiliae (Hay)

Testudo emiliae Hay 1908, p. 419.
Gopherus emiliae Williams 1950a, p. 30.

TYPE.—American Museum of Natural History; an almost entire shell.

TYPE LOCALITY AND HORIZON.—On Porcupine Creek, South Dakota, U.S.A.; Lower Rosebud Formation, Arikareean faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Southern South Dakota, U.S.A.

REMARKS.—Presumably close to *G. copei*, according to Koerner (1940).

Gopherus flavomarginatus Legler

Gopherus polyphemus Duges 1888, p. 146-147 (part).
Gopherus flavomarginata Legler 1959, p. 337.
Gopherus polyphemus flavomarginatus Wermuth and Mertens 1961, p. 174.

TYPE.—U.S. National Museum; a mounted specimen.

TYPE LOCALITY.—30-40 miles north of Ciudad Lerdo, Durango, Mexico.

GEOLOGIC RANGE.—Middle Pleistocene and Recent.

GEOGRAPHIC RANGE.—In a living state known only from the Bolson de Mapimi, northeastern Chihuahua, western Coahuila and northern Durango, Mexico. Pleistocene fossils known from Aguascalientes, Mexico.

REMARKS.—Most closely related to *G. polyphemus* (Legler 1959, Auffenberg in press). Grant's statement (1960) that this species is closest to *G. agassizii* is not followed here. Legler and Webb (1961) described additional specimens.

REFERENCES.—Morphology. Skull: Legler 1959; Skeleton: Auffenberg 1966b, in press.

Gopherus †hexagonatus (Cope)

Testudo hexagonata Cope 1893, p. 77.
Gopherus hexagonata Williams 1950a, p. 30.

TYPE.—Univ. of Texas; originally a partial shell, now represented by a few badly broken pieces.

TYPE LOCALITY AND HORIZON.—Rock Creek, Tule Canyon, Briscoe County, Texas, U.S.A.; Tule Formation, Rock Creek Local fauna, Irvingtonian faunal age, Middle Pleistocene.

GEOLOGIC RANGE.—Middle to Late Pleistocene.

GEOGRAPHIC RANGE.—Most of Texas, north to Kansas, U.S.A.

REMARKS.—For best description see Auffenberg (1962b). The end-

ing of the species name has been changed to correspond with the masculine gender of *Gopherus*. Probably a synonym of *G. laticaudatus*.

Gopherus †hollandi (Hay)

Testudo hollandi Hay 1907, p. 18.
Gopherus hollandi Williams 1950a, p. 30.

TYPE.—Carnegie Museum; a complete shell.

TYPE LOCALITY AND HORIZON.—Near Running Water Creek, Sioux County, Nebraska, U.S.A.; Harrison Formation, Arikareean faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Western Nebraska, U.S.A.

REMARKS.—Probably close to *G. edae*.

Gopherus †huecoensis Strain

Gopherus huecoensis Strain 1966, p. 24.

TYPE.—Memorial Museum, Bureau of Economic Geology, Univ. of Texas; plastron and various appendicular skeletal elements of same individual.

TYPE LOCALITY AND HORIZON.—Madden Arroyo, Hudspeth County, Texas, U.S.A.; Fort Hancock Formation, Early Pleistocene.

GEOLOGIC RANGE.—Early Pleistocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Clearly a member of the *polyphemus* group on the basis of the carpus and probably a synonym of *G. flavomarginatus*.

Gopherus †laticaudatus (Cope)

Testudo laticaudata Cope 1893, p. 75.
Testudo luticaudata Wilson 1950, p. 115 (typographical error).
Geochelone laticaudata Auffenberg 1963, p. 93.

TYPE.—Univ. of Texas; an epiplastron and xiphiplastron.

TYPE LOCALITY AND HORIZON.—Rock Creek, Tule Canyon, Briscoe County, Texas, U.S.A.; Tule Formation, Rock Creek local fauna, Irvingtonian age, Middle Pleistocene (incorrectly stated as Pliocene by Hay 1908).

GEOLOGIC RANGE.—Middle Pleistocene.

GEOGRAPHIC RANGE.—Northwestern Texas, U.S.A.

REMARKS.—*Gopherus laticaudatus* is a new combination, based on the similarity of *laticaudatus* and *G. pertenuis*. The ending of the species name has been changed to correspond with the masculine gender of *Gopherus*. It is probably a synonym of *G. hexagonatus*.

Gopherus †laticuneus (Cope)

Testudo laticunea Cope 1873a, p. 6.
Gopherus laticunea Williams 1950a, p. 30.

TYPE.—American Museum of Natural History; an almost complete carapace, pelvis, and some limb elements.

TYPE LOCALITY AND HORIZON.—Head of Horsetail Creek, Weld County, Colorado, U.S.A.; Horsetail Creek Member, White River Formation, Chadronian faunal age, Early Oligocene.

GEOLOGIC RANGE.—Early and Middle Oligocene.

GEOGRAPHIC RANGE.—Northeastern Colorado, southeastern Wyoming, southwestern South Dakota, and western Nebraska, U.S.A.

REMARKS.—*Gopherus praeextans* and *G. neglectus* may be synonyms of *G. laticuneus*. Hay (1908) refers fossils from the Colorado Oreodon beds to this species, but this stratigraphic assignment was based on an error in geologic interpretation. The ending of the species name has been changed to conform with the masculine gender of *Gopherus*.

Gopherus †mohavetus (Merriam)

Testudo mohavense Merriam 1919, p. 456.
Testudo mohavensis Bataller 1926, p. 155.
Gopherus mohavense Williams 1950a, p. 30.
Gopherus mohavetus Des Lauriers 1965, p. 1.

TYPE.—Univ. of California Museum of Paleontology; a complete shell.

TYPE LOCALITY AND HORIZON.—Barstow syncline, Mojave Desert, San Bernardino County, California, U.S.A.; Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Southeastern California, U.S.A.

REMARKS.—Close to *G. brattstromi* (as *G. depressus*) and *G. pansus* according to Brattstrom (1961).

Gopherus †neglectus (Brattstrom)

Gopherus neglectus Brattstrom 1961, p. 544, figs. 1-5.

TYPE.—California Institute of Technology; an almost entire shell.

TYPE LOCALITY AND HORIZON.—Key Quarry, Ventura County, California, U.S.A.; Upper Sespe Formation, Whitneyan faunal age, Late Oligocene.

GEOLOGIC RANGE.—Late Oligocene.

GEOGRAPHIC RANGE.—California, U.S.A.

REMARKS.—Close to *G. praeextans* and *G. laticuneus* according to

Brattstrom (1961). *G. neglectus* and *G. praeextans* may be synonyms of *G. laticuneus*.

Gopherus †pansus (Hay)

Testudo pansa Hay 1908, p. 420, pl. 71, figs. 1-2, text figs. 550-1.
Gopherus pansa Williams 1950a, p. 30.

TYPE.—American Museum of Natural History; a complete shell and pelvis.

TYPE LOCALITY AND HORIZON.—Near the state lines of Colorado and Nebraska, north of Sterling, Weld County, Colorado, U.S.A.; Pawnee Creek Formation, Barstovian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Southwestern Nebraska and northeastern Colorado, U.S.A.

REMARKS.—Close of *G. brattstromi* (as *depressus*) and *G. mohavetus*, according to Brattstrom (1961). The ending of the species name has been changed to correspond with the masculine gender of *Gopherus*.

Gopherus †pertenuis (Cope)

Testudo pertenuis Cope 1892b, p. 226.

TYPE.—Univ. of Texas; only a few fragments remain of the original, almost complete type shell (Wilson 1950).

TYPE LOCALITY AND HORIZON.—Near Mt. Blanco, Crosby County, Texas, U.S.A.; Early Blancan faunal age, Late Pliocene.

GEOLOGIC RANGE.—Late Pliocene.

GEOGRAPHIC RANGE.—Northwestern Texas, U.S.A.

REMARKS.—Probably very close to *G. canyonensis* and *G. laticaudatus*.

Gopherus polyphemus (Daudin)

Testudo polyphaemus Bartram 1791, p. 18 (nomen nudum).
Testudo polyphemus Daudin 1802.
Testudo depressa Guerin-Meneville 1829, p. 5, pl. 1, fig. 1.
Testudo gopher Gray 1844, p. 4.
Xerobates carolinus Agassiz 1857, p. 447.
Gopherus polyphemus Stejneger 1893, p. 161.
Gopherus carolinus Shaler 1888, p. 37.
Gopherus praecedens Hay 1916a, p. 55 (Late Pleistocene, Vero, Florida).
Gopherus polyphemus polyphemus Mertens and Wermuth 1955, p. 371.

TYPE.—None designated.

TYPE LOCALITY.—Savannah, Georgia, U.S.A. (by Schmidt 1953).

GEOLOGIC RANGE.—Late Pleistocene to Recent of Florida (Hay 1930, Holman 1958, 1959) and South Carolina.

RECENT GEOGRAPHIC RANGE.—Southeastern United States (Georgia, Florida, and South Carolina west to the Mississippi River along the Gulf Coast).

REMARKS.—Closely related to *G. flavomarginatus* (Auffenberg 1966b, in press). *G. praecedens* was originally believed to originate from Early Pleistocene beds (Hay 1916a), but these have since been shown to be Late Pleistocene and Recent in age (Weigel 1962).

Gopherus †praeextans (Lambe)

Testudo praeextans Lambe 1913, p. 61.
Gopherus praeextans Williams 1950a, p. 29.

TYPE.—Geological Survey (Canada); a shell.

TYPE LOCALITY AND HORIZON.—Sage Creek, Niobrara County, Wyoming, U.S.A.; Orellan faunal age, Lower Brule age, Middle Oligocene.

GEOLOGIC RANGE.—Middle Oligocene.

GEOGRAPHIC RANGE.—Southeastern Wyoming, U.S.A.

REMARKS.—Probably only a chronologic race of *G. laticuneus*. Gilmore (1946) described the osteology of an almost entire skeleton.

Gopherus †undabunus (Loomis)

Testudo undabuna Loomis 1909, p. 25.
Gopherus undabuna Williams 1950a, p. 30.
Geochelone undabuna Auffenberg 1964a, p. 6.

TYPE.—Amherst College; shell.

TYPE LOCALITY AND HORIZON.—Muddy Creek, Laramie County, Wyoming, U.S.A.; Upper Harrison beds, Arikareean faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Eastern Wyoming, U.S.A.

REMARKS.—The ending of the species name has been changed to the masculine gender of *Gopherus*. My earlier assignment to *Geochelone* is here believed incorrect.

Genus *Homopus* Dumeril and Bibron

Lorica Walbaum 1782, p. 71.
Testudo Thunberg 1787, p. 181 (part).
Chersine Merrem 1820, p. 30 (part).
Homopus Dumeril and Bibron 1835, p. 145.
Chersobius Fitzinger 1835, p. 108 (*Testudo signata* Schoepff).
Horopus Haycroft 1891, p. 341 (typographical error).
Pseudomopus Hewitt 1931, p. 496 (*Testudo signata* Schoepff).

GENOTYPE.—*Homopus areolatus* (Thunberg).

DEFINITION.—Small Old World tortoises, with triturating surfaces of

maxilla and premaxilla without ridges; maxillary not entering roof of palate; prootic narrowly exposed dorsally; quadrate enclosing stapes; centrum of third cervical biconvex, no submarginal scutes; gulars divided; gular region only slightly thickened.

GEOLOGIC RANGE.—No fossils known.

GEOGRAPHIC RANGE.—South Africa (possibly into Southwest Africa).

REMARKS.—Contains four extant species: *H. areolatus, H. boulengeri, H. femoralis,* and *H. signatus.* The most recent monographic treatment is Loveridge and Williams (1957).

REFERENCES.—Skeleton: Boulenger 1889, 1890a, Auffenberg 1966b, Gray 1873c, Williams 1950b.

Genus *Kinixys* Bell

Kinixys Bell 1827, p. 398.
Cinothorax Fitzinger 1835, pp. 108, 111, 121.
Cinixys Fitzinger 1843, p. 29.
Kinothorax Gray 1873a, p. 16.
Testudo Shaw 1802, p. 59 (part).
Homopus Lataste 1886, p. 286 (part).
Malacochersus Loveridge 1942, p. 248 (in error).

GENOTYPE.—*Kinixys erosa* (Schweigger).

DEFINITION.—No ridges on triturating surfaces of maxillary and premaxillary; prootic well exposed dorsally; quadrate enclosing stapes; third cervical biconvex; carapace of adult hinged; submarginal scutes present; gular region greatly thickened and projected; gulars divided.

GEOLOGIC RANGE.—?Oligocene of France to Recent (see Remarks).

GEOGRAPHIC RANGE.—Africa from 17° N., S. to Bechuanaland and Natal, South Africa. May be introduced in Malagasy Republic.

REMARKS.—Three extant species are recognized: *K. belliana, K. erosa, K. homeana. Cinixys couzieri,* Oligocene of France, is here tentatively placed in *Ptychogaster* on the basis of basic shell morphology.

REFERENCES.—Skeleton: Gray 1873b, Boulenger 1889, Siebenrock 1910, Ruckes 1937, Williams 1950b, Kilias 1957, Villiers 1958, Auffenberg 1966b.

Genus *Malachochersus* Lindholm

Cinicys Tornier 1896, p. 2 (part) [sic] (not of Gray).
Cinixys Procter 1922, p. 515.
Malacochersus Lindholm 1929, p. 285.
Testudo Siebenrock 1903a, p. 185.

GENOTYPE.—*Testudo tornieri* Siebenrock (=*Malacochersus tornieri* [Siebenrock]).

DEFINITION.—An African genus with a persistently fenestrated, very

flat shell; a single suprapygal; gular region not thickened or projected; gulars divided; triturating surface of maxilla strongly rigid; no median premaxillary ridge; prootic well exposed dorsally; quadrate enclosing stapes; submarginal scutes absent.

GEOLOGIC RANGE.—No fossils known.

GEOGRAPHIC RANGE.—Kenya, south to Tanganyika, Africa.

REMARKS.—The remark by Szalai (1934) that this genus possesses teeth, and that it is thus similar to *Stegochelys* is incorrect. There is only one extant species, *M. tornieri.*

REFERENCES.—Skeleton: Proctor 1922, Wettstein-Westersheim 1924, Siebenrock 1904, Williams 1950b, Richmond 1964.

Genus *Psammobates* Fitzinger

Testudo Linnaeus 1758, p. 199 (part).
Chersine Merrem 1820, p. 32 (part).
Psammobates Fitzinger 1835, pp. 108, 113, 122.
Psammobates Fitzinger 1843, p. 29 (part).
Emys Gray 1844, p. 28 (part).
Clemmys Strauch 1862, p. 32 (part).
Peltastes Gray 1869, p. 173 (part).
Homopus Boettger, 1893, p. 8 (part).
Chersinella Hewitt 1933, p. 259 (not of Gray).

GENOTYPE.—*Testudo geometricus* Linnaeus (=*Psammobates geometricus* [Linnaeus]).

DEFINITION.—Small South African tortoises with triturating surfaces of maxilla not ridged; prootic narrowly exposed dorsally; quadrate enclosing stapes; submarginal scutes absent; gulars divided; gular region not greatly thickened or projected; anterior neurals hexagonal.

GEOLOGIC RANGE.—No fossils known.

GEOGRAPHIC RANGE.—Southern Africa.

REMARKS.—Of all the genera of tortoises, living and extinct, this one has suffered the greatest vacillation in terminology. The most recent species account is in Loveridge and Williams (1957). Three extant species are recognized: *P. geometricus, P. oculifer, P. tentorius.*

REFERENCES.—Skeleton: Siebenrock 1897, Power 1932, Williams 1950b, Auffenberg 1966b.

Genus *Pyxis* Bell

Pyxis Bell 1827, p. 395.
?*Testudo* Boulenger 1889, p. 45.
Bellemys Williams 1950b, p. 553 (in error).

GENOTYPE.—*Pyxis arachnoides* Bell.

DEFINITION.—A monospecific genus of small tortoise from the Mala-

gasy Republic, characterized by a hinge at the anterior lobe of the plastron.

GEOLOGIC RANGE.—No fossils known.

GEOGRAPHIC RANGE.—Malagasy Republic.

REMARKS.—Relationships not clear. Only one species recognized, *P. arachnoides*.

REFERENCES.—Skeleton: Gray 1873c, Williams 1950b.

Genus †*Stylemys* Leidy

Stylemys Leidy 1951a, p. 173 (not of Maack 1869).
Emys Leidy 1851a, p. 173.
Testudo Leidy 1851b, p. 173.
Geochelone Auffenberg 1963, p. 87 (part).
Gopherus Brattstrom 1961, p. 547 (part).

GENOTYPE.—*Stylemys nebrascensis* Leidy.

DEFINITION.—An extinct Holarctic genus of tortoises characterized by a premaxillary ridge; a symphyseal dentary groove; pleurals only slightly alternately narrower and wider laterally; moderately long unspecialized tail with some vertebrae lacking interpostzygopophyseal notches; posterior epiplastral excavation shallower or absent; no hinge on plastron or carapace; pleural bones not, or only slightly differentiated; free proximal portion of ribs long; a single supracaudal scute; nuchal scute longer than wide. The most recent description is that by Auffenberg (1964d). Glaessner (1933) discussed the general problem of "stylemiform" tortoises.

GEOLOGIC RANGE.—Eocene to Miocene of North America, Miocene of Europe and Oligocene of Turkestan, U.S.S.R.

GEOGRAPHIC RANGE.—United States (Oregon, California, Nebraska, Colorado, South Dakota, Utah, Texas), France, and Turkestan.

REMARKS.—Shells described as *Stylemys bottii* from the Miocene of France (Stefano 1902a) and *Stylemys karakolensis* from the Oligocene of Turkestan (Riabinin 1927) may belong to this genus and are provisionally placed here.

Stylemys amphithorax (Cope)

Testudo amphithorax Cope 1873a, p. 6.
Stylemys amphithorax Auffenberg 1962d, p. 9.
Geochelone amphithorax Auffenberg 1963, p. 81 (in error).

TYPE.—American Museum of Natural History; cotypes, various parts of three shells.

TYPE LOCALITY AND HORIZON.—Head of Horsetail Creek, Weld County, Colorado, U.S.A.; Horsetail Creek Member, White River Formation, Chadronian faunal age, Early Oligocene.

GEOLOGIC RANGE.—Early Oligocene.

GEOGRAPHIC RANGE.—Northeastern Colorado and (?) South Dakota, U.S.A.

REMARKS.—For description of skeleton see Auffenberg (1962d).

?*Stylemys †botti* Stefano

?*Stylemys bottii* Stefano 1902a, p. 72.
Stylemys botti Williams 1950a, p. 23.

TYPE.—Presumably in the Museum of the School of Mines in Paris, but not located on inquiry; most of carapace and plastron.

TYPE LOCALITY AND HORIZON.—France; Miocene.

GEOLOGIC RANGE.—Miocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Generic assignment uncertain.

?*Stylemys †calaverensis* Sinclair

?*Stylemys calaverensis* Sinclair 1903, p. 243.

TYPE.—Univ. of California Museum of Paleontology; a partial shell.

TYPE LOCALITY AND HORIZON.—2 mi. S. of Vallecito, Calaveras County, California, U.S.A.; auriferous gravels, Miocene.

GEOLOGIC RANGE.—Miocene.

GEOGRAPHIC RANGE.—Northern California, U.S.A.

REMARKS.—Generic assignment not entirely clear because of fragmentary nature of the specimen.

Stylemys †capax Hay

Stylemys nebrascensis Cope 1885, p. 770 ("No. 2") (part).
Stylemys capax Hay 1908, p. 392, figs. 498-499.

TYPE.—American Museum of Natural History; a complete shell.

TYPE LOCALITY AND HORIZON.—Near junction of North and South Forks of John Day River, Grant County, Oregon, U.S.A.; Middle John Day series, Arikareean faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Central Oregon, U.S.A.

Stylemys †conspecta Hay

Stylemys nebrascensis Cope 1885, p. 769 (part).
Stylemys conspecta Hay 1908, p. 393.

TYPE.—American Museum of Natural History; a shell.

TYPE LOCALITY AND HORIZON.—Near junction of North and South

Forks of John Day River, Grant County, Oregon, U.S.A.; Middle John Day series, Arikareean faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Central Oregon, U.S.A.

Stylemys †karakolensis Riabinin

Stylemys karakolensis Riabinin 1927, p. 193.
"Stylemys" karakolensis Glaessner 1933, p. 360 [sic].

TYPE.—Geological Institute, Academy of Sciences (Leningrad, U.S.S.R.); a complete shell.

TYPE LOCALITY AND HORIZON.—Karakul, E. of Lake Issukkul, Sihkiang Province, Turkestan, U.S.S.R.; Oligocene (or Early Miocene).

GEOLOGIC RANGE.—Oligocene (?).

GEOGRAPHIC RANGE.—Turkestan.

REMARKS.—Thought to be close to *S. conspecta* by Riabinin (1927). Perhaps part of *Geochelone,* subgenus *Indotestudo.*

?Stylemys †ligonia (Cope)

Testudo ligonius Cope 1873a, p. 6.
Testudo ligonia Cope 1873b, p. 19.
?Stylemys ligonia Auffenberg 1962d, p. 8 [sic].
Geochelone ligonia Auffenberg 1963, p. 92 (in error).

TYPE.—American Museum of Natural History; part of nuchal bone, some peripherals and parts of the plastron.

TYPE LOCALITY AND HORIZON.—Head of Horsetail Creek, Weld County, Colorado, U.S.A.; Horsetail Creek Member, White River Formation, Chadronian faunal age, Early Oligocene.

GEOLOGIC RANGE.—Oligocene.

GEOGRAPHIC RANGE.—Northeastern Colorado, U.S.A.

REMARKS.—Probably conspecific with *S. amphithorax* (see Auffenberg 1962d).

Stylemys †nebrascensis Leidy

Emys hemispherica Leidy 1851a, p. 173.
Emys hemispherica Leidy 1851a, p. 173.
Testudo lata Leidy 1851a, p. 173.
Emys oweni Leidy 1851a, p. 327.
Emys culbertsonii Leidy 1852a, p. 34.
Testudo hemispherica Leidy 1852a, p. 59.
Testudo nebrascensis Leidy 1852a, p. 59.
Testudo oweni Leidy 1852a, p. 59.
Testudo culbertsonii Leidy 1852a, p. 59.
Emys nebrascensis Leidy 1852b, p. 65.
Emys lata Leidy 1852b, p. 65.
Stylemys culbertsonii Cope 1870, p. 124.

TYPE.—U. S. National Museum; most of the carapace and plastron.

TYPE LOCALITY AND HORIZON.—South Dakota, U.S.A.; Brule series, Orellan member, White River Formation, Orellan faunal age, Middle Oligocene.

GEOLOGIC RANGE.—Middle Oligocene.

GEOGRAPHIC RANGE.—Nebraska, Colorado, Wyoming, North Dakota, and South Dakota, U.S.A.

REFERENCES.—Skeleton: Case 1925, 1936, Auffenberg 1961, 1964d, 1966b, Hay 1907.

Stylemys †uintensis (Gilmore)

Testudo uintensis Gilmore 1915, p. 150.
?*Stylemys uintensis* Auffenberg 1962d, p. 10.

TYPE.—Carnegie Museum; a complete shell.

TYPE LOCALITY AND HORIZON.—South of Kennedy's Hole, 100 rods west Dragon-Vernal Road, Uinta Basin, Uinta County, Utah, U.S.A.; Horizon B or C., Uinta Formation, Uintan faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Eastern Utah, U.S.A.

REMARKS.—A primitive member of the genus, little differentiated from *Geochelone*.

Genus *Testudo* Linnaeus

Testudo Linnaeus 1758, p. 197.
Chersine Merrem 1820, p. 43 (Type: *T. graeca*).
Emys Meyer 1834, p. 121 (part).
Chersus Brandt 1852, p. 331 (part).
Homopus Blyth 1854, p. 642 (part) (Type: *H. burnesii*).
Peltastes Gray 1869, p. 171 (Type: *T. graeca* L.).
Chersinella Gray 1870b, p. 725 (Type: *T. graeca* L.).
Testudinella Gray 1870b, p. 658 (Type: *T. horsfieldii* Gray).
Peltonia Gray 1872a, p. 4 (Type: *T. graeca* L.).
Medaestia Wussow 1916, p. 170 (Type: *T. graeca* L.).
Stylemys Auffenberg 1964d, p. 121 (part).
Agrionemys Khozatsky and Mlynarski 1966, p. 123 (part) (Type: *T. horsfieldi* Gray).
Agrione Khozatsky and Mlynarski 1966, p. 123 (typographical error).
Protestudo Chkikvadze 1970c, p. 7 (part) (Type: *T. bessarabica*).

GENOTYPE.—*Testudo graeca* Linnaeus.

DEFINITION.—A Eurasian and North African genus of tortoises characterized by the presence of a nuchal scale; suprapygal single or divided and, if divided, a larger anterior one embracing a smaller posterior scale; posterior lobe of plastron more or less movable in one or both sexes. Three subgenera are recognized here: *Pseudotestudo, Agrionemys,* and *Testudo*.

GEOLOGIC RANGE.—Miocene to Recent.

GEOGRAPHIC RANGE.—Recent forms are distributed in Southern Europe, western and south central Asia, and northern Africa. Fossils are found over much of the central and southern part of the Palearctic.

REMARKS.—*Protestudo* of Chkikvadze (1970c) is here considered a synonym of *Testudo* because the generic characters given are not sufficiently distinct in view of those for the remaining testudinid taxa.

Subgenus *Agrionemys* Khozatsky and Mlynarski

Testudo Pallas 1811, p. 19 (part).
Chersus Brandt 1852, p. 331 (part).
Homopus Blyth 1854, p. 642 (Type: *H. burnesii*).
Testudinella Gray 1870b, p. 658.
Agrionemys Khozatsky and Mlynarski 1966, p. 123 (as genus).
Agrione Khozatsky and Mlynarski 1966, p. 123 (typographical error).

TYPE SPECIES.—*Testudo horsfieldi* Gray.

DEFINITION.—A subtropical Asian subdivision of the genus *Testudo* characterized by moderately ridged maxillary; four toes on the anterior limbs; humero-pectoral scute usually crossing posterior part of the entoplastron; and two suprapygal bones in which the upper embraces the lower.

GEOLOGIC RANGE.—Recent only at this writing, but undoubtedly with many Pliocene and Pleistocene members in Asia.

GEOGRAPHIC RANGE.—Turkestan to northwestern West Pakistan.

REMARKS.—Apparently a primitive subgroup of the genus *Testudo*. It may eventually be found that many of the small globular Tertiary and Pleistocene tortoises of Southern Russia and China belong to this subgenus.

Testudo (*Testudo*) *horsfieldi* Gray

Testudo geometrica Pallas 1811, p. 19 (part).
Testudo horsfieldii Gray 1844, p. 74 (Afghanistan).
Chersus iberus Brandt 1852, p. 331 (part).
Homopus burnesii Blyth 1854, p. 642 (Afghanistan).
Testudinella horsfieldii Gray 1870b, p. 658.
Homopus horsfieldi Syevertzov 1873, p. 71.
Testudo baluchiorum Annandale 1906, pp. 75, 205, pl. 2, fig. 1 (Baluchistan).
Agrionemys horsfieldi Khozatsky and Mlynarski 1966, p. 123.

TYPE.—British Museum (Natural History); mounted specimen.

TYPE LOCALITY.—Afghanistan.

GEOLOGIC RANGE.—No fossils known, but included here because some of Plio-Pleistocene fossils will certainly be referred here with further study.

GEOGRAPHIC RANGE.—Eastern shore of the Caspian Sea, Turkestan

to Aral 'Skoye More' (Aral Sea), Iran, Afghanistan, and northwestern West Pakistan.

REMARKS.—The report of a Nepalese specimen (Günther 1864) and verbal accounts of tortoises in the Dera-Dun area of India that seem to represent this tortoise suggest *horsfieldi* will eventually be found to inhabit much of the foothill area of the Himalaya Mountains. The recent erection of *Agrionemys* for reception of *horsfieldi* (Khozatsky and Mlynarski 1966) is not followed here because I consider the purported generic characters within the generic spectrum of variability of *Testudo*.

REFERENCES.—Morphology. Skeleton: Auffenberg 1966b, Williams 1950b, Mlynarski 1966b, Khozatsky and Mlynarski 1966. Serology. Obst and Ambrosius 1971.

Subgenus *Pseudotestudo* Loveridge and Williams

Testudo Lichtenstein 1823, p. 91 (part).
?*Chersus* Fitzinger 1955, p. 252 (part).
Peltastes Gray 1870b, p. 657 (part).
Pseudotestudo Loveridge and Williams 1957, p. 276 (as subgenus).

TYPE SPECIES.—*Testudo* (*Pseudotestudo*) *kleinmanni* Lartet.

DEFINITION.—An African subdivision of the genus *Testudo* characterized by usually having a single supracaudal; maxillary without ridges; larger exposed anterior palatine foramina; quadrate not enclosing stapes; plastron of all adults with clearly movable posterior lobe.

GEOLOGIC RANGE.—No fossils known.

GEOGRAPHIC RANGE.—Western Cyrenaica, Libya east to northern United Arab Republic and northern Sinai.

REMARKS.—Composed of only one species, *T. kleinmanni*, which is close to the *graeca* group according to Loveridge and Williams (1957).

REFERENCES.—Skeleton: Siebenrock 1906, Williams 1950b, Loveridge and Williams 1957.

Subgenus *Testudo* Linnaeus

Testudo Linnaeus 1758, p. 198.
Emys Meyer 1834, p. 121 (part).
Peltastes Gray 1870c, p. 11 (part).
Chersinella Gray 1873c, p. 725, pl. 60, fig. 4 (part).
Stylemys Auffenberg 1964d, p. 121 (part).

TYPE SPECIES.—*Testudo graeca* Linnaeus (=*Testudo* [*Testudo*] *graeca* Linnaeus).

DEFINITION.—A Eurasian subdivision of the genus *Testudo* characterized by a weakly or moderately ridged maxillary; anterior palatine foramen, partially concealed in ventral view; quadrate enclosing stapes;

plastron of adults with more or less movable posterior lobe in one or both sexes.

GEOLOGIC RANGE.—Miocene to Recent.

GEOGRAPHIC RANGE.—Northern Africa, southern Europe, and western Asia.

REMARKS.—Contains three extant species, *T. marginata, T. hermanni,* and *T. graeca,* in addition to the many fossil forms.

REFERENCES.—Morphology. General Anatomy: Thompson 1932; Skeleton: Simonetta 1960.

Testudo †alba (Chkikvadzé)

Protestudo alba Chkikvadze 1971, p. 245, fig. 1.

TYPE.—Georgian Academy of Science (Tbilisi); right epiplastron.

TYPE LOCALITY AND HORIZON.—Georgian S.S.R., eastern Kazakhstan, Zaisan Valley; Upper Oligocene to Lower Miocene.

GEOLOGIC RANGE.—Upper Oligocene to Lower Miocene.

GEOGRAPHIC RANGE.—Georgian S.S.R.

REMARKS.—Originally placed in the genus *Protestudo,* but here considered a synonym of *Testudo.*

Testudo (*Testudo*) *†antiqua* Bronn

Testudo antiqua Bronn 1831, p. 215.
Emys striata Meyer 1834, p. 121.
Testudo striata Giebel 1847, p. 58.
Emys mellingi Peters 1869, p. 122.
Testudo amiatae Pantanelli 1893, p. 129 [sic] (Vindobonian Miocene, Italy).
Testudo noviciensis (Nouel MS) Deperet 1895, p. 412 (Burdagalian Miocene, Austria).
Testudo amiatae Reinach 1900, p. 17 (part).
Testudo promarginata Reinach 1900, p. 74 (part).
?*Testudo neoviciensis* Koch 1904, p. 60 (part) (typographical error).
Testudo antiqua var. *noviciensis* Glaessner 1933, p. 364.
Testudo antiqua noviciensis Mlynarski 1955a, p. 173.
Testudo praeceps Haberlandt 1876, p. 243 (Vindobonian Miocene, Austria).
Testudo kalksburgensis Toula 1896, p. 915 (Vindobonian Miocene, Austria).
Testudo leithi Siebenrock 1915, p. 84 (part).
Testudo antiqua var. *praeceps* Glaessner 1933, p. 362.
Testudo antiqua praeceps Glaessner 1935, p. 125.
Testudo craverii Portis 1879, p. 121 [sic] (Sarmatian Miocene, Italy).
Testudo craveri Pantanelli 1893, p. 135.
Testudo olawari Teppner 1913, p. 384 (typographical error).
Testudo claweri Riabinin 1915, p. 11 (typographical error).
Testudo graweri Bataller 1926, p. 149 (typographical error).
Testudo crawenii Riabinin 1926, p. 60 (typographical error).
Testudo escheri Pictet and Humbert 1856, p. 17 [sic] (Vindobonian Miocene, Switzerland).
Testudo minuta Fraas 1870, p. 51 (in error).

Testudo kalksbergensis var. *steinheimensis* Straesche 1931, p. 4 (Vindobonian Miocene, Germany).
Testudo graeca Koch 1902, p. 311 (part).
Testudo syrmiensis Koch 1904, p. 61 (Pontian Pliocene, Hungary).
Testudo canetotiana Lartet 1851, p. 38 (Vindobonian Miocene, France).
Testudo cannetotiana Szalai 1935, p. 380 (typographical error).
Stylemys canetotiana Auffenberg 1964d, p. 121.
Testudo csakvarensis Szalai 1934, p. 119 (Sarmatien Miocene, France).
Testudo csakvariensis Mlynarski 1966a (typographical error).

TYPE.—Fürsten von Fürstenberg? collection; a shell.

TYPE LOCALITY AND HORIZON.—Hohenhöven, Engen in Hegau, Germany; Late Miocene.

GEOLOGIC RANGE.—Early Miocene to Early Pliocene.

GEOGRAPHIC RANGE.—Early Miocene of Austria. Late Miocene of France, Germany, Austria, Italy, Greece, and Switzerland. Early Pliocene of Poland (Mlynarski 1962) and Hungary (Mlynarski 1955a).

REMARKS.—Good descriptions are found in Campana (1917a) of specimens referred to *T. amiatae* from Tuscany, Italy, and in Meyer (1867) of the type.

Not all workers will agree with my disposition of most species placed in the synonomy of *T. antiqua.* The principal philosophy behind this action is outlined in a series of often confusing statements expressing the close relationship and possible conspecificity of these forms in one combination or another. A comparison of conclusions by Roger 1902, Stefano 1902b, Siebenrock 1915, Glaessner 1933, 1935, Szalai 1934, 1935, Thenius 1951, and Mlynarski 1955a, 1956, 1962, regarding the relationships of these forms (often named on the most meager material) should prove the practicality of the present action.

Siebenrock (1915) and Mlynarski (1955a) consider *Testudo praeceps* Haberlandt to be quite distinct from *antiqua* and the latter states it may be close to *Stylemys.* Thenius (1952) considers the "stylemys" characters of *praeceps* as an individual variation of *antiqua,* with which I concur.

Testudo (*Testudo*) †*bosporica* Riabinin

Testudo bosporica Riabinin 1945, p. 127.

TYPE.—Paleontological Museum (Leningrad); a poor shell.

TYPE LOCALITY AND HORIZON.—Mt. Opouk, near Kertch, Crimea, U.S.S.R.; Sarmatian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Crimea.

REMARKS.—Close to *T. hermanni* or *T. graeca* according to Riabinin (1945); in the *antiqua-graeca* phyletic line according to Khozatsky (1947).

Testudo (*Testudo*) †*catalaunica* Bataller

Testudo catalaunica Bataller 1926, p. 149.

TYPE.—Seminario Councilar de Barcelona (Spain); a shell.

TYPE LOCALITY AND HORIZON.—St. Quirce, near Barcelona, Barcelona Province, Catalonia region, Spain; Vindobonian Miocene.

GEOLOGIC RANGE.—Middle Miocene.

GEOGRAPHIC RANGE.—Northeastern Spain.

REMARKS.—Relationship close to *graeca* group and probably a synonym of *T. antiqua*. *T. catalaunica* var. *irregularis* Bergounioux (1958) is intended as a morphotype, not a subspecies, and therefore has no validity as a trinomial. It is from the same locality as the type.

Testudo (*Testudo*) †*celonica* Bergounioux

Testudo celonica Bergounioux 1958, p. 171; figs. 13, 14; pls. 30, 31.

TYPE.—Seminario Councilar de Barcelona (Spain); a partial shell.

TYPE LOCALITY AND HORIZON.—San Celoni, near Barcelona, Catalonia region, Spain; Vellesian Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Northeastern Spain.

REMARKS.—Probably a synonym of *T. antiqua*.

Testudo (*Testudo*) †*cernovi* Khozatsky

Testudo cernovi Khozatsky 1948, p. 92.

TYPE.—Zoology Institute, Academy of Sciences (Ukranian S.S.R.); anterior parts of carapace and plastron.

TYPE LOCALITY AND HORIZON.—Village Gol'ma, Baltsk region, Ukrainian S.S.R.; Kucurgan deposits, Late Pliocene.

GEOLOGIC RANGE.—Pliocene.

GEOGRAPHIC RANGE.—Ukraine.

REMARKS.—Close to the *antiqua-graeca* line, according to Mlynarski (1955a), and particularly to *T. graeca* and *T. hermanni* (Mlynarski 1968).

Testudo (*Testudo*) †*corroyi* Bergounioux

Testudo corroyi Bergounioux 1933a, p. 508.

TYPE.—Geologic Laboratory, Faculty of Sciences (Marseille, France); a carapace.

TYPE LOCALITY AND HORIZON.—Lutetian Basin of Palette, Aix-en-Provence, Bouches-du-Rhone Dept., France; Lutetian faunal age, Middle Eocene.

GEOLOGIC RANGE.—Middle Eocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Related to the *graeca* group according to Bergounioux (1933a) and near base of the genus *Testudo*. Discussed further by Bergounioux (1935).

Testudo †*darewskii* (Chkikvadze)

Protestudo darewskii Chkikvadze 1971, p. 46, fig. 2.

TYPE.—Georgian Academy of Science (Tbilisi); right epiplastron.

TYPE LOCALITY AND HORIZON.—Georgian S.S.R., eastern Kazakhstan, Zaisan Valley; Middle to Upper Miocene.

GEOLOGIC RANGE.—Middle to Upper Miocene.

GEOGRAPHIC RANGE.—Georgian S.S.R.

REMARKS.—Originally placed in the genus *Protestudo*, but is here considered a synonym of *Testudo*. *T. darewskii* is probably close to *T. alba*.

Testudo (*Testudo*) †*denizoti* Bergounioux

Testudo denizoti Bergounioux 1935, p. 87, pl. 5, fig. 1.
Testudo denizotti Mlynarski 1955a, p. 49 (typographical error in English version only)

TYPE.—Paleontological Laboratory of Geology, Faculty of Sciences (Marseille); a carapace.

TYPE LOCALITY AND HORIZON.—Near Puy Laurens, Tarn Department, France; Stampian faunal age, Middle Oligocene.

GEOLOGIC RANGE.—Middle Oligocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Close to *T. catalaunica* according to Bergounioux (1935). In *antiqua-graeca* phyletic line according to Mlynarski (1955a), Bergounioux (1935), and Bräm (1951).

Testudo (*Testudo*) †*doduni* Gray

Testudo doduni Gray 1831b, p. 47.

TYPE.—Location unknown to author; fragments of shell.

TYPE LOCALITY AND HORIZON.—Castelnaudary, Aude Department, France; Lutetian faunal age, Middle Eocene.

GEOLOGIC RANGE.—Eocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Probably indeterminate.

Testudo (*Testudo*) †*globosa* Portis

Testudo globosa Portis 1890, p. 3.

TYPE.—Firenze Museum; a shell.

TYPE LOCALITY AND HORIZON.—Valley of the Arno River, Tuscany, Italy; Villafranchian faunal age, Early Pleistocene.

GEOLOGIC RANGE.—Early Pleistocene.

GEOGRAPHIC RANGE.—Northern Italy.

REMARKS.—Presumed to be close to the *graeca-hermanni* line by Portis (1890), closest to *T. hermanni* (Mlynarski 1962). *T. szalaii* may be a synonym of *T. globosa.* In *antiqua-graeca* phyletic line and perhaps a synonym of *T. antiqua* (Glaessner 1933).

Testudo (*Testudo*) *graeca* Linnaeus

Testudo graeca Linnaeus 1758, p. 198.
Testudo pusilla Linnaeus 1766, p. 353 (part).
Testudo terrestris Forskal 1775, p. 12 (=*Testudo* [*Testudo*] *graeca terrestris* Forskal, Lebanon Mts., Israel, by Wermuth 1958) (not *Testudo terrestris* of Fermin 1765).
Testudo ibera Pallas 1814, p. 18 (=*Testudo* [*Testudo*] *graeca ibera* Pallas, Middle Kura-Tales in Caucasus by Mertens 1946).
Testudo georgicana Guldenstedt 1814 (*In* Pallas) (nomen nudum)
Testudo ecaudata Pallas 1827, p. 19 (Tiflis, Iran at the Caspian Sea).
Testudo geometrica Hohenacker 1831, p. 364 (Caucasus) (part).
Testudo zolkafa Forskal 1831a, p. 13, *In* Gray (Arabia) (nomen nudum).
Testudo zohalfa Forskal 1835, p. 44, *In* Dumeril and Bibron (Arabia) (nomen nudum).
Testudo mauritanica Dumeril and Bibron 1935, p. 44 (part).
Testudo mauritonica Kercado 1835, p. 35 (typographical error).
Testudo marginata Gervais 1836, p. 309 (not of Schoepff).
Testudo ibera Gervais 1836, p. 309 (not of Pallas).
Testudo whitei Bennett 1840, p. 361 (*In* White).
Testudo graeca var. *mauritanica* Schlegel 1841, p. 106.
Testudo pusilla Strauch 1862, p. 67 (Transcaucasia) (part).
Peltastes marginatus var. *whitei* Gray 1870c, p. 11.
Chersinella graeca Gray 1873b, p. 725, pl. 60, fig. 4.
Testudo zarudyni Nikolsky 1869, p. 369 (=*Testudo* [*Testudo*] *graeca zarudnyi* Nikolsky, Birdschau Prov., Eastern Iran, by Mertens 1946).

TYPE.—Location unknown to author.

TYPE LOCALITY.—Santa Cruz, Oran, Algeria, Africa (by Mertens and Müller 1928).

GEOLOGIC RANGE.—Pleistocene of Morocco (Lecointre 1926), France (Henri-Martin 1946) and Recent.

GEOGRAPHIC RANGE.—Northwestern Africa from Morocco and Malta to Cyrenaica region of Libya.

REMARKS.—See Mertens (1946) for monographic treatment, and Obst and Ambrosius (1971) for a recent discussion of relationships to European members of the genus.

REFERENCES.—Morphology. Tympanum: Filogamo 1849; Bone Histology: Amprino and Godina 1947; Skull: Gray 1873c, Siebenrock 1897,

Bellairs 1949, Staesche 1961; Myology: Favaro 1903, Hacher and Schumacher 1955, Stammer 1959; Hyobranchial Apparatus: Siebenrock 1898, Bender 1914; Skeleton: Lydekker 1889a, Brühl 1896, Siebenrock 1910, Nopsca 1926a, 1926b, Mertens 1936, Khozatsky 1941, Bannikov 1947, Williams 1950b, Loveridge and Williams 1957, Staesche 1961, Auffenberg 1966b; Serology: Obst and Ambrosius 1971.

Testudo (*Testudo*) *hermanni* Gmelin

Testudo hermanni Gmelin 1788, p. 1041 (unknown).
?*Testudo* (*Emys*) †*canstadiensis* Plieninger 1847, p. 208 (Sinterkalk of Wurttemberg).
Testudo graeca bettai Lataste 1881, p. 396 (unknown).
Testudo graeca Boulenger 1889, p. 177 (part).
Testudo graeca var. *boettgeri* Mojsisovics 1888, p. 242 (not *T. boettgeri* Siebenrock) (Orsova, Banat).
Testudo graeca var. *hercegovinensis* Werner 1899, p. 818 (Trebinje, Hercegovina).
Testudo enriquesi Parenzan 1932, p. 1160 (Conca di Elbasson, Skumbi, Central Albania).
Testudo hermanni hermanni Wermuth 1952, p. 161.

TYPE.—None designated originally (Wermuth 1952).

TYPE LOCALITY AND HORIZON.—None designated.

GEOLOGIC RANGE.—Pleistocene of Italy (Campana 1917b) and Wurttemberg (Plieninger 1847) to Recent.

GEOGRAPHIC RANGE.—Southern Italy, Sicily; the Balkans south of the Danube River (except in Dobrua), to the Peloponnesus in Greece, north of the Danube River only in southwestern Romania. Intergrades with *T. h. robertmertensi* on Corsica, Sardinia, and in (?) northern Italy.

REMARKS.—In *antiqua-graeca* phyletic line according to Glaessner (1933).

REFERENCES.—Morphology. Skeleton: Siebenrock 1910, Loveridge and Williams 1957, Auffenberg 1966b; Shell: Staesche 1961; Serology: Obst and Ambrosius 1971.

Testudo (*Testudo*) †*hipparionum* Wiman

Testudo hipparionum Wiman 1930, p. 41, pl. 6, fig. 2-2b.
Geochelone hipparionum Mlynarski 1968, p. 95.

TYPE.—Institute of Vertebrate Paleontology and Paleonanthropology (Peking); a shell.

TYPE LOCALITY AND HORIZON.—Wuhsiang-Hsien, Shansi Province, China; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Northern China.

REMARKS.—Represented in the Shansi Steppe fauna. Yeh (1963a) described and figured a complete specimen referred to this species. Very

poorly defined by Wiman (1930) and undoubtedly conspecific with several of his other species from the same horizon and area. I see no morphological basis for including the species in *Geochelone*.

Testudo (*Testudo*) †*honanensis* Wiman

Testudo honanensis Wiman 1930, p. 43.
Testudo hannonensis Mlynarski 1955b, p. 170 (typographical error).

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking); a shell.

TYPE LOCALITY AND HORIZON.—Hsin-An-Hsien, Honan, China; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene and ?Miocene.

GEOGRAPHIC RANGE.—Honan, Shansi, and Kansu Provinces, China.

REMARKS.—In *antiqua-graeca* phyletic line according to Mlynarski (1955b). Undoubtedly conspecific with other described species from the same horizon and area.

Testudo (*Testudo*) †*hypercostata* Wiman

Testudo hypercostata Wiman 1930, p. 35, pl. 5, fig. 3-36.

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking); a shell.

TYPE LOCALITY AND HORIZON.—Ho Ch'u-Hsien, Shansi Province, China; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Shansi, China.

REMARKS.—A very poorly defined species, probably an individual variant and quite likely conspecific with *T. shensiensis*.

Testudo †*illiberalis* (Chkikvadze)

Protestudo illiberalis Chkikvadze 1971, p. 246, fig. 3.

TYPE.—Georgian Academy of Science (Tbilisi); nearly complete plastron imbedded in nodule.

TYPE LOCALITY AND HORIZON.—Georgian S.S.R., eastern Kazakhstan, Zaisan Valley; Lower to Middle Pliocene.

GEOLOGIC RANGE.—Lower to Middle Pliocene.

GEOGRAPHIC RANGE.—Georgian S.S.R.

REMARKS.—Perhaps close to *Testudo horsfieldi*.

Testudo (*Testudo*) †*kegenika* Khozatsky

Testudo kegenika Khozatsky 1955, p. 51.

TYPE.—Geological Museum, Academy of Sciences (U.S.S.R.); a shell.

TYPE LOCALITY AND HORIZON.—Upper Course Kegen River, Chuladir Ridge, Kazakhstan, S.S.R., U.S.S.R., Alura-Atiau Province, Kegen Region, Tienshan "Neogene" (=Upper Miocene?).

GEOLOGIC RANGE.—"Neogene" (=Upper Miocene?).

GEOGRAPHIC RANGE.—Kazakhstan, S.S.R.

REMARKS.—The age of this fossil tortoise is questionable (Bazhanov and Pigulevsky 1955). Mlynarski (1968) places this species in the genus *Geochelone* without comment. Its characters are such that I prefer to leave it in *Testudo* until proof of another assignment is forthcoming.

Testudo (*Testudo*) †*kucurganica* Khozatsky

Testudo kucurganica Khozatsky 1948, p. 94.

TYPE.—Zoology Institute, Academy of Sciences (Ukrainian S.S.R.); comprised of numerous fragments of shell from 40-50 specimens of different sizes.

TYPE LOCALITY AND HORIZON.Novopetrovka, Alekseeva and other localities in the valley of the Kucurgan River, District Odessa, Ukrainian S.S.R.; Kucurgan deposits, Late Pliocene.

GEOLOGIC RANGE.—Pliocene.

GEOGRAPHIC RANGE.—Ukraine.

REMARKS.—Close to the *antiqua-graeca* group according to Mlynarski (1955a). Close to *T. graeca* and *T. hermanni* according to Khozatsky (1948).

Testudo (*Testudo*) †*lamanoni* Cuvier

?*Testudo* sp. Lamanon 1780, p. 868.
Testudo lamanonii Cuvier 1836, p. 486.
Testudo lamanoni Gervais 1859, p. 438.
Testudo lamanonis Bergounioux 1933a, p. 515 (typographical error).

TYPE.—Museum of Natural History (Paris); an internal mold of a carapace.

TYPE LOCALITY AND HORIZON.—Near Aix-en-Provence, Bouches du Rhone Department, Provence region, France; Oligocene.

GEOLOGIC RANGE.—Oligocene.

GEOGRAPHIC RANGE.—Provence, France.

REMARKS.—In *antiqua-graeca* phyletic line according to Mlynarski (1956). According to Bergounioux (1932) the specimen of this species described by Gervais (1859) belongs to *Clemmys vidali.*

Testudo (*Testudo*) †*lunellensis* Almera and Bofill

Testudo lunellensis Almera and Bofill 1903, p. 106 [sic].
Testudo lunellensis Deperet 1906, p. 12.

TYPE.—Museo Municipales Barcelona; a shell.

TYPE LOCALITY AND HORIZON.—Cavern in Park Guell, Barcelona, Spain; Early Pleistocene.

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Near Barcelona, Spain.

REMARKS.—In the *antiqua-graeca* phyletic line according to Bergounioux (1935). *T. lunellensis* var. *iberica* Bergounioux (1958) is intended as the designation of a morphotype, not a subspecies, and therefore has no validity as a trinomial.

Testudo (*Testudo*) *macarovicii* Mlynarski

Testudo praegraeca ibera Marcarovici and Vancea 1960, p. 377 (nomen illicit.).
Testudo macarovicii Mlynarski 1969b, p. 152 (new name).

TYPE.—Designated by Mlynarski (1969b) as the many isolated fragments of the carapace and plastron in the Geological Institute, A. I. Cuza University (Iasi, Romania).

TYPE LOCALITY AND HORIZON.—Malusteni, Moldavia, Romania; Astian faunal age, Late Pliocene?

GEOLOGIC RANGE.—Late Pliocene?

GEOGRAPHIC RANGE.—Besides the type locality, known from Manastirea, Minzatesti, Plesea, Beresti, Pruth, Roscani, and a number of other localities, all in Moldavia, Romania.

REMARKS.—As Mlynarski (1969b) states this species is extremely close to *T. graeca ibera*. It is indeed a pity that he formally renamed Macarovici and Vancea's *Testudo praegraeca ibera*, when the illegality of their name (Art. 52 and 57, Int. Code Zool. Nomen.) would have afforded a convenient method to place it where it probably belongs—a synonym of *T. graeca*.

Testudo (*Testudo*) *marginata* Schoepff

Testudo tabulata var. *campanulata* Walbaum 1782, p. 124 (nomen illegitum).
Testudo marginata Schoepff 1792, p. 58, pls. 11-12, fig. 1 (unknown).
Testudo graja Hermann 1804, p. 219 (Greece, by Mertens and Wermuth, 1955).
Chersine marginata Merrem 1820, p. 31.
Chersine marginatus Wagler 1833, p. 138.
Testudo campanulata Strauch 1862, p. 65 (Greece).
Peltastes marginatus Gray 1869, p. 173.
Testudo nemoralis Schreiber 1875, p. 557 (Greece).

TYPE.—Location unknown to author.

TYPE LOCALITY—Unknown.

GEOLOGIC RANGE.—No fossils known but included here because of my conviction that further study of European fossils of *Testudo* will indicate its presence.

GEOLOGIC RANGE.—Southern Greece, north to Olymp, the island of Skiros, southern Albania, and (?) Sardinia.

REMARKS.—Considered very close to *T. graeca* by Siebenrock (1910) and placed in *antiqua-graeca* phyletic line by Glaessner (1933). Serological analysis (Obst and Ambrosius 1971) suggests a somewhat more distant relationship to *graeca* and *hermanni*.

REFERENCES.—Morphology. Skeleton: Siebenrock 1910, Williams 1950b, Auffenberg 1966b; Hyobranchial Apparatus: Siebenrock 1898; Skull: Siebenrock 1897; Serology: Obst and Ambrosius 1971.

Testudo (*Testudo*) †*marmorum* Gaudry

Testudo marmorum Gaudry 1862, p. 502.
Testudo (*Chersis*) *marmorum* Hoernes 1892, p. 245.
Testudo marmorem Nafiz and Malik 1933, p. 120 (typographical error).

TYPE.—Paris Museum; almost complete shell.

TYPE LOCALITY AND HORIZON.—Pikermi, Greece; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Greece and adjacent Turkey.

REMARKS.—Posterior part of plastron movable. Best description in Gaudry (1862-7). Nuchal scute *very* narrow. Perhaps in *antiqua-graeca* line, though Mlynarski (1955a) and Glaessner (1933) think not.

Testudo (*Testudo*) †*oriens* Portis

Testudo oriens Portis 1890, p. 9.

TYPE.—Location unknown to author; a shell.

TYPE LOCALITY AND HORIZON.—Valley of the Arno River, Tuscany, Italy; Villafranchian faunal age, Early Pleistocene.

GEOLOGIC RANGE.—Early Pleistocene.

GEOGRAPHIC RANGE.—Italy.

Testudo (*Testudo*) †*pusilla* Bergounioux

Testudo pusilla Bergounioux 1936a, p. 21 (not *T. pusilla* Linn.).

TYPE.—Location unknown to author; partial shell.

TYPE LOCALITY AND HORIZON.—Near Marseilles, Bouches du Rhone Department, France; Stampian faunal age, Middle Oligocene.

GEOLOGIC RANGE.—Middle Oligocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Close to *Geochelone nana* according to Bergounioux (1936a), but retained in *Testudo* here on basis of available material.

Testudo (*Testudo*) †*roguesi* Bergounioux

Testudo rougesi Bergounioux 1936b, p. 58.

TYPE.—Geological Laboratory (Clermont-Feuant, France); a shell.

TYPE LOCALITY AND HORIZON.—Bard near Brioude, Haute Loire Department, France; Oligocene.

GEOLOGIC RANGE.—Oligocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Close to *Testudo antiqua* according to Bergounioux (1936b).

Testudo (*Testudo*) †*semenensis* Bergounioux

Testudo semenensis Bergounioux 1955, pp. 145-152.

TYPE.—Location unknown to author; a carapace.

TYPE LOCALITY AND HORIZON.—Djeber Semene, 110 km SE of Tunis, Tunisia; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Probably in *antiqua-graeca* line.

Testudo (*Testudo*) †*seminota* Portis

Testudo seminota Portis 1890, p. 10, pl. 2, fig. 13.

TYPE.—Location unknown to author; a shell.

TYPE LOCALITY AND HORIZON.—Valley of the Arno River, Tuscany, Italy; Villafranchian faunal age, Early Pleistocene.

GEOLOGIC RANGE.—Early Pleistocene.

GEOGRAPHIC RANGE.—Italy.

REMARKS.—Close to *hermanni-graeca.*

Testudo (*Testudo*) †*serresi* Pictet

Testudo serresii Pictet 1845, p. 20.
Testudo serresi Bergounioux 1938a, p. 279.

TYPE.—Location unknown to author; a shell.

TYPE LOCALITY AND HORIZON.—Montpellier, Herault Department, France; Astian faunal age, Late Pliocene.

GEOLOGIC RANGE.—Late Pliocene.

GEOGRAPHIC RANGE.—Montpellier, France.

REMARKS.—Said to be in same group with *T. globosa, T. oriens,* and *T. seminota* (Bergounioux 1938a).

Testudo (*Testudo*) †*shensiensis* Wiman

Testudo shensiensis Wiman 1930, p. 28, pl. 5, figs. 1-16.
Testudo shansiensis Wiman 1930, p. 36 (not a typographical error).

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking); a shell.

TYPE LOCALITY AND HORIZON.—Fu-Ku-Hsein, Shensi Province, China; Pontian faunal age, Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Shensi and Shansi Provinces, China.

REMARKS.—In *antiqua-graeca* phyletic line according to Glaessner (1933), which see for discussion of *T. shansiensis* and *T. shensiensis*. Yeh (1963a) and Gilmore (1931) describe additional specimens.

Testudo (*Testudo*) †*sphaerica* Wiman

Testudo sphaerica Wiman 1930, p. 33, figs. 2-26.
Terrapene sinica Young 1950, p. 2, figs. 1-2 (Pliocene, China).
Testudo sinica Mlynarski 1955a, p. 164 (Pliocene, China).
Testudo yushensis Yeh 1963a, p. 40 (Pliocene, China).
Testudo honanensis Yeh 1963a, p. 40, pl. XIII (Pliocene, China).
Geochelone shaerica Mlynarski 1968, p. 95 (typographical error).

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking); a shell.

TYPE LOCALITY AND HORIZON.—Pao-Te-Chou, Shansi Province, China; Early Pliocene.

GEOLOGIC RANGE.—Early Pliocene.

GEOGRAPHIC RANGE.—Shansi and Kansu Provinces, North China.

REMARKS.—Not a typical member of the *antiqua-graeca* line, according to Mlynarski (1955a); perhaps closely related to *T.* (*Agrionemys*) *horsfieldi*. Probably conspecific with some other described Pliocene species from North China. Mlynarski (1968) places it in the genus *Geochelone*, but its characters seem more like those of *Testudo*, where I prefer to keep it. The type of *T. yushensis* Yeh is placed here in view of its similarity in morphology and geologic age.

Testudo (*Testudo*) †*suttoensis* Szalai

Testudo suttoensis Szalai 1932, p. 222 (manuscript name).
Testudo suttoensis Szalai 1934, p. 131.
Testudo graeca Kormos 1932, p. 3 (part).

TYPE.—National Museum of Hungary; humerus, femur, coracoid and parts of plastron.

TYPE LOCALITY AND HORIZON.—Sutto, Komarom County, Hungary; Middle Pleistocene.

GEOLOGIC RANGE.—Middle Pleistocene.

GEOGRAPHIC RANGE.—Hungary.

REMARKS.—A poorly defined form close to *T. marginata* (Szalai 1934) and in the "*graeca*-group" (Szalai 1936).

Testudo (*Testudo*) †*szalai* Mlynarski

Testudo szalaii Mlynarski 1955b, p. 164.

TYPE.—Polish Zoologic Institute (Krakow); part of the posterior portion of the shell.

TYPE LOCALITY AND HORIZON.—Bone breccia of Weze, near Dzialoszyn, Lodz Region, Poland; Late Astian and/or Early Villafranchian faunal ages, Late Pliocene and/or Early Pleistocene (perhaps a mixed fauna).

GEOLOGIC RANGE.—Late Pliocene or Early Pleistocene.

GEOGRAPHIC RANGE.—Poland.

REMARKS.—Close to *T. hermanni* according to Mlynarski (1955b). In the *antiqua-graeca* phyletic line and perhaps a synonym of *T. globosa* according to Mlynarski (1962).

Testudo (*Testudo*) †*tunhuanensis* Yeh

Testudinidae Bohlin 1953, p. 63.
Testudo tunhuanensis Yeh 1963a, p. 42, fig. 23-24, pl. XIV, 1-2.

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking); two cotypes: a complete plastron and partial carapace.

TYPE LOCALITY AND HORIZON.—Taben-buluk, Tunhuang, Kansu, China; Miocene?

GEOLOGIC RANGE.—Probably Miocene in age.

GEOGRAPHIC RANGE.—Northern China.

REMARKS.—Probably close to *T. sphaerica.*

Testudo (*Testudo*) †*turgaica* Riabinin

Testudo turgaica Riabinin 1926, p. 54, fig. 2, pl. 4.

TYPE.—Geological Museum, Academy of Sciences (Leningrad); a partial shell.

TYPE LOCALITY AND HORIZON.—Dzhilanchik River, near the Kushuka Wintering Station (Kugaly-Dzhar Land Section) Turgai area, U.S.S.R.; Chattian faunal age, Late Oligocene.

GEOLOGIC RANGE.—Late Oligocene.

GEOGRAPHIC RANGE.—Turgai area, U.S.S.R.

REMARKS.—In *antiqua-graeca* phyletic line according to Glaessner (1933).

Genus Uncertain

?*Testudo* †*castrensis* Bergounioux

Testudo castrensis Bergounioux 1935, p. 53.

TYPE.—Museum d'Histoire Naturelle de Toulouse; a carapace.

TYPE LOCALITY AND HORIZON.—Near Castres, Tarn Department, France; Ludian faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—France.

REMARKS.—Close to *Geochelone richardi* according to Bergounioux (1938a). If correct, this species is probably a *Geochelone.*

?*Testudo* †*chienfutungensis* Yeh

Testudinidae sp. Bohlin 1953, p. 99, pl. IX, figs. 3-4.
Testudo chienfutungensis Yeh 1963a, p. 100, figs. 25-26, pl. XV, 1, 2.

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking); a nearly complete carapace.

TYPE LOCALITY AND HORIZON.—Taben-buluk, Tunhuang, Kansu, China; ?Miocene.

GEOLOGIC RANGE.—?Miocene.

GEOGRAPHIC RANGE.—Type locality only.

REMARKS.—The very narrow shell and presence of intergular scutes suggest that this turtle may not even be a land tortoise. Both Bohlin (1953) and Yeh (1963a) consider these additional scutes as abnormalities.

?*Testudo* †*comptoni* (Bell)

Emys comptoni Bell *In* Owen 1849.
Homopus comptoni Lydekker 1889a, p. 91.
Testudo comptoni Loveridge and Williams 1957, pp. 218-353.

TYPE.—British Museum (Natural History); a partial shell.

TYPE LOCALITY AND HORIZON.—Isle of Sheppey, England; London Clay, Cuisian faunal age, Early Eocene.

GEOLOGIC RANGE.—Early Eocene.

GEOGRAPHIC RANGE.—Isle of Sheppey, England.

REMARKS.—For a discussion of relationships see Loveridge and Williams (1957), who consider it close to *T. scutella.*

?*Testudo* †*ptychogastroides* Reinach

Testudo ptychogastroides Reinach 1900, p. 19.

TYPE.—?Frankfurt Museum, Germany; shell fragment.

TYPE LOCALITY AND HORIZON.—Near Frankfurt a. M., Germany; Burdigalian faunal age, Early Miocene.

GEOLOGIC RANGE.—Early Miocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—Probably not a member of the genus *Testudo.*

?*Testudo* †*reidlii* Hoernes

Testudo reidlii Hoernes 1892, p. 243.
"Testudo"(Ocadia) reidlii Siebenrock 1915, p. 360 [sic].

TYPE.—Vienna Museum; internal cast of shell.

TYPE LOCALITY AND HORIZON.—Oligocene (Sotzka layer) in Trifail.

GEOLOGIC RANGE.—Oligocene.

GEOGRAPHIC RANGE.—Austria.

REMARKS.—Redescribed by Teppner (1913) who placed it in the *antiqua-graeca* line. Possibly an emydid rather than a true tortoise, according to Siebenrock (1915) and Riabinin (1926), with which I concur.

?*Testudo* †*scutella* (Meyer)

Emys scutella Meyer 1845, p. 17, pl. 7, fig. 2.
Homopus scutella Lydekker 1889a, p. 91.
Testudo scutella Loveridge and Williams 1957, p. 353.

TYPE.—Teyler Museum (Haarlem); a partial carapace.

TYPE LOCALITY AND HORIZON.—Switzerland; (?) Late Miocene.

GEOLOGIC RANGE.—(?) Late Miocene.

GEOGRAPHIC RANGE.—Switzerland.

REMARKS.—Thought by Lydekker (1889a) to be close to *Homopus areolatus.* For discussion of relationships see Loveridge and Williams (1957), who considered it close to *Testudo comptoni.*

?*Testudo* †*stehlini* Reinach

Testudo stehlini Reinach 1900, p. 113.

TYPE.—Naturhistorischen Museum (Basel, Switzerland); natural cast of most of carapace, some carapacial bones, and most of the plastron.

TYPE LOCALITY AND HORIZON.—Mathod, near Yverdon, Vaud Canton, Switzerland; Stampian faunal age, Middle Oligocene.

GEOLOGIC RANGE.—Middle Oligocene.

GEOGRAPHIC RANGE.—Switzerland.

REMARKS.—See Bräm (1951) for best description; if his statement is correct that *stehlini* is closely related to *pyrenaica,* then it probably belongs in the genus *Geochelone.*

?*Testudo tungia* Yeh

Testudo tungia Yeh 1963b, p. 224, fig. 1, pl. 1.

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking); a carapace.

TYPE LOCALITY AND HORIZON.—*Gigantopithecus* Cave, Liucheng, Kwangsi, China; Lower Pleistocene.

GEOLOGIC RANGE.—Pleistocene.

GEOGRAPHIC RANGE.—Kwangsi, China.

REMARKS.—Probably not even a testudinid; perhaps referable to the genus *Cuora*.

Genera *Inquirendae*

Genus †*Cheirogaster* Bergounioux

Cheirogaster Bergounioux 1935, p. 78.

GENOTYPE.—*Cheirogaster maurini* Bergounioux (by monotypy).

DEFINITION.—If correctly described, this is a monotypic genus characterized by lack of entoplastron and contact between gular and pectoral scutes.

TYPE LOCALITY AND HORIZON.—Gironde, France; Eocene.

GEOLOGIC RANGE.—Eocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—If correctly interpreted the type shell represents a distinct genus. The presumed distinctive characters are so unusual that a reexamination of the type material is suggested. Bergounioux (1958) correctly points out that his earlier reconstruction of the type species (1935) is greatly in error when compared with the specimen available.

Cheirogaster †*maurini* Bergounioux

Cheirogaster maurini Bergounioux 1935, p. 78.

TYPE.—M. Maurin Borbereaux collection (Gironde, France); a complete shell.

TYPE LOCALITY AND HORIZON.—Gironde, France; Ludian faunal age, Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Type locality.

Cheirogaster †*arrahonensis* Bergounioux

Cheirogaster arrahonensis Bergounioux 1957, p. 1237 (Preliminary notice).
Cheirogaster arrahonensis Bergounioux 1958, p. 175, figs. 15, 16, pls. 32, 33.

TYPE.—Museo de Sabadell (Spain); a partial shell.

TYPE LOCALITY AND HORIZON.—Sabadell, Penedes District, Spain; Vallesian faunal age, Late Miocene.

GEOLOGIC RANGE.—Late Miocene.

GEOGRAPHIC RANGE.—Northeastern Spain.

REMARKS.—Very poorly defined.

Genus †*Floridemys* Williams

Bystra Hay 1916a, p. 53 (preoccupied by *Bystra* Cameron 1902).
Floridemys Williams 1950a, p. 27 (substitute name).

GENOTYPE.—*Bystra nanus* Hay (=*Floridemys nana* [Hay] [by monotypy]).

DEFINITION.—A monotypic genus distinguished by its small size and a transverse gulo-humeral sulcus.

GEOLOGIC RANGE.—Miocene (originally thought to be Pliocene).

GEOGRAPHIC RANGE.—Central Florida.

REMARKS.—The Miocene age here assigned to the species is based on both the stratigraphy at the type locality and additional material from a Miocene site in Alachua County, Florida.

Floridemys †*nana* (Hay)

Bystra nanus Hay 1916a, p. 53, pl. 1.
Floridemys nanus Williams 1950a, p. 27.

TYPE.—U. S. National Museum; a shell.

TYPE LOCALITY AND HORIZON.—Holder Phosphate Mine, near Inverness, Citrus County, Florida, U.S.A.; Hawthorne Formation, Miocene (Early?).

GEOLOGIC RANGE.—Miocene (Early?).

GEOGRAPHIC RANGE.—Central Florida, U.S.A.

REMARKS.—Perhaps congeneric with *Stylemys*, but the small adult size (105 mm. carapacial length) and the transverse gulo-humeral sulcus suggests that *nana* should be retained in a distinct genus. Final judgment will have to await additional material. The ending of the species name has been changed to correspond with the feminine gender of *Floridemys*.

Genus †*Kansuchelys* Yeh

Kansuchelys Yeh 1963a, p. 28.

GENOTYPE.—*Kansuchelys chiayukuanensis* Yeh.

DEFINITION.—Small to medium tortoises with hexagonal neurals throughout the series, and a doubly notched epiplastral projection.

GEOLOGIC RANGE.—Tertiary (Oligocene or Eocene?).

GEOGRAPHIC RANGE.—China.

REMARKS.—A very poorly defined genus, undoubtedly very close to, and perhaps a synonym of the subgenus *Manouria* (Genus *Geochelone*). Almost the entire reference to this genus by Mlynarski (1968) is incorrect.

Kansuchelys †chiayukuanensis Yeh

Kansuchelys chiayukuanensis Yeh 1963a, p. 28.

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking); a nearly complete shell.

TYPE LOCALITY AND HORIZON.—Shih-erh-ma-cheng, north of Hui-hui-p'u, Chia-yu-kuan, Kansu, China; Tertiary, exact horizon unknown.

GEOLOGIC RANGE.—Oligocene or Eocene?

GEOGRAPHIC RANGE.—Type locality only.

REMARKS.—A good specimen of fossil tortoise and important zoogeographically; unfortunately with very poor data.

Kansuchelys †ovalis Yeh

Kansuchelys ovalis Yeh 1963a, p. 33.

TYPE.—Institute of Vertebrate Paleontology and Paleoanthropology (Peking).

TYPE LOCALITY AND HORIZON.—Unknown, probably from Yushe, Shansi, China.

GEOLOGIC RANGE.—Unknown.

GEOGRAPHIC RANGE.—Unknown.

REMARKS.—It is unfortunate that this poorly defined species was ever described.

Genus *†Sinohadrianus* Ping

Sinohadrianus Ping 1929, p. 232.

GENOTYPE.—*Sinohadrianus sichuanensis* Ping.

DEFINITION.—An extinct Asiatic genus with neural plates comparatively narrow, most neurals hexagonal; plastron extensively united to carapace; entoplastron wholly in front of pectoral scutes.

GEOLOGIC RANGE.—Eocene.

GEOGRAPHIC RANGE.—Honan, China and Japan.

REMARKS.—The single imperfect shell of the type displays almost no distinctive features. If it is a tortoise, it is probably more primitive than *Hadrianus*. Yeh (1963a) states that it is not close to *Hadrianus*, and I agree.

Sinohadrianus †eozensis Shikama

Sinohadrianus eozensis Shikama 1953, p. 20, figs. 1-4, pl. 2.

TYPE.—?Natural Science Museum (Tokyo); carapace.

TYPE LOCALITY AND HORIZON.—Utosinai Coal Mine, Utosinai, Japan; Eocene.

GEOLOGIC RANGE.—Eocene.

GEOGRAPHIC RANGE.—Japan.

REMARKS.—Not well defined.

Sinohadrianus †sichuanensis Ping

Sinohadrianus sichuanensis Ping 1929, p. 232, figs. 1-2, pls. 1-2.

TYPE.—Institute of Paleontology and Paleoanthropology (Peking); a poorly preserved shell.

TYPE LOCALITY AND HORIZON.—Fan Chuang, Si Chuan, Hsien, Honan, China; Late Eocene.

GEOLOGIC RANGE.—Late Eocene.

GEOGRAPHIC RANGE.—Type locality.

REMARKS.—See *Sinohadrianus*.

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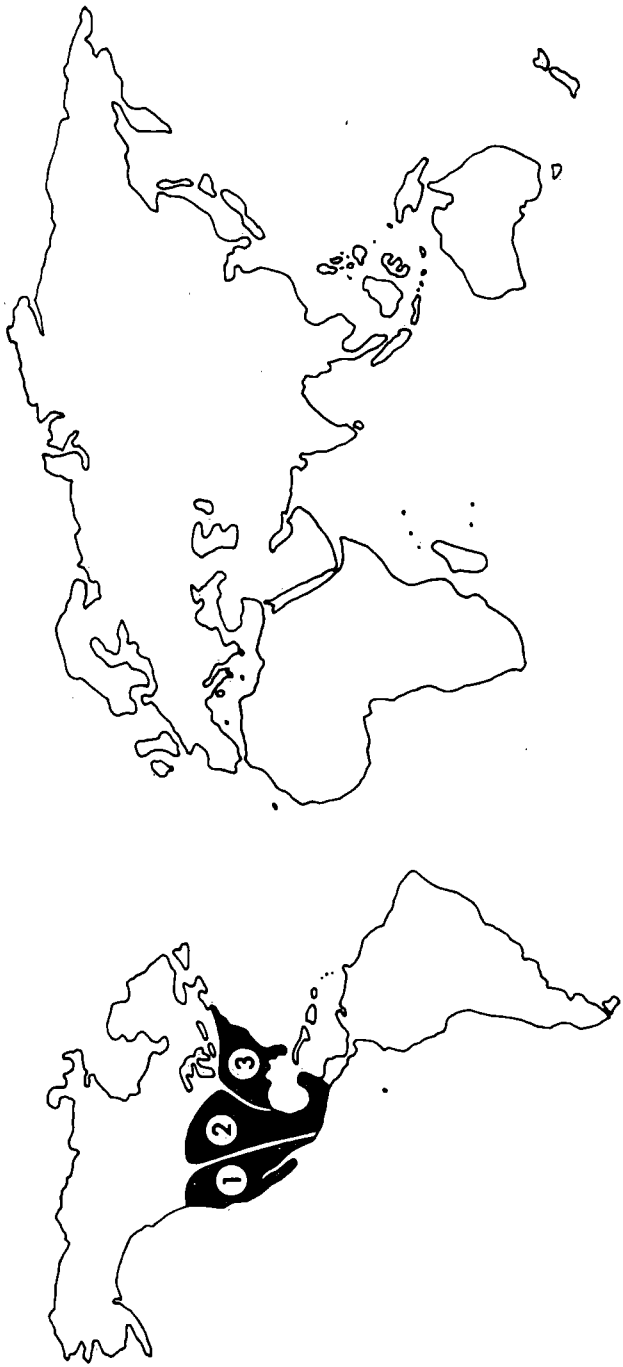
APPENDIX A

The Geologic and Geographic Distribution of Valid Land Tortoise Species Known as Fossils

1.—The Genus *Gopherus*.

Time	Area 1	2	3
Recent	*agassizii*	*berlandieri* *flavomarginatus*	*polyphemus*
Pleistocene	*agassizii*	*huecoensis* *laticaudatus* *flavomarginatus* *atascosae* *canyonensis*	*polyphemus*
Pliocene		*pertenuis*	sp.
Miocene	*brattstromi* *dehiscus* *mohavetus*	*pansus* *brevisternus* *copei* *undabunus* *edae* *emiliae*	
Oligocene	*neglectus*	*laticuneus* *praeextans*	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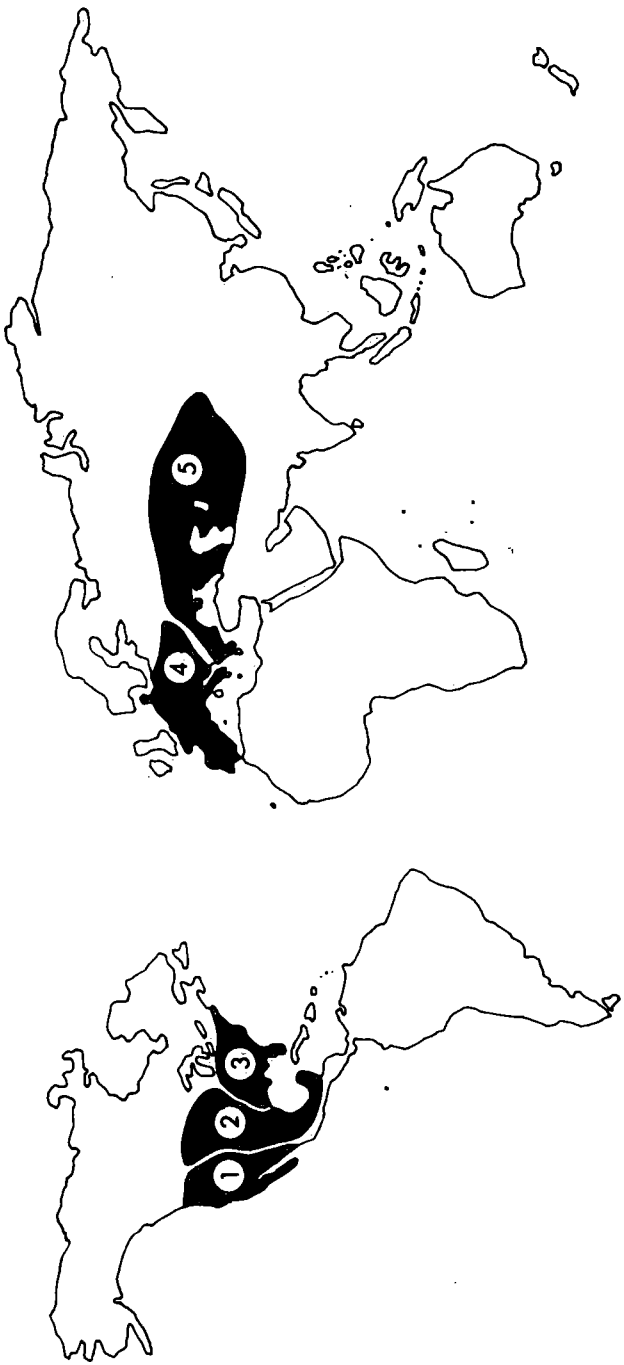
APPENDIX A (CONTINUED)

2.—THE GENUS *Stylemys**

Time	Area 1	2	3	4	5
Recent					
Pleistocene					
Pliocene					
Miocene	*calaverensis* *capax* *conspecta*		genus (*Floridemys*?) sp. *botti*(?)		
Oligocene		*amphithorax* *ligonia*(?) *nebrascensis*			*karakoliensis*(?)
Eocene		*uintensis*			

*(?) = generic designation not definite.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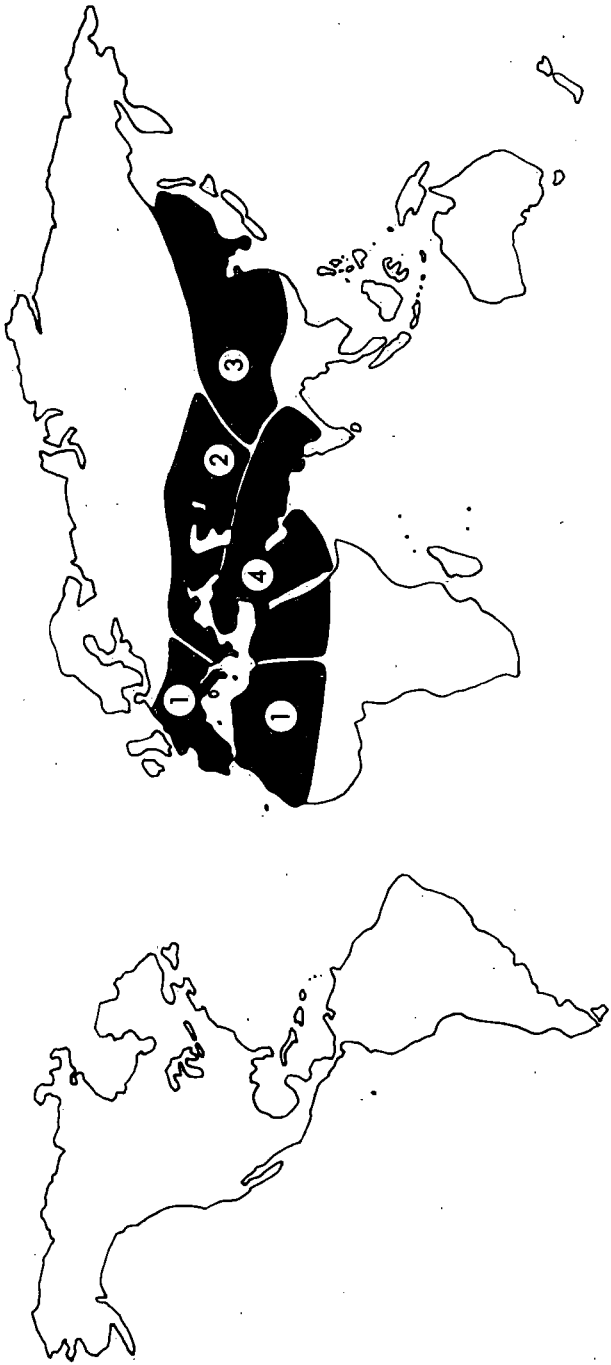
APPENDIX A (CONTINUED)

3.—THE GENUS *Testudo*[*]

Time	Area 1	2	3	4
Recent	*graeca* *hermanni* *lunellensis*	*graeca* *hermanni* *marginata*		*horsfieldi* *graeca* *kleinmanni*
Pleistocene	*graeca* *seminota* *globosa* *oriens*	*hermanni* *suttoensis*	*tungia*(?)	
Pliocene	*szalai* *antiqua* *serresi* *semenensis*	 *cernovi* *kucurganica* *marcarovicii* *illiberalis* *marmorum*	 *sinica*(?) *shensiensis* *sphaerica* *hypercostata* *honanensis* *hipparionarum*	 *marmorum*
Miocene	*celonica* *scutella*(?) *catalaunica* *ptychogastroides*(?) *antiqua*	*darewskii* *bosporica* *kegenika*	*tunhuanensis*	
Oligocene	*stehlini*(?) *lamononi* *denizoti* *pusilla* *roguesi* *reidli*(?)	*alba* *turgaica*		
Eocene	*doduni* *corroyi* *castrensis*(?) *comptoni*(?)			

[*](?) = generic designation not certain. Subgeneric designations have been avoided in view of the unsettled taxonomic situation in both fossil and living populations belonging to this genus.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APPENDIX A (CONTINUED)

4.—FOSSIL SPECIES OF THE GENUS *Geochelone*, SUBGENUS *Manouria**

Time	Area 1	2	3	4	5
Recent				*impressa* *emys*	
Pleistocene					
Pliocene			*punjabiensis*		
Miocene					
Oligocene					
Eocene	*corsoni* *gilmorei* *majusculus* *tumida* *utahensis*	*eocaenica*			*insolitus* *obailiensis* genus (*Kansuchelys*?) genus (*Sinohadrianus*?)

*Genera *Kansuchelys* and *Sinohadrianus* may be synonyms.


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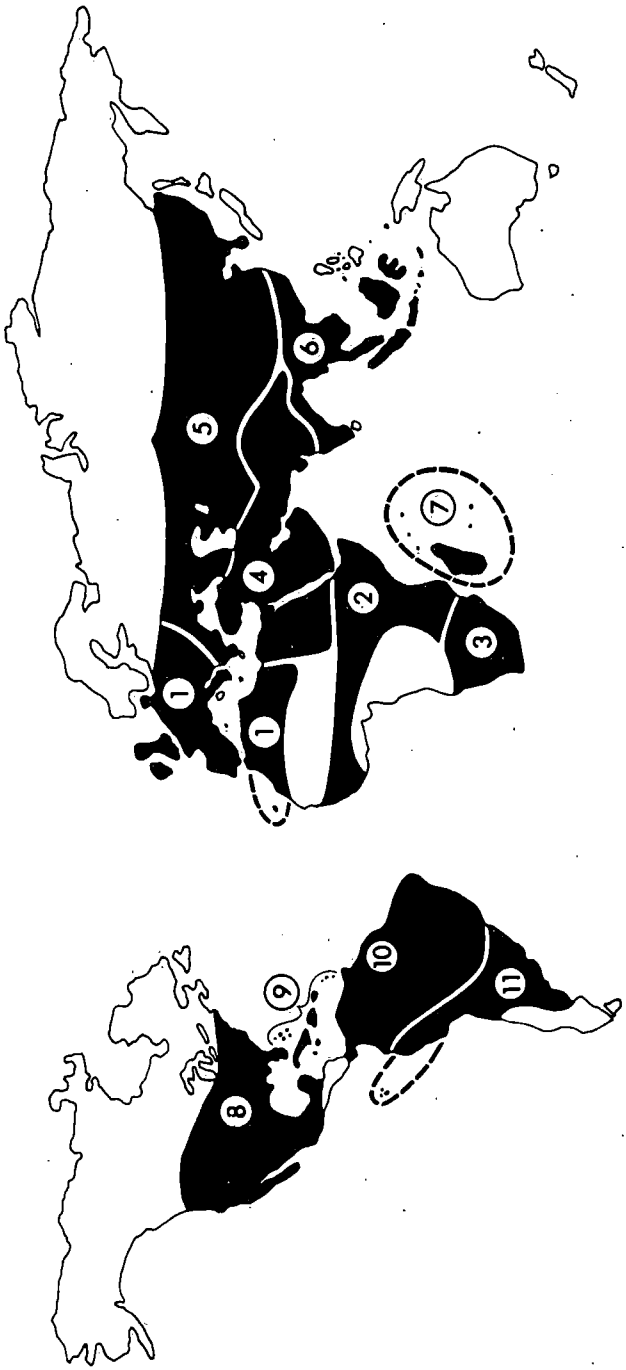
APPENDIX A (CONTINUED)

5.—FOSSIL SPECIES OF THE GENUS *Geochelone* (EXCEPTING SUBGENUS *Manouria*)* (See next page for figure).

Time	1	2	3	4	5
Recent		*pardalis* (Ge)	*pardalis* (Ge)	*elegans* (Ge)	
Pleistocene	*amberiacensis* (Ge) *burchardi* (Ge) *gymnesica* (Ge) *robusta* (Ge)	*pardalis* (Ge)	*pardalis* (Ge)	*atlas* (Me) *cautleyi* (Me)	*kalganensis* (He)
Pliocene	*perpiniana* (Ge) *pyrenaica* (Ge)			*schafferi* (?) *sloanei* (?)	*grandis* (Ge) *bessarabica* (?) *oskarkuhni* (?)
Miocene	*bolivari* (Ge) *picteti* (Ge) *vitodurana* (Ge) *larteti* (?)	*crassa* (Ge)	*namaquensis* (Ge)		*turgae* (Ge) *tarakliensis* (?)
Oligocene	*richardi* (Ge) *chaileoti* (?) *phosphoritarum* (?)				*nana* (In) *yunnanensis* (?) *meschetica* (Ge)
Eocene				*ammon* (Ge) *beadnelli* (Ge) *isis* (Ge)	*kaiseni* (In) *ulanensis* (?)

*Subgeneric designations in parentheses behind species names, as follows: Al=*Aldabrachelys*, As=*Asterochelys*, Ca=*Caudochelys*, Ch=*Chelonoides*, Cm=*Cymatholcus*, Cy—*cylndraspis*, Ge =*Geochelone*, He=*Hesperotestudo*, In=*Indotestudo*, Me=*Megalochelys*, Mo=*Monochelys*, ?=subgenus inquirendae, *=species became extinct within historic times.

6	7	8	9	10	11
travancorica (In) *forsteni* (In) *elongata* (In) *platymota* (Ge)	*peltastes** (Cy) *vosmaeri** (Cy) *yniphora* (As) *radiata* (As) *gigantea* (Al) *indica** (Cy) *sumeirei** (Al) *grayi** (Cy)		*carbonaria* (Ch)	*carbonaria* (Ch) *denticulata* (Ch)	*chilensis* (Ch) *elephantopus* (Ch)
atlas (Me)	*radiata* (As) *gigantea* (Al) *abrupta* (Al) *grandidieri* (Al) *grayi* (Cy) *gadowi* (Me)	*annae* (Ca) *crassiscutata* (Ca) *francisi* (Ca) *equicomes* (He) *incisa* (He) *johnstoni* (He) *wilsoni* (He)	*cubensis* (Ch) *sombrerensis* (Ch) *monensis* (Mo)	*elata* (Ch)	*chilensis* (Ch) *sellowi* (Ch)
		orthopygia (He) *riggsi* (He) *turgida* (He) *undata* (He) *hayi* (Ca) *alleni* (He) *campester* (He) *niobrarensis* (He)			*gallardoi* (Ch)
		inusitata (He) *impensa* (He) *arenivaga* (He) *klettiana* (He) *orthopygia* (He) *primaeva* (He) *vaga* (He) *gilberti* (He) *farri* (He) *williamsi* (Ca) *tedwhitei* (Ca) *milleri* (Ca) *ducatelli* (Ca)		*hesterna* (Ch)	*gringorum* (Ch)
		quadrata (?) *peragrans* (?) *cultrata* (?) *exornata* (He) *brontops* (Ca) *thompsoni* (?)		*costaricensis* (?)	
		longus (Cm) *schucherti* (Cm)			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Index to Species and Subspecies[5]

[5] Valid taxa are italicized. Page numbers in bold face type indicate the major species reference.

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