A. Carr

ARCHIE CARR

BULLETIN

OF THE

FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 3 Number 2

FOSSIL TURTLES OF THE GENUS TERRAPENE IN FLORIDA

Walter Auffenberg

UNIVERSITY OF FLORIDA
Gainesville
1958

The numbers of THE BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, will be published at irregular intervals. Volumes will contain about 300 pages and will not necessarily be completed in any one calendar year.

All communications concerning purchase or exchange of the publication should be addressed to the Curator of Biological Sciences, Florida State Museum, Seagle Building, Gainesville, Florida. Manuscripts should be sent to the Editor of the BULLETIN, Flint Hall, University of Florida, Gainesville, Florida.

Published 27 June 1958 Price for this issue $.60

FOSSIL TURTLES OF THE GENUS *TERRAPENE* IN FLORIDA

WALTER AUFFENBERG [1]

SYNOPSIS: Recent paleontological work in the Pleistocene of Florida has made available a larger series of fossil box turtles, *Terrapene*, than has been studied previously. A large number of modern specimens were examined to determine the extent of variation existing in various populations and to evaluate characters found in the fossils. It is shown that two box turtles are represented in the known Pleistocene localities of the area. There is some evidence of intergradation between them, and the two fossil forms are thus considered subspecies of the Recent form, *Terrapene carolina*. The smaller Pleistocene form represents the modern *T. c. carolina* or *T. c. bauri* or both. The larger fossil form is termed *T. c. putnami*. *Terrapene innoxia* and *T. formosa* are considered synonyms of *T. c. carolina* or *T. c. bauri* or both. *Terrapene canaliculata* and *T. antipex* are synonyms of *T. c. putnami*. *Terrapene singletoni* seems to represent a specimen intermediate between *T. c. carolina* and *T. c. putnami*. Certain fossil populations are intermediate between these same two forms and are considered intergrades. A probable history of the genus *Terrapene* in southeastern United States is presented. The Pleistocene localities of Florida are tentatively correlated on the basis of the box turtles now available from them.

Fossil box turtles are fairly common over much of eastern North America. Their remains are almost always composed of fragmentary elements of the carapace and plastron. Occasionally complete shells are found; rarely a skull. Most vertebrate paleontologists are only casually interested in fossil turtles, particularly Pleistocene forms. As a result, much remains to be learned concerning late Cenozoic turtles. No single comprehensive study has ever been attempted of the anatomy of *Terrapene* or its evolutionary history, though several good regional studies have been published recently. Earlier papers tend to obscure relationships of fossil and Recent forms under a profusion of new names based, in many cases, on individuals so fragmentary as to make identification of new material almost impossible. This is particularly true in Florida, where six species have been described from Pleistocene deposits alone.

The Recent species of *Terrapene* of the United States, *ornata* and *carolina*, are rather well understood, at least in broad outline. The Mexican species, *T. mexicana, coahuila, klauberi,* and *nelsoni* are little known. Some, if not all of them, are close to *T. carolina*. *T. coahuila* seems to be the most primitive member of the genus and most distantly

[1] The author is an Associate in the Florida State Museum, Assistant Professor of Biological Sciences, and curator in vertebrate paleontology of the University of Florida Collections. His most important contributions are concerned with the fossil history of small amphibians and reptiles. Manuscript submitted 23 May 1958.—ED.

related to *T. carolina*. The latter includes four currently recognized geographic races: *T. c. carolina, major, bauri,* and *triunguis*. The geographical and morphological limits of these forms are not clearly defined at present. Their relationships are not adequately understood, though *major* certainly seems the most primitive member of the species as now defined. Little is actually known of their subspecific characters other than that they are rather variable. This last fact is important when considering the described fossil forms, since it has been almost entirely ignored by past workers with the exception of Milstead (1956) and Barbour and Stetson (1931). The degree of variability in Pleistocene populations has never been fully demonstrated. In the present study it is assumed to be as great as in the Recent forms.

Abbreviations and Acknowledgments

The following abbreviations are used when referring to collections: ACM—Amherst College Museum; AMNH—American Museum of Natural History; FGS—Florida Geological Survey; MCZ—Museum of Comparative Zoology; UF—University of Florida Collections; USNM—United States National Museum; and VU—Vanderbilt University. I wish to thank the persons responsible for the collections in the various institutions mentioned above for the loan of specimens in their care. To A. Holman and R. Weigel, University of Florida, I wish to express appreciation for allowing me to examine fossil box turtles collected by them while working on particular vertebrate deposits in the state and which have not as yet been deposited in a public institution. I also wish to thank W. Milstead and E. E. Williams for their valuable criticisms.

Discussion of Previous Studies on *Terrapene*

The earliest fossil referred to this genus is *Terrapene longinsulae* Hay (1908a) from the lower Pliocene of Phillips County, Kansas. It has been thought to be somewhat closer to *T. ornata* than to *T. carolina,* but the specimen deserves additional study. So far box turtle remains are unknown from the Florida Miocene or Pliocene. The Pleistocene forms from Florida obviously belong to the *carolina* complex, so *T. longinsulae* has not been seriously considered as a possible close relative in this study.

Terrapene carolina appears first in the Pleistocene of North America. Remains have been found from Maryland to Texas and from Pennsylvania to Florida. A number of fossil species obviously belonging to the *carolina* group have been described from Florida and Georgia, largely by Hay. These are as follows:

TERRAPENE PUTNAMI Hay (1907).—The holotype is represented by a single hypoplastral element (AMNH 6097), dredged from the Alafia River, Hillsborough County, Florida, about one mile above its entrance into Tampa Bay. Described on the basis of its large size and the thickness of the element, Hay estimated the carapace to have been about 265 mm. long. He also assigned two additional fragments of a carapace of a large box turtle in the collections of Vanderbilt University to the same species. He estimates the carapace length of one of these specimens to have been about 320 mm. long. The holotype was taken from what was then termed the Peace Creek beds, originally thought to represent the Pliocene. Subsequent work has shown that the Peace Creek beds include both Pliocene and Pleistocene vertebrate remains (Wood, *et al.*, 1941). Hay placed the species in the Pliocene with some reservation, however some subsequent authors have referred it to this period without question. New material indicates that the pieces are almost certainly Pleistocene.

TERRAPENE CANALICULATA Hay (1907).—The holotype (USNM 5500) is composed of several fragmentary pieces of the carapace and plastron of a large box turtle estimated to have had a carapace length of about 200 mm. The type was collected from Pleistocene deposits on either Whitemarsh or Skedaway Islands, below Savannah, Georgia. The most important diagnostic features are the large size, a sharp longitudinal keel on the peripherals above the bridge, and a broad gutterlike groove above this keel.

TERRAPENE ANTIPEX Hay (1916).—The holotype, originally in the collection of the Florida Geological Survey, is now in the United States National Museum (USNM 8820). It is represented by the posterior lobe of the plastron of a large box turtle estimated to have had a carapace length of about 220 mm. The specimen was presumably collected from stratum 3, Vero Beach, Indian River County, Florida. Stratum 2 has been shown to represent the Pleistocene bed. Stratum 3 is a much more recent deposit, containing Recent vertebrates as well as Pleistocene forms eroded from stratum 2. *Terrapene antipex* is here assumed to have originated from stratum 2, as will be discussed below. In addition to the type, another posterior lobe, part of an anterior lobe, and a few small pieces of carapace from the same locality are referred by Hay to this species. Still another posterior lobe from 28 miles south of St. Augustine, St. Johns County, Florida, and a fragment of a carapace from the same locality are also referred to this species by Hay. *Terrapene antipex* is said to differ from *T.*

canaliculata in having a less conspicuous lateral keel, a thinner shell, and peripherals which are less flaring at the posterolateral margin of the shell. From *putnami* it is said to differ chiefly in size, being much smaller, and having a proportionately thinner hypoplastron.

TERRAPENE INNOXIA Hay (1916).—The holotype (USNM 8824) is a complete carapace, said to come from stratum 2, Vero Beach, Indian River County, Florida (fig. 1). In the same collection a second carapace bearing the same locality data, and several fragments of the carapace and plastron of a similar-sized turtle from the same beds, are referred to this species by Hay. The major diagnostic features of this fossil species concern the size of the pieces, which represent a turtle much smaller than *T. canaliculata, antipex,* or *putnami.* The lateral keel so well developed in *antipex* and *canaliculata* is almost absent. The posterior peripherals are much less flared. From *T. carolina* (*T. major* of Hay, 1916) it differs in having the highest point of the carapace over the middle of the shell rather than posterior to the middle (Hay was using modern specimens of populations now termed *T. c. bauri*); in having a slightly less excavated nuchal bone at its anterior edge; in having a well-developed nuchal scale, which is said to be suppressed in Recent forms; and in having the rear marginal scutes uniformly lower than in Recent shells he examined from Florida.

TERRAPENE FORMOSA Hay (1916).—The holotype is represented by the greater part of the posterior two thirds of a carapace (USNM 8825) taken from a Pleistocene fissure in the Ocala limestone at Ocala, Marion County, Florida (fig. 2) This is a poorly defined species that seems to have been described as new only because it came from Pleistocene beds and was slightly different than the type and referred material of *T. innoxia* from Vero Beach.

TERRAPENE SINGLETONI Gilmore (1927).—The holotype (USNM 11181) consists of the greater part of a carapace from the Melbourne bone beds (presumably equivalent to stratum 2 of Vero Beach), two miles west of Melbourne, Brevard County, Florida. It is distinguished from all other fossil and Recent species of eastern United States, with the exception of *T. canaliculata* and *putnami,* in being much larger, the shell being 200 mm. long. From *canaliculata* it differs in being slightly smaller, in having a thinner shell, in lacking a lateral keel above the bridge, in being narrower, and in having peripherals which are less flared posteriorly.

Gilmore placed Hay's *T. antipex* in the synonymy of *T. canaliculata* Hay, largely on the basis of similar proportions of the posterior lobe of the plastron. Several complete carapaces from Melbourne in the

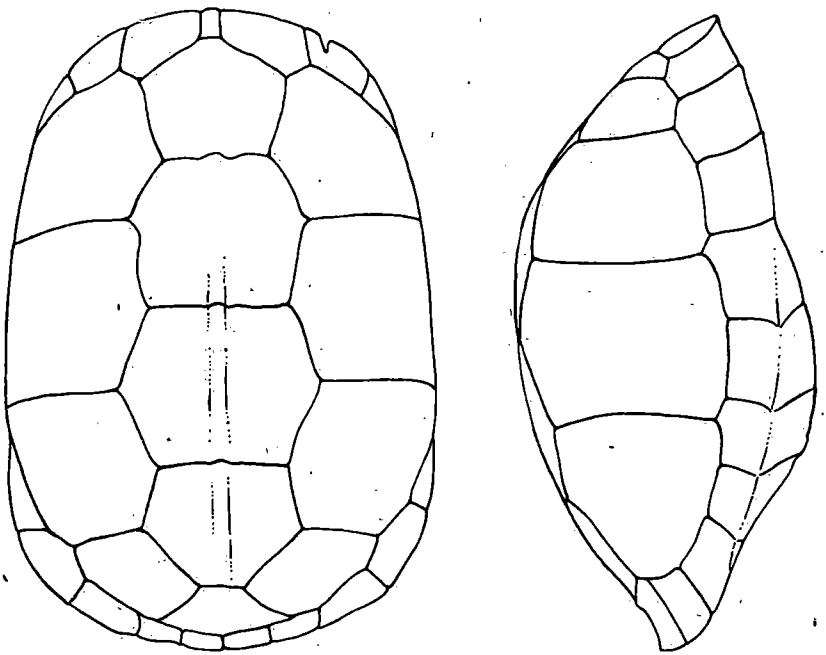

Figure 1.—Type of *Terrapene innoxia* Hay, USNM 8824, stratum 2 (?), Vero Beach, Indian River County, Florida, late Pleistocene (or Recent ?), referred to *Terrapene carolina bauri*. (A) dorsal view. (B) lateral view.

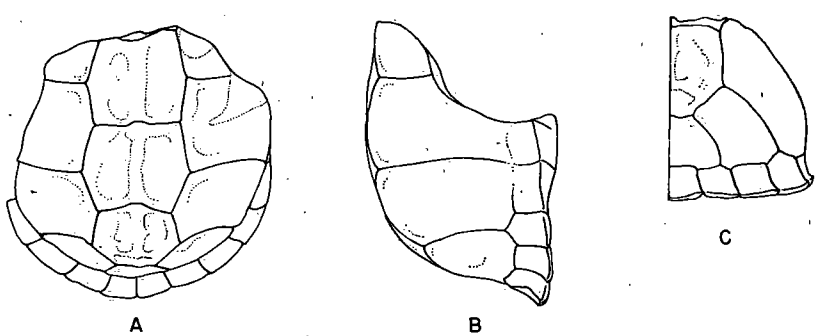

Figure 2.—Type of *Terrapene formosa* Hay, USNM 8825, from fissure fill in limestone quarry at Ocala, Marion County, Florida, Pleistocene, referred to *Terrapene carolina* (*bauri* or *carolina*). (A) dorsal view. (B) lateral view. (C) posterior view, right half.

collections of Amherst College and the United States National Museum (some of which are now in the Museum of Comparative Zoology) are referred by Gilmore to *canaliculata* (fig. 3). One specimen (USNM 11428) is provided with an associated complete plastron. The definite association of a plastron fitting Hay's description of *antipex* with a carapace identical to his description of *canaliculata* leaves little doubt that Gilmore is correct in placing the former in the synonymy of the latter.

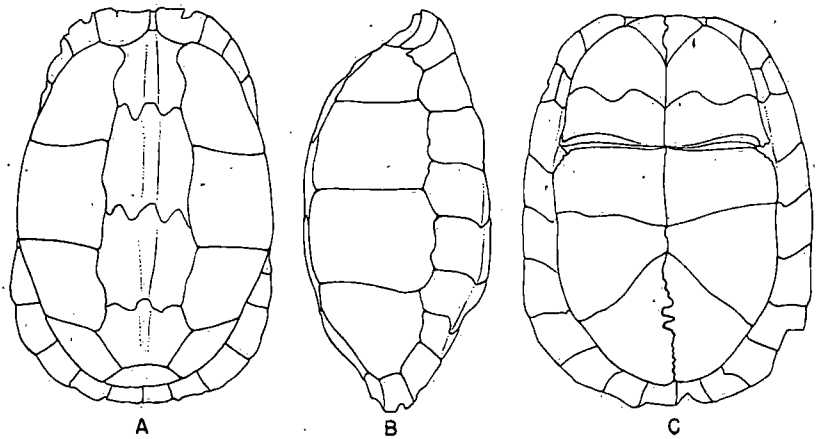

Figure 3.—Specimens typical of those referred to *Terrapene carolina putnami* (Hay), all from Golf Course locality, approximately three miles west of Melbourne, Brevard County, Florida, late Pleistocene. (A) dorsal view, AMC 25-144. (B) lateral view, AMC 25-145. (C) ventral view of carapace and plastron, showing axillary scale in contact with the third, fourth, and fifth marginal scutes, USNM 11428.

Barbour and Stetson (1931), in reviewing the fossil box turtles then known from Florida, placed *T. singletoni, T. innoxia,* and *T. formosa* in the synonymy of *T. canaliculata,* basing this action largely on a realization of the extreme variation within the shells of Recent *T. carolina.* The Pleistocene form, *T. canaliculata,* was diagnosed mainly on size alone. *Terrapene putnami* was retained as a much larger Pliocene species.

Oelrich (1953), in describing a new Pleistocene species related to the *carolina* group (*llanensis* from Kansas), suggests that *formosa, innoxia,* and *singletoni* may be valid, but gives no evidence for the statement.

Milstead (1956) agrees with Barbour and Stetson as to the synonymy of *T. innoxia, formosa, singletoni,* and *canaliculata.* He also places

llanensis in the synonymy of *canaliculata* and refers a series of shells from Friesenhahn Cave, Bexar County, Texas, to *T. canaliculata*. Two species described from the Pleistocene of Texas, *Terrapene impensa* and *T. bulverda*, are also placed in the synonymy of *canaliculata*. Although the western fossils of the genus are not considered in detail in the present study, it is significant to point out that Milstead re-emphasizes the conclusions of Barbour and Stetson that the only distinctive difference between *T. canaliculata* and *T. carolina* lies in the larger size of the former.

Milstead's work is certainly the most comprehensive so far in that it takes into account the variability of the Recent form, *T. carolina*, as well as illustrating for the first time the variability in a series of fossil shells. Even more important is the fact that in comparing the Friesenhahn Cave specimens with a small series from Ingleside, San Patricio County, Texas, and with published measurements of *canaliculata* from Florida, reference is made to intermediacy, a concept which, unfortunately, was not considered by earlier workers. The Ingleside specimens are said to be close to the Florida specimens of *canaliculata*, and the larger number of Friesenhahn Cave specimens intermediate between these and the Recent *carolina*. In the present paper it is hoped that it can be shown that two types of turtles occur in the Florida Pleistocene, rather than only one as Barbour and Stetson indicated. Furthermore, there are intermediates between the two extremes, representing two races of the species *carolina*.

Shell shape, sulcus patterns, and scute proportions are all highly variable within *Terrapene carolina*, as has been pointed out by a number of herpetologists. In some cases identification of Recent specimens from several areas of the United States by means of these characters becomes almost impossible. However, regardless of the nomenclatural problems confronting the herpetologist working with Recent forms, certain extremes can certainly be discerned. Thus, *Terrapene c. bauri* from central and southern peninsular Florida tends to be a rather small turtle with a high shell, with the highest point posterior to the middle of the carapace. Its shell is usually more triangular in cross section than any of the other subspecies. The peripherals are not as greatly flared as in *T. c. major*. In the latter subspecies the shell is not as gabled, but more flattened dorsoventrally and frequently with a depressed area on either side of the middorsal keel (fig. 4). The lateral keel above the bridge is much more obviously developed, and the posterior peripherals are much more strongly flared. In addition, the turtle attains considerably greater size. Though variable, the first vertebral is usually straight-sided in *bauri* from extreme south-

ern Florida but is decidedly urn-shaped in specimens of *major*. An axillary scale is rarely absent in specimens of *major* and rarely present in *bauri*. Most of these differences appear to be clinal, though the degree of difference per unit distance may be different for each character. The shells of *T. c. triunguis* and *T. c. carolina* are intermediate between those of *bauri* and *major*. *T. c. triunguis* is certainly one of the most variable of the races as regards shell shape.

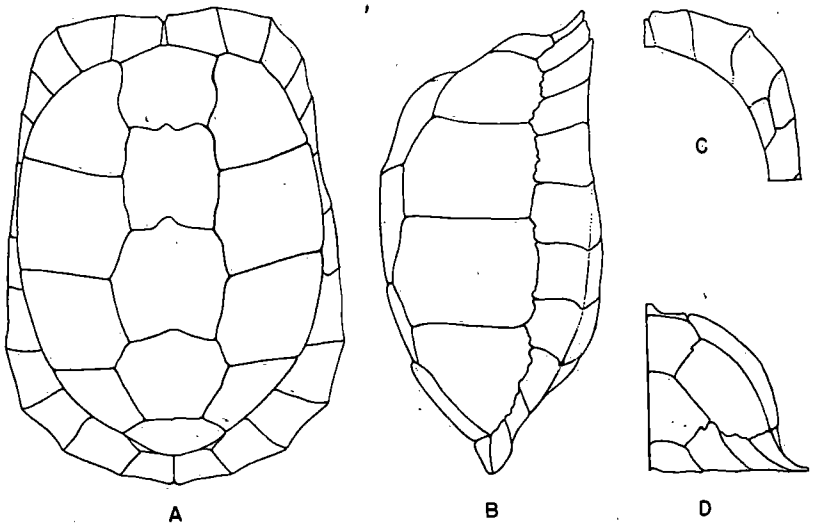

Figure 4.—Recent specimen of *Terrapene carolina major*, St. Josephs Island, Gulf County, Florida. (A) dorsal view. (B) lateral view. (C) ventral view of anterior peripherals, left side, showing axillary scale in contact with the third, fourth, and fifth marginal scutes. (D) posterior view, right half, showing flared posterior peripherals.

Most important to the present study is the fact that at least two basic shell types are represented in the Pleistocene beds of Florida: (1) a small, high-domed, or even gabled-shelled turtle with peripherals not greatly flared and a well-developed axillary scale lacking, and (2) a much larger type in which the shell is usually depressed dorsoventrally, peripherals widely flared, and an axillary scale always well developed. Both of these types are being termed *canaliculata* at the present time. As far as is presently known, except in deposits where admixture of faunas has definitely occurred, either one or the other is found. They are never found together in unmixed deposits.

The smaller box turtle found so commonly in the Pleistocene of Florida certainly represents the species *carolina*. Furthermore, it is closer to *T. c. bauri* and *T. c. carolina* than to *T. c. major*. It is indis-

tinguishable from *bauri* and *carolina* in shape, proportions of the scutes, and in sulcus patterns of both the carapace and plastron.

The larger turtle in the Pleistocene of Florida is certainly closer to the Recent subspecies *major*. The only character by which it can be separated from the modern subspecies is maximum size. The Pleistocene form grows much larger.

Terrapene c. carolina, major, and *bauri* intergrade at their mutual borders at the present time (table 4). Fossil specimens intermediate between the smaller and larger Pleistocene forms occur at some localities. Whether these are temporal or geographic intermediates is unknown at present. The smaller Pleistocene form, which lacks an axillary scale, is here considered synonymous with *Terrapene carolina bauri* or *Terrapene carolina carolina* or both, and the larger form in which an axillary scale is always found is designated by the new nomenclatural combination *Terrapene carolina putnami*. The morphological characters on which these designations are based are discussed below.

Material Examined

In order to evaluate variation in shell shape and sulcus pattern in Pleistocene specimens from Florida, 475 Recent specimens of *Terrapene carolina,* including the cotypes of *T. c. bauri* and *T. c. major,* were examined for particular characters. Specimens of *T. carolina* examined come from the following states: Florida 165, Georgia 81, Tennessee 73, Arkansas 12, Louisiana 5, Texas 17, Illinois 6, Missouri 12, Alabama 22, South Carolina 4, Mississippi 8, North Carolina 3, Virginia 11, Maryland 11, New Jersey 6, West Virginia 3, Ohio 13, New York 9, Pennsylvania 8, Massachusetts 3. Of the specimens from extreme southeastern United States, 54 can be termed "good" *major,* possessing all of the diagnostic characters presently used to separate this form from the others. Most of these specimens come from the general region of the lower reaches of the Apalachicola River in Florida. Specimens termed "good" *bauri,* in view of the fact that they possess all of the diagnostic characters of this race, total 59. These all come from peninsula Florida south of Marion County. The remaining 52 specimens from Florida are intermediate in at least some of their characters; intermediate between *bauri* and *major, bauri* and *carolina,* or *major* and *carolina.* These specimens come from the northern tier of counties of Florida southward on the peninsula to include Marion County.

The study of Recent *Terrapene carolina* is necessarily Florida-centered for two reasons. Specimens from this area are more com-

mon in collections than from other southeastern states, and data from the fossil box turtles of Florida indicate that populations in and near Florida today are the most important from a comparative standpoint.

In addition to Recent specimens of *Terrapene carolina*, 27 specimens of *T. ornata* from various parts of its range were also examined. One of the paratypes of *T. coahuila* (MCZ 53931), several individuals of *T. mexicana* (MCZ 4041, 4997, 9512, 56032, 56050), and one *T. klauberi* (MCZ 46855) were studied with regard to particular shell characters.

The study of fossil box turtles from Florida is based largely on 34 complete or nearly complete shells in which at least one entire half of the carapace is available. There are a few exceptions, namely, type specimens and *Terrapene formosa* in which the anterior quarter of the carapace is missing. In addition, a large number of fragments, particularly of the anterior and posterior peripherals were studied from several deposits.

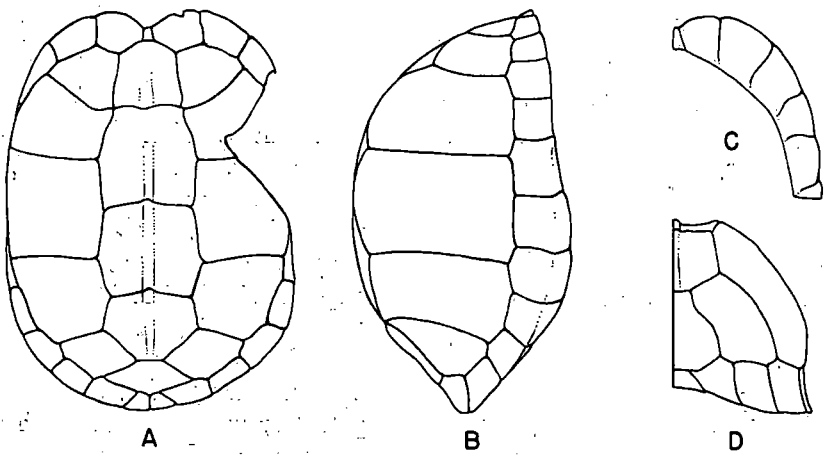

Figure 5.—Specimen referred to *Terrapene carolina carolina*, UF 9973, Arredondo I C, Alachua County, Florida, Pleistocene. (A) dorsal view. (B) lateral view. (C) ventral view of anterior peripherals, left side, showing absence of axillary scale. (D) posterior view, right half, showing nonflared posterior peripherals.

It is indeed fortunate that a fine series of 16 complete or almost complete shells are available from one Pleistocene locality—a quarry of the Dixie Lime Products Company, approximately one-mile south of Reddick, Marion County, Florida. Most of these are in the University of Florida Collections, although several are in the collections of the Florida Geological Survey. This series of shells constitutes the

largest yet assembled of *Terrapene* from any single Pleistocene locality in North America.

A specimen from Arredondo I, Locality C, Alachua County, Florida (UF 9973), is a particularly fortunate find since it is provided with a perfect skull attached to the inner surface of the anterior lobe of the plastron (figs. 5 and 8).

A small series of complete and partial shells is also available from the Melbourne area. These are deposited in the collections of Amherst College, the Museum of Comparative Zoology, and the United States National Museum. Single shells of less importance, which are complete or nearly complete, are available from several localities and are discussed below.

In addition to the excellent specimens mentioned above, 106 non-associated anterior and posterior plastral lobes are available from the Pleistocene deposits of Florida, as are hundreds of fragmental pieces of carapace and some partial skulls. Some of the more noteworthy of these are discussed below.

Analysis and Discussion of the Genus *TERRAPENE*

The name *canaliculata* is now applied to all Pleistocene box turtle remains from Florida. It has been applied to several populations outside the state as well. This form in the restricted sense is best described by Gilmore (1927). He redefines the species on the basis of newer, more complete material than was previously available. He outlines the main distinguishing features of this species as, " . . . large size; shell thick and heavy; carapace with its free borders curved upwards; posterior peripherals widely flaring; keel over the bridges connecting free borders of the front and back peripherals; gutter-like groove above this keel; first vertebral strongly urn-shaped with portion posterior to the middle as wide but usually wider than the anterior end; strongly elevated median longitudinal ridge, extending full length of first vertebral; median . . . keel [not] interrupted by transverse sulci."

All of the characters mentioned in the description above, as well as several others, have been examined to determine their variability in Recent specimens of *carolina*, as well as in the better and more abundant fossil material now available from Florida.

One character of considerable interest, and never before mentioned by workers in this group, is the presence of a well-developed axillary scale in shells belonging to the large *canaliculata*-type turtles in Florida. Recent specimens of *Terrapene c. major* almost always possess a well-developed axillary scale in contact with the third and fourth,

or third, fourth, and fifth marginal scales. Color, size, and shell shape are the main characters used to diagnose this subspecies so far. Examination of specimens of *T. carolina* from outside the range of *major* shows some variation in the development of the axillary scale. Rarely it is broken into a series of small scales. A similar abnormality occurs in other genera of turtles (Zangerl and Johnson, 1957). When present as a single structure in *Terrapene* it varies from a large obvious scale to one of small size. In some it is totally absent. For purposes of this study variation is simply tabulated as a presence or absence of the scale. If present, the marginal scutes with which the axillary scale comes in contact is noted. No attempt is made to evaluate individual

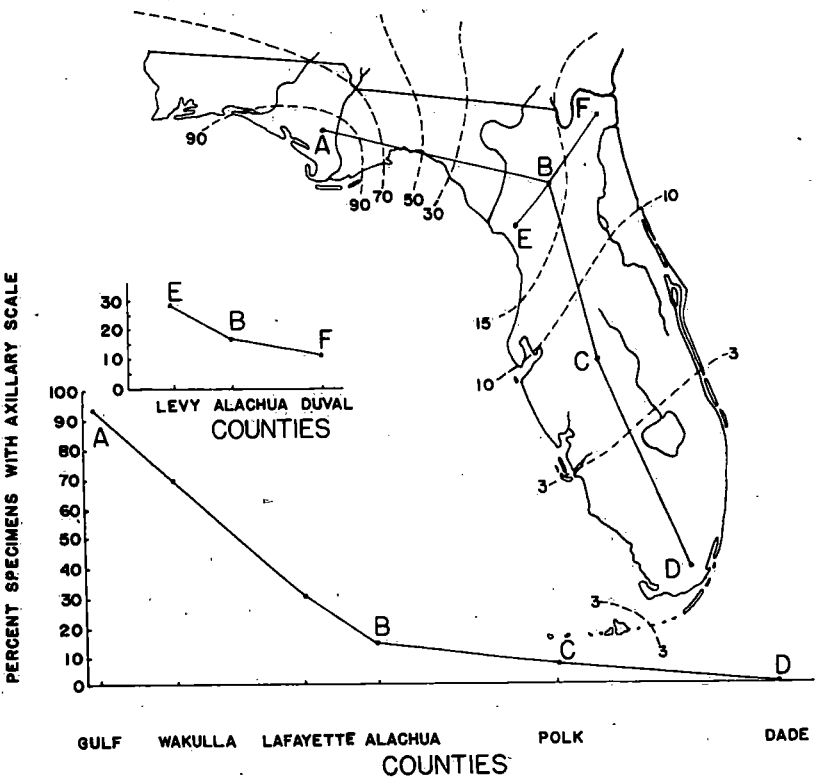

Figure 6.—Geographic variation in the percentage of specimens in various populations in Florida that possess axillary scales. The representation is a generalization and is meant to illustrate only major trends in this clinal type variation. Variations among small localized inter-breeding populations in the same general area are not of sufficient magnitude to alter the broad trends indicated here.

variation in its size since the material at hand indicates that such a study would in no way alter the general conclusions attained by means of the simpler method.

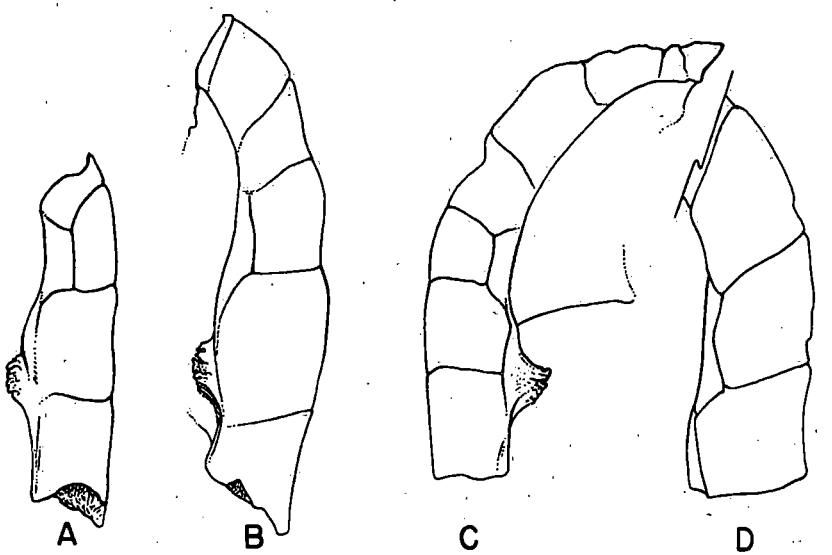

Figure 7.—Variation in development of the axillary scale in *Terrapene carolina putnami*. (A) UF 9928, Seminole Field, Pinellas County, Florida. (B) UF 2258, Bone Cave, Citrus County, Florida. (C) UF 2362, 51st St. locality, Bradenton, Manatee County, Florida. (D) UF 2211, Haile VII A, Alachua County, Florida. All specimens Pleistocene.

The axillary scale is absent in approximately two thirds of the specimens of *Terrapene c. carolina* from the eastern seaboard. It is absent in populations of *bauri* from southern Florida. It is variable in specimens of *triunguis* and *c. carolina* from the middle and western parts of the species range, but is never as frequent in *c. carolina* as in *major*. The specimens from northern and central Florida are intermediate as regards the number of individuals possessing the scale. Furthermore, a cline is suggested in Florida in which the scale becomes less frequent in populations from more southern areas of the state. Populations from the western half of the peninsula have the scale more frequently than do those from the eastern half. Presumably this is due to the influence of *major* existing in western Florida. Within the range of *major* in the panhandle of the state, the populations which most frequently have the scale present occur nearest the Gulf coast. Figure 6 illustrates variation in this character in Recent individuals of the species. Figure 7 illustrates variation in the size and shape of this

scale in several shells of the large Pleistocene box turtle called *canaliculata* in the restricted sense of Hay (1907, and later) and Gilmore (1927).[2]

An axillary scale is present in the single *Terrapene coahuila* and *T. klauberi* examined. It is present in two of the six individuals of *T. mexicana* examined.

No skull of *T. canaliculata* (*sensu stricto*) has yet been found. However, a fossil of a *carolina bauri*-type animal (UF 9973) from the Pleistocene deposits at Arredondo I, Locality C, Alachua County, Florida, possesses a fine skull. The associated shell is rather small (128 mm. in length), the peripherals are only slightly flared, the first vertebral is straight-sided, not urn-shaped, and the area above the bridge lacks a keel. Unlike *T. c. major* and most specimens of *bauri*, the quadratojugular portion of the postorbital bar is completely lacking, though this element may have dropped out while the specimen was rotting. (It frequently does this in macerating specimens of *bauri* because this element is somewhat loosely attached to its neighbors.) The presence or absence of the bar is apparently variable, at least in *T. carolina*. Unfortunately, the situation is much more complex than that indicated by Zangerl (1948a). In the fossil skull from Arredondo the postorbital is narrow and high as in *T. c. triunguis* and *carolina*, and a more robust element is found in *T. c. bauri* and *major*. The squamosal is relatively long and more like that in *carolina* and *major* than in *triunguis* and *bauri*. The posterior palatine foramina are small, and thus similar to those found in all of the North American subspecies with the exception of *major*, where they are usually rather large (fig. 8). As a unit the skull seems closest to that usually found in populations of *T. c. carolina*. The shell, because it is so high in proportion to its length, is more nearly like that typical of *T. c. bauri* (figs. 5 and 9), but is certainly encountered in some *carolina* specimens as well. The fossil shell lacks the axillary scale found in *canaliculata*-type specimens and almost all Recent *T. c. major*. Of the fossil forms described from Florida, it is obviously close to *T. innoxia* Hay and *T. formosa* Hay (figs. 1 and 2).

The characters utilized by Gilmore in redefining *Terrapene canaliculata* are discussed in detail below, with particular emphasis being placed on variation in both Recent and fossil samples from Florida.

[2] A similar pattern of geographic variation has been shown in the snake *Coluber constrictor* (Auffenberg, 1955). In the absence of any direct evidence bearing on the origin of such a geographic pattern it is quite reasonable to infer that its basis rests in dispersal patterns of particular organisms during the Pleistocene.

Differences between the recent subspecies *bauri* and *major* are stressed in order to illustrate parallel differences between the two Pleistocene forms on the one hand represented by *canaliculata* from Melbourne, and on the other by the Arredondo specimen mentioned above as well as the types of *formosa* and *innoxia*.

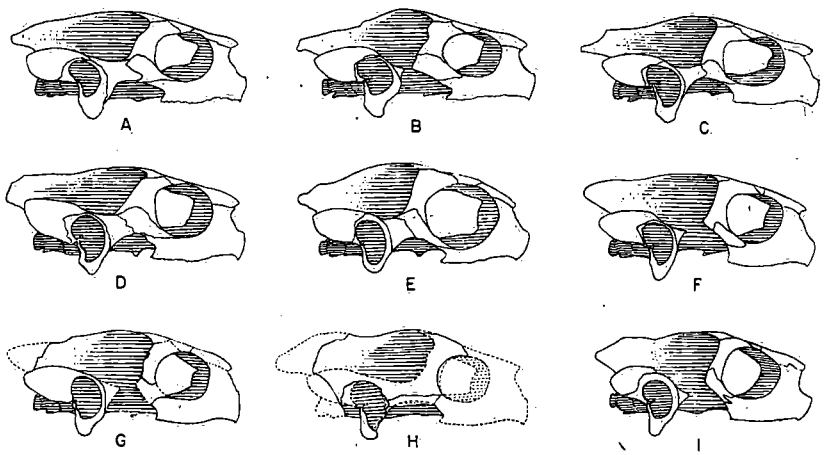

Figure 8.—Variation in the development of the postorbital bar in Recent and Pleistocene specimens of *Terrapene carolina*. Dotted lines represent reconstructed parts. (A, B, and C) Recent specimens of *T. c. bauri*, showing extremes of development; all from Gainesville, Alachua County, Florida. Drawing C represents the typical condition found in this part of the state. (D) Recent adult *T. c. major*, St. Josephs Island, Gulf County, Florida. (E) Recent juvenile *T. c. major*, 5 mi. W Apalachicola, Franklin County, Florida. (F) Recent *T. c. carolina*, Massachusetts. (G) UF 9973, Pleistocene, Arredondo I C, Alachua County, Florida, referred to *T. c. carolina*. (H) UF 9933, Reddick I B, Marion County, Florida, Pleistocene, referred to *T. c. ?carolina* × *T. c. putnami*. (I) Recent *T. c. triunguis*, (after Zangerl, 1948b).

SIZE.—This has been one of the characters most persistently used not only in describing several fossil forms from Florida and Texas but also in separating *canaliculata* from *carolina* (Milstead, 1956; Barbour and Stetson, 1931).

Size is a character of restricted diagnostic value when dealing with closely related reptiles. However, the several recognized subspecies of *T. carolina* show considerable differences in maximum size, as well as average size. Thus, *T. c. major* definitely attains a greater size than does *carolina* or *triunguis*. *T. c. bauri* is the smallest subspecies of the group. Maximum and average sizes of the samples of Recent specimens of *T. c. bauri, major,* and *carolina* are given in table 1. The available sample of *triunguis* is much too small to be signifi-

cant. Furthermore, the more western range of this form suggests that it need not be considered seriously in comparing Recent forms of *carolina* with the fossils from Florida.

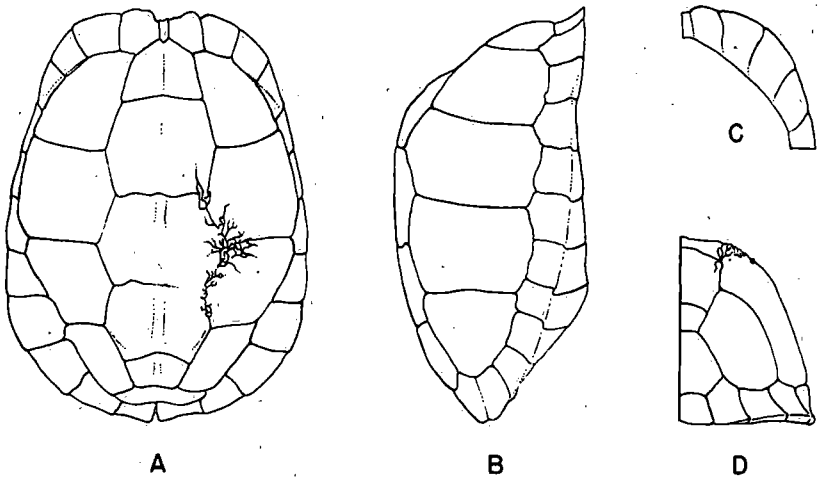

Figure 9.—Recent shall of *T. c. bauri,* Gainesville, Alachua County, Florida. (A) dorsal view showing dendritic scale abnormalities caused by fire, and an extra vertebral scute. (B) lateral view. (C) ventral view of anterior peripherals, left side, showing absence of axillary scale. (D) posterior view, right side, showing nonflared peripherals.

Similar measurements for the fossil shells from Florida are given in table 2. The entire sample is divided into three categories; the fine series of shells from a single locality at Reddick, Marion County, Florida, the small *bauri*-like shells from several localities, and the available specimens clearly referable to *T. canaliculata* (*sensu stricto*).

The specimens of *canaliculata* (*sensu stricto*) are obviously much larger than any of the Recent forms. Their size is approached most closely by *Terrapene c. major,* less so by the Reddick sample. The latter is intermediate between the Recent *major* and *carolina.* The *bauri*-type shells from the remaining fossil localities in Florida are essentially identical to *T. c. bauri* in size.

The smallest living box turtles in Florida are found at the extreme southern end of the peninsula. Individuals from the Keys seem to be somewhat larger, approaching those of northern peninsular Florida in shell length. They also possess a flatter shell than those from the adjacent mainland, and the peripherals are more widely flared. The largest living box turtles in North America are found along the Gulf coast from Bay County to Wakulla County, Florida.

Two specimens from St. Vincents Island are the largest box turtles I have measured (210 and 216 mm. respectively before the scutes were removed in preparing their skeletons). Northward from this coast the average carapace length becomes progressively less, so that at the Georgia border the turtles are only slightly larger than typical specimens of the subspecies *carolina* over the remainder of its range. Milstead (1956) was unaware that *major* attain so large a size. The largest Recent specimen of *Terrapene* that he measured is 162 mm. long. The largest fossil individual he measured is 208 mm., although fragments indicate that some specimens have attained lengths of from 240 to 260 mm. Living *major* from a restricted area along the Gulf coast attain a greater size than the majority of specimens from Friesenhahn Cave referred to *canaliculata*. It is obvious that if size is the only difference between Recent *carolina* and the Friesenhahn Cave sample, the reference of that fossil series to an extinct species seems

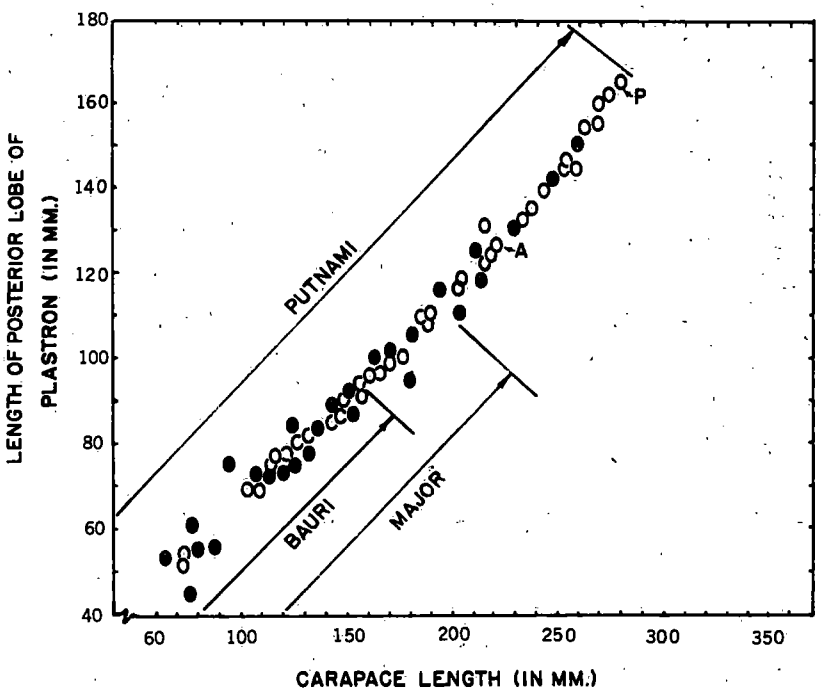

Figure 10.—Correlation of carapace length against hypoplastral length in Recent and fossil *Terrapene carolina*. Solid circles represent actual measurements; hollow circles represent specimens in which only the hypoplastron is available and the carapace length is estimated. The size ranges for both fossil and Recent nomenclaturally distinct races are indicated.

unwarranted, especially in view of the considerable variation demonstrated in living material from Florida. However, the Florida specimens of *canaliculata* (*sensu stricto*) considerably exceed in size the largest Recent *major* measured so far.

Partial plastra are by far much more abundant than complete carapaces. Of the plastral elements available from Florida, the posterior lobe is preserved complete most frequently. The posterior lobes of all Recent and fossil individuals were measured if a definite association with a particular carapace was possible. These measurements are plotted against carapace length (fig. 10). It then becomes possible to estimate carapace lengths of individuals represented only by the posterior lobe of the plastron, thus making it possible to obtain a better idea of size distribution in the various fossil populations than could be gained solely from the complete specimens now available. The results of these estimates are presented in table 3.

It is obvious that two turtles can be distinguished in the Florida Pleistocene on size alone. Of particular interest is the fact that the type of *Terrapene putnami,* described by Hay on the basis of its larger size, is not unduly larger than *canaliculata* (see fig. 10). A second fragment referred to *putnami* by Hay (1908b) is estimated to have originated from a specimen 320 mm. in length. There is every reason for believing that *putnami* bears the same relation to *canaliculata* (*sensu stricto*) as the latter does to *T. c. major,* and as *major* does to *carolina,* that is, a continuous trend toward increasing size from *bauri* on the one hand, through *carolina, major, canaliculata* (*sensu stricto*), to *putnami.* As members of a continuous series that can be separated by no other means, it seems unreasonable to assume that the relationship of all of these forms to one another is any more than a subspecific one, if indeed one should go even that far on size alone. *T. c. major* from the coastal areas of northwestern Florida, Alabama, Mississippi, and Louisiana is clearly differentiated from other nominal races of the same species on several characters other than size. This is also true of *T. c. bauri.* The fossil forms, *canaliculata* and *putnami* Hay 1907, are indistinguishable. *T. putnami* is considered to be subspecifically related to *T. carolina,* and of all the forms in this latter species, it is closest to *T. c. major.* The name *T. carolina putnami* as used below thus refers to the large, flared-shelled, Pleistocene box turtles of Florida possessing an axillary scale.

Shell Thickness.—Shell thickness is related to total size, and by itself a poor character with which to separate populations of Recent or fossil turtles. As a diagnostic tool it is valueless except as a cri-

TABLE 1

STANDARD CARAPACE LENGTH (IN MILLIMETERS) OF RECENT SPECIMENS OF *Terrapene carolina*

Subspecies	Mean	Maximum	Number
major	178	216	46
bauri	133	158	44
carolina	156	168	101

TABLE 2

STANDARD CARAPACE LENGTH (IN MILLIMETERS) OF FOSSIL SHELLS OF *Terrapene* FROM FLORIDA

Population	Mean	Maximum	Number
Reddick I B	154	181	24
bauri-type, several localities	128	156	4
canaliculata (*sensu stricto*)	230	262	6

TABLE 3

ESTIMATED CARAPACE LENGTH (IN MILLIMETERS) OF FOSSIL *Terrapene* FROM FLORIDA

Population	Mean	Maximum	Number
Reddick I B	150	190	51
bauri-type, several localities	132	173	63
canaliculata (*sensu stricto*)	227	285	20

terion of total size in small fragments of shells. This view is also held by Milstead (1956).

FLARED PERIPHERALS.—The degree of flare of the posterior peripherals has been used by several workers as a character considered to be of some merit in the description of fossil forms. It has been condemned by others as a character so variable that its use is deplored. That the peripherals are widely flared in some Pleistocene shells and little flared in others is quite obvious to even the casual observer (figs. 1, 2, 5, and 7). The same is true, but to a lesser extent, in Recent forms. Some objective estimate of the variability of this character in both Recent and fossil forms thus seems warranted.

The major problem involved in obtaining an estimate of variability in this character is one of measurement. Two factors seem to be involved, namely, the curvature of the posterior peripherals, and the distance to which they extend posterolaterally. A radius gauge was found to be most useful in describing the amount of curvature. The 10th peripheral was measured in all specimens. The radius was measured in the sulcus between the 10th and 11th element, since the surface of the peripheral is usually somewhat irregular while that at the bottom of the groove describes a smooth curve. The greater the radius the less the curvature, and thus the less flared the peripheral area is. The average radius of the available specimens of *T. carolina putnami* (14.6 mm.) is less than that of any other series of Recent or fossil shells. *T. carolina major* approaches most closely with an average radius of 15.8 mm. The slight difference between the two is not statistically significant. In the fossil series from Reddick I B the average radius is 23.6 mm. In *bauri*-type fossils from the remainder of the state the average radius is 30.1 mm. The average radius of Recent specimens of *T. c. bauri* is 26.7 mm. The difference between the two samples is not statistically significant.

The size of the flange is measured with dividers as the distance from the sulcus between the 10th marginal and the adjacent costal scute to the outer edge of the peripheral. The radial and linear measurements are then increased three times and drawn to scale. The radius is represented as an arc, and the size of the flange as a line segment. The angle formed between the line segment and the perpendicular is also measured. In this manner specimens with similar radii can be compared, regardless of size, so that differences in the size of the flanges can be demonstrated. Figure 11 illustrates the method of measurement of both the radii and the size of the peripherals, as well as comparing specimens of Reddick I B fossils with individuals of *Terrapene c. putnami* that possess a similar radial measure-

ment. After comparing specimens of Recent and fossil shells it is found that in specimens of similar radial measurements the flange in *putnami* is decidedly larger than in other forms. The flanges of fossils from Reddick I B are intermediate between those of *putnami* and those of *bauri*-type fossils in the same radial class. Recent *major* compared with *bauri* show that the former possess larger peripherals than the latter within the same radius class.

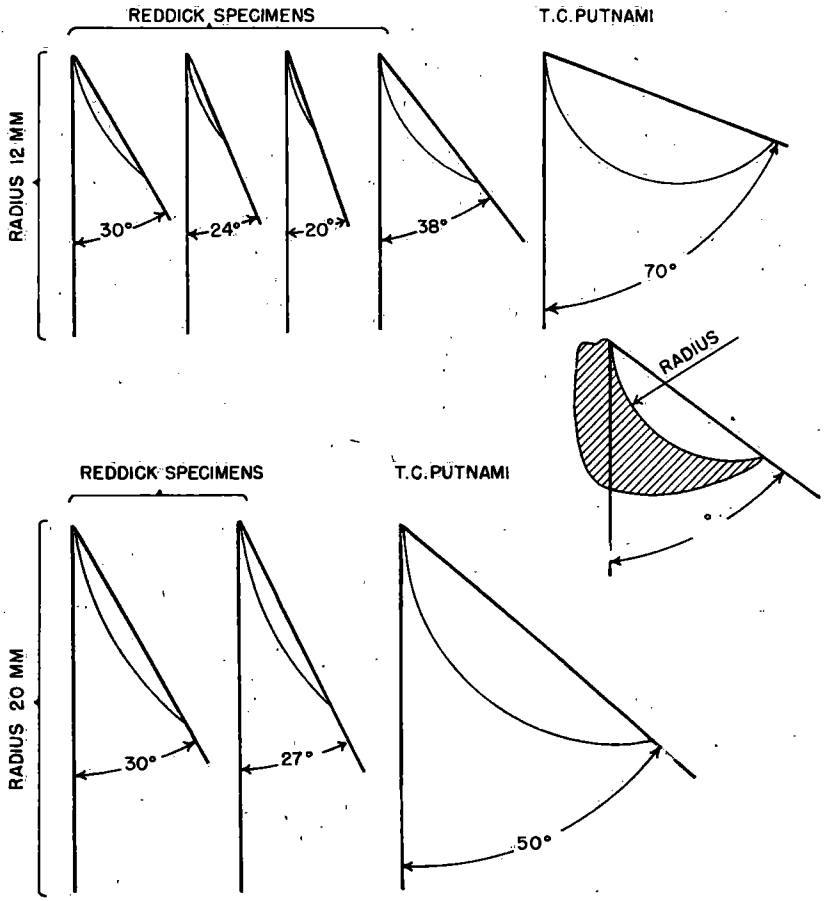

Figure 11.—A comparison of fossil specimens from Reddick I B and *T. c. putnami* having similar radial measurements of the 10th peripheral in two radius classes (12 mm. and 20 mm.) and showing the difference in the angle formed between the extended line segment and the perpendicular for specimens of any one radius class. The method of obtaining the radial measurement, the extended line segment, and the angle between it and the perpendicular is shown at the right. The shaded area represents a cross section through the 10th peripheral.

Of possible interest to future workers, I point out that in Recent box turtles there is a tendency for individuals from the lower Keys to be less gabled and provided with a more flared shell than that possessed by specimens from the closest part of the mainland. Comparable divergences between populations on the mainland and the lower Keys may be a common phenomenon in reptiles and amphibians of Florida (McConkey, 1957; Auffenberg, 1955).

KEEL ON THE BRIDGE.—As has been pointed out by Milstead (1956) the lateral keel above the bridge in *Terrapene* is rather variable. Furthermore, its development seems to vary with age, so that younger specimens of all forms possess a stronger keel than do older specimens. Apparently in some forms, such as Recent *T. c. major* and fossil *T. c. putnami* the sharp keel characteristic of the juvenile is retained into adulthood. The fact that the keel is well developed in the large Pleistocene shells is not particularly significant since it is rather variable even there, but it does provide another character pointing to the closer relationship of this fossil population to *major* than to *bauri*.

GUTTERLIKE GROOVE ABOVE THE LATERAL KEEL.—This character exhibits considerable variation and is of little diagnostic value. In specimens with a strong keel the edge is turned dorsolaterally producing a deep gutter. The nature of the groove is thus determined by the development of the keel on the bridge.

URN-SHAPED FIRST VERTEBRAL.—The shape of the first vertebral has been given considerable weight in the past. Milstead (1956) points out that the shape of this scute is extremely variable and of little use in diagnosis (fig. 12). However, I point out that in specimens of Recent *T. c. bauri* from extreme southern Florida the first vertebral is usually straight-sided. The shape is exceedingly variable in *carolina* and *triunguis*. It is always urn-shaped in adult specimens of *major*. Juvenile specimens of the last race usually possess a straight-sided scute, so that vertebral shape seems to be ontogenetically controlled, at least in this population. The type of *T. innoxia* Hay from Vero Beach has a first vertebral in which the sides are straight (fig. 1). The same is true of UF 9973 from Arredondo I C (fig. 5). It is urn-shaped in all specimens of *T. c. putnami* (cf. fig. 3) except one, and is rather variable in the fossil series from Reddick and the remaining *carolina*-type shells.

An urn-shaped vertebral is common in many species of emydine turtles. Its great development in *T. c. major* and *putnami* is another character suggesting the primitive nature of these forms.

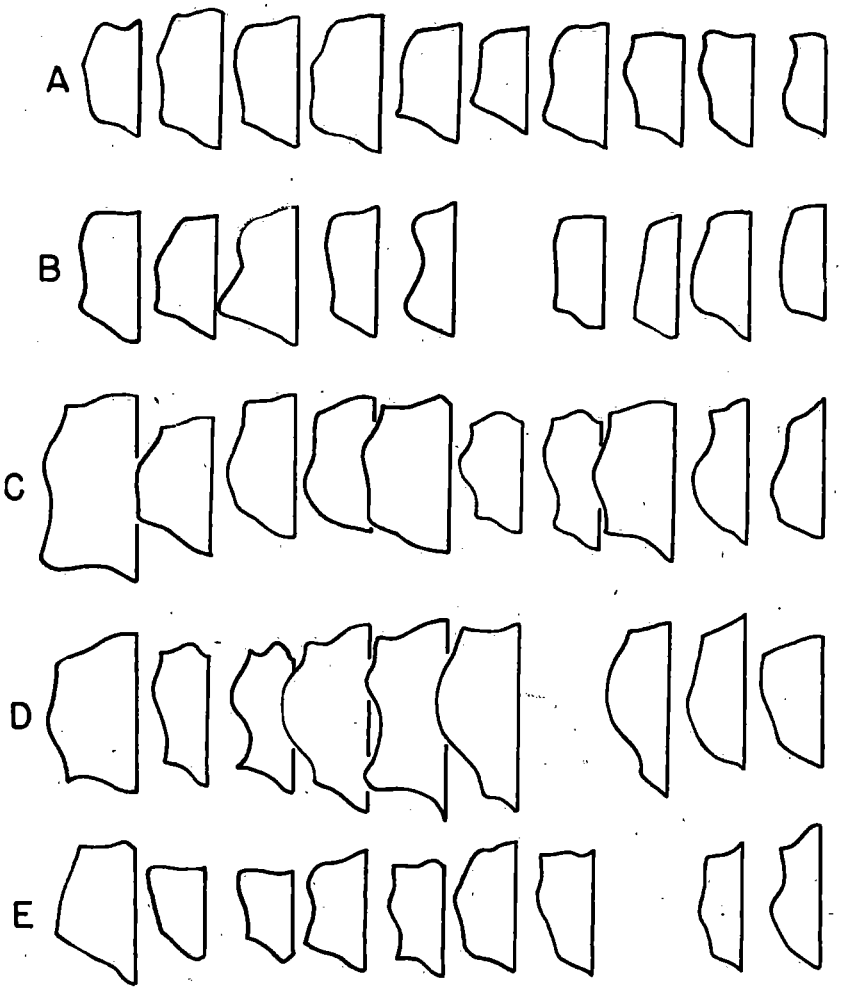

Figure 12.—Variation in the shape of the first vertebral scute. Only the right half of each scute is shown. (A) Gainesville, Florida. (B left) Baker County, Georgia. (B right) Dade County, Florida. (C) Gulf County, Florida. (D left) *T. c. putnami*, Pleistocene, Florida. (D right) Maryland. (E left) *T. c. ?carolina* × *T. c. putnami*, Pleistocene, Reddick I B, Marion County, Florida. (E right) eastern Tennessee.

ELEVATED MEDIAN LONGITUDINAL KEEL.—The degree of supravertebral carination of the shell is also a character showing considerable variation. It tends to be well developed in large fossil and Recent specimens. It is of course most obvious when the area on each side of the median line is depressed.

A fair proportion of fossil shells of both types of *Terrapene* from the Pleistocene of Florida have the seventh pleural bones in contact medially. One of Cope's specimens, referred to *Terrapene eurypygia* from the Pleistocene of Maryland, possesses a similar contact. A similar condition is also found in Recent specimens of *T. carolina*. Unfortunately, most shells of *Terrapene* have all of the bones of the carapace fused into a single unit. The sutures are obscure in almost all Recent and fossil specimens, so that the character is not easily studied unless numerous juvenile specimens are available for examination. I do not mean to imply, however, that all larger specimens have the bones of the carapace fused, since many large fossil and Recent specimens are provided with clear sutural articulations. In the type of *T. eurypygia* (Cope, 1869) the 5th vertebral comes in contact with the 10th peripheral. The type of *T. llanensis* (Oelrich, 1953) from the Pleistocene of Kansas differs from other fossil and Recent forms mainly in the size and shape of some of the posterior marginal scutes. However, Milstead (1956) finds the same condition in a few individuals of a series of fossil shells from Texas. He interprets this condition as an abnormality, and refers *llanensis* to the synonymy of *canaliculata*. Recent and fossil specimens possessing a fifth costal or a sixth vertebral are common (fig. 9). The fusion or articulation of the seventh and eighth vertebral centra of the carapace in *Terrapene* varies considerably. Zangerl and Johnson (1957) point out that the posterior part of the shell is more subject to areal abnormalities than any other. This suggests even more strongly that all of the cases mentioned above are abnormalities, and the species described on these characters should be placed in synonymy. However, the presence of a medial contact of the seventh pleural bones is, presumably, a character of considerable importance in separating pelomedusid turtles into the pelusiine and pelomedusine subgroups (Zangerl, 1948a). The eighth neural bone is usually absent in *Terrapene*, though it is sometimes represented as a long narrow element between the eighth pleurals (Hay, 1908b).

The disposition of still another fragment referred by Hay to a new species should be discussed. "*Trachemys* (?) *nuchocarinata*" Hay (1916) is described from a fragmental nuchal bone collected from the Florida Coast Line Canal, 20 miles north of St. Augustine, Florida. It is stated to be " . . . so peculiar that it can hardly be confused with any other nuchal." The diagnostic characters concern a well-developed, median, longitudinal keel. A similar keel occurs in several species of Recent and fossil *Pseudemys* and *Graptemys*. It is undoubtedly on this basis that Hay refers the fragment to *Pseudemys scripta* (= *Trachemys* of earlier workers), even though he does so with reser-

vation. The large keel projects anteriorly between the first marginal scutes. The nuchal scale is small; much smaller than in any Recent or fossil species of *Pseudemys*. A large keel and small nuchal scute occurs in *Terrapene*. The type of *Trachemys* represents a rather large turtle. The anterior parts of carapaces of fossil species described from Florida up to that time were unknown to Hay. The keel, its shape, and all the proportions and sulcus patterns can be duplicated in complete specimens of *Terrapene c. putnami* or even large specimens of Recent *T. c. carolina* or *major* (fig. 13). Because of its much larger size it is not difficult to see why Hay failed to compare the fragment with skeletons of Recent *Terrapene*. A similar keel occurs in modern subspecies, though it is not quite as evident except in large specimens of *T. c. major*. Subsequent authors either ignore the fragment described by Hay, or assume that he placed it in the correct genus. *Trachemys nuchocarinata* Hay is unquestionably a synonym of *Terrapene carolina putnami* Hay.

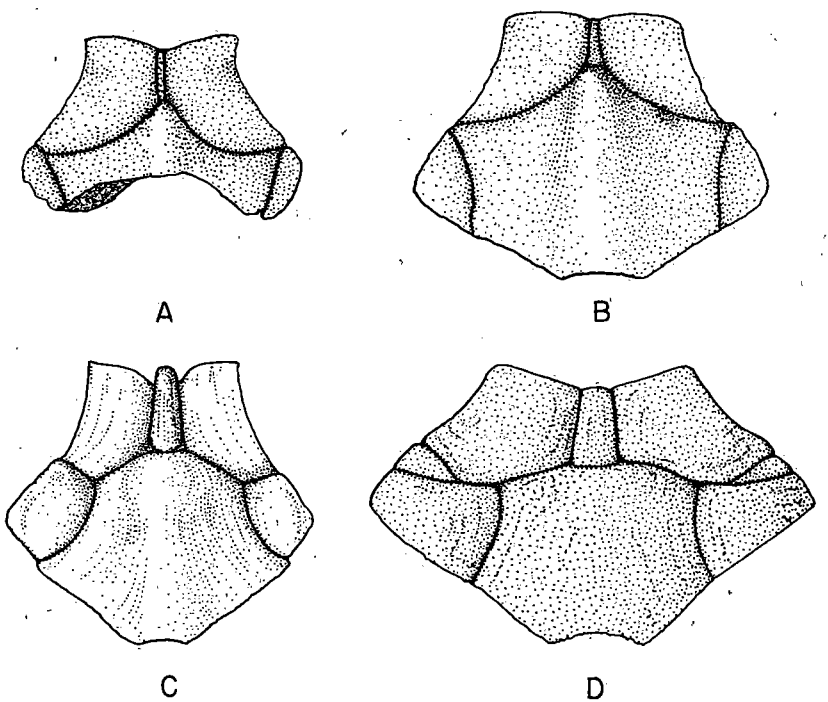

Figure 13.—Shape of the nuchal bone in: (A) Type of "*Trachemys* (?) *nuchocarinata*" Hay, referred to *Terrapene carolina putnami* (Hay). (B) Recent *T. c. major*, St. Josephs Island, Florida. (C) Recent *Pseudemys scripta*, Gainesville, Florida. (D) Recent *Pseudemys floridana suwanensis*.

It is shown above that at least two types of turtles are present in the Pleistocene of Florida. Previously these were both included under the name *canaliculata*. One of these forms clearly belongs to the Recent species *carolina*. This is, strangely enough, the first record of the species from the Pleistocene, all fossil forms previously being referred to extinct species. The other type found in the Pleistocene of Florida is synonymous with Hay's *putnami*. *Terrapene canaliculata* Hay is here considered synonymous with *T. putnami*, since the only distinguishing feature of *canaliculata* seems to be a smaller size, at least as represented by the specimens at hand. The name *putnami* antedates that of *canaliculata*. *Terrapene innoxia* Hay and *Terrapene formosa* Hay are definitely synonyms of the Recent species *T. carolina*. *T. innoxia*, taken from stratum 2 of the Vero Beach section, may have originated from stratum 3, since the differentiation in these is obscure, particularly on the south bank of the canal. Stratum 3 is now considered to represent post-Pleistocene time. The fact that the type of *innoxia* is identical with turtles living in peninsular Florida at the presnt time is thus not surprising. The type of *T. formosa* is from a Pleistocene fissure fill near Ocala, Marion County, Florida, so that *T. carolina* was definitely present on the peninsula during this time regardless of the true stratigraphic association of the type of *innoxia*. A well-preserved shell and skull from the Pleistocene deposits of pit 1, locality C, at the village of Arredondo, is definitely referable to *T. carolina*, probably *T. c. carolina*. All three of these shells—*innoxia, formosa*, and the Arredondo specimen—are much closer to *T. c. carolina* or *bauri* than they are to *T. c. major*. The large Pleistocene form, *T. c. putnami*, is closest to *major* (figs. 3 and 4), a thesis already advanced by Milstead (1956). The only difference between these two forms is that the Pleistocene form is larger. A few modern shells of *major* are as large, and even larger, than some fossil specimens referred to *putnami*. As shown above there is a gradual increase in size from *T. c. bauri* to *carolina* to *major*, culminating in the large specimens of *major* found near the mouth of the Apalachicola River, Florida, and particularly on the offshore islands. This trend continues through the Pleistocene fossils of the *canaliculata* type (*sensu stricto*) to terminate in the fossil form originally described as *T. putnami*. It thus seems unreasonable to suppose, in the absence of other diagnostic characters, that the fossil types are any more than subspecifically differentiated from *Terrapene carolina*. Hence the names *canaliculata, antipex, nuchocarinata*, and *singletoni* are placed in the synonymy of *T. c. putnami*. The only change in our concept of the species *T. carolina* involves the maximum size attained. At present this is recognized as

216 mm. The inclusion of *putnami* in this species raises the maximum size to perhaps 320 mm. The over-all range of size within the species is certainly no greater than that in the rattlesnake *Crotalus viridis,* in which the several populations vary greatly in length.

The fine series of shells from the Pleistocene of Reddick appear to be intermediate between *Terrapene carolina major* and *T. c. carolina,* or *bauri,* or both, in size, percentage of specimens with an axillary scale, and degree of flare of the posterior peripherals. In all of these characters they are closer to *bauri* or *carolina,* especially the latter, than they are to *major.* The same deposit contains other northern herpetofaunal elements (Auffenberg, 1956, MS) suggesting somewhat cooler climates than the current ones. The population of box turtles at Reddick may represent one intermediate between two either chronological or geographical races. Brodkorb (1957) recently suggested that the deposits at Reddick may represent Illinoian time, but the situation is rather complex (Bader, 1957).

The type of *Terrapene singletoni* Gilmore is unique in several regards. It is large, suggesting the *canaliculata*-type turtle. The peripherals are little flared and possess a large radial measurement. It also lacks an axillary scale. The last two characters indicate a close relationship to *bauri-carolina.* The shape of its shell, that is its elongation, is duplicated in populations on the east coast of Florida at the present time, although not in other populations in peninsular Florida. *Terrapene coahuila* also possesses a long narrow shell with little flare, but in at least one of the paratypes (MCZ 53931) an axillary scale is present. The type of *T. singletoni* is here interpreted as an intermediate between *T. carolina putnami* and another race of *T. carolina,* being closer to the former on the basis of its size. Similar intermediate individuals are described from several localities in Texas (Milstead, 1956). In the case of the Texas material, the intermediate condition may be the result of intergradation or some other sort of genetic exchange between one or more of the little-known Mexican species of *Terrapene* and *T. carolina,* rather than between *T. carolina* and the large Florida Pleistocene box turtle. The intermediate shells from Florida are here interpreted as the result of geographic or temporal intergradation, or both.

In addition to the intact shells discussed above, many fragmentary specimens from the Florida Pleistocene were examined. Of particular importance are fragments of the anterior part of the shell including the peripheral areas of the third and fourth marginal scutes; the presence or absence of an axillary scale can be demonstrated in such material. Posterior parts of the shell including the peripherals were

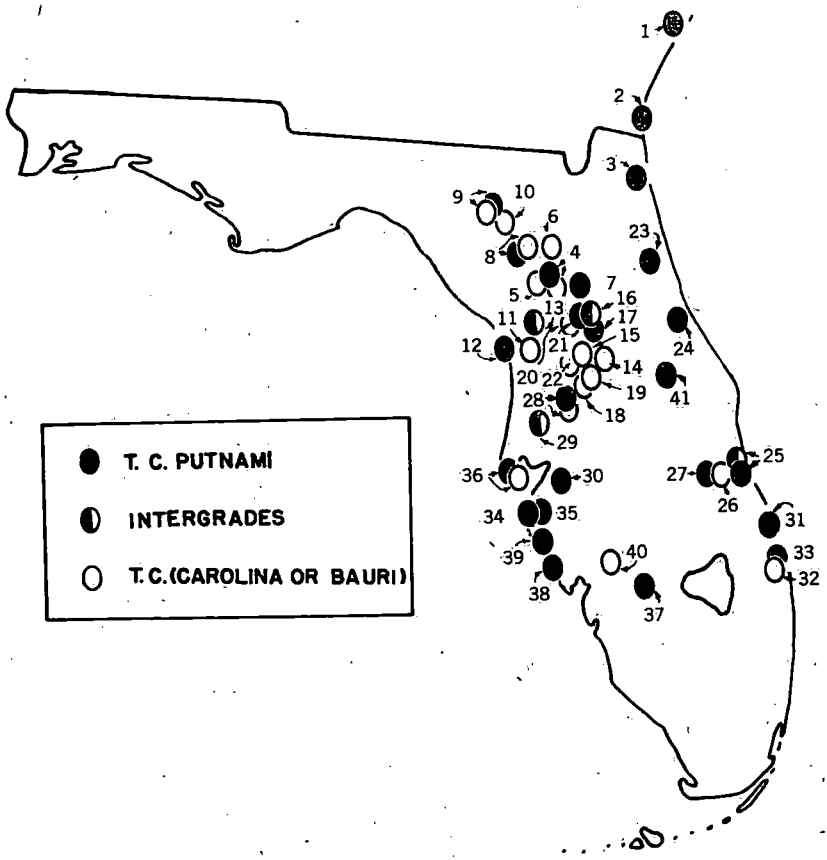

Figure 14.—Fossil localities in Florida and Georgia from which specimens of *Terrapene* have been examined. (1) Skedaway or Whitemarsh Islands, Georgia. (2) St. Marys, Georgia. (3) Jacksonville. (4) Arredondo I. (5) Arredondo II. (6) Wall Company Pit. (7) Paynes Prairie B. (8) Haile VII. (9) Itchatucknee River. (10) Three Rivers Development. (11) Wekiva Springs. (12) Waccasassa River. (13) Williston. (14) Ocala. (15) Zuber I. (16) Reddick I. (17) Reddick II. (18) Eichleberger Cave. (19) "Uranium" Cave. (20) Mefford Cave I. (21) Mefford Cave II. (22) Kendrick I. (23) 20 mi. N St. Augustine. (24) 28 mi. S St. Augustine. (25) Golf Course locality, 3 mi. W Melbourne. (26) 8 mi. W Melbourne. (27) 10 mi. W Melbourne. (28) Bone Cave. (29) Lecanto or Saber Tooth Cave. (30) Alafia River. (31) Winter Beach locality. (32) Vero Beach, stratum 2. (33) Vero Beach, stratum 3. (34) Bradenton, 51st St. locality. (35) Tamiami Blvd. locality. (36) Seminole Field. (37) LaBelle. (38) Venice. (39) Sarasota. (40) Prairie Creek. (41) Apopka Creek.

examined for degree of flare. General size was also considered. Specimens were referred to either *Terrapene carolina* (*carolina* or *bauri*) or *Terrapene carolina putnami*. With additional material from some of the deposits it might be demonstrated that the populations from which some of the fragmentary specimens are drawn are actually intermediate. The distribution of these two types of box turtles in the Florida Pleistocene is shown in figure 14.

As pointed out above, the populations of Recent *T. c. major* adjacent to the Gulf coast contain not only the largest living *Terrapene*, but the highest percentage of individuals with a well-developed axillary scale. Only *T. c. putnami* of the Pleistocene are larger. With the possible exception of *singletoni*, which may be an intergrade, all of the large fossil shells possess well-developed axillary scales. Recent *major* are obviously close to Pleistocene *putnami*. It is entirely conceivable that a large part of the range of what we are calling *major* may, in actuality, represent an area of intergradation between Recent *T. c. carolina* or *triunguis* or both on the one hand and Pleistocene *putnami* on the other. Thus, *T. c. major* may represent a relict integrade population.

Terrapene c. major is more aquatic than any of the other Recent subspecies (Carr, 1952). *T. c. putnami* is closest to *T. c. major*, and remains of the former are most abundant in deposits laid down in marshes, swales, or extensive low areas—Vero Beach, Winter Beach, Melbourne, Bradenton, Seminole Field, etc. Most of the localities are coastal, extending from near Savannah, Georgia, around the peninsula of Florida to the Waccasassa River in Levy County. To date *putnami* is known from seven inland localities, namely: Bone Cave, Citrus County, is a cavern in the Ocala limestone, the mouth of which is located on a very slight rise overlooking a rather extensive low area to the northeast, part of which is covered with a body of water; the remainder is swampy. Reddick II is a deposit obviously laid down in an extensive marshy area. LaBelle, Hendry County, is near extensive marshy areas. Paynes Prairie, Alachua County, is still a large marsh. Arredondo I A deposits apparently were laid down when Kanapaha Prairie was much more extensive than it is at present. Itchatucknee River run, during former times, apparently had along it extensive marshes. Apopka Creek is located near extensive lowground. There are two exceptions to the seemingly general association of this type of turtle with extensive marshy areas, at least during the period of deposition. One of these is represented by a series of bones of the plastron and carapace of a turtle from Mefford Cave II, approximately one and a half miles south of Reddick, Marion County.

Florida. As far as is known there are no other marsh-dwelling faunal elements in the deposit along with the turtles. The next cave west of Mefford II (Mefford Cave I) contains remains of only the smaller Pleistocene *Terrapene*. A single large fragment of *T. c. putnami* is also available from Haile VII, locality A, Alachua County, Florida. A pond, probably of rather small extent, was present during some part of the Pleistocene. Unfortunately the specimen was not found in place, so its exact origin is unknown. Other specimens of *Terrapene* found in place at Haile VII A, and in a fissure locality nearby (Haile VII B) are referred to *T. c. carolina* or *bauri*.

Neill (1957) points out the importance of a highway of dispersal for certain land vertebrates entering Florida from more western areas during a period of decreased rainfall sometime during the Pleistocene. Most of the forms he discusses are organisms inhabiting dry and rather open habitats. However, during the Pleistocene glacial periods when sea levels were low, animals of certain marsh-inhabiting types might use as a highway of dispersal a circumferential Gulf route much broader than the one indicated by the present coastal marshes and lagoons. That Recent *major* is more aquatic than the other recognized races has been pointed out. Most of the Pleistocene localities from which *putnami* has been taken represent marshes or low-lying areas. It is thus conceivable that *putnami* entered coastal peninsular Florida along this route. If so, it is likely that most of the range of Recent *major* represents a relict intergradient population, rather than being directly evolved from *T. canaliculata* (*T. c. putnami*) as Oelrich (1953) has suggested.

The name *major* is here retained as a convenient label for a distinct Recent population, though it may represent either a temporally or geographically intergradient one, or both. *T. c. putnami*, undoubtedly derived from more western areas, must then have either fossil or Recent representatives in that area. Better collections of Mexican species of *Terrapene* may show that one or more of them is closely related to *T. c. major* or *putnami* or both.

The series of fossil turtles from Friesenhahn Cave and the Ingleside locality, both in Texas, may bear the same relation to *T. c. triunguis* and Pleistocene *putnami* as *major* does to *T. c. carolina* and Pleistocene *putnami* in Florida. A large (215 mm.) specimen of *Terrapene* from San Diego County, Texas, referred by Hay to *T. marnocki* (AMNH 3936) conceivably could be close to *major* or *putnami* or both, or to some Mexican relative. These problems are best referred to workers in that area who are more familiar with the local depositional

phenomena, correlation of isolated Pleistocene localities, and who have adequate series of both fossil and Recent shells available.

Apparently *Terrapene carolina putnami* had an extensive range during at least a part of the Pleistocene. There is no reason to suppose that all of the localities in which this form is found are contemporaneous. In fact, some evidence supports this idea. Unfortunately, the Pleistocene deposits are far from being adequately correlated. Hence we know almost nothing of the sequence of events that led to the present distribution of the populations of *Terrapene carolina* in Florida. There is, however, some reason to believe that stratum 2 of the coastal localities is a reasonably contemporaneous bed from one locality to the next. Stratum 3 may also be contemporaneous at its various coastal localities, and is one in which mixture of faunas has occurred. Some recent workers consider stratum 2 at least in some of the coastal localities to be correlated with Altithermal time, or about 5000 B.C. Other authors believe this bed to be much older (Nebraskan, Hay, 1923; substage of the Wisconsin, Cooke, 1945). *Terrapene c. putnami* is known from this stratum in almost all of the localities in which it is found. This race must have had a wide distribution, at least along the coast, during this time. In the same coastal localities *Terrapene carolina—carolina* or *bauri* or both, but probably the latter—occurs in stratum 3, now considered post-Pleistocene (Van Valkenburgh beds of Rouse, 1951). Most inland localities, such as Reddick I, Marion County; Haile VII, locality A, Alachua County; Ocala, Marion County, from which the same type turtle has been taken, are certainly considerably older than post-Pleistocene. Unfortunately, in none of these inland localities is there any really definite evidence that either of the two types preceded the other. There remains the possibility that they are, at least in part, contemporaneous, in which case their subspecific relationship might be open to question.

At the Arredondo I locality a *carolina*-type shell has been taken from a deposit (C) stratigraphically higher than one (A) in which a *putnami*-type shell has been found. In Bone Cave, Citrus County, the *putnami*-type shells are found in the older breccias on the walls of one of the chambers, while the apparently more recent *bauri*-type shells are mixed with the former on the floor of the same chamber. I suggest that *T. c. putnami* inhabited the area around these two localities—Arredondo I C and the floor deposits of Bone Cave—before the time represented by the smaller shells. However, the peculiarities of depositional factors associated with fossils originating from sinks, such as those at the Arredondo locality, leaves much to be desired in regard to correlation. The floor deposits of Bone Cave are almost useless

for more detailed correlation, since very recent remains are scattered among the older bones.

If Brodkorb (1957) is correct in assigning the Reddick I deposits to the Illinoian, it would appear that an intergradient population (*carolina* × *putnami*) was present in at least the central part of the peninsula during this time; that at some stage in the Wisconsin or during Altithermal time, *T. c. putnami* dispersed eastward, probably from Texas, along almost continuous coastal lowland areas as far north as Savannah; and that in post-Pleistocene time a *bauri* type replaced *putnami* over all of peninsular Florida, and *carolina* replaced *putnami* in coastal Georgia. The relationship between *T. c. bauri* (or *c. carolina* or both) and *putnami* during Wisconsin or Altithermal time must have been similar to that between *c. carolina* and *c. major* at present, with *major* being found near and in the coastal marshes, and the smaller form farther inland.

However, this does not explain the distribution of *putnami* in more inland localities during the Pleistocene. If the dispersal of this form during the Wisconsin was so extensive that it covered all of the peninsula, it must be assumed that *bauri* retained its identity during this period and was distributed to the north of peninsular Florida, perhaps in southern Georgia. This seems unreasonable, since *bauri* is, presumably, an animal adapted to the warm conditions of peninsular Florida and would hardly be expected to range much farther north during a glacial period. However, it might be assumed that *bauri* is a post-Wisconsin product of evolution in the box turtles. This too seems unwarranted, since some of the fossil specimens from definitely Pleistocene deposits are clearly identical to *bauri*, or at least closely related to it. Furthermore, on the scant evidence from the Arredondo I and Bone Cave localities it appears that *T. c. putnami* preceded at least some populations of *carolina* or *bauri* or both in this area. The most reasonable explanation seems to be that the inland records of *putnami* represent a different time period than stratum 2; probably much earlier.

Until more data are accumulated on the age of many of the deposits in the central part of the state, the period during which *putnami* inhabited this area will remain highly speculatve. Specimens from Reddick I B seem to be somewhat intermediate between *T. c. carolina* and *T. c. putnami* or *major*. This is based on a number of characters. The same locality includes other northern herpetofaunal elements (Auffenberg, 1956, MS). Brodkorb (1957) suggests that the locality may represent at least a part of the Illinoian glacial period. Thus it is not surprising that the fossils from this locality reflect influences from

northern forms, for example, *T. c. carolina*. The population seems intermediate between this race and the larger *major-putnami* type. More typical populations of the latter may have occurred to the west of the Reddick locality. One then wonders whether *T. c. bauri* was already differentiated in Illinoian time, and if so, where it was located. Those questions must remain unanswered at present.

The remaining herpetofauna from Reddick indicates cooler climatic conditions than are now found in the area, but not much cooler than Virginia. The least change necessary to bring these northern elements into Florida would be one in which the climate became similar to that of the area around the South Carolina-Georgia boundary. Although it is not known how cold it became in Florida during the height of a glacial period, the suggested herpetofaunistic shift seems minor. Thus, the Reddick deposits may not represent the Illinoian maximum, but some period before or after.

Terrapene from the deposit at Reddick suggest a close proximity to *T. c. putnami* or *major*, if indeed the latter was at all present in the peninsula during Pleistocene time. During Sangamon interglacial time many islands were apparently produced in what is now the peninsula. *T. c. putnami* may be an indicator of near-shore environments in the Pleistocene, as "good" *major* is at present. If true, then I suggest that sea level was relatively higher when the Reddick materials were accumulating than at present; that is, the locality represents the beginning or end of the Illinoian. *T. c. bauri* may have been located on one or more of the Sangamon islands, and may or may not have become reconnected with *T. c. carolina*. It is conceivable that *bauri* became differentiated on one or more of these islands during this time, although it may have evolved much earlier.

In any event, it is important to emphasize that at least some of the subspecies of *T. carolina* are much older than post-Pleistocene. A turtle essentially identical to *T. c. bauri* was already differentiated from the primitive *T. c. putnami* in the Pleistocene. Figure 15 depicts the hypothetical distributional stages of the subspecies of *T. carolina* in Florida in Pleistocene and post-Pleistocene time. Fossil records attest to the occurrence of particular races in particular areas. However, correlation of the deposits is quite unproven at present. Even in the absence of details of correlation of deposits in Florida it seems fairly obvious that the range of the primitive type of *Terrapene* (*putnami*) has become more and more restricted, even withstanding possible expansions in range during the glacial periods. It may be less obvious from this study that *T. c. putnami* is represented at present, at

least in part, by a geographically somewhat restricted intermediate population, *T. c. major.*

A tentative arrangement is presented in table 4 as a speculative correlation of Pleistocene vertebrate-bearing strata; this is based on taxonomic determinations of fossil *Terrapene* populations from Florida and the available stratigraphic data. Table 5 summarizes the taxonomic determinations made from complete or fragmentary shells of *Terrapene* for all of the deposits from which box turtles are now known in Florida.

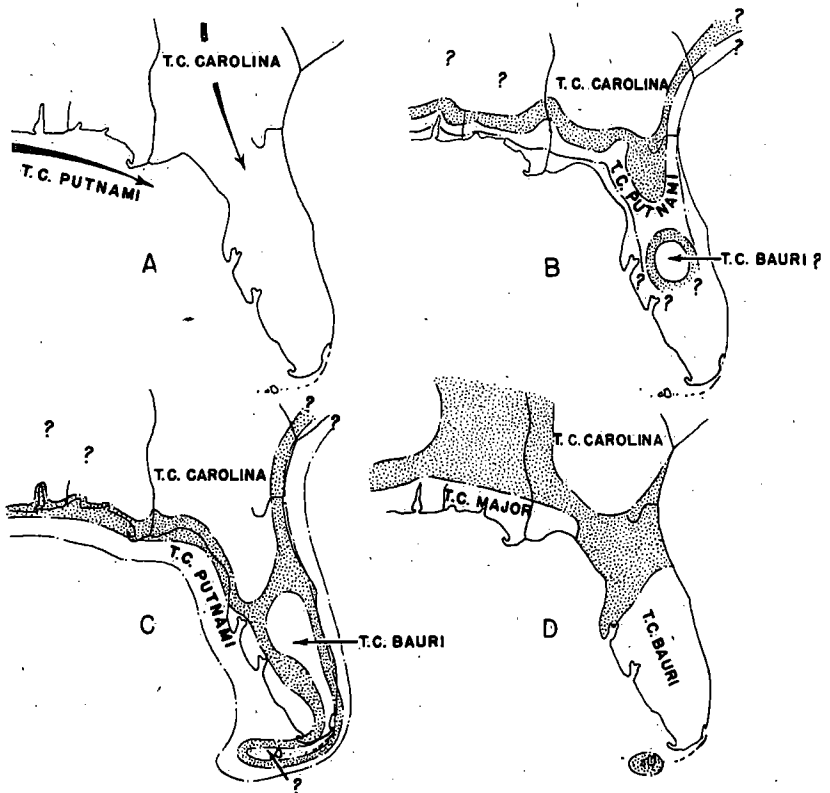

Figure 15.—Major distributional stages in the evolution and dispersal of *Terrapene carolina* in southeastern United States. (A) movement of a large, primitive stock (*T. c. putnami*) eastward along a circumferential Gulf coast marsh route sometime in the early Pleistocene. (B) hypothetical stage during some interglacial period when sea level was much higher than at present. (C) hypothetical stage during some later glacial period when sea level was much lower than at present. (D) present distribution of the subspecies. *T. c. major* is assumed to represent a relict intergrade population between *T. c. carolina* to the north and Pleistocene *T. c. putnami* to the south. Stippled areas represent areas of intergradation.

TABLE 4

TENTATIVE CORRELATION OF FOSSIL *Terrapene* LOCALITIES IN FLORIDA

Time	Bauri	Bauri × Putnami	Putnami
RECENT	Vero Beach, stratum 3 Seminole (in part) Wekiva Springs Itchatucknee River (in part) Bone Cave (in part)		
PLEISTOCENE			
Wisconsin maximum ►	8 mi. W Melbourne Eichleberger Cave A and B "Uranium" Cave Mefford Cave I Kendrick I Itchatucknee River (in part) Three Rivers Development	3 mi. W Melbourne	Seminole Field (in part) LaBelle Sarasota Venice Vero Beach, stratum 3 Waccasassa River near St. Augustine 3 mi. W Melbourne 10 mi. W Melbourne Alafia River Winter Beach Bradenton Field
Sangamon maximum ►		Lecanto Cave	Itchatucknee River (in part)
			Bone Cave (in part) Mefford Cave II Reddick II Arredondo I A Paynes Prairie B Haile VII A (in part) Apopka Creek
		Reddick I B Zuber I Williston	
Illinoian maximum ►	Arrendondo I C; II Wall Company Pit Haile VII A (in part) Haile VII B		

TABLE 5

DETERMINATIONS OF FOSSIL *Terrapene* FROM THE PLEISTOCENE BEDS OF GEORGIA AND FLORIDA

Locality	Subspecies of *Terrapene carolina*	Remarks
GEORGIA		
Skedaway or Whitemarsh Islands	*putnami*	Types of *T. canaliculata*, USNM 5500
FLORIDA		
Alachua County		
Arredondo I, A	*putnami*	UF 2429
Arredondo I, B	*Terrapene* sp.	UF 2045
Arredondo I, C	*?carolina*	A complete shell and skull, UF 9973
Arredondo II	*?carolina*	UF 2094
Wall Co. Pit	*carolina* or *bauri*	UF 2017, 5023–4, 5028
Paynes Prairie B	*putnami*	UF 6408
Haile VII, A	*putnami*	UF 2211
	carolina or *bauri*	Complete shell and plastron. Private collection; not available for further study. Also FGS uncataloged and UF 1790, 9936.
Haile VII, B	*carolina* or *bauri*	FGS V-5708
Brevard County		
3 mi. W Melbourne (Gold Course loc.)	*putnami*	USNM 11428 AMC 25-144, 25-145 MCZ 1024–1028
	putnami × *?bauri*	Type of *T. singletoni*, USNM 11181
8 mi. W Melbourne	*bauri*	UF 1586
10 mi. W Melbourne	*putnami*	UF 1594
Citrus County		
Bone Cave	*putnami*	Large part of shell, UF 2258
		Large pieces of shells, plastra, etc., UF 2257, 2616, 2625, 6520
	bauri	Anterior parts of carapaces, numerous plastra, UF 2622, 2623
Lecanto Cave (Saber Tooth)	*putnami* × *?bauri*	FGS uncataloged.

[continued]

TABLE 5—(continued)

DETERMINATIONS OF FOSSIL *Terrapene* FROM THE PLEISTOCENE BEDS OF GEORGIA AND FLORIDA

Locality	Subspecies of *Terrapene carolina*	Remarks
Columbia County		
Itchatucknee River	*carolina* or *bauri*	UF 1986
	putnami	UF 1616
Three Rivers Development	*carolina* or *bauri*	UF 1611
DeSoto County		
Prairie Creek	*Terrapene* sp.	UF 6613
Hardy County		
Near LaBelle	*putnami*	UF 5817
Hillsborough County		
Alafia River	*putnami*	Type of *T. putnami*, AMNH 6097
Indian River County		
Winter Beach Locality	?*putnami*	UF 1865
Vero Beach, stratum 2	*bauri*	Type of *T. innoxia*, USNM 8824
		Also FGS V-5471, 7085
Vero Beach, stratum 3	*putnami*	Type of *T. antipex*, USNM 8820
		Also FGS V-4435, 5478, 5480, 5255
Levy County		
Wekiva Springs	*bauri*	UF 2588
Waccasassa River	*putnami*	UF 4267
Williston (Holman locality)	*carolina* × *putnami*	FGS uncataloged
Manatee County		
Bradenton, 51st Street locality	*putnami*	Large parts of carapaces and plastra, UF 2309, 2362, 2663, 9862
Marion County		
"Ocala"	*carolina* or *bauri*	Type of *T. formosa*, USNM 8825
Zuber I	?*carolina* × *putnami*	Entire rear of shell, UF 5019
Reddick I, B	?*carolina* × *putnami*	Entire, or large parts of shells, UF 1479, 2059, 2179, 2333, 2552, 4747-a, -b, -c, 5697, 5699, 5700, 6137, 6415, 6422, 6612
		FGS V-5709

[continued]

TABLE 5—(continued)

DETERMINATIONS OF FOSSIL *Terrapene* FROM THE PLEISTOCENE BEDS OF GEORGIA AND FLORIDA

Locality	Subspecies of *Terrapene carolina*	Remarks
		Plus many plastra, skull pieces, etc.
Reddick II	*putnami*	Almost complete shell, UF 9972, and large piece of shell, UF 9918
Eichleberger Cave A	*?bauri*	UF 1476–9
Eichleberger Cave B	*?bauri*	UF 1658
"Uranium Cave," 2 mi. north Bellview	*?bauri*	UF 1453
Mefford Cave I	*carolina* or *bauri*	UF 2115
Mefford Cave II	*putnami*	UF 6521–2
Kendrick I	*carolina* or *bauri*	UF 2650
Orange County		
Apopka Creek	*putnami*	FGS V-1694
Pinellas County		
"Seminole Field"	*putnami*	UF 9928
Sarasota County		
Near Sarasota	*putnami*	UF 1054
St. Johns County		
28 mi. S St. Augustine	*putnami*	Uncataloged, Allen collection (Hay 1916)
20 mi. N St. Augustine	*putnami*	FGS V-4435

LITERATURE CITED

Auffenberg, W.

1955. A reconsideration of the racer, *Coluber constrictor,* in eastern United States. Tulane Studies Zoöl., vol. 2, no. 6, pp. 89-155.

1956. Additional records of Pleistocene lizards from Florida. Quart. Jour. Florida Acad. Sci., vol. 19, nos. 2-3, pp. 157-167.

[MS.] The fossil snakes of Florida. Thesis, submitted to University of Florida, 1956. 128 pp.

Bader, R.

1957. Two Pleistocene mammalian faunas from Alachua County, Florida. Bull. Florida State Mus., vol. 2, no. 5, pp. 53-75.

Barbour, T., and H. C. Stetson

1931. A revision of the Pleistocene species of *Terrapene* of Florida. Bull. Mus. Comp. Zoöl., vol. 72, no. 8, pp. 295-299.

Brodkorb, P.
1957. New passerine birds from the Pleistocene of Reddick, Florida. Jour. Paleontol., vol. 31, no. 1, pp. 129-138.

Carr, A. F., Jr.
1952. Handbook of turtles. Ithaca, New York: Cornell Univ. Press, pp. i-xviii, 1-542.

Cooke, C. W.
1945. Geology of Florida. Florida State Geol. Surv., Geol. Bull., no. 29, pp. 1-339.

Cope, E. D.
1869. Synopsis of extinct Batrachia, Reptilia and Aves of North America. Trans. Amer. Phil. Soc., vol. 14, pp. 1-124.

Gilmore, C. W.
1927. On fossil turtles from the Pleistocene of Florida. Proc. U.S. Natl. Mus., vol. 71, art. 15, pp. 1-10.

Hay, O. P.
1907. Descriptions of seven new species of turtles from the Tertiary of the United States. Bull. Amer. Mus. Nat. Hist., vol. 23, art. 34, pp. 847-863.
1908a. Descriptions of five species of North American fossil turtles, four of which are new. Proc. U.S. Natl. Mus., vol. 35, no. 1640, pp. 161-169.
1908b. The fossil turtles of North America. Carnegie Inst. Washington, publ. no. 75, pp. 1-568.
1916. Descriptions of some Floridian fossil vertebrates belonging mostly to the Pleistocene. Florida State Geol. Surv., 8th Ann. Rept., pp. 39-76.
1923. The Pleistocene of North America and its vertebrate animals from the states east of the Mississippi River, and from the Canadian Provinces east of longitude 95°. Carnegie Inst. Washington, publ. no. 322, pp. 1-405.

McConkey, E. H.
1957. The subspecies of *Eumeces egregius*, a lizard of the southeastern United States. Bull. Florida State Mus., vol. 2, no. 2, pp. 13-23.

Milstead, W. W.
1956. Fossil turtles of Friesenhahn Cave, Texas, with the description of a new species of *Testudo*. Copeia, 1956, no. 3, pp. 162-171.

Neill, W. T.
1957. Historical biogeography of present-day Florida. Bull. Florida State Mus., vol. 2, no. 7, pp. 175-220.

Oelrich, T. M.
1953. A new box turtle from the Pleistocene of southwestern Kansas. Copeia, 1953, no. 1, pp. 33-38.

Rouse, I.
1951. A survey of Indian River archeology. Yale University Publ., Anthropol., no. 44, pp. 1-296.

Wood, H. E., *et al.*
1941. Nomenclature and correlation of the North American continental Tertiary. Bull. Geol. Soc. Amer., vol. 52, no. 1, pp. 1-48.

Zangerl, R.

1948a. The vertebrate fauna of the Selma formation of Alabama. II. The pleurodiran turtles. Fieldiana, Geology Memoirs, vol. 3, pp. 23-56.

1948b. The methods of comparative anatomy and its contribution to the study of evolution. Evolution, vol. 2, no. 4, pp. 351-374.

Zangerl, R., and R. G. Johnson

1957. The nature of shell abnormalities in the turtle shell. Fieldiana, Geology, vol. 10, no. 29, pp. 341-362.

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM may be in any field of biology. Manuscripts dealing with natural history or systematic problems involving the southeastern United States or the Caribbean area are solicited especially.

Manuscripts should be of medium length—12 to 200 printed pages. Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges only. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this, fifty copies are furnished the author without cost.

PREPARATION OF MANUSCRIPT

Highly recommended as a guide is the "Style sheet for the scientific serial publications of the American Museum of Natural History," second edition, revised, 1953.

Manuscripts should be typewritten with double spacing, with ample margins, and on only one side of the paper. The author should keep a copy; the copy submitted must be the original. Tables, legends of figures, and all footnotes should be assembled separate from the text. Several legends or footnotes may be placed on a single sheet.

Illustrations, including maps and photographs, should be referred to as "figures" wherever possible. All illustrations are reduced to a maximum of 4¼ by 7⅛ inches. The scales, wherever it is necessary, should be incorporated into the figure.

All references to literature should conform with the bibliographic style used in recent numbers of the BULLETIN. Spell out in full the titles of non-English serials.

Footnote material should be kept to a minimum. However, provide copy for a footnote detailing the title, affiliations, and address of the author (see recent numbers of the BULLETIN).

Manuscripts must be accompanied by a synopsis—a brief and factual summary (not a mere description) of the contents and conclusions, which points out the presence of any new information and indicates its relevance. In it list all new organisms described and give their ranges; indicate all taxonomic changes proposed. The synopsis, written in full sentences, should be concise, but completely intelligible in itself without reference to the paper, thereby enabling the busy reader to decide more surely than he can from the title alone whether the paper merits his reading. The synopsis will be published with the paper, hence it does not replace the usual conclusions or summary sections. It will also serve as copy for the abstracting services.

Manuscripts and all editorial matters should be addressed to:

Editor of the BULLETIN
Flint Hall
University of Florida
Gainesville, Florida