BULLETIN

OF THE

FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 10 Number 5

THE CARPUS OF LAND TORTOISES (TESTUDININAE)

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1853

UNIVERSITY OF FLORIDA
Gainesville
1966

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

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Communications concerning purchase or exchange of the publication and all manuscripts should be addressed to the Managing Editor of the Bulletin, Florida State Museum, Seagle Building, Gainesville, Florida. 32601

Published February 18, 1966 Price for this issue $.55

THE CARPUS OF LAND TORTOISES (TESTUDININAE)

by

WALTER AUFFENBERG [1]

SYNOPSIS: This study of the manus of 30 species of living and fossil tortoises shows their structure to be considerably more variable than formerly presumed. The carpal pattern of each of the species studied is described and most are illustrated diagrammatically. Certain basic structural patterns reflect both the phyletic relationships of these species and the kinetics of the foot and stresses placed on it during locomotion.

The carpal architecture of tortoises is easily derived from that of a generalized amphibian or a primitive reptilian arrangement. Some species of tortoises possess a distinct proximal centrale, here reported for the first time in any reptile. Other dissimilarities between the carpus of the tortoises and those of other reptiles are probably due to simple loss and/or fusion of elements, fusion being apparently much more common than loss in tortoises. The probable homologies of tortoise carpal elements are discussed. Trends in morphological and functional evolution of the carpus are: (1) subradial and subulnar lateral migration of elements, (2) fusion of proximal subradial and subulnar elements, and (3) fusion of distal carpal elements.

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[1] The author is Associate Curator in Herpetology, Florida State Museum. Most of his researches have dealt with the evolutionary biology of amphibians and reptiles. Earlier contributions to the Bulletin concern fossil turtles and the musculature of salamanders. Manuscript submitted 7 October 1965.—ED.

Auffenberg, Walter. 1966. The Carpus of Land Tortoises (Testudininae). Bull. Florida State Mus., vol. 10, no. 5, pp. 159-191.

INTRODUCTION

The aim of this paper is to describe the morphology and major functional features of the carpus of land tortoises. It is part of a continuing study of the evolution and systematics of fossil and Recent tortoises of the world.[2] A study of the tarsus of land tortoises is presently under way.

A summary of the functions and evolution of the amphibian and reptilian tarsus has been published (Schaeffer, 1941), but no similar study has been made of the carpus. Some general accounts of the carpus in reptiles are available (Hoffman, 1890; Romer, 1933 and 1956; Sieglbaurer, 1909; Williston, 1925; *et al.*), and numerous isolated papers describe the carpus of specific reptile and amphibian groups (Baur, 1885, 1888; Dollo, 1929; Gegenbauer, 1864; Gregory, Miner and Noble, 1923; Hartmann-Weinberg, 1929; Howell, 1935; Nauck, 1924; Rabl, 1916; Ribbing, 1909; Romer, 1933, 1956; Sieglbaurer, 1909; Sjögren, 1940; Steiner, 1920-1921; Wiedersheim, 1876; Williston, 1914; *et al.*). The carpus of the land tortoises has never been extensively studied, and those of only a few species have been described in detail (Flower, 1924, 1933; Hewitt, 1937; Schmidt, 1919; *et al.*). Though no comprehensive treatise is available on the development of the carpus of land tortoises, Hoffman (1890) discusses certain aspects of the carpal embryology of *Geochelone denticulata*, Walker's paper on *Chrysemy's* (1947) is pertinent, and Shah and Patel (1964) have recently described the myology of the front limb of a land tortoise.

The present study indicates that the carpus of tortoises exhibits considerably more individual and ontogenetic variation than was generally presumed. Yet within this extreme range of individual diversity a series of basic structural patterns is manifest, each characterizing the major tortoise groups currently recognized. The structural patterns reflect the relationships of these groups to one another, as well as the kinetics of the foot and the stresses placed upon it during locomotion.

The articulated front feet of 30 species of land tortoises were examined. Individual and ontogenetic variations were studied in those species for which a number of skeletons was available. Diagrammatic drawings of each of the feet examined provide a more uniform basis for comparison of the considerable variation in the shape of the individual elements. Articular details and the presence or absence of certain units are considered more important than minor variations in shape.

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[2] Partially supported by NSF GB1362, GB2725, and the American Philosophical Society.

Discussion of the functional aspects is necessarily superficial because of the lack of living material representing all the major carpus patterns known in tortoises. The function of the carpus and its relation to the movements of the front limb and body as a whole was studied from slow motion photographs showing the locomotor patterns of tortoises of several different genera. Analysis of these photographs, together with experiments on the kinetics of preserved feet and skeletal material, provided data useful in interpreting the variation and pattern of carpal architecture.

This study could not have been completed without the assistance of a great number of persons, to whom I owe my deepest appreciation. In particular I wish to thank the individual curators of the collections listed below for permision to examine skeletal material in their care:

AMNH—American Museum of Natural History (Charles M. Bogert)
BMNH—British Museum of Natural History (Alice G. C. Grandison)
BNHS—Bombay Natural History Society (J. C. Daniel)
CAS—California Academy of Sciences (A. Leviton)
CMNH—Chicago Museum of Natural History (Robert Inger)
MCZ—Museum of Comparative Zoology (Ernest E. Williams)
PPHM—Panhandle-Plains Historic Museum (Jack Hughes)
SNHM—Stanford Natural History Museum (George Myers)
UCM—University of Colorado Museum (Paul Maslin)
UK—University of Kansas (William Duellman)
UMMP—University of Michigan Museum of Paleontology (Claude H. Hibbard)
UMMZ—University of Michigan Museum of Zoology (Charles Walker)
USNM—United States National Museum (D. Cochran)
UT—University of Texas (Frank Blair)
UT-A—University of Tel-Aviv (H. Mendelsohnn)
VNHM—Vienna Naturhistorishe Museum (Josef Eiselt)
ZSI—Zoological Survey, India (M. N. Archarji)

HOMOLOGIES AND MAJOR PATTERNS

The distal ends of both the radius and ulna of land tortoises are always expanded in the same plane, forming a firm, linear foundation for the carpals, which are similarly aligned. The structural plan of the manus is usually plantigrade or digitigrade; the phalangeal arrangement is always palmate. Being in a single plane, the carpus is effective in transferring the weight of the front part of the animal to the toes. Shrearing stresses are controlled by strong, sheet-like ligaments that bind the entire bony complex together.

The usual number of bones in the carpometacarpus of extant tortoises is 12, though fusion and/or loss may reduce them in some species to as few as 5. Regardless of number or homology, the elements comprising the carpus in the tortoises tend to be distributed in three rows. The upper row is usually composed of three bones; one articulates with the distal end of the radius, a more medial and usually smaller element articulates with both the radius and the ulna, and the last articulates with the distal end of the ulna. The two lateral elements may be fused to more distal members in some species. The number of elements comprising the middle row varies from one to three. Each is normally articulated with one or more elements in the proximal series and with one or more distal carpals; or these middle elements may be fused with either of these series or with adjacent lateral elements. A median element lying between the proximal row of central and the distal carpals is often all that remains of this series. Five distal carpals (true carpals) usually comprise the lower row, though fusion with one another, or with adjacent medials (centrals), or with metacarpals is common. The outer distal carpals may articulate with either the radius or the ulna.

Metacarpals I-V are usually present, but fusion with adjacent phalanges or with the distal carpals is common. There are never more than two phalanges in each digit, though the proximal phalanges may be fused with the adjacent metacarpals. Most species have 5 digits, a few only 4, and in some species the number characteristically varies between 4 and 5. The pisiform when present usually articulates with the ulna and one of the external carpals; when absent it is represented by a cartilaginous element of variable density in the sheet of connective tissue that binds the carpals together.

The homologies of the elements comprising the turtle carpus have not yet been established beyond question. In fact the problem of homology in even the generalized reptilian carpus has not been completely solved. This is due partly to the fact that the carpal structure of early tetrapods is quite variable (Romer, 1956, *et al.*). The pattern found in rhachitomous amphibians, such as *Eryops*, is presently believed to be close to the ancestral type (Gregory, Miner, and Noble, 1923; Romer, 1956). In these amphibians four elements make up the proximal carpal series, the radiale, proximal centrale, intermedium, and ulnare (Fig. 1A). The intermedium and radiale are separated by the proximal centrale. A series of medial centrals (medialia) extends from below the radiale to below the proximal centrale, and between the proximal series and the distal carpals. For convenience these centrals are usually distinguished as medialia 1, 2, and 3. Most

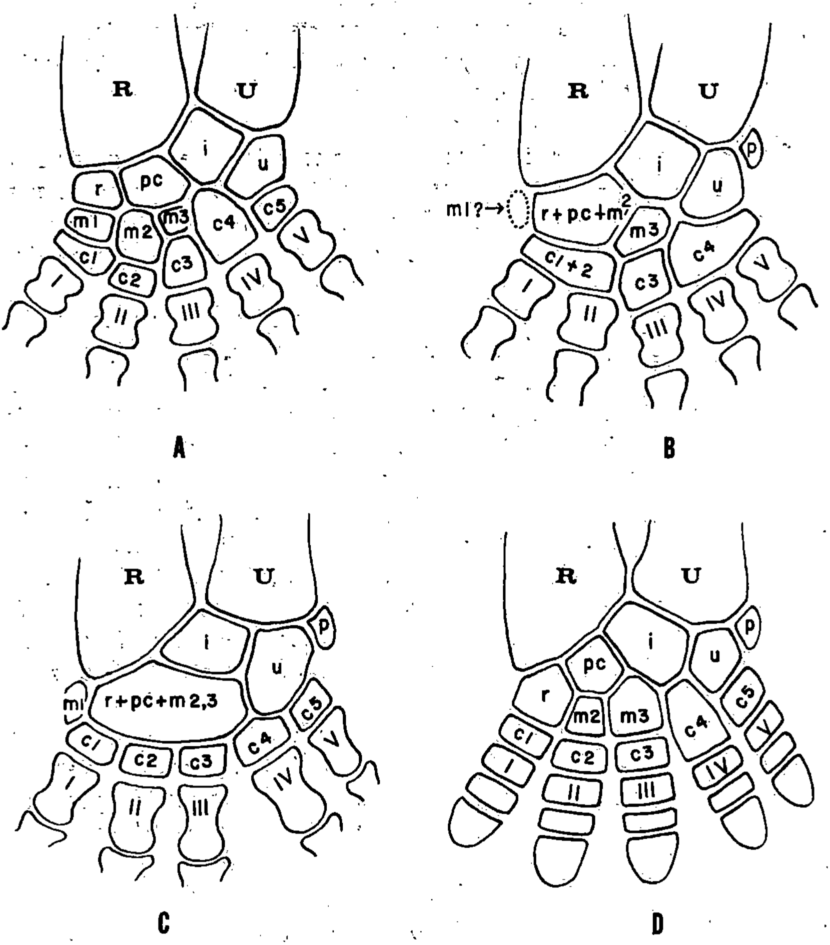

FIGURE 1. (A) The carpus of a primitive, generalized amphibian, such as *Eryops* (modified from Romer, 1956). (B) The carpus of a primitive, generalized reptile (modified from Romer, 1956). (C) The carpus of a pond turtle, genus *Chrysemys*. (D) Hypothetical carpal pattern of a primitive tortoise.
Abbreviations: R = radius, U = ulna, r = radiale, pc = proximal centrale, i = intermedium, u = ulnare, p = pisiform, m 1-3 = medialia 1-3, c 1-5 = carpals 1-5, I-V = metacarpals of digits one through five; me = metacarpal, ph = phalange.

reptilian anatomists believe that medialia 2 and 3 were lost by the time the early reptilian carpal arrangement had become firmly established (Romer, 1956). Mediale 1 is believed to have been lost soon thereafter.

In the early reptilian carpal pattern the weight transmitted from the radius is borne by the radiale and thence through the carpals to digits one and two. Digit three is supported by the proximal centrale and digits four and five by the ulnare. This arrangement permits a more even distribution of weight through all the digits than does the generalized amphibian type.

The pisiform makes its first appearance with the early reptiles, where it is associated with the insertion of the *M. flexor carpi ulnaris.* It is present in some tortoises. When it is absent the tendon of the *flexor carpi ulnaris* inserts on the surface of the sheet of connective tissue that surrounds the carpus.

The carpal architecture of most tortoises is actually more easily derived from the generalized amphibian type than that believed to represent the earliest reptilian arrangement. This is because the number and disposition of carpal elements in tortoises is similar to that in generalized rhachitomes. Thus the differences between the carpus of tortoises and generalized reptiles are probably only a matter of loss and/or fusion of elements. Though phylogenetic evidence is lacking, irrevocable structural data prove that in at least the tortoises, fusion of carpal elements is much more common than loss. This proof is founded partly on the fact that all stages of such fusion can be seen in a selected series of certain species of tortoises, from two discreet adjacent elements to adjacent elements fused in either the left or right carpus and still divided on the other side, to complete fusion of the same elements. Different degrees of fusion are occasionally seen between the right and left carpi of one individual. Furthermore, the tendency to fuse increases with age; in several species the juveniles and subadults often lack the fusion patterns characteristic of the adults.

In addition to structural evidence suggesting fusion of carpal elements in tortoises, Hoffman's (1890) embryological studies have clearly demonstrated the presence of two or more centers of ossification in some elements that in the adult stage are represented by only one large unit.

Though fusion of carpal elements is the commoner tendency in tortoises, simple loss of elements also occurs. This is clearly the case in the lack of ossification of the pisiform in some species or the loss of a complete digit, as in *Testudo horsfieldi.*

In at least the genus *Gopherus,* an additional element between the radiale and intermedium articulates with the radius. This is interpreted here as being homologous to the proximal centrale of the early amphibians. Not only is the element in the same position, but it functions in a similar manner. To my knowledge the proximal centrale has not been reported previously in any other reptile genus.

The element usually referred to as the radiale in all other tortoises is undoubtedly the proximal centrale plus the radiale of more generalized amphibians. These two elements remain distinct in some species of tortoises. The intermedium and ulnare of the testudinines are probably homologues of those elements given the same names in primitive amphibians. As in the rhachitomous amphibians, carpals 4 and 5 usually articulate with the ulnare, and carpal 3 articulates with mediale 3. Carpals 1 and 2 have migrated inwards with the loss of the hypothetical prepollex.

This interpretation, based mainly on the carpus of *Gopherus,* does not modify the conclusions of others regarding the homology of the generalized reptile or cotylosaur carpus, but simply suggests that the variation in basic carpal patterns within the early reptiles was probably even greater than is generally presumed. An alternate, less tenable interpretation is that the element between the composite radiale and the intermedium in tortoises is a new, additional central member, not homologous to any found in the early reptiles or the Paleozoic amphibians.

Another important feature of the carpus of *Gopherus* is that carpal 4 completely separates the ulnare from mediale 3. This pattern is also found in the primitive amphibian carpus and is approached in some of the early reptilian types. All these structural features suggest that some of the tortoises may be less modified from a generalized primitive amphibian or reptilian carpal arrangement than is often implied. Unfortunately no specimen of the earliest of fossil tortoises (*Geochelone*?, *Testudo,* and *Stylemys* from Middle and Upper Eocene deposits) has a complete carpus, nor has a complete carpus been found with the earliest fossil specimens of the genus *Gopherus* (Lower Oligocene of central North America).

In reconstructing the primitive or pretortoise carpal pattern from embryological evidence, from structural patterns of later fossil and Recent tortoises, and from the evidence afforded by both normal and abnormal conditions in modern species, one is led to the conclusion that this carpus must have been composed of 12 elements distributed in three rows (Fig. 1, D), as in generalized rhachitomes. Below a proximal series of four elements, the radiale, proximal centrale, intermedium, and ulnare aligned side to side under most of the radius and ulna, must have been two elements, probably homologous with medialia 2 and 3 of Romer (1956). Mediale 1 was already lost by this stage, though it may be represented by a small, medial subradial element in less specialized genera such as *Pseudemys* and *Podocnemys*. Proximally mediale 2 articulated with the radiale and the proximal central, and mediale 3 articulated with the proximal central and the intermedium. Distally was a series of five carpals; proximally carpal 1 articulated with the radiale, carpals 2, 3, and 4 with the mediale 2 and 3 respectively, and carpal 5 with the ulnare. Distal to the five carpals were five metacarpals. A pisiform, still of common occurrence in diverse turtle groups, was probably present.

Following the primary stages, the general trends of carpal evolution in the tortoises seem to have included (1) migration of subulnar and subradial elements externally, (2) fusion of subulnar and subradial elements, and (3) fusion of more distal elements (Fig. 2). Loss of elements seems most frequent at the external border of the carpus below the outer edge of the ulna. The same tendencies are observed in the modification of the digital elements as well.

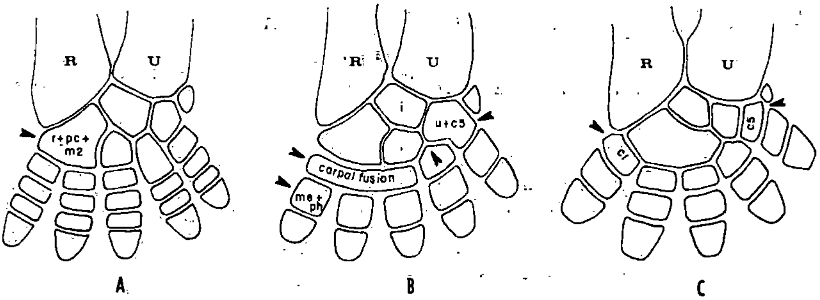

FIGURE 2. Major trends in the evolution of the tortoise carpus: (A) Fusion of subradial elements. (B) Fusion of more distal elements, fusion of proximal subulnar elements, and failure of carpal 4 to contact the intermedium. (C) Lateral migration of subulnar and subradial elements and fusion of medialia.

The external migration of subradial and subulnar carpal elements is apparently affected by the decrease of the proximal, sub-brachial elements (radiale through ulnare), and the upward rotation of the lateral distal carpals 1 and 5 until they come in contact with the radius and ulna respectively (Fig. 2, C). This trend apparently begins on either the internal or the external carpal surfaces, but never on both at the same time. This is clearly shown in both fossil and primitive living species of tortoises. Whether this migration initiated on one surface or the other seems to have phylogenetic import, and the tortoise genera that show some form of distal carpal migration can be divided into two major groups on other characters. Groups that initiated carpal migration in one direction often migrate later in the other direction as well.

DESCRIPTIONS

Because of the complexity of the fusions and losses often observed, the following accounts of the characteristic structure of the carpus of each of the genera examined begin with the simpler arrangements and proceed through progressively more complex and modified types. Strict adherence to this arrangement is not possible in large, diverse genera, such as *Geochelone,* which contain both primitive and advanced carpal types. Thus the sequence of taxa in the following section is not meant to reflect phylogeny entirely. The classification of living and extinct land tortoises proposed by Loveridge and Williams (1957) is followed throughout and commented upon under "Phylogenetic Aspects."

Gopherus polyphemus (Daudin) (Fig. 3A)

Thirty-two specimens from 105 to 255 mm in shell length were available for study (AMNH, MCZ, PPHM, UF, UMMZ, USNM). Except for a slight difference in degree of fusion in digit 5, little variation was observed from the smaller to the larger specimens. The proximal centrale is present in all specimens examined; carpal 1 is fairly large and articulates broadly with the radius; the radius is bordered below by four elements (carpal 1, radiale + mediale 2, proximal centrale, and intermedium); no intercarpal fusions are evident; the metacarpals are typically fused to adjacent phalanges (14 of 32 specimens in all 5 digits, 18 in all digits except number 5); carpal 4 is wedged between the ulnare and mediale 3, but not so extensively as in *G. agassizii* and *G. berlandieri;* the pisiform is absent in all but 3 of the 32 specimens examined; carpal 5, the ulnare, and intermedium are in broad contact with the ulna.

Gopherus flavomarginatus Legler (Fig. 3B)

Three specimens of this highly interesting, recently described species of *Gopherus* were available for study (UF). The carpus is similar to that of *G. polyphemus,* with 4 subradial elements (carpal 1, radiale + mediale 2, proximal centrale, and intermedium), and 3

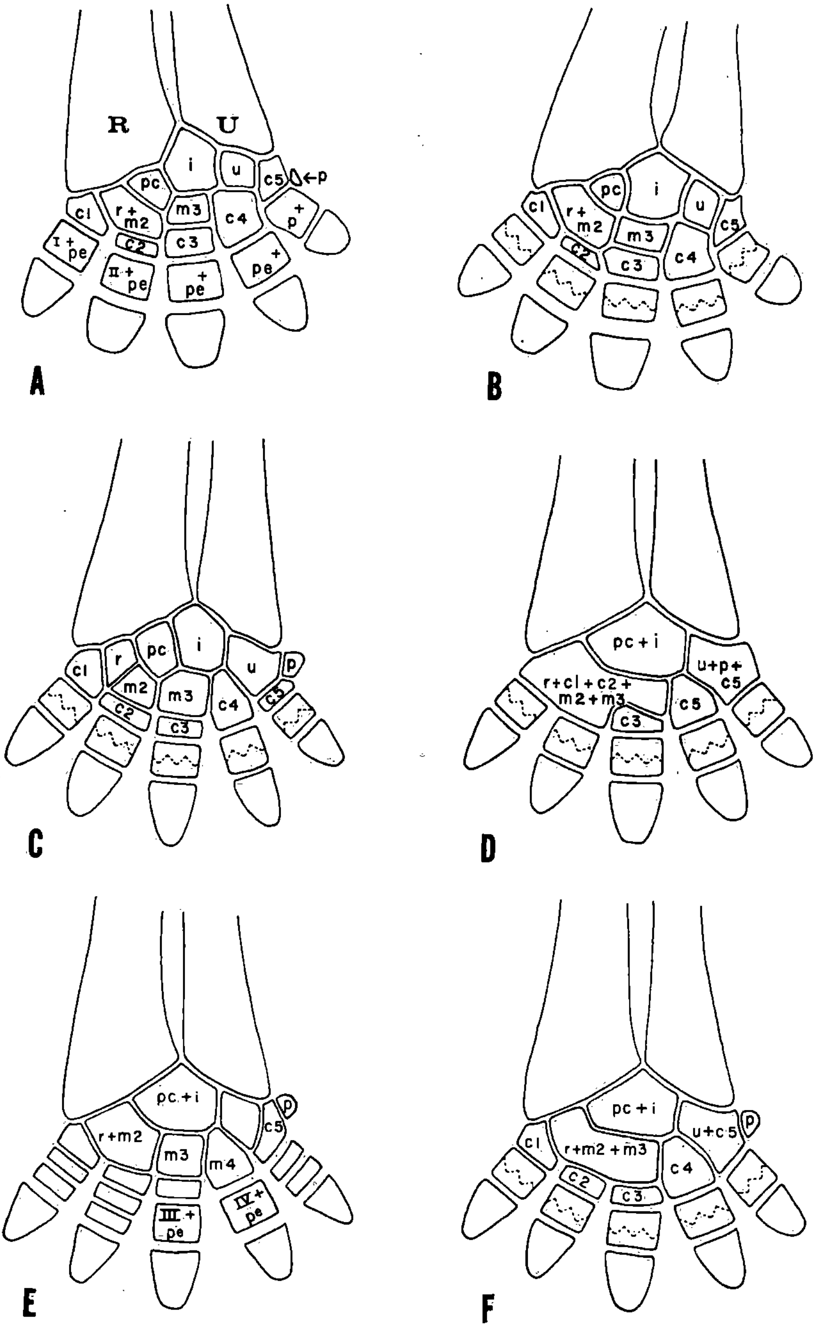

FIGURE 3. Carpi (diagramatic) of various tortoises: (A) Typical adult *Gopherus polyphemus.* (B) Adult *Gopherus flavomarginatus.* (C) Juvenile *Gopherus agassizii.* (D) Adult *Gopherus agassizii.* (E) Juvenile *Gopherus berlandieri.* (F) Adult *Gopherus berlandieri.*

subulnar elements (intermedium, ulnare, and carpal 5); metacarpals I through V are fused to the adjacent phalanges in all three specimens.

Gopherus agassizii (Cooper) (Figs. 3C, 3D)

Thirty-one specimens were available for study (MCZ, SNHM, UCM, UF, UK). The arrangement of elements is different from those of *G. polyphemus* and *G. flavomarginatus* and similar to that of *G. berlandieri*. On the basis of difference in carpus structure, as well as on a number of other anatomical features (True, 1892; Bogert and Oliver, 1945; Legler, 1959; Legler and Webb, 1961), two species groups may be recognized, the Polyphemus group containing *G. polyphemus* and *G. flavomarginatus*, and the Agassizii group containing *G. agassizii* and *G. berlandieri*. The proposal by Wermuth and Mertens (1961) that all four species of *Gopherus* are only subspecifically distinct is untenable in view of present evidence which includes, besides considerable anatomical data, the fossil history of *Gopherus* in the Pleistocene and important differences in habits. The view of Grant (1960) that *G. flavomarginatus* may represent *G. agassizii* or a subspecies thereof is strongly contradicted both by differences in gross anatomical features (Legler, 1959; Legler and Webb, 1961) that place them in different species groups, and by their carpal structure.

In 4 out of 8 specimens of *Gopherus agassizii* smaller than 150 mm, the proximal centrale is a separate element between the composite radiale and the intermedium, as in the Polyphemus group. In those small individuals in which the proximal centrale is absent, the space it usually occupies is filled by the intermedium, suggesting that the proximal centrale is fused with the intermedium in these specimens. In 11 out of 23 specimens over 150 mm in shell length, the proximal centrale is a separate element. In all 11 specimens with a separate proximal centrale, carpal 1 is fused to the composite radiale, while in all but 2 of the 12 specimens in which the centrale is fused to the intermedium, carpal 1 is free and in contact with the radius. Mediale 2 is fused to at least the radiale in 21 of the 23 specimens over 150 mm, though in some of these the fusion is not quite complete. No such fusion is manifest in 6 out of 8 specimens less than 150 mm in shell length. The radiale and medialia 2 and 3 are solidly fused together in 11 specimens over 150 mm, and all these individuals have carpals 1 and 2 also fused to this mass (Fig. 3D). Carpals 1 and 2 are fused together in 21 of the specimens over 150 mm. All the metacarpals are firmly fused to the adjacent phalanges in all specimens examined, regardless of size. Carpal 5 is fused to both the pisiform and ulnare in 13 of the 23 specimens over 150 mm; in every larger individual in which carpal 5 is free, the pisiform is fused to the ulnare. The pisiform is free in all smaller specimens examined.

The data above suggest that the carpus of *Gopherus agassizii* is much more variable than that of *G. polyphemus*, particularly in the lateral elements of the subradial and subulnar complexes.

Gopherus berlandieri (Agassiz) (Fig. 3E, 3F)

Thirty-seven specimens with an articulated carpus were available for study (AMNH, MCZ, UCM, UF, UK), varying in shell length from 90 mm to 314 mm. The latter is the largest individual of this species reported so far.

The lack of a separate proximal centrale, plus a number of other anatomical features suggest that *Gopherus berlandieri* is closer to *G. agassizii* than to the other two species of *Gopherus*. This is supported by behavioral similarities within the two species groups. Breeding has occurred in captivity between *G. berlandieri* and *G. agassizii* (Mertens, 1956; Woodbury, 1952), but has not been demonstrated between *G. polyphemus* and *G. berlandieri*, or *G. polyphemus* and *G. agassizi*.

In six specimens under 100 mm in shell length, mediale 2 is not fused to the composite radiale as it is in all the larger specimens. In none of the specimens is the proximal centrale separate from the intermedium. Carpal 1 is separate and in contact with the radius in all the specimens and is never fused to the composite radiale. While metacarpals 3 and 4 are always fused to the adjacent phalanges, metacarpals 1, 2, and 5 are fused to the adjacent phalanges in only the larger specimens. The pisiform is present in all specimens. Carpal 5 is fused to the ulnare in 22 of 41 specimens over 100 mm, and carpal 4 separates mediale 3 and the ulnare in all specimens. The radiale is fused to mediale 2 in all individuals, and these are fused to mediale 3 in all adult specimens.

Stylemys nebrascensis Leidy (Fig. 4A)

The carpus of the North American Oligocene tortoise *Stylemys nebrascensis* is known from an articulated foot in the collection of the University of Michigan Museum of Paleontology. I have discussed previously (1961) this important specimen which Case (1928) described fully. The radiale, proximal centrale, and medialia 2 and 3 are completely fused to one another; carpal 1 is separate and in contact with the radius; the pisiform is missing (perhaps fused to the ulnare?);

and no fusion of the distal carpals to either metacarpalia or medialia is evident.

The carpus of this genus, as shown by the one articulated foot known, represents one of the least modified carpal arrangements known in tortoises. This is to be expected in view of the unspecialized structure of the rest of the skeleton and its early geologic age.

Geochelone emys (Schlegel and Muller) (Fig. 4B)

Only three adult specimens were studied (UF, VNHM, and ZSI). The radiale, proximal centrale, and medialia 2 and 3 are all firmly fused to one another; carpal 1 is separate and in contact with the radius, and therefore shares directly with the composite radiale the weight transmitted through the radius to the medial digits; the pisiform is separate in one specimen and fused to either the ulnare or carpal 5 in the other two; carpal 5 is fused to the ulnare in all specimens; carpals 1 through 4 and metacarpals I through V are never fused to adjacent elements.

Except in its large composite radiale, this species seems to represent one of the more primitive of the known carpal arrangements.

Geochelone impressa (Gunther)

Only one subadult specimen of this species was available for study (UF). Except for a lack of subradial fusion, the manus of this species is practically identical to that of *G. emys*. The radiale, proximal centrale, and medialia 2 and 3 are all separate. Carpals 1 and 5 are not completely ossified, and are in contact with the radius and ulna respectively. Carpal 5 is not fused to the ulnare, as in the larger specimens of *G. emys* examined.

Geochelone radiata (Shaw) (Fig. 4F)

In the 8 adult specimens examined (AMNH, CNHM, and UF) the carpus shows little fusion or loss of elements in comparison with other species of tortoises. The composite radiale is composed of the radiale, proximal centrale, and medialia 2 and 3 in 4 of the 8 specimens, and of the radiale, proximal centrale, and mediale 2 in the remaining 4; the pisiform is missing in all specimens; carpal 5 is in contact with the ulna; carpal 1 is excluded from contact with the radius by the composite radiale.

Geochelone travancorica (Boulenger) (Fig. 4D)

In the 18 adult specimens examined (UF) the carpus is simplified by the fusion of many of the elements. The composite radiale is

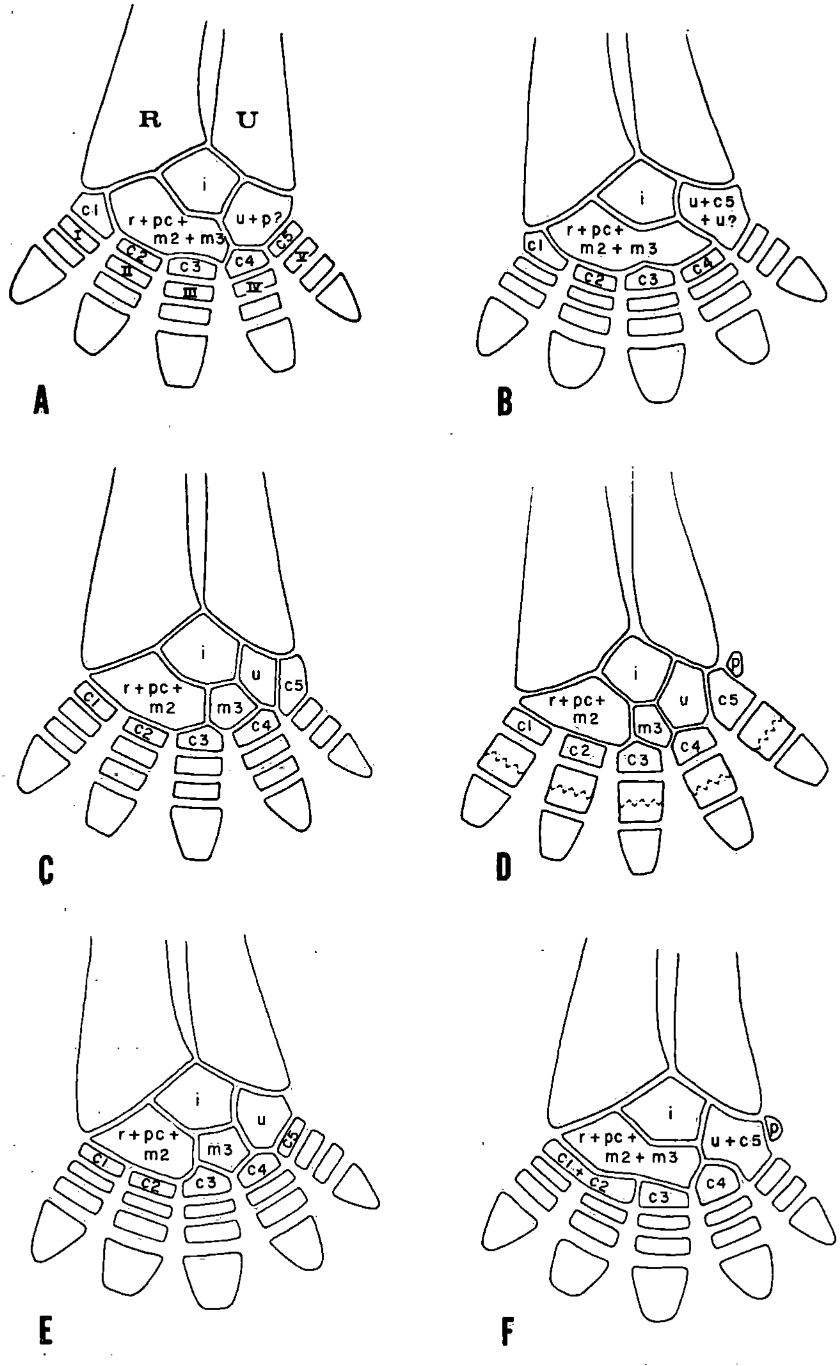

FIGURE 4. Carpi (diagramatic) of various tortoises: (A) *Stylemys nebrascensis*. (B) *Geochelone emys* (*G. impressa* almost identical). (C) *Geochelone radiata*. (D) *Geochelone travancorica*. (E) *Geochelone sulcata*. (F) *Geochelone pardalis*.

made up of the radiale, proximal centrale, and medialia 2 and 3 in 15 specimens, and of the radiale, proximal centrale, and mediale 2 in the remaining 3 individuals; the intermedium is always distinct; carpals 1 through 5 are separate; carpal 5 is in broad contact with the ulna; the composite radiale intervenes between carpal 1 and the radius; metacarpals I through V are apparently fused to the adjacent phalanges; the pisiform is cartilaginous in all specimens.

Geochelone sulcata (Miller) (Fig. 4E)

In the 6 adult specimens examined (UT-A and VNHM) the general arrangement of the carpal bones is simple and like that in *G. radiata*. Mediale 2 is fused to the composite radiale in 4 of the 6; the pisiform is absent in all specimens; carpal 5 is not in contact with the ulna, and with only the ulnare proximally; carpal 1 is excluded from contact with the radius by the composite radiale; all remaining elements are separate.

Geochelone pardalis (Bell) (Fig. 4F)

In the 10 adult specimens examined (AMNH, CNHM, and UF) many of the carpal elements are fused. Mediale 2 is fused to the composite radiale in 6 of the 10 skeletons; the pisiform is present in all; carpal 4 is consistently fused to the ulnare; carpal 1 is fused to carpal 2 in 8 of the 10 specimens; the metacarpals are never fused to their adjacent elements.

Geochelone elegans (Schoepff) (Fig. 5A)

The 17 specimens available for study (AMNH, UF, and ZSI) show the carpus to be very similar to that of *Geochelone pardalis*. The composite radiale in adults over 100 mm is composed consistently of the radiale, proximal centrale, and mediale 2 and 3; in smaller specimens mediale 3 is often separate; the pisiform is present in all but 2 specimens; carpals 1 through 5 are always separate; carpal 5 is in contact with the ulna; the composite radiale keeps carpal 1 from contacting the radius; the metacarpals are never fused to adjoining bones.

Geochelone chiliensis (Gray) (Fig. 5B)

In the 13 articulated forefeet available (UF) the carpus shows considerable fusion. The intermedium is large; the proximal centrale is never incorporated into the composite radiale; the latter is composed of the true radiale and medialia 2 and 3; the ulnare is fused to

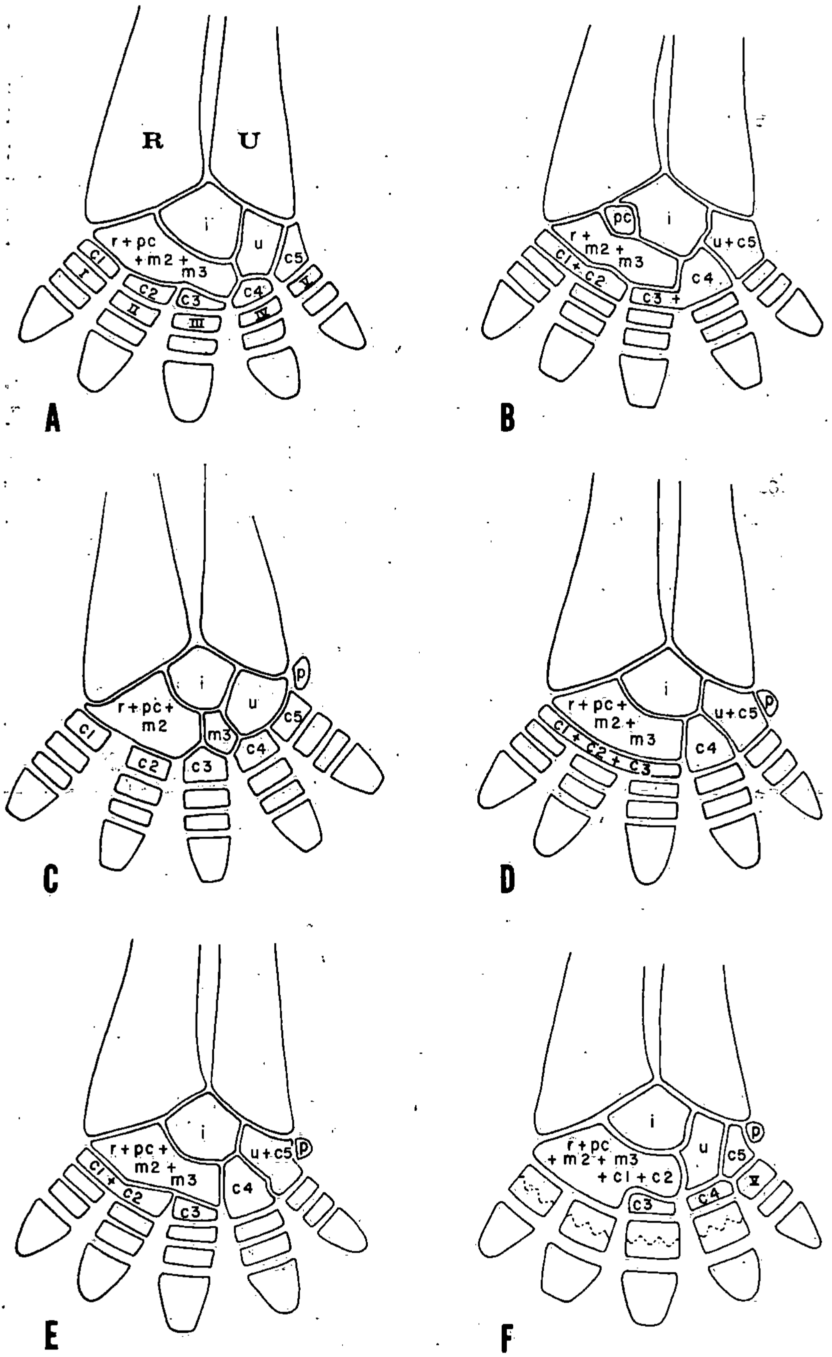

FIGURE 5. Carpi (diagramatic) of various tortoises: (A) *Geochelone elegans.* (B) *Geochelone chiliensis.* (C) *Geochelone elephantopus.* (D) *Geochelone denticulata.* (E) *Geochelone carbonaria.* (F) *Geochelone grandidieri.*

ments of its front foot show more fusion and atrophy than in any other carpal 5 in 8 specimens and distinct in the remaining 5; when fused this composite element is in turn fused to carpal 3 in 7 specimens; carpals 1 and 2 are fused to one another in all but 3 specimens; metacarpals I through V are never fused to adjacent elements; the pisiform is absent in 8 specimens.

Geochelone elephantopus (Harlan) (Fig. 5C)

In the 18 adult specimens available (AMNH, CAS, SNHM, and UF), the composite radiale is composed of the true radiale, the proximal centrale, and mediale 2. In larger specimens the true radiale is often represented by a flat wedge of cartilage attached to the osseous remainder of the composite radiale. Mediale 3 is always a distinct element; the pisiform is usually cartilaginous; carpals 1 through 5 are distinct, none are in contact with either the radius or ulna; the metacarpals are also distinct; digit three is so situated that its carpal is in contact with both medialia 2 and 3, and both digits four and five are in contact with the ulnare.

Geochelone denticulata (Linn.) (Fig. 5D)

Ten specimens were available for study (UF and VNHM). Though the carpus is fairly conservative, the tendency to intercarpal fusion is strong in this species. The composite radiale is composed of the true radiale, the proximal centrale, and medialia 2 and 3 in all the specimens except two, in which mediale 3 is a separate element; the pisiform is always present; carpal 5 is fused to the ulnare and carpal 1 is fused to carpal 2; in two individuals carpal 3 is, in turn, fused to carpals 1 and 2 on one side only.

Geochelone carbonaria (Spix) (Fig. 5E)

In the 12 specimens examined (UF and VNHM) the carpus is very similar to that of *G. denticulata.* In all specimens the composite radiale is composed of the true radiale, the proximal centrale, and medialia 2 and 3; the pisiform is present in eight specimens; carpal 5 is always fused to the ulnare; carpal 4 separates the composite radiale and the ulnare; carpals 1 and 2 are fused in two specimens.

Geochelone grandidieri (Vaillant) (Fig. 5F)

Whether the one specimen of *Geochelone grandidieri* (an extinct Madagascar Pleistocene species) available for study (BMNH) is typical of the carpus structure in this species is uncertain. The bony eletortoise examined. The pattern differs greatly from that found in other species of *Geochelone* and, if validated by additional material, will strengthen the distinctness of the subgenus in which the species has been placed.

The composite radiale is composed of the true radiale, proximal centrale, medialia 2 and 3, and carpals 1 and 2. The inclusion of carpals 1 and 2 in the composite radiale is particularly noteworthy. Carpal 1 (in a fused condition) must have originally (juvenile condition?) been in contact with the external lower border of the radius. Carpals 3 through 5 are separate, and 5 is in broad contact with the ulna; the pisiform is present in the notch between the outer surface of carpal 5 and the ulna; the ulnare is in contact with the composite radiale; metacarpals I through IV are fused with their adjacent phalanges. The basic modification of the carpus of this species is fusion of externally placed subradial carpals, metacarpal-phalangeal fusion in all but the outer digit, and ventro-medial migration of the outer subradial elements.

Geochelone gigantea (Schweigger) (Fig. 6A)

Six adult specimens were examined (AMNH and UF). The composite radiale is composed of the true radiale, proximal centrale, and mediale 2; digit three makes contact with both the composite radiale and mediale 3; digit four makes contact with mediale 3 and the ulnare; carpals 1 through 5 are discreet, and neither 1 nor 5 makes contact with the radius or ulna; the metacarpals are never fused to adjacent elements; the pisiform is represented by a block of cartilage only.

Psammobates oculifera (Kuhl) (Fig. 6B)

One specimen was available for study (VNMH). The composite radiale is composed of the true radiale, proximal centrale, and medialia 2 and 3; carpal 5 is fused to the ulnare; the pisiform is absent; carpal 4 separates the ulnare and the composite radiale; carpals 1, 2, and 3 are all fused to one another. Hewitt (1937) states that the intermedium and ulnare are fused in one of his adult specimens, as are metacarpal V and the proximal phalange. I did not find these fusions in the Vienna Museum specimen.

Homopus areolatus (Thunberg) (Fig. 6C)

Eight specimens were examined (UF, VNHM). The presence of only four toes on the front feet of this species is notable. Hewitt (1937) believed digit one to be the missing toe. I believe digit five has disappeared, on the basis of (1) the normal articulation of digits one and two with the composite radiale, (2) the normal articulation of digit three with the unfused mediale 3, (3) the separation of the composite radiale and the ulnare by mediale 3 and (4) the fact that only one digit articulates with the ulnare.

The composite radiale is comprised of the true radiale, proximal centrale, and mediale 2; mediale 3 is always discreet; carpals 1 through 4 are fused to the adjacent metacarpals; carpal 5 may be fused to the ulnare. No pisiform is present.

Homopus signatus (Schoepff)

No specimens of this species were examined in the present study and the following description is based on that by Hewitt (1937). Five toes are always present; the composite radiale is composed of the true radiale and proximal centrale; the intermedium is small but distinct; mediale 2 is separate; mediale 3 has apparently moved dorsally to articulate with the ulna, pushing the small ulnare laterally; the pisiform is present; carpals 1 and 2, and 4 and 5 are fused (as in *H. femoralis,* according to Hewitt, *Ibid*); metacarpals I through V seem to have fused to their adjacent phalanges.

Pyxis arachnoides Bell (Fig. 6D)

Only two specimens of this interesting tortoise were examined (VNHM). The composite radiale is composed of the true radiale, the proximal centrale, and medialia 2 and 3; the ulnare is separate but small; carpal 5 is in broad contact with the ulna; carpals 1, 2, and metacarpal I are all fused together; the mediale 3 portion of the composite radiale is in contact with the ulnare, thereby excluding carpal 4 from articulation with the intermedium. The remainder of the elements comprising the foot are unmodified.

Chersine angulata (Schweigger) (Fig. 6E)

Ten specimens were studied (UF). The carpus of this odd tortoise is unlike that of any other species examined. Most notable is the very small intermedium with a large proximal centrale lying completely under it and making contact with the very large ulnare; the composite radiale is probably composed of the true radiale and mediale 2; mediale 3 is very large and articulates with the proximal centrale dorsally, the ulnare externally, and both carpals 3 and 4 distally; carpal 4 articulates with both mediale 3 and the ulnare. The remaining elements and their positions are normal.

Kinixys homeana Bell (Fig. 6F)

In all members of this genus the carpus is most unusual in that the radius projects farther distally beyond the ulna than in other tortoises. The consequent shifting of the carpal elements makes their homologues so difficult to determine that the following interpretations for the *Kinixys* species are entirely tentative.

Four specimens of *K. homeana* were available for study (UF). The intermedium is very large, as is the discreet adjacent ulnare; the composite radiale is composed of the true radiale, the proximal centrale, and medialia 2 and 3; carpal 5, though small, is discreet and in contact with the ulna proximally and the ulnare medially. The dorsal shift of this element brings the elongated metacarpal V even with carpal 4. Carpals 1, 2, and 3 are discreet, and the latter has migrated slightly laterally to articulate with carpal 4 as well as its normal articulation with the mediale 3 portion of the composite radiale. The proximal phalange of digit five is elongate to accommodate the proximal migration of its corresponding carpal and metacarpal units. The pisiform is absent. The remaining elements are normal.

Kinixys erosa (Schweigger) (Fig. 7A)

Two specimens were studied (UF and VNHM). The carpal arrangement is slightly more modified than that of *Kinixys homeana*. The composite radiale is composed of the true radiale, the proximal centrale, and mediale 2; mediale 3 is discreet and in its normal position; the intermedium is very large; carpal 5 is fused to the ulnare; carpal 3 is probably fused to metacarpal III. The pisiform is absent. The remaining elements are normal.

Kinixys belliana Gray (Fig. 7B)

In the six specimens available (UF) the composite radiale is composed of the true radiale, the proximal centrale, and medialia 2 and 3. As in the other species of the genus the intermedium is large and located high in the proximal series; the composite ulnare is composed of the true ulnare and carpal 5; carpals 1 and 2 are fused together, as are carpal 4 with metacarpal IV and metacarpal V with the most proximal phalange of digit five; carpal 3 is only a thin wedge of bone, but in its normal position; no pisiform is present. Some specimens have only 4 toes (Schmidt, 1919). The missing toe is usually five (Hewitt, 1937), but may be four in some specimens (Loveridge and Williams, 1957).

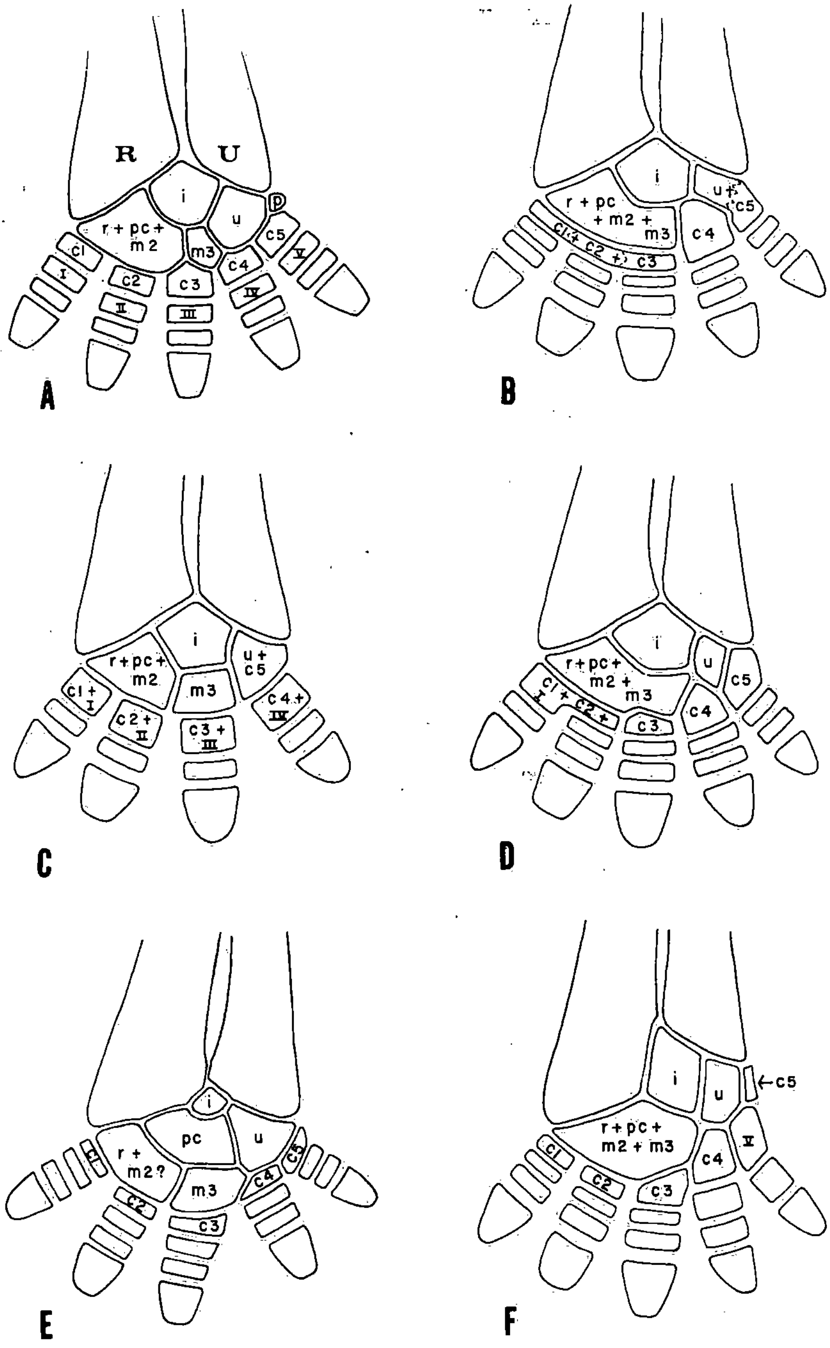

FIGURE 6. Carpi (diagramatic) of various tortoises: (A) *Geochelone gigantea.* (B) *Psammobates oculifera.* (C) *Homopus areolatus.* (D) *Pyxis arachnoides.* (E) *Chersine angulata.* (F) *Kinixys homeana.*

Testudo graeca Linn. (Fig. 7C)

Twenty-one adult specimens were studied (UF and VNHM). Thompson's (1932) plate 23 is in error in showing three phalanges for this species. The composite radiale is composed of the true radiale, the proximal centrale, and medialia 2 and 3 in 16 specimens, of the radiale, proximal centrale and only mediale 2 in 5 specimens; carpal 4 is excluded from contact with the intermedium by the lateral extension of the composite radiale in all individuals; carpals 1 and 2 are fused; the pisiform is present; the ulnare includes carpal 5 from articulation with the ulna; the composite radiale includes carpal 1 from articulation with the radius; metacarpal 1 is often fused to the proximal phalange, an individual characteristic according to Siebenrock (1906) which this study confirms.

Testudo hermanni Gmelin

Eighteen specimens were examined (UF and VNHM). As the carpus of this species is apparently identical to that of *Testudo graeca,* no description or illustration seems necessary.

Testudo marginata Schoepff (Fig. 7D)

Three specimens were studied (VNHM). The composite radiale is composed of the true radiale, the proximal centrale, and medialia 2 and 3; the intermedium is fused to the ulnare in both carpi of one individual and fused on only one side in another; the pisiform is present in all the carpi studied; the ulnare excludes carpal 5 from articulation with the ulna; carpals 1 and 2 and metacarpal 1 are fused into a solid mass in one specimen; carpal 1 contacts the radius.

Testudo horsfieldi Gray (Fig. 7E)

Four specimens were examined (BNHS and UF). The presence of only four toes in the manus makes it difficult to determine homologies. Digit four is probably the lost one. The composite radiale is composed of the true radiale, proximal centrale, and mediale 2; mediale 3 is probably fused with carpals 3 and 4; the composite ulnare probably formed of the true ulnare and carpal 5; carpal 1, which is in contact with the radius, is fused to metacarpal I; digit two is normal; metacarpal III and its adjacent phalange are fused in two specimens and free in the other two; metacarpal V(?) is apparently fused to its adjacent phalange in three individuals.

Testudo kleinmanni Lortet (Fig. 7F)

Two specimens of this tortoise were studied (VNHM). It is known sometimes to have only four toes (Flower, 1933). The composite radiale is composed of the true radiale, proximal centrale, and mediale 2 in both specimens; carpal 1 is in contact with the radius and is also fused to carpal 2; the ulnare excludes carpal 5 from contact with the ulna; no pisiform is present; metacarpals IV and V are fused to their respective adjacent phalanges. Perhaps one of the most unusual features of this carpus is that metacarpal I is also in contact with the radius.

FUNCTIONAL ASPECTS

As Romer (1933) points out, the way a turtle moves its limbs is, despite the presence of the shell, probably as close to that of the primitive tetrapod method of locomotion as can be found among living reptiles. In tortoises the well-developed humerus head is attached to the shaft by a constricted neck, and is oriented more medially to the shaft than dorsally. The articulating surface of the head shows considerable interspecific variation in shape, from almost hemispheric in a few species to ovate with the long axis horizontal in most. The so-called glenoid cavity of the tortoise shoulder girdle is similarly shaped to accommodate it. Strongly ovate articulating surfaces (the usual case in species with narrow shell openings) restrict limb movement to the horizontal plane and greatly limit vertical movement.

Of the two elements comprising the brachium, the radius is usually the longer and more slender. Both are often in broad contact near their distal ends, where strong ligaments and muscles bind them tightly together. Torsional movement may be further reduced by an interdigitating articulation between the two elements at their distal ends.

The restriction of the movement of the humerus to the horizontal plane, the reduction of rotation in the brachium, and the fusion of many of the carpals and metacarpals all limit movement to those planes where shell shape permits it. Some distal movement is obviously necessary, because when the flexor musculature pushes the foot against the ground the brachium and carpus serve as a sort of stationary pivot on which the humerus rotates. The great structural variation in the degree of fusion in the elements comprising the carpus of tortoises is apparently related to (1) reduction of mobility in certain areas, and (2) failure of the component elements to serve a definite mechanical need.

The ulna makes the most extensive articulation with the humerus

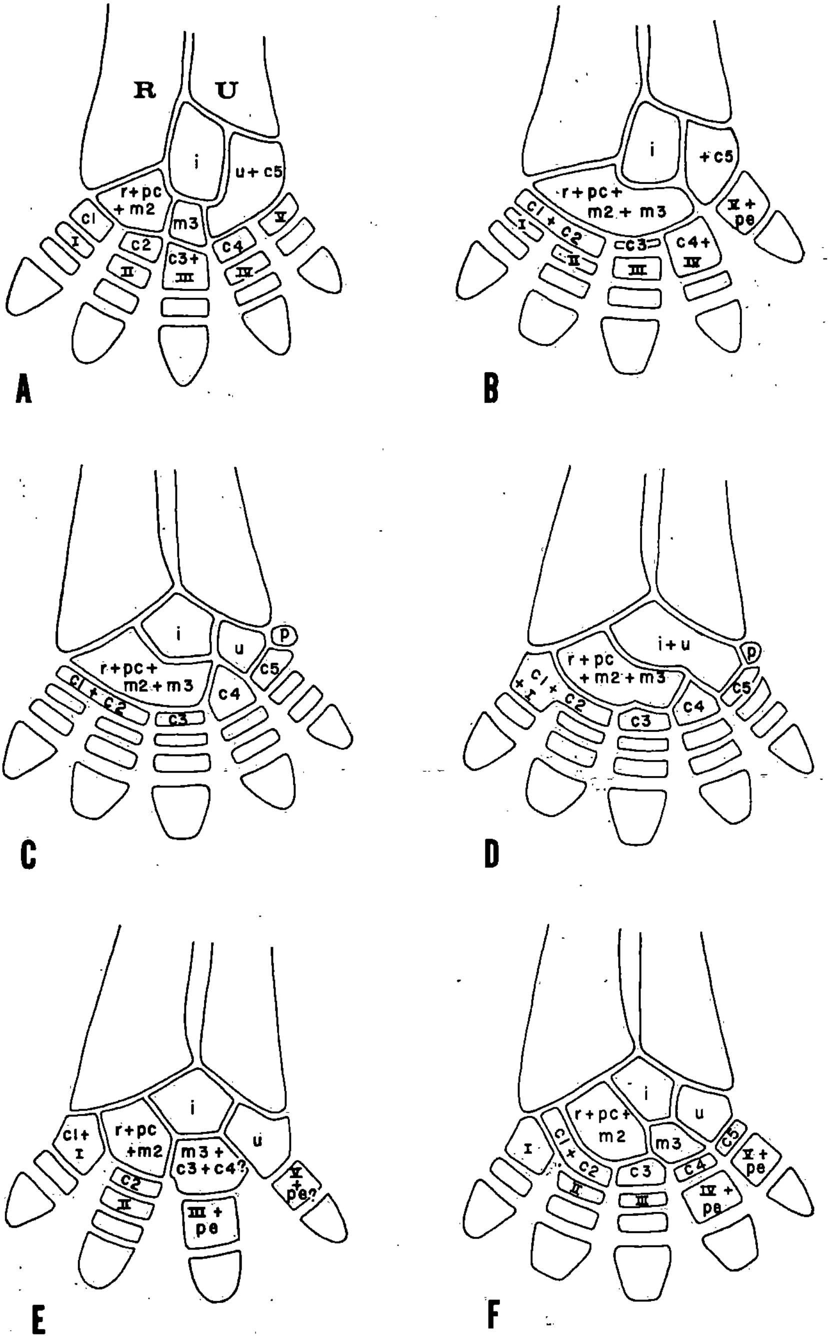

FIGURE 7. Carpi (diagramatic) of various tortoises: (A) *Kinixys erosa.* (B) *Kinixys belliana.* (C) *Testudo graeca* (*Testudo hermanni* almost identical). (D) *Testudo marginata.* (E) *Testudo kleinmanni.*

and is certainly the major weight-bearing element of the upper brachium. At the beginning of the propulsive phase the foot is placed on the ground in such a way that the radius bears all the weight, which is then transferred gradually to the ulna as the body moves forward and the limb pivots inward. This shift is accomplished by certain muscles, particularly *M. interosseus brachis*.

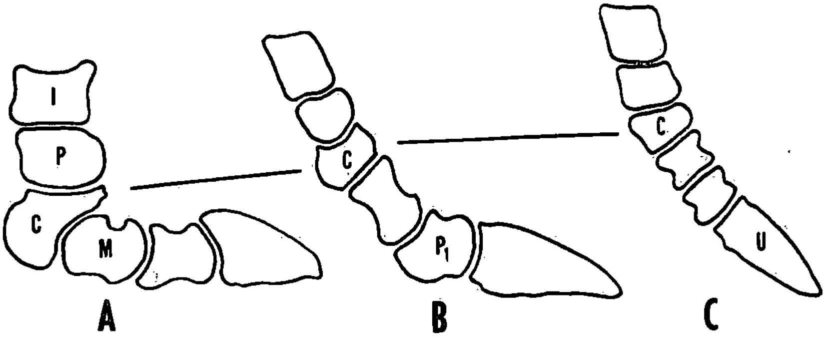

FIGURE 8. Cross sections of digit three and the carpus through the intermedium of, (a) *Geochelone radiata*, an essentially plantigrade genus, (B) *Kinixys homeana*, a digitigrade genus, and (C) *Gopherus polyphemus*, an unguligrade genus. Abbreviations: I = intermedium, P = proximal centrale, C = carpal, M = metacarpal, P_1 = penultimate phalanyx, U = unguinal phalanyx.

As pointed out above, the considerable variation in the tortoise manus is due principally to the fusion of elements. That of the genus *Stylemys*, which represents one of the earliest fossil tortoises known, shows a primitive pattern both in the number of elements and in their relative positions. In *Stylemys* and in the extant genus *Geochelone*, most of the weight is transferred to the substrate through the carpals. These elements are usually thickened ventrally where they rest on a thick cushion of connective tissue and enlarged dermal scutes, and they bear all the weight as the metacarpals and phalanges extend forward at almost right angles to the brachial axis. Tortoises with this arrangement are essentially plantigrade. The extent of the fleshy cushion between the carpals and the substrate varies between species. In true digitigrade forms the penultimate phalange transfers the weight to the substrate and is thickened ventrally. Of all the tortoises only the genus *Gopherus* is truly unguligrade (Fig. 8). Whether or not the early members of the genus were also unguligrade is unknown.

In most genera of tortoises, as the foot moves forward into its new position during locomotion digits two and three usually provide the

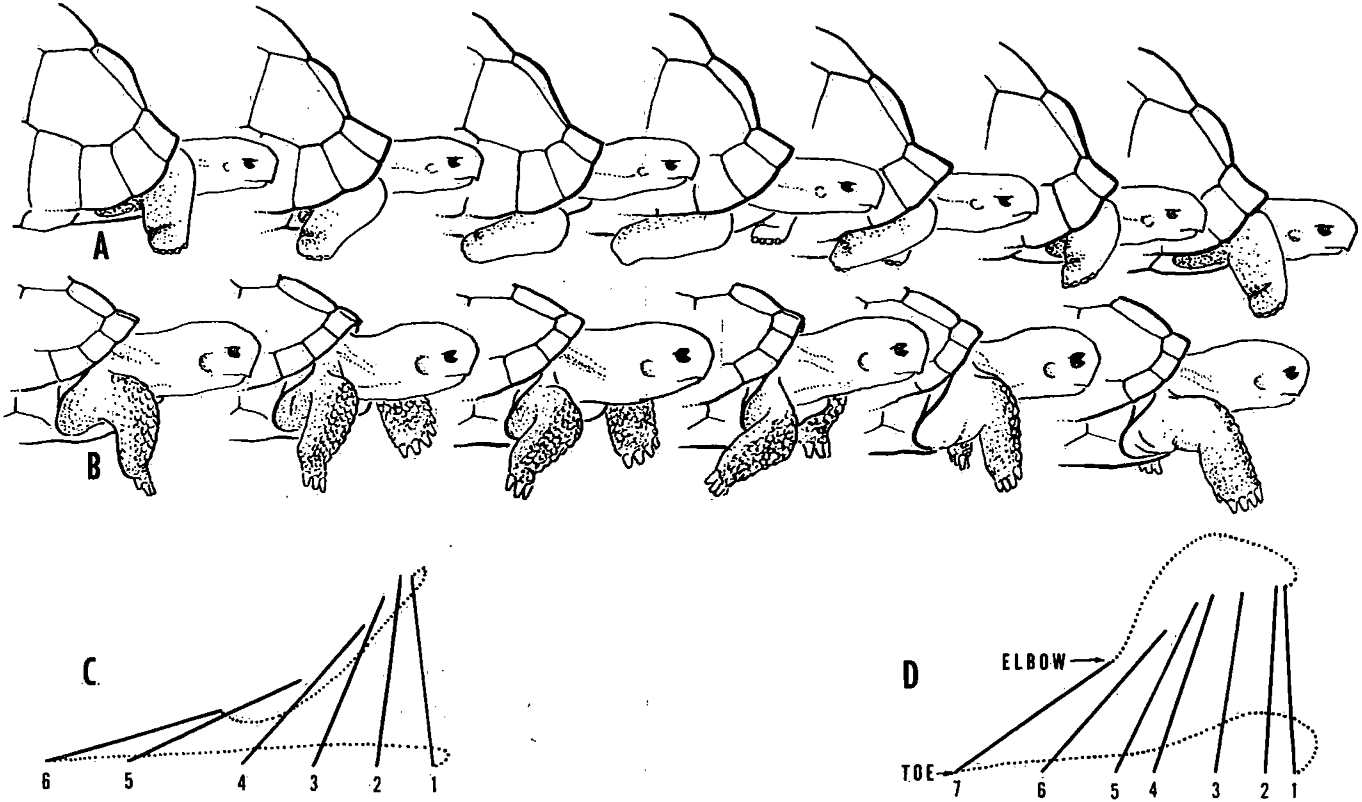

FIGURE 9. Movement of the front limbs during locomotion. (A) *Geochelone radiata*. (B) *Gopherus polyphemus*. (C) Positions of front right limb of *Geochelone radiata* during propulsion (solid lines) and retrieval (dotted lines). (D) Same, *Gopherus polyphemus*. A to D all prepared from slow-motion photographs.

final propulsive force. This is indicated by analysis of slow motion photography and reflected in wear patterns on the toenails.

Tortoises have two major patterns of limb positions and movement during walking, one represented by *Geochelone*, the other by *Gopherus*. In *Geochelone radiata* the distal end of the humerus describes an oval with its major axis at approximately 45° (Fig. 9A, 9C). The ulna and radius rotate but little on the humerus, except near the forward part of the arc, when the brachium rotates slightly outward. The arc of the moving humerus and the relative immobility of the brachio-humeral articulation bring the foot down with the toes directed slightly inward. At this point the humerus rotates anteriorly on the radio-ulnar articulation, moving the body slightly upward and forward.

As the body continues its forward motion, the weight is slowly transferred from the radius to the intermedium and then to the subulnar elements. The foot continues to rotate so that the toes face even farther inward. The weight is now transferred to the ulna as the forward-moving body rolls the foot until digits one and two are lifted off the ground at the end of the propulsive phase. The retrieval phase begins as the weight is transferred to the opposite forelimb, now near the end of its retrieval phase. Its propulsive phase is triggered by a shift of gravity to that side of the body, accomplished by (1) the weight of the laterally suspended limb moving into its new position, (2) the flexion of the opposite hind limb, and (3) the lateral force of the front limb still on the ground near the end of its cycle.

Geochelone has two major planes of flexure at the carpus, at the metacarpo- and brachio-carpal junctures. Kinesis in both flexures is most pronounced near the end of the propulsive cycle, when the toes are directed inward and at almost right angles to the brachium. In most plantigrade tortoises the intermedium is below the brachio-carpal flexure, but in the more digitigrade types such as *Kinixys*, the intermedium lies above the flexure. The small size of the intermedium in *Kinixys* and its position permit more rotation at the brachio-carpal juncture than in most species of *Geochelone*.

In the second major locomotor pattern, exhibited only by the unguligrade *Gopherus*, the lower limb passes through a broader oval than in *Geochelone* (Fig. 9B, 9D). Though the propulsive phase is somewhat shorter, the body is lifted higher and farther forward. The lower leg is oriented more vertically throughout the entire sequence, probably largely because of the relative immobility of the carpus. Most important, the foot is rotated outward rather than inward during the propulsive phase, and to a much greater degree than in *Geoche-*

lone. Both the greater vertical movement of the distal end of the humerus and the greater rotation of the brachium in *Gopherus* are accomplished largely at the proximal head of the humerus, which is much more nearly spherical than that of most species of *Geochelone* or *Kinixys*. These two genera depend for vertical limb movement on the humero-ulnar joint, which is much more flexible than in *Gopherus*.

PHYLOGENETIC ASPECTS

In the more primitive tortoises 12 elements, including the pisiform, comprise the carpus. The reduction in the number of elements in more advanced tortoises is probably in response to stresses placed on the carpus during locomotion.

The radius, which receives the initial shock of sudden weight support during the propulsive phase, must transfer this weight to both the ulna and the subradial elements. In the primitive tortoise carpus the weight is transferred to four subradial elements (carpal 5, radiale, proximal centrale, and intermedium), thence to five more distal elements (carpals 1, 2, 3, and medialia 2 and 3). During this phase a number of important shearing forces develop between the subradial elements. In more advanced forms some of the subradial elements are usually fused into a composite radiale (radiale + proximal centrale + mediale 2), and carpal 1 is no longer in contact with the radius. This arrangement solidifies the carpus and makes it less flexible in the area of greatness stress by reducing the total number of potential interacting surfaces. A similar reduction in subulnar articular surfaces through fusion occurs in some advanced forms as well, though never as extensively as in the subradial series. The subulnar articular reduction is apparently related to shearing forces operative during the middle and last parts of the propulsive phase, when the ulna bears much of the weight of the front part of the animal.

In the most advanced forms this subradial modification is carried even further, so that carpal 1 may fuse to the composite radiale. Metacarpals I and II, and sometimes even III also fuse into one large mass, and carpal 5 may fuse to carpal 4. Thus the number of carpal and metacarpal elements is reduced from 12 elements in the most primitive condition to 5 in the most simplified condition known. The most extreme degree of fusion and loss known so far in tortoises occurs in the extinct Pleistocene species *Geochelone grandidieri* (Fig. 5F).

When the carpal structures of the major groups of living and extinct tortoises are compared, a heirarchial system of increasing or decreasing complexity becomes evident. That the direction of the sequence is toward simplicity is suggested by the arrangements found in the earlier fossil tortoises such as *Stylemys* and in such presumed primitive groups of extant genera as the subgenus *Manouria* of the genus *Geochelone*. It is also reflected by the development of the carpus in living species.

In the major stages in the evolution of the tortoise carpus, the first (Fig. 1D) is represented by the primitive condition of three subradial and two subulnar elements. In the next stage (Fig. 2A) various subradial elements fuse, different ones in different phyletic lines. This is apparently followed (Fig. 2B) by fusion of subulnar elements, of carpals, and of metacarpals with phalanges. The last stage (Fig. 2C) involves the movement outward of both carpals 1 and 5, so that they contact the radius and ulna respectively. The eventual development of carpo-brachial contact on both sides is derived independently in two phyletic lines.

The phyletic scheme proposed by Loveridge and Williams (1957) based largely on shell structure (Fig. 10) corresponds remarkably well with one based on carpal structure (Fig. 11). The only areas of disagreement between the two schemes are in the positions of the subgenus *Aldabrachelys* and the genus *Chersine*.

The genus *Gopherus*, as pointed out previously, exhibits a primitive carpal pattern, though the manus is highly specialized for digging. The foot and entire lower leg are flattened antero-posteriorly. More important, carpus flexion is reduced by both the flattened articular surfaces of the carpal elements and by a strong ligamentous sheet over the entire carpus and adjacent brachium. Of all the extant genera of tortoises, it is the only one that is completely unguligrade.

Perhaps the most important single character of phylogenetic significance is the position of carpal 4. In *Geochelone pardalis* and *G. elegans* of the subgenus *Geochelone*, all species of the subgenus *Chelonoides* and of the genus *Gopherus*, carpal 4 contacts the intermedium and separates the ulnare and mediale 3. In all other tortoises the ulnare contacts mediale 3, and carpal 4 fails to contact the intermedium. On the basis of the position of carpal 4 in the generalized amphibian and reptilian carpus, the more primitive arrangement is a contact with the intermedium. Unfortunately, no articulated carpus is available for the primitive, extinct subgenus *Hadrianus*. Carpi of this subgenus and of earlier fossils of the genus *Stylemys* than are now available can be expected to show a contact between carpal 4 and the intermedium.

On the basis of carpal structure, the species of the Neotropical subgenus *Chelonoides* seem least modified from the presumed primitive condition, with *Geochelone pardalis* and *G. elegans* of the subgenus *Geochelone* only slightly more modified. The carpi of the remaining taxa represent a complex of specializations, often independently derived, and from which few phylogenetic conclusions can be drawn. The carpus of *Kinixys* seems to represent the greatest deviation from the presumed primitive condition.

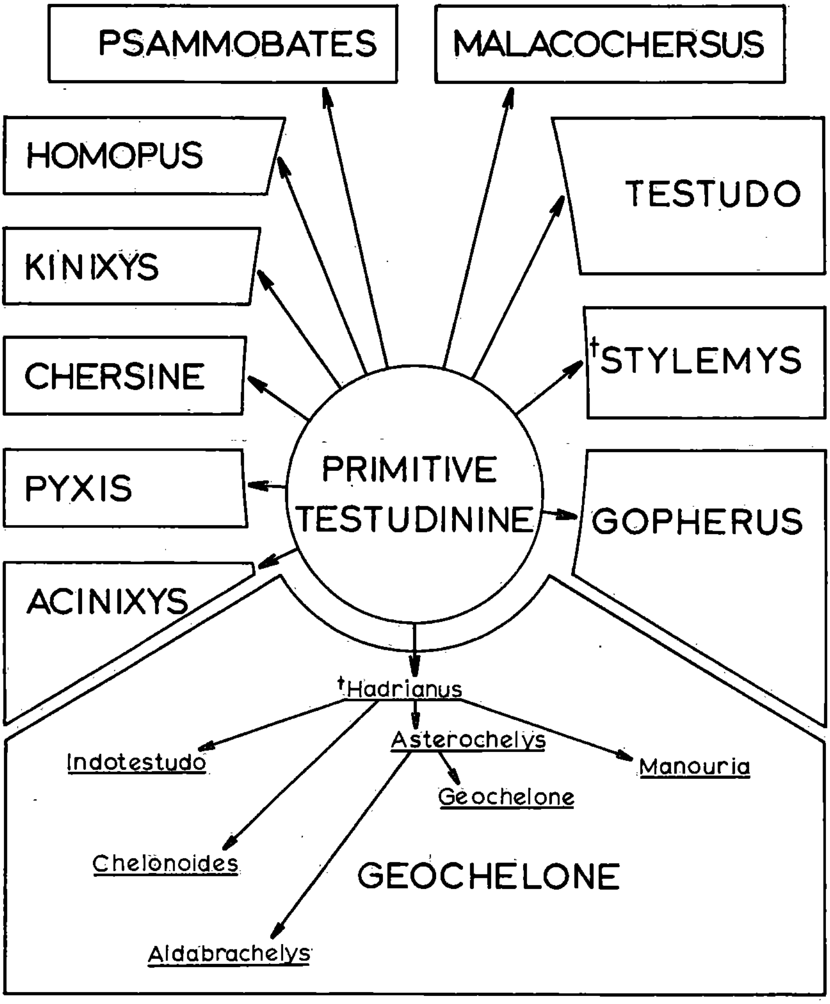

FIGURE 10. The hypothetical relationships of tortoises based on shell characters (modified from Loveridge and Williams, 1957).

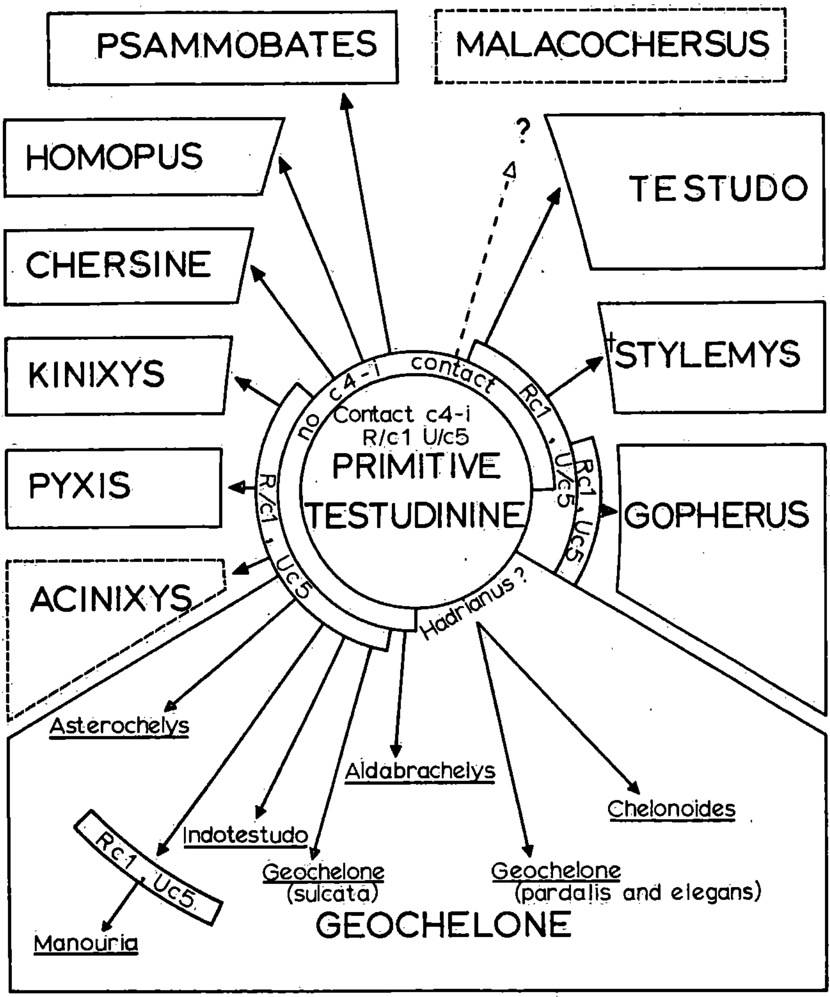

FIGURE 11. The hypothetical relationships of tortoises based on carpal architecture. Abbreviations: R = radius, U = ulna, c = carpal (1, 4 or 5), i = intermedium, / = no contact between radius or ulna and carpals 1 or 5, no slash represents contact of elements.

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