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STUDIES ON THE EVOLUTION OF BOX TURTLES (GENUS TERRAPENE)

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STUDIES ON THE EVOLUTION OF BOX TURTLES (GENUS *TERRAPENE*)

WILLIAM W. MILSTEAD[1]

SYNOPSIS: Describes and analyzes important North American fossil and Recent box turtle material. Characters investigated include osteological features of the shell and skull as well as scutellation and color. Salient morphologic features, past and present distribution, and evolutionary history of each of the recognized taxa are discussed. No nomenclatorial changes are proposed.

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[1] The author is Professor of Biology and Chairman of the Biology Department at the University of Missouri — Kansas City. Most of his researches have been evolutionary and ecological studies of amphibians and reptiles. This is his first contribution to the Bulletin. Manuscript received 3 September 1968 — Ed.

Milstead, William W. 1969. Studies on the evolution of box turtles, (Genus *Terrapene*). Bull. Florida State Mus., vol. 14, No. 1, pp. 1-113.

The basic plan of this study was formulated at a meeting between Walter Auffenberg, Donald Tinkle, and myself at the University of Florida in January, 1959, where we compared specimens of Texas fossils reported by me (Milstead, 1956) with Florida fossils reported by Auffenberg (1958). At that time we decided that the first step in understanding evolution in the genus *Terrapene* should be a comprehensive study of living box turtles to discover osteological characteristics that could be used to distinguish the various species and subspecies. We began by examining specimens from the extremes of the subspecies ranges where there could be little question of identification. The forms and areas considered in this initial phase of the study were: *T. carolina bauri*, Dade County, Florida; *T. carolina carolina*, New Jersey and New York City-Long Island area; *T. carolina major*, Tallahassee, Florida, area; *T. carolina triunguis*, south-central Texas; *T. ornata ornata*, Oswego, Kansas area; and *T. ornata luteloa*, Arizona. After characters were identified in the initial approach, we planned to refine them by applying them more generally to the subspecies ranges, and finally to apply the refined characters to the fossils. Concentration was on osteological features of the plastron, partially because plastral elements are more frequently preserved as fossils than carapacial elements, and partially because plastral elements appear to be less variable than carapacial elements. Other than those of the plastron, the characters used initially were those of the nature of the postorbital bar of the skull, size, presence or absence of axillary scales on the carapace, shape of the first central scute, flaring of the marginal scutes, and position of the plastral hinge in relation to the marginal scutes. Other characters were added as the work progressed.

Difficulties in packaging and shipping the many box turtle specimens in the major collections made us decide early in the study that it would be best to visit the various collections personally; this was the procedure followed except in a few cases. Visits to the collections also provided the opportunity to exchange views with other herpetologists, and these exchanges yielded many valuable ideas and suggestions, as well as considerable information on box turtle habits and habitats. It also seemed advisable to visit areas where box turtles had been collected in order to gain first hand information on habitats. During the study I visited a number of fossil localities and one or more localities for each of the living species and subspecies. Efforts to collect personally at least one specimen of each of the living forms, however, were not successful.

Acknowledgments and Abbreviations

Visits to museums in the United States and most of the field trips in the United States and Mexico were supported by National Science Foundation grants G19421 and GB1232. Visits to European museums and support during the time the manuscript was in preparation were provided by a John Simon Guggenheim Memorial Fellowship and a sabbatical leave grant from the University of Missouri-Kansas City. A 1962 field trip to the Mexican states of Coahuila, Nayarit, and Sonora was supported by National Science Foundation grant G23042. A small pen and pond for studies on captive turtles was built with funds provided by the Kansas City Regional Council for Higher Education and the UMKC Biology Department. A 1965 trip to Alamos, Sonora, Mexico, was made possible by a UMKC Faculty Research Grant. I am grateful to these institutions and organizations for their support.

I am indebted to numerous people for ideas and information obtained through lengthy discussions of turtle evolution and of changing climatic conditions during the Pleistocene. Foremost among the contributors were Walter Auffenberg, the late Norman Hartweg, Claude Hibbard, Ernest Lundelius, Bob H. Slaughter, and Donald Tinkle. I am also indebted to many people for permission to exmine material in their charge. The names of these people, most of whom also contributed ideas and information, are given below with the institution or collection with which they are associated:

AMNH – American Museum of Natural History, Charles M. Bogert, Richard G. Zweifel
ANSP – Academy of Natural Sciences of Philadelphia, James E. Böhlke
ASU – Arizona State University, W. L. Minckley
BCB – private collection of Bryce C. Brown
BMNH – British Museum of Natural History, Alice G. C. Grandison
BUSM – Baylor University Strecker Museum, Bryce C. Brown
FMNH – Field Museum of Natural History, Robert F. Inger, Hymen Marx
KU – Kansas University Museum of Natural History, William E. Duellman
MCZ – Museum of Comparative Zoology, Harvard University, Ernest E. Williams
MRHN – Musee Royal d' Histoire Naturelle de Belgique, G. F. de Witte
NMS – New Mexico State University, James Dixon (then at NMS)
RC – private collection of Roger Conant
RMNH – Rijksmuseum van Natuurlijke Historie, M. S. Hoogmoed
SM – Senkenberg Museum, Robert Mertens, Konrad Klemmer
SMU – Southern Methodist University, Bob H. Slaughter
TCW – Texas Cooperative Wildlife Collection, Texas A & M University, W. B. Davis, Richard Bauldauf
TNW – Tulane-Northwestern University Collection, Tulane University, Harold Dundee
TT – Texas Technological College, John S. Mecham
UCB – University of California (Berkely), Robert Stebbins
UCM – University of Colorado Museum, T. Paul Maslin
UF – University of Florida (Florida State Museum), W. Auffenberg

UF-RMJ – University of Florida, R. M. Johnson field numbers
UMKC – University of Missouri (Kansas City), James L. Vial
UMMP – University of Michigan Museum of Paleontology, Claude W. Hibbard
UMMZ – University of Michigan Museum of Zoology, Charles F. Walker, Donald W. Tinkle
USNM – United States National Museum, the late Doris Cochran, James Peters
UT – University of Texas, W. Frank Blair
VNHM – Vienna Naturhistorishe Museum, Josef Eiselt

I am also indebeted to J. Douglas Walter for preparing the figures and the final composition of plates, and to secretaries Maureen Arnold, Mary Alice Crivello, and Toni Gregory for loyal service. I am very grateful to members of my family for having endured my frequent absences from home, trips to Europe and Mexico, and for having continuously shared their home with a small herd of box turtles.

SYMBOLS

Several symbols are used consistently throughout the following report. In most cases the symbols are composed of a numeral and one or more letters. The numerals are sample numbers and the letters are abbreviations for taxonomic identifications of the samples. (The symbol 3C, for example, refers to sample number 3, composed of 53 specimens of *Terrapene carolina carolina* from New Jersey.) The abbreviations are:

B – *T. carolina bauri*
BM – *T. c. bauri x major*
C – *T. c. carolina*
CB – *T. c. carolina x bauri*
C(B) – *T. c. carolina* (with *bauri* influence)
CMT – *T. c. carolina x major x triunguis*
Co – *T. coahulia*
CT – *T. c. carolina x triunguis*
C(T) – *T. c. carolina* (with *triunguis* influence)
K – *T. nelsoni klauberi*
L – *T. ornata luteola*
Lo – *T. o. longinsulae*
M – *T. c. major*
MT – *T. c. major x triunguis*
Mx – *T. c. mexicana*
N – *T. n. nelsoni*
P – *T. c. putnami*
PB – *T. c. putnami x bauri*
PT – *T. c. putnami* x^t *triunguis*
R – *T. o. ornata* (R is used to avoid confusion between the alphabetical O and the numerial 0.)
RL – *T. o. ornata x luteola*
R(L) – *T. o. ornata* (with *luteola* influence)
T – *T. c. triunguis*
T(C) – *T. c. triunguis* (with *carolina* influence)
T(M) – *T. c. triunguis* (with *major* influence)
T(P) – *T.c. triunguis* (with *putnami* influence)
Y – *T. c. yucatana*
x – horizontal intermediate form
x^t – vertical intermediate form

MATERIALS AND METHODS

Box turtles are extremely variable morphologically, a fact first noted by Barbour and Stetson (1931), and re-emphasized by Milstead (1956) and Auffenberg (1958). No single characteristic can be depended upon to identify a series of box turtles, and no series of characteristics can be depended upon to identify a single box trutle below the species level. It has been necessary, therefore, to use many characteristics and to apply them to series of specimens drawn together from various collections to form adequate samples of local populations. An annotated list of the characters used is given below, and the approximate localities of the samples used are shown in figure 1. Three factors were given strong consideration in assembling individual specimens to form samples: (1) to reduce errors caused by ontogenetic influences on the characters, only specimens over 99 mm were used, (2) all specimens in any one sample are from the same biotic province, and (3) all specimens in any one sample are from localities as close together as possible. Unfortunately it was necessary to be opportunistic in regard to the third point. The 10 specimens of *T. ornata luteola* from Brewster, Jeff Davis, and Presidio counties, Texas (sample 54L), for example, come from a much wider area than the 45 specimens of *T. carolina carolina* from the Baltimore-Washington area (sample 5C). It would be much more desirable to have a sample composed of 5% to 10% of the entire adult population of any one decade collected within a radius of 25 miles from a given point on a map, but this was not possible. Although it is sometimes difficult to establish the number of individuals represented in a sample of fossils, a total of at least 2,050 adult box turtles were examined and included in the 87 samples shown in figure 1 and Tables 2-4. Data from several hundred other specimens were discarded because the specimens from which they were obtained did not conform to all three criteria outlined above.

CHARACTERS STUDIED

In view of the abundance of box turtles over the eastern United States, museums hold surprisingly few skeletons of them. Thus, no statistically sound series of skulls has been examined for any one form or character. Although skull characters are generally considered among the most stable used in taxonomy, the high degree of variation found in other box turtle characters permits some skepticism regarding the stability of those of box turtle skulls.

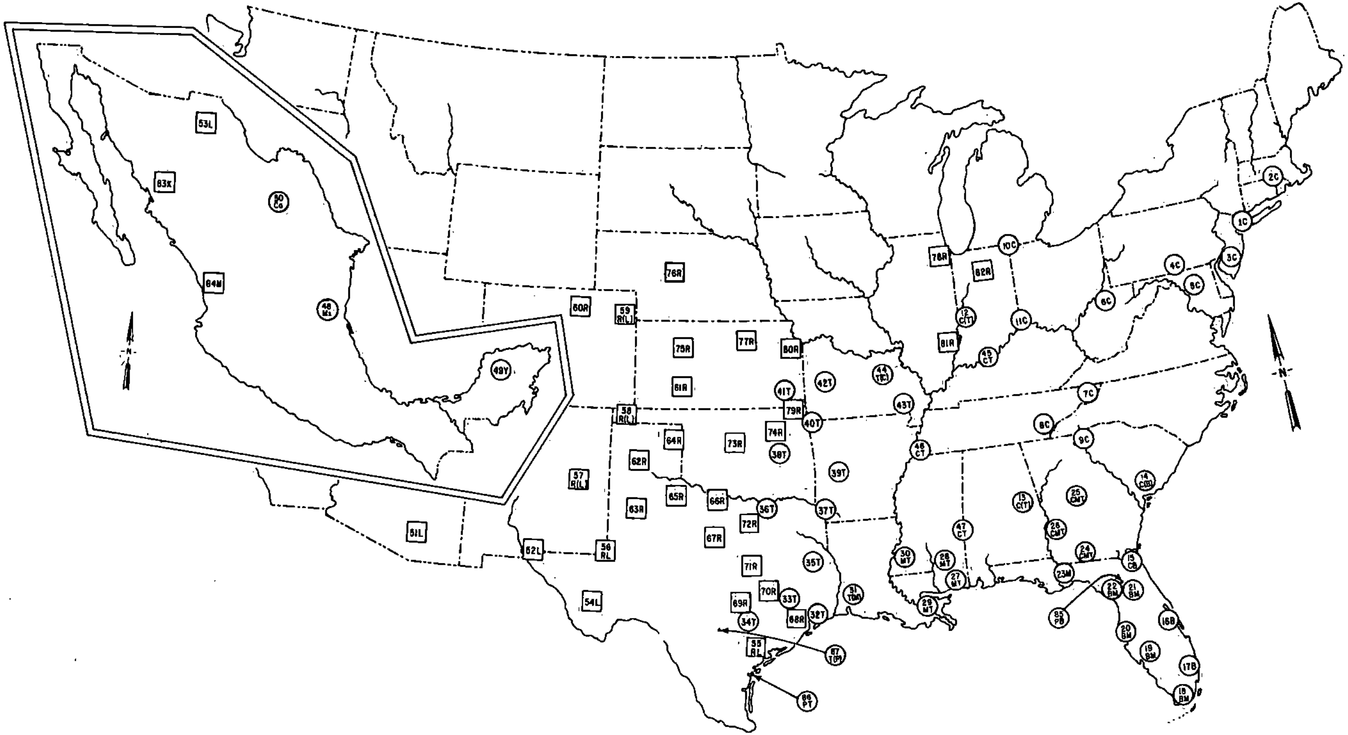


FIGURE 1. Map of the eastern United States with inset map of Mexico showing approximate localities for box turtle samples used in this study. Circles = Carolina Group samples, squares = Ornata Group samples. The three circles in the Gulf of Mexico = fossil Carolina Group samples. See text for additional explanation.

POSTORBITAL BAR. — This is a span of several bones extending from the posterior border of the orbit to the anterior border of the tympanum. In *Terrapene* it is composed of the squamosal, anterior edge of the quadrate, posterio-ventral portion of the postorbital, and posterio-dorsal portion of the jugal. In the Carolina Group of box turtles, the squamosal bone may be thick and broad (Figure 5B), reduced to a thin bar of bone (Auffenberg, 1958, figure 8C; 1959, figure 1B), present only as a span of cartilage, or absent Figure 5C). Even when the squamosal is totally lacking, the posterior portions of the postorbital and jugal bones retain their contributions to the postorbital bar. These are seen (Figure 5C) as a posteriorly directed bony process behind the orbit. In the Ornata Group, all traces of the postorbital bar have been lost, the jugal and postorbital bones are reduced in thickness, and the posterior border of the jugal-postorbital junction is smooth (Figure 5D, E).

ANGULAR BONE. — McDowell (1964) has noted that in the American box turtles (*Terrapene*) and other members of the testundinid subfamily Emydinae, the angular bone forms the floor of the canal for Meckel's cartilage. Although this characteristic appears to be stable in the two species of the genus *Coura* (*amboinensis* and *trifasciata*) for which skeletal material is available, it varies in *Terrapene* and *Clemmys*. One *Terrapene carolina bauri*, two *T. c. triunguis*, one *T. coahuila*, one *T. nelsoni nelsoni*, and one *Clemmys marmorata* had the angular excluded from contact with Meckel's cartilage.

BASIOCCIPITAL. — The subfamily Batagurinae has a strong lateral process (batagurine process), which forms the floor of the recessus scalae tympani, but the subfamily Emydinae lacks the process (McDowell, 1964). No species of *Terrapene* appears to have the process, but both species of *Cuora* examined do have it. Associated with the batagurine process is a posterior extension of the mesial border of the pterygoid. This process and the batagurine process, give the batagurine turtles a much heavier and more solid bony armor on the underside of the skull than is found in the emydines.

CAROTICOPHARYNGEAL FORAMINA. — McDowell (1964) has related *Terrapene* to *Clemmys* chiefly on the point that both genera have enlarged caroticopharyngeal foramina. I found these foramina quite variable in both size and location in the *Terrapene* and *Emys* specimens I examined. Within only one subspecies, *Terrapene carolina carolina*, did the size of the foramina vary from large (as in *Clemmys*) to small (as in *Emys*) to absent.

FRONTAL. – McDowell (1964) has noted that the frontal bone enters the orbital margin in *Terrapene* and *Clemmys*, while in *Emys* the frontal is excluded from the orbit by a strong contact between the prefrontal and postorbital. I have found this character variable in *Emys* and *Terrapene*. In *Emys* the association between the prefrontal and postorbital varied from a point-to-point contact (one specimen) to a broad contact (most specimens), while in *Terrapene* the association varied from no contact (most specimens) to a broad contact (11 specimens). The specimens of *Terrapene* with a broad contact included 2 *T. carolina carolina*, 7 *T. c. bauri*, 1 *T. c. major*, and 1 *T. nelsoni nelsoni*.

JUGAL. – McDowell (1964) found that *Emys* has the "lower end of the jugal expanded inward along the posterior border of the maxilla to meet the pterygoid," while *Clemmys* and *Terrapene* have the lower end of the jugal narrowing to a point without meeting the pterygoid. My investigations have shown that this character is useful as a taxonomic tool, but that there are some variations of significance in considering the relationships of the three genera. Most specimens of *Terapene*, and all specimens of *Clemmys*, examined had a jugal that tapered to a point without any inward expansion onto the posterior border of the maxilla. But in 1 *Terrapene carolina carolina*, 10 *T. c. bauri*, 1 *T. c. mexicana*, 2 *T. c. triunguis*, 1 *T. c. yucatana*, 4 *T. coahuila*, and 1 *T. nelsoni nelsoni*, the jugals were expanded to cover about half of the posterior border of the maxilla. The one specimen of *T. carolina major* examined had a complete contact between the jugal and pterygoid, exactly as found in most specimens of *Emys*. A number of skulls of *Clemmys* and *Terrapene*, particularly those that were poorly cleaned, had a membranous bridge from the lower end of the jugal to the pterygoid. Adult specimens of *Emys* exhibited an osseous expansion of the jugal, but five juvenile specimens showed only a membranous bridge, as found in *Clemmys* and *Terrapene*. One juvenile *Emys* showed no contact between the jugal and pterygoid, and one young adult showed only a partial contact. Both of the latter specimens were fully cleaned, however, and membranous bridges may have existed in life. Thus it appears that the lower end of the jugal tends to become ossified in *Emys*, but tends to remain membranous in *Terrapene* and *Clemmys*.

CERVICAL VERTEBRAE. – Members of the testudinid subfamilies Emydinae and Batagurinae show a slight difference in the morphology of the cervical vertebrae (McDowell, 1964). In *Terrapene* and other emydines, the 1st, 2nd, 3rd, and 4th joints between the centra of the vetebrae are simple joints with a single condyle and socket, but both the condyle and the socket expand progressively laterally until the 4th joint has a bar-shaped condyle with a weakened medial area. The 5th joint has a complete separation to produce a double condyle. In *Coura* and other batagurines, the separation does not occur until the 6th joint. This characteristic is somewhat subjective, in that some specimens of *Coura* come very close to having double condyles at the 5th joint, while some *Terrapene* specimens have poorly-developed double condyles at the 5th joint.

CARAPACE LENGTH.— This is used throughout the study as an indication of size. It has some disadvantages in that it is only one parameter of size, but it is useful in supporting statements of relative size (e.g. *Terrapana carolina major* is the largest living box turtle). Carapace length was measured with calipers from the anterior edge of the nuchal scute to the posterior edges of the 12th marginal scutes. Ranges of sample averages are given in table 1, and the individual sample averages are given in tables 2, 3, and 4.

CARAPACE SHAPE. — Four characteristics of carapace shape are used: (1) whether round or elongate as seen in dorsal view; (2) curvature, or general outline, of the carapace as seen in lateral view (median saggital section); (3) highest point of the carapace, particularly as to whether it comes before the bridge (Ornata Group) or behind the bridge (Carolina Group); and (4) sculpturing of the shell, as, for example, the presence of a hump (or boss) on the third central scute of *T. carolina triunguis* and depressions in the posterior; pleural bones of *T. carolina mexicana* and *T. carolina yucatana.* Differences in shapes of the various box turtles are shown in figures 2 and 4-18.

FIRST CENTRAL SCUTE. — Auffenberg (1958) used the shape of the 1st central scute in dorsal view in working with Florida box turtles, and the shape in lateral view was used by Milstead (1967) and Milstead and Tinkle (1967) in working with the Ornata Group. Although the shape of the 1st central in dorsal view shows extreme variation (Auffenberg, 1958, Figure 12), most of the specimens from some Floridian populations have a straight-sided scute, while most of the specimens from other populations throughout the range of the genus have something other than a straight-sided scute, usually an urn-shaped scute similar to Auffenberg's (1958) Figure 12D, third

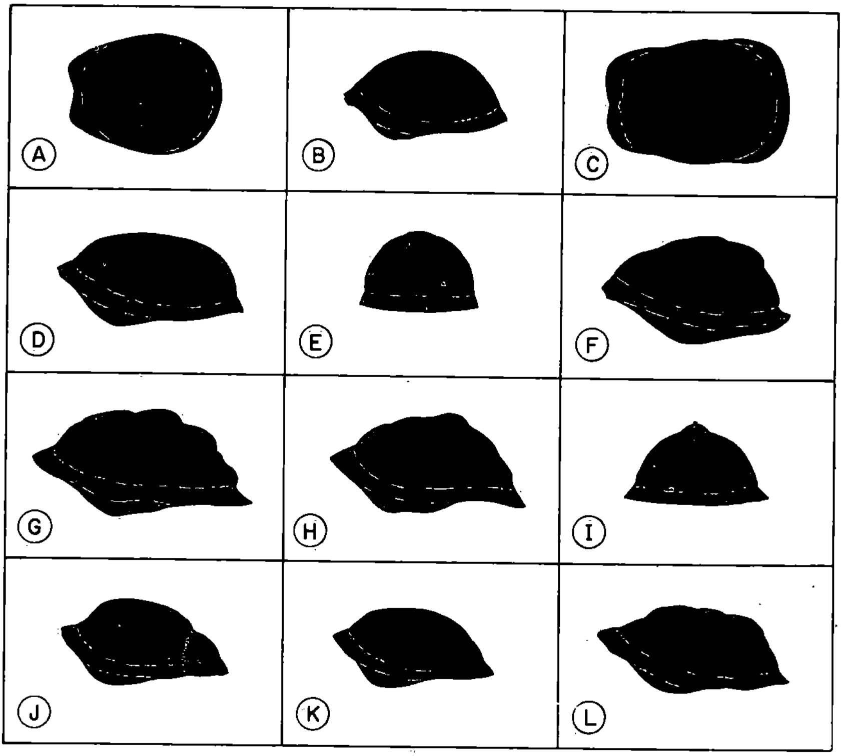


FIGURE 2. Box turtle silhouettes. A-B, dorsal and lateral views, *Terrapene c. carolina*, New York City area. C-D, dorsal and lateral views, *T. c. carolina*, Michigan. E, posterior view, *T. c. carolina* from almost any area in its range. F, lateral view, *T. c. bauri*, Dade county, Florida, G, lateral view of *T. c. major*, St. Joseph's Island, Florida. H-I, lateral and posterior views, *T. c. triunguis*, Oklahoma.. J, lateral view, *T. c. yucatana*, Piste, Yucatan. K, lateral view, *T. o. ornata*, Kansas City, Missouri. L, lateral view, *T. n. nelsoni*, Pedro Pablo, Nayarit.

from left. In collecting data for this study, the shape of the 1st central scute of specimens examined was recorded by a number given in reference to Auffenberg's figure.

The shape of the 1st central scute in lateral view appears to be an important character for distinguishing the various forms of the Ornata Group and in distinguishing between the Ornata and Carolina Groups. The Carolina Group has the 1st central elevated at a steep angle, while the Ornata Group has it elevated at a low angle. Some forms (e.g., *T. nelsoni nelsoni*) have such a low angle that the anterior third of the carapace appears flattened, somewhat reminescent of acquatic members of the subfamily Emydinae. Unfortunately the importance of this character did not develop until late in the study, and measurements of the angle of elevation referred to later were taken from only a few specimens. They are, thus, not to be relied upon as anything more than an approximate quantification of a trait that can readily be seen (Figures 2 and 4-18).

The elevation of the 1st central scute actually represents the elevation of the underlying neural and pleural bones, but in this character and other characters of the carapace and plastron, the bones have been ignored and measurements have been taken on the scutes. This was done because preserved specimens, which constituted most of the material examined, have the bones obscured by the scutes. Fossil and skeletal specimens, on the other hand, show the seam lines of the scutes on the bones.

AXILLARY SCALES.—These are epidermal scutes that occur just anterior to the bridge on the ventral, medial edges of the marginal scutes. *Terrapene* usually has a single scute, while in *Cuora* the scute is usually double. Auffenberg (1958) notes that the scute is usually present in *T. carolina major* and *T. c. putnami*, and rarely present in *T. c. bauri*. The present study has shown (Table 2) that an auxillary scale is present in 100% of the specimens of *major* examined, in up to 91% of the specimens of one sample of *T. c. triunguis*, in up to 80% of the specimens of one sample of *T. c. carolina*, in 78% of the specimens of *T. c. coahuila*, and is present in less than 20% of the specimens of *T. c. bauri*, *T. c. mexicana*, and *T. c. yucatana*. When present in the Carolina Group, the scale is usually on the 4th marginal, or occasionally overlies the adjacent halves of the 4th and 5th marginals. The scale is present only rarely in the Ornata Group, and usually overlies the 5th marginal when it is present. Auffenberg (1958) noted that the size of the axillary scale varied when it was present, but considered the scale to be an important character only in terms of presence or absence. Milstead (1957) treated it as enlarged (covering half of the ventral side of the 4th marginal scute), reduced (less than half of the ventral side of the fourth marginal scute), or absent. This treatment produced the semblance of a cline around the Gulf Coast from Florida to Texas, but if such a cline exists, it is only along the Gulf Coast. No clinical relationship was found in other directions, and the data were found to be more meaningful when the auxillary scale was treated simply as either present or absent.

MARGINAL SCUTES. – Auffenberg (1958) notes that the degree to which the marginal scutes flare outwards and upwards from the carapace is important in recognizing the various box turtles of Florida, and he presented data on both the radius of curvature and the angle of flare for the turtles he studied. It now appears that the degree of marginal flare is an important character when applied to all members of the genus *Terrapene*. I gathered no quantitative data on this character during the present study, but I have relied heavily on Auffenberg's data in comparing specimens visually. Another character of the marginals appears to be of some use in distinguishing the two species groups in the genus *Terrapene*. In members of the Carolina Group, the shape of the 1st marginal scute is normally rectangular, while in members of the Ornata Group, it is usually irregularly oval or triangular (Milstead and Tinkle, 1967).

KEELS. – An important distinction between the Carolina and Ornata groups is a prominent mid-dorsal keel usually present on the 2nd, 3rd, and 4th central scutes of members of the Carolina Group. Although a keel is frequently present in some members of the Ornata Group (60% of specimens of *T. nelsoni nelsoni*), it is only weakly developed and usually limited to the posterior half of the 3rd and anterior half of the 4th central scutes. The prominence of the keel in the Carolina Group is frequently enhanced by a shallow trough or groove on each side of the keel. Some members of both species groups frequently have a lateral keel above the bridge. This is generally associated with flaring marginal scutes anterior and posterior to the bridge. The lateral keel is of some use in distinguishing between subspecies in both groups.

PLASTRAL HINGE. – When a box turtle is viewed laterally, the plastral hinge may be opposite the 5th marginal scute of the carapace, opposite the seam between the 5th and 6th marginals, or opposite the 6th marginal scute. Members of the Carolina Group usually have the hinge opposite the 5th marginal, while members of the Ornata Group usually have it located more posteriorly. Within the Ornata Group, *T. o. ornata* usually has the hinge opposite the seam between the 5th and 6th marginals, while *T. o. luteola* usually has it opposite the 6th marginal (Table 3).

PLASTRAL RATIOS. – These include seven ratios: (1) anterior lobe length/posterior lobe length, (2) intergular suture length/-

anterior lobe length, (3) interhumeral suture length/anterior lobe length, (4) interpectoral suture length/anterior lobe length, (5) interabdominal suture length/posterior lobe length, (6) interfemoral suture length/posterior lobe length, and (7) interanal suture length/-posterior lobe length. The seam lengths were taken with calipers on the mid-line of the plastron. In cases where the scute of one side extended farther posteriorly than the scute of the other side, measurements were taken from a point midway between the two, and the next succeeding measurement began at the same point. The length of the anterior lobe was obtained by adding the lengths of the intergular, interhumeral and interpectoral seams, and the length of the posterior lobe was obtained by adding the lengths of the interabdominal, interfemoral, and interanal seams. By this method the length of each lobe is equal to the sum of its parts. This made work with the ratios easier, and at the same time served to reduce some of the error produced by the curvature of the plastron. Because of the plastral curvature, a direct measurement of length of either lobe by calipers yields a figure that is less than the sum of the parts. The dorsal lip of the plastral hinge was not included in figures recorded for anterior lobe lengths. It was omitted because it is hidden by the ventral lip of the posterior lobe of articulated specimens and cannot be measured. Samples of all of the living forms of the genus *Terrapene* were studied with the sexes treated separately. When it was found that no significant sexual dimorphism existed in any of the plastrial ratios, the figures for the two sexes in all samples were combined. This lack of sexual dimorphism greatly facilitated work with fossil specimens, in which sex determination is occasionally little more than guesswork.

Sample averages of plastral ratios are shown in Tables 1-4. The importance of these ratios as taxonomic tools varies, but some generalizations can be made: (1) the plastral ratios are useful in distinguishing the various species of the genus; (2) they are also useful in distinguishing the various subspecies, but in this respect they are somewhat more useful in the Carolina Group than in the Ornata Group; (3) anterior lobe ratios as a whole are more useful than posterior lobe ratios; and (4) the most consistently important ratios are those of the interhumeral and interfemoral seams. This last generalization is related at least in part to the central location of these two seams on their respective lobes. They show their own variations and also reflect changes in the other seams.

Some of the plastral ratios show definite clines around the Gulf

Coast from Florida to Texas in the Carolina Group (Table 2, and Milstead, (1967). Generalized clines exist in the Ornata Group, but the circumferential Gulf Coast clines are the only distinct ones. They may be the result of coincidence, but the fact that the clines do occur in more than one ratio may be used as additional evidence of the close relationship between *triunguis* and *putnami-major*, as evidence of the importance of the Gulf circumferential corridor (Auffenberg and Milstead, 1965) in Pleistocene movements and faunal exchanges of box turtles, or as evidence for both.

Posterior Lobe. – Apart from the seam ratios, the posterior plastral lobe shows three characteristics useful in distinguishing members of the Carolina Group from members of the Ornata Group. First, males of the Carolina Group have a smooth to deeply concave posterior plastral lobe (Figure 4D) while males of the Ornata Group have a smooth lobe. Second, the posterior margin of the plastron is rounded in the Carolina Group (Figure 4-14), but may be straight-edged in the Ornata Group (Figures 15-18). Third, large specimens of the Carolina Group sometimes show a deep indentation of the lateral margin of the posterior lobe at the femero-anal seam. This gives the plastron the appearance of being tri-lobed (Figures 10C; 12D, F).

Digits. – Two characters of the digits were used in reference to Recent specimens of box turtles. First, in the Carolina Group, it has been known since the original descriptions of *T. c. bauri* and *T. c. triunguis* that some forms have three toes on each hind foot while others have four. This has generally been thought to be a highly variable character, and was ignored at the beginning of this study. As work progressed, however, it was noted that the number of toes appeared to be a more stable character than previously thought. It is now known that this character is highly stable in "pure" lines of box turtles, and varies only in populations of one subspecies showing some influence of another subspecies. Most members of the Ornata Group have four toes on each hind foot. Only an insignificant number of individuals have three toes.

The second character used in relation to digits is sexually dimorphic, Legler (1960) first noted that *T. o. ornata*, *T. o. luteola*, and *T. n. klauberi* have the ability to extend the medial hind toe inward to serve as a clasper during copulation. Milstead and Tinkle (1967) noted that males of *T. n. nelsoni* have the same ability. Members of the Carolina Group appear to lack this ability.

COLOR PATTERN. — Coloration as a whole was generally ignored during this study because fossils lack coloration completely and in specimens preserved in spirits colors are generally faded. The one exception was the recording of the color pattern for most of the Recent specimens examined. Legler (1960: 654) states, "Personal observations of interspecific and ontogenetic variation of color patterns of box turtles has convinced me that a basic pattern of more or less linear radiations is the one from which all other patterns (including spots, blotches, rosettes, and unicolored condition) can be derived, and that the radial patten is generalized and primitive for *Terrapene* (possibly for all emyids and testudinids as well)." I am in complete agreement with this conclusion of Legler's, but have some reservations about one of his following statements, "I suspect, however, that the pattern of a living species most closely approaching that of the primitive ancestral stock of *Terrapene* is the pattern of fine, wavy, dark radiations (on a paler background) present in young examples of *T. coahuila*." I agree that a pattern of dark radiating lines may have been the, or one of the, patterns exhibited by early box turtles, but disagree with the implication that *T. coahuila* is closely related to the ancestral stock of the genus. I think that the pattern displayed by *T. coahuila* came to it through *T. carolina triunguis* or *T. carolina putnami*.

TAXONOMIC INTERPRETATIONS

Recent years have seen increased interest in the Quanternary and its twilight zone betwen zoology and paleontology (see e.g. papers presented and cited in Wright and Frey, 1965). This has created some problems in taxonomy as horizontally-developed terms (e.g., species, subspecies, intergrade, isolation) have come into wider use in a vertical sense. I think it advisable, therefore, to present my interpretations of the lower taxonomic categories as they are used in the following pages.

The most important taxon, of course, is the species, and my definition is fairly simple: I regard a species as a group of organisms recognizable (at least to each other) by definite characteristics, and, in general, reproductively distinct from other groups of organisms through biochemical, ethological, or morphological barriers. Abstractly, I think of a species at any one moment in time as being represented by a circle that encompasses all of the possible allelic combinations that can be transmitted by that particular group of organisms (the gene pool). In this sense a biotic community could be represented by a handfull of coins placed side by side on a table. The limited area in which two coins contact one another would represent all of the interrelationships between the two species from predation to gene exchange. (The analogy is already weak at this point and should not be carried further.)

Through time, I see the circle of any one species as a column of variable diameter (relative to increases or decreases in the size of the gene pool), which at its base merges with another column. Once they have diverged, I regard the columns of two species as being distinct in both time and space, but do not regard isolation in either time or space as being by itself a criterion for recognizing a species. Thus, I feel that one or more populations of a species may become isolated in space because of changing environmental conditions, or may appear to be isolated in time because of an incomplete fossil record, but I do not consider these gaps in space and knowledge as being by themselves reason for recognizing the isolated populations as distinct species

Terrapene carolina mexicana, for example, considered as a distinct species until recently (Milstead, 1967), is isolated in space from all other forms of the genus by unsuitable ecological conditions. Its morphology, however, is very close to that of two other turtles (*T. c. triunguis* and *T. c. yucatana*) and apparently gene flow occurred between the three within the last few thousand years. That *mexicana* could evolve into a new species if it continues to remain isolated is not denied, but it does not appear to have developed morphological traits during its relatively short period of isolation, and nothing guarantees that climatic factors will maintain the isolation long enough for isolating mechanisms to arise. A good example of isolation in time is provided by *Terrapene ornata longinsulae.* Its line to modern examples of the species has a gap from the Aftonian interglacial stage to the Wisconsin glacial stage, but it is almost impossible to distinguish *T. o. longinsulae* from the modern *T. o. luteola,* and it is expected that fossils connecting the two will eventually be found. There is no question that a species of box turtles could have existed from Aftonian to Wisconsin times, because the fossil record for *Terrapene carolina* is almost complete from mid-Pliocene to Recent times.

The word "subspecies" by virture of the meaning of its prefix refers to something less than a species, but this is a very poor definition biologically, because it provides no lower limit, and it has led to extensive misuse of the taxon. In some cases nomenclature below the species level has been carried to the point of recognizing local populations and even individuals as distinct subspecies. Such extensive nomenclaturial recognition of genetic variation is not useful to studies of evolution, and has precipitated frequent proposals to eliminate the term "subspecies" from formal taxonomy. I feel that the deletion of a term because it has been misused is equally as bad as the misuse, because those who, through lack of understanding of the goals of taxonomy, misused the first term will simply misuse its substitute or another term. Furthermore, I feel that the term "subspecies" when properly applied is very useful to studies of evolution. Thus I define a subspecies as an ecological or geographical grouping of organisms that is almost a species. By this, I mean that the morphological or behavioral traits of a subspecies allow it to be easily distinguished from other members of its species, but it is still a member of that species through genetic exchange with one or more of the other members, even though at times that gene exchange may be interrupted (as in the case of *T. carolina mexicana* above). The subspecies of *T. carolina* provide good examples of subspecies that are "almost species." All but one of the forms considered in the following pages as subspecies have been treated as distinct species by various authors within the last two decades.

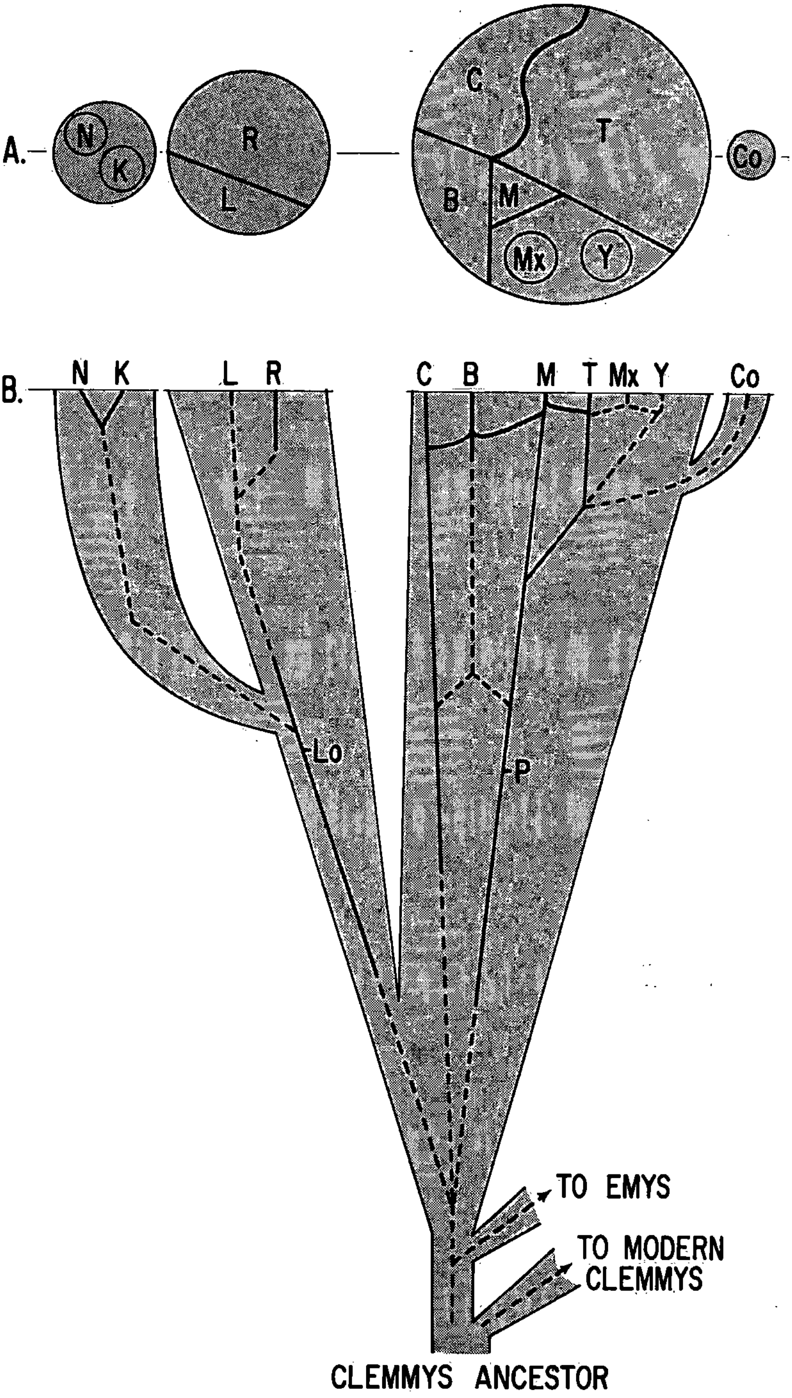
What I consider an excellent example of the proper use of the subspecies taxon is provided by *Natrix sipedon* in the San Jacinto River of southeastern Texas and other rivers emptying into the Gulf of Mexico. *Natrix sipedon confluens* is a large, heavy-bodied water snake more than a meter in length with a pattern of broad bands and a round tail. It lives along the San Jacinto River in areas of fresh water, and spends most of its time on the shore. *Natrix sipedon clarkii,* on the other hand, is a small, slender water snake about half a meter in length with a pattern of four narrow stripes and a laterally flattened, oar-like tail. It lives in the Gulf of Mexico and spends most of its time in the water. A person seeing the two for the first time would not hesitate to call them different species, but in the brackish water at the mouth of the San Jacinto River, the two snakes come together and interbreed freely to produce intergrades that are intermediate in size, body form, tail shape, and color pattern. The latter presents the most obvious intermediacy. The bands of *confluens* and the stripes of *clarkii* come together in a decorator's nightmare of bands, stripes, bands that trail off into stripes, and stripes that run together to form bands.

It would be unreasonable to demand that all named subspecies be as distinct as the two water snakes, but it would not be unreasonable to demand that all subspecies be as distinct as those of the box turtles. A simple test of a subspecies would be to consider it as a species. Is this sample sufficiently distinct from its closest relatives to be considered as a separate species? If the answer is affirmative, the sample in question may be considered as a separate species or as a subspecies, depending largely, but not entirely (see discussion of *T. c. mexicana* above), on the amount of gene flow between the sample population and closely related populations. If the answer is negative, the sample in question may represent something less than a subspecies. Obviously this test will not serve as a panacea to cure all of the ills of lower-category taxonomy, but if it is used even loosely it will put a stop to some of the "hair-splitting" that has long cluttered biological literature and been a nuisance in studies of evolution.

Abstractly I visualize subspecies as polygons with varying degrees of contact between each other (to represent varying degrees of genetic exchange) within the circle that represents the species. Isolated subspecies can be represented by small circles within the large circle. The present-day forms of the genus *Terrapene*, therefore, may be represented by a number of small circles and polygons contained within four large circles as shown in figure 3,A.

Vertical representation of subspecies is more difficult because the nature of subspecies makes them more easily illustrated horizontally. A subspecies is, in a sense, a sub gene-pool, because certain genetic combinations are expressed more frequently than others, but, if there are enough individuals, a subspecies may contain the gene

FIGURE 3. Suggested relationships of box turtles: A at present, B through time. Outer circles in A and columns in B represent species: (left to right) *nelsoni, ornata, carolina,* and *coahuila.* Small circles, semicircles, triangles, and polygons within the larger circles of A represent relationships between subspecies showing relative amounts of territory occupied by each subspecies and relative amounts of contact between subspecies. Ranges of *carolina-bauri* and *major-bauri* intergrades are added to the *bauri* area, *carolina-triunguis* and *major-triunguis* intergrade areas are added to *triunguis*, and *ornata-luteola* intergrade areas are added to *luteola.* Solid lines in B, except for those shown for *T. nelsoni,* are vertical relationships suggested by fossils. Dash lines and all lines for *nelsoni* in B are vertical relationships suggested by occurrences of similar traits, but without fossil substantiation. Letters are symbols for species and subspecies. See text for additional explanation.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pool of the species. That is, it is possible that the number and kind of allelic combinations that can be produced by the species as a whole may not exceed the number that can be produced by one or more of its subspecies. This means, ignoring the possibility of non-adaptive genetic drift, that the particular phenotype of a subspecies is maintained by natural selection, and that under changing environmental conditions one subspecies through successive generations could change into another by genetic recombinations, or into a new subspecies by new combinations. Or, in other words, subspecies, unlike species, are fully reversable and reproducible. A young species with two newly-formed subspecies could be represented accurately by two small vertical columns within a larger vertical column, but representation of an older species with several subspecies and a turbulent history would require a piece of sculpture put together with a number of pastel colors to show reversals, divergence, convergence, intergradation, etc. Inaccurately, however, evolution in *Terrapene* (as reconstructed below) can be illustrated by a series of intersecting lines (used to represent columnar polygons) as shown in Figure 3,B.

At times in the past, it has been argued that subspecies are only two dimensional; i.e. they can be recognized only in a horizontal sense. The nature of the great number of specimens and the amount of information now being accumulated from the Cenozoic offer a material defeat for the argument, but it should have been defeated on philosophical grounds long ago. An individual after birth or emergence from an egg has a life expectancy ranging from a few days to a century or more, depending upon its species, health, activity, and genetic potential. Although the longest individual life spans are insignificant in terms of geological time, a subspecies would ordinarily be expected to have a life span that brackets the life spans of many individuals. In forms with long-lived individuals, the subspecies life span could certainly be significant in terms of geologic time.

A subspecies is recognized by a certain phenotype shared by the majority of individuals in a definite geographical range or ecological niche. Horizontally a subspecies is recognized as long as its phenotype can be recognized, and in my opinion, this rule of thumb applies equally well vertically. There are important biological differences between horizontal and vertical distribution, but in general, those differences are of the same order of magnitude, and do not interfere with the convenience of using the subspecies taxon in both senses. It is important, however, to distinguish between the horizontal and the vertical intermediate forms, and I have done this above (under symbols) and in the following pages by using x for horizontal intermediates and x^t for vertical ones. Thus, turtles intermediate between the modern *Terrapene c. major* and the modern *T. c. triunguis* are identified as *T. c. major x triunguis*, while those intermediate between the extinct *T. c. putnami* and modern *T. c. triunguis* are identified as *T. c. putnami* x^t *triunguis*.

Although I have presented two cases in the following pages where the use of the tetranomial might be justified, I do not feel that anything below the trinomial is very useful. With the refined techniques of today and the aid of computers, it is possible to divide any population of a subspecies into finer and finer groupings, ultimately ending with the individual. Certainly such detailed studies of variation are useful in understanding evolution, particularly in identifying traits that show similar degrees and directions of evolution, but I do not feel it is particularly useful or necessary to recognize such divisions formally beyond the trinomial. Additional subdivision brings about the dissolution of Linnaeus's greatest contribution to taxonomy: a reasonable degree of assurance coupled with maximum convenience.

Terrapene Merrem (1820)

DEFINITION AND COMPOSITION.

The genus *Terrapene* is included in the subfamily Emydinae of the Family Testudinidae, and displays the major features of both the subfamily and family. McDowell (1964: 277) describes the salient morphological traits of the genus as follows:

> jugal tapering to a point ventrally, not in contact with pterygoid, not excluding maxilla from border of inferior temporal fossa; frontal entering orbital margin; posterior palatine foramen little, if at all, expanded; caroticopharyngeal foramen large, on pterygoid-basisphenoid suture, or connected to it by a short suture; plastron with a hinge between hyoplastron and hypoplastron; plastron connected to carapace by suture, the buttresses absent; cloacal bursae very small or absent.

Members of the genus are predominantly terrestrial in habitat, but variations in habitats range from the aquatic or semi-aquatic *T. coahuila* to the desert-inhabitating *T. o. luteola*. All members of the genus are omnivorous. As presently known, the genus is limited in distribution to North America (Milstead, 1965) where it is widely distributed east of the cordilleras. Only one species (*T. nelsoni*) has its distribution west of the cordilleras. One specimen of *T. ornata* (AMNH 73720) has been recorded from the west coast of Mexico, but its natural occurrence there needs substantiation.

The living and fossil members of the genus may be divided into two species groups on the basis of a number of morpholigical characteristics. These were defined by Milstead and Tinkle (1967). Completion of this study has provided data for some refinements and additions, and it seems advisable to present the new version, although it does not differ markedly from the original:

	Carolina Group	Ornata Group
1.	Postorbital bar usually present, although the central portion (squamosal bone) may be cartilaginous; when squamosal is absent, postorbital and jugal bones have posteriorly directed processes (Figure 5, B-C).	Postorbital bar absent; posterior border of postorbital bone smooth (Figure 5, D-E).
2.	Inner toe of male not capable of being turned inward.	Inner toe of male capable of being turned inward at sharp angle to foot.
3.	Highest part of carapace posterior to hinge (Figures 4-14).	Highest part of carapace at or anterior to hinge except in some males of *T. n. nelsoni* (Figures 5-18).
4.	First central scute elevated at a steep angle (50° or more); anterior third of carapace rounded or tapering gradually upward posteriorly.	First central scute elevated at a low angle (45° or less); anterior third of carapace may be distinctly flattened (Figures 15, C; 18, A).
5.	Posterior margin of plastron rounded (Figures 4-14).	Posterior margin of plastron either rounded or straight, frequently straight (Figures 15-18).
6.	Lateral margin of plastron may be indented at the femero-anal seam (Figures 10, C; 12, D,F).	Lateral margin of plastron usually entire.
7.	First marginal scute usually rectangular in shape.	First marginal scute usually irregularly oval or triangular in shape.

8.	Posterior lobe of plastron in males varies from smooth or only shallowly concave to deeply concave.	Posterior lobe of plastron in males smooth or only shallowly concave.
9.	Carapace elongate except in some *T. carolina carolina.*	Carapace generally round or oval except in *T. nelsoni nelsoni* and some *T. nelsoni klauberi.*
10.	Carapace rounded dorsally. General appearance in both sagittal and cross sections is of a highly vaulted carapace. *T. coahuila,* one of the flattest members of the genus is an exception to this.	Carapace flattened dorsally. General appearance in both sagittal and cross sections is of a flat turtle, although height in proportion to length in *T. ornata ornata* may be greater than in some forms of the Carolina Group.
11.	Axillary scale frequently present, and usually on the fourth marginal scute.	Axillary scale usually absent, but usually on the fifth marginal scute, when present.
12.	Interhumal seam long (averaging 18% to 33% of the anterior lobe length; see Tables 1, 2).[1]	Interhumal seam short (averaging 11% to 19% of the anterior lobe length; see Tables 1, 3).[1]
13.	Interfemoral seam short (averaging 10% to 21% of the posterior lobe length; see Tables 1, 2).[1]	Inferfemoral seam long (averaging 16% to 23% of the posterior lobe length; see Tables 1, 3).[1]
14.	Three or four toes on each hind foot, dependent upon the species and subspecies being considered.	Usually four toes on each hind foot in all species and subspecies; three toes occur very rarely.
15.	Hinge usually opposite the fifth marginal scute when specimens are viewed laterally.	Hinge usually opposite the seam between the fifth and sixth marginal scutes or opposite the sixth marginal scute when specimens are viewed laterally.
16.	A mid-dorsal keel is usually present and prominent.	When present, a mid-dorsal keel is only weakly developed.

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[1] Forms of the two species groups in which percentages for this character overlap are not contiguously distributed at present (Figure 1, Tables 2 and 3).

The 16 characters are grouped in sequence to facilitate identification: numbers 1-3 may be applied to single specimens, 4-11 may be applied with discretion to single specimens or small series, and 12-16 require good series of specimens. In each of the three groupings (1-3, 4-11, 12-16), the characters are listed in what I consider to be order of decreasing importance and/or utility in reference to the species groups.

Application of these characteristics to the specimens from which they were drawn yields the following arrangement of species and subspecies into the two species groups:

CAROLINA GROUP	ORNATA GROUP
T. carolina bauri	*T. nelsoni klauberi*
T. c. carolina	*T. n. nelsoni*
T. c. major	*T. ornata ornata*
T. c. mexicana	*T. o. longinsulae* (extinct)
T. c. putnami (extinct)	*T. o. luteola*
T. c. triunguis	
T. c. yucatana	
T. coahuila	

ORIGIN AND AFFINITIES

The oldest known fossils of the genus are of Pliocene age. They are fully differentiated as to both generic characters and species group characters, and thus give no clues to the origin either of the genus or of the species groups. The oldest fossil of the Ornata Group (*T. o. longinsulae*) is of middle Pliocene age, as are the oldest fossils of the Carolina Group (*T. c. putnami*). Although the fossils provide no definite clues, it seems best to assume that the Ornata Group evolved from the Carolina Group. It might be suggested that the converse possibility was the case, but this thesis is rejected because: (1) the Carolina Group would have had to develop a postorbital bar during the process; and (2) members of the Ornata Group are among the most xeric-adapted species of emydinid turtles, and a mesic or hygric-adapted ancestor to the Carolina Group seems mandatory. Another possible hypothesis is that the groups evolved from a common ancestor. In any case the high degree of development of *T. carolina putnami* and *T. ornata longinsulae* by middle Pliocene times indicates that the genus and both of the species groups must have had their origin in Miocene or pre-Miocene times.

A description of a common ancestor for both species groups can be drawn easily from the Pliocene and early Pleistocene fossils (*T. ornata longinsulae, T. carolina putnami,* and *T. c. carolina*) and from trends and parallelisms in various characteristics that seem evident from my interpretations of evolution in the two groups given in the following pages. Such an ancestor would have been a medium-sized box turtle, 130-150 mm in carapace length; round in shape, although some may have had a tendency to be elongate; relatively flat in carapacial curvature; a weak mid-dorsal keel posteriorly was present in some; marginal scutes were generally nonflaring, but some may have had a low degree of flare; plastral hinge was located opposite the seam between the 5th and 6th marginal scutes; the posterior margin of the plastron was rounded; the interhumeral and interfemoral scutes were long (averaging 30% or more of their respective lobe lengths); the posterior plastral lobe of males was smooth or only shallowly concave; the postorbital bar was solid and broad in most, but some individuals had varying degrees of reduction; each hind foot had four toes; an axillary scale was present in some, probably overlying the seam between the 4th and 5th marginals; the color pattern in most was probably a pattern of dark radiating lines, but some had light lines developed between the dark lines, some had uniform coloration, and some may have had a tendency toward melanism. The ancestral turtles were probably marsh and moist-meadow inhabitants in central North America in the ecotone between the eastern forests and the western plains.

The necessity of depending heavily on modern turtles to construct a description of the common ancestor yields a picture of the ancestor as it was on the point of evolving into the forest-inhabiting *T. carolina* on one hand and the grassland-inhabiting *T. ornata* on the other. How much evolution and how much time were required to get the common ancestor to this point depend largely on the group to which the genus *Terrapene* is related. Of the genera that seem to be closest to *Terrapene* morphologically, the Asiatic genus *Cuora* seems at first glance to be the closest. Modern forms of the genus *Cuora* display a phenotype that is almost an exact match with the phenotype of the ancestral *Terrapene* described above, but in evolving from *Cuora, Terrapene* would have had to change a number of major features in the skeleton, including: resorption of the bataguridid process into the basioccipital, resorption of the longitudinal flange on the prearticular, movement of the double condyle on the 6th vertebral centrum anterior to the 5th centrum, and reduction of the superacaudal scutes to the extent that they fall short of the suture between the pygal and suprapygal. These four differences between the two genera appear to be the most important because they constitute the major differences between the subfamilies Emydinae and Batagurinae (McDowell, 1964).

I examined more skeletons of *Terrapene* and *Cuora* than McDowell did in order to test the stability of the first three of the four characters in particular reference to these two genera. I consider the first three of the four characters as being the most important because they have to do with the axial skeleton rather than with the shell. My examination was made because there is always the possibility that one or both of the subfamilies had a polyphyletic origin, and that the characteristics of the subfamilies are the result of convergent evolution. Failure of the three traits to be exhibited appropriately in numbers of specimens, or even extensive variation in the traits, would be sufficient grounds for suggesting that the two subfamilies are artificial divisions based on convergent characters. Aside from the main goal of this study in seeking generic affinities for *Terrapene*, two genera resembling each other as closely as do *Terrapene* and *Cuora* would seem to be the logical place to look for weaknesses in the characters.

The greatest variation in the three traits was found in the longitudinal flange of the prearticular. In *Terrapene* a flange existed in several of the 67 specimens examined, and it was long enough in 5 specimens to exclude the angular from contact with Meckel's cartilage. No specimen of *Cuora* lacked the flange or failed to have it exclude the angular. Thus, of a total of 86 *Cuora* and *Terrapene* examined only 5 (5.8%) exhibited a significant deviation from the expected.

Although, as noted above, the position of the first double condyle in the cervical vertebrae is a somewhat subjective characteristic, it appears to be more stable than the preceding character. The presence or absence of the batagurine process appears to be the most stable of the three characters. The process was present in all batagurines examined and was missing from all emydines. The only variations noted were those of size, shape, and position of the process in the batagurines.

It seems best, therefore, to conclude that no relationship exists between the American and Asiatic box turtles, and that their close resemblance is the result of convergence. As noted above, the resemblance is superficial. Only one trait possessed by both, the hinged plastron, would require major genetic rearrangements (in both soft and hard parts) in order for convergence to have occurred. Although it would seem to require less genetic change to make a *Terrapene* skeleton out of a *Cuora* skeleton than it would for both genera to produce a hinge, this may not be true when all the differences between the two genera are considered, and it must also be remembered that both genera were probably under vigorous selective pressure to develop the hinge. In assuming a terrestrial habitat, turtles could follow only a few courses to protect their soft parts: (1) develop a plastral hinge to enable the plastron to be drawn up against the carapace, (2) develop a carapacial hinge to enable the carapace to be lowered against the plastron, (3) develop armored plates on the appendages, (4) reduce armour to allow greater and more rapid movements, and (5) combinations of the first four. Several otherwise unrelated groups could be expected to solve the problem in the same way. Legler (1960) and McDowell (1964) concluded previously that a hinged plastron arose independently in several groups of terrestrial turtles.

Emydoidea is a North American emydine genus which also resembles *Terrapene,* but the resemblance is between modern forms of the two genera, and is not so close as the resemblance between the modern forms of *Cuora* and the projected ancestral form of *Terrapene.* *Emydoidea* and *Terrapene* also differ in major features of the skeleton, which relate *Emydoidea* to the aquatic *Deirochelys* (Tinkle, 1962; McDowell, 1964). Thus, the *Emydoidea-Terrapene* resemblance appears to be another case of convergence.

Clemmys and *Emys* are two emydine genera to which *Terrapene* appears to be closely related through possession of the same major skeletal features, although neither resembles *Terrapene* as closely as do *Cuora* and *Emydoidea.* Of the two, *Emys* (Africa, Asia, and Europe) more closely resembles both the proposed description of the ancestral *Terrapene* and the modern forms of *Terrapene* than does *Clemmys* (North America). This resemblance is seen in the possession of a plastral hinge, in adsorption of the plastral buttesses, and in similar shapes of the posterior plastral lobes and plastral scutes.

McDowell (1964) considered *Terrapene* an offshoot of *Clemmys* because both genera differ from *Emys* by having large carotico-pharyngeal foramina, but my own investigations show these foramina, vary in size in all three genera. Two other characters, the contact between the jugal and the pterygoid and the contact between the prefrontal and postorbital, also exhibit extensive variation. I suggest that both *Terrapene* and *Emys* evolved from a common ancestor that evolved from *Clemmys* in either Asia or North America, that the common ancestor had the traits that all three genera hold in common plus the beginnings of the traits that unite *Terrapene* and *Emys* apart from *Clemmys*, and that all three genera subsequently developed the traits that now distinguish them.

The two species groups of the genus *Terrapene* and suggested evolutionary lines within those groups are discussed below. Speculation on the origin of the genus *Clemmys* lies outside the scope of this study.

The following skeletal specimens were examined with particular reference to the subfamilial and generic characters discussed above:

BATAGURINAE

Coura amboinensis, BMNH 48.10.31.14, 51.11.10.76, 67.4.2.145, 71.9.1.52; MRNH 4544, 4870; RMNH, 2 unnumbered skeletons; SM 32973-5; USNM 78128, 104345, 129253; VNHM 1799-1903

Coura trifasciata, VNHM 1785.

Cyclemmys dentata, BMNH 48.10.31.15, 67.3.5.24, 68.4.3.153, 97.11.22.3; KU 47170.

EMYDINAE

Terrapene carolina bauri, KU 20506, 20508-16.

T c. carolina, BMNH 58.12.30.2, 59.9.6.435, 1900.7.12.3, 1900.7.12.6; KU 2846, 2850, 2854, 2870, 16383-4, 16386-7, 16389, 16393; RMNH, 3 unnumbered skulls; SM 29974; VNHM 1775-7.

T. c. major, UMKC 0502.

T. c. mexicana, KU 24075, 47902.

T. c. triunguis, KU 48264, 48266-73, 48276.

T. c. yucatana, KU 71773.

T. coahuila, KU 46924-27, 51432, 92623; UMKC 0496.

T. n. nelsoni, KU 92630-31; UMMZ 128400; UF 27138.

T. o. ornata, KU 2844, 2860, 2866, 2901, 3538, 3540-1, 5033, 6862, 22969.

Clemmys guttata, KU 1114; VNHM 1723-4.

Clemmys insculpta, KU 2843; VNHM 1725.

Clemmys mamorata, VNHM 1731, 1733.

Clemmys muhlenbergi, VNHM 1730.

Emys orbicularis, VNHM 32-4, 37-9, 105-7.

THE CAROLINA GROUP

This group includes two species: *Terrapene carolina,* with one extinct and six living subspecies distributed over eastern North America, and *Terrapene coahuila,* which is known only from a bolson in central Mexico. Morphological differences between the two species are discussed under *T. coahuila.*

In general the Carolina Group may be considered forest-inhabiting The one exception is *T. coahuila,* the only known aquatic member of the genus, and I presume that it evolved from a forest form. *T. carolina carolina* inhabits the northeastern deciduous forests of the United States in the Carolinian biotic province of Dice (1943), and because of this distribution in relation to the glacial periods, it was apparently the most geographically stable member of the genus during the turbulent conditions of the Pleistocene epoch. While other forms of the genus seem to have undergone one or more important range shifts, which set the stage for isolation and speciation, *T. c. carolina* appears to have lasted out the Pleistocene in almost the same geographic range it occupies today, with only minor fluctuations of range relative to expansions and contractions of the deciduous forests. *T. c. bauri, T. c. mexicana,* and *T. c. triunguis* occupy mixed pine and deciduous forests in their respective ranges in the United States and Mexico, and *T. c. yucatana* inhabits tropical scrub forests on the Yucatan Peninsular. *T. c. major* occupies palmetto-pine forests and coastal marshes along the northern coast of the Gulf of Mexico. Trees in the habitat of *major* may be close together or widely scattered, and there may be relatively open areas with very few trees. Underbrush is usually thick with dense stands of palmettos, and frequently the forest floor has pools of water. The habitat of the extinct *T. c. putnami* is presumed to have been the same as, or similar to, the habitat of *T. c. major.*

The earliest known representative of the Carolina Group is *T. c. putnami* from middle Pliocene deposits in Florida. *T. c. carolina* appeared in late Blancan times, *T. c. bauri* appeared during the early Rancholabrean, *T. c. triunguis* evolved in the Rancholabrean, and *T. c. major* is an extension of *T. c. putnami* into the Recent era. *T. c. mexicana, T. c. yucatana,* and *T. coahuila* are known only from the Recent.

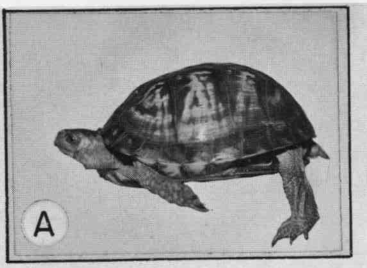
At present we have no clues to the origin of either *T. c. putnami* or *T. c. carolina,* although *carolina* may have evolved from *putnami* in the interval between the first appearance of *putnami* and the first appearance of *carolina* (Aftonian interglacial of the Pleistocene in Florida). No evidence either supports or denies this thesis, and theoretical arguments can be presented on both sides. It seems best for the present to ignore the problem, and simply note that in the early Pleistocene the Carolina Group was represented by two forms: *T. c. carolina,* an upland, forest-inhabitating form that lived east of the Appalachian Mountains; and *T. c. putnami*, a palmetto-pine-forest-inhabiting form that lived along the Gulf Coast and west of the Appalachian Mountains. The two forms presumably came into contact and intergraded in Florida during a time of low sea levels in a glacial stage. *T. c. bauri* is presumed to have evolved from these intergrade populations.

Following the initial emergence of the Florida peninsula, high Pleistocene sea levels divided Florida into a series of islands, and it is suggested that these provided the physical mechanism for the isolation of the *carolina x putnami* populations that evolved into *bauri*. High Pleistocene sea levels also caused extensive embayments along the Mississippi River at times, and these or some other barrier divided *putnami* into eastern and western populations. The western populations ultimately evolved into *triunguis*, and the eastern ones into *major*. The evolution of *major* is presumed to have differed from that of *bauri* and *triunguis* in that it apparently did not involve the appearance of new characters through mutation or recombination, but appears to have resulted from the swamping of some *putnami* characteristics through intergradation with *carolina* and secondary intergradation with *bauri* and *triunguis*.

The western populations of *putnami* that ultimately became *triunguis* may have been the source from which the Mexican box turtles evolved. It is suggested that at times in the Pleistocene *T. carolina* ranged around the Gulf of Mexico from Florida to Yucatan, and that *T. c. yucatana* evolved from a population of *T. c. putnami* or *T. c. putnami* x^t *triunguis* that became isolated on the Yucatan Peninsula in pre-Sangamon or Sangamon times. During the Wisconsin, *triunguis* and *yucatana* came into contact and intergradation occurred. Isolation of the intergrade populations, first from *yucatana* by rising sea levels and then from *triunguis* by arid conditions in northern Mexico, in post-Wisconsin times marked the beginning of *T. carolina mexicana*. I suggest further that the evolution of *T. coahuila* was similar to that of *T. c. yucatana* in that it appears to have begun with the isolation of a population of *T. c. putnami* or *T. c. putnami* x^t *triunguis*.

The existing fossils of the Carolina Group leave little doubt that *T. c. carolina* and *T. c. putnami* evolved before or in the early

FIGURE 4. *Terrapene carolina carolina*. A, Living specimen, Long Island, N. Y. B, AMNH 6406, Massachusetts. C, UMMZ S443, Massachusetts. D, AMNH 71292, New Jersey. E, UMMZ 78519, Michigan. F, UMMZ 53003, Michigan. G-H, UMMZ 40833, Michigan.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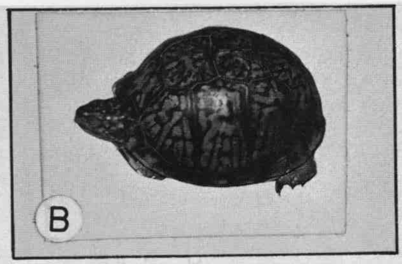
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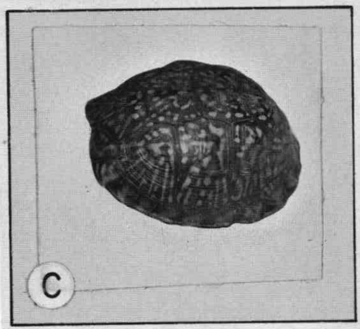
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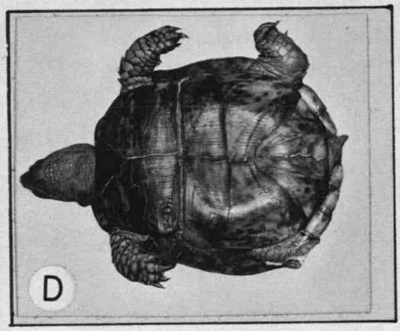
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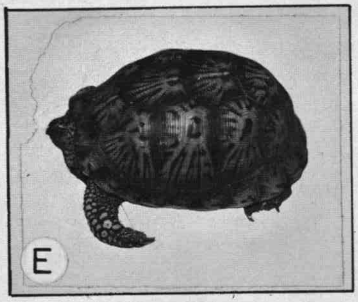
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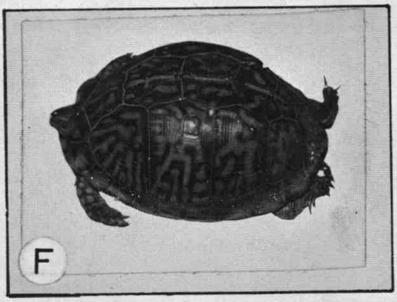
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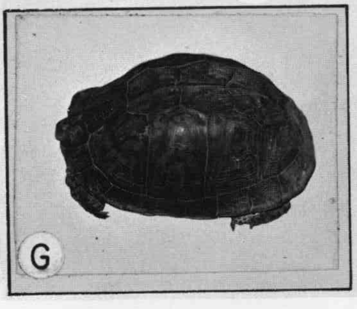
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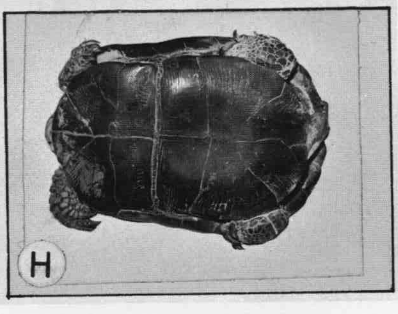
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Pleistocene, while *bauri, major* and *triunguis* evolved during the Pleistocene. Evolution of the Mexican members of the group as given above and in the following pages, however, is largely speculation. Additional fossil material may show that *putnami* evolved from *yucatana* or *coahulia* rather than vice versa. These possibilities and reasons for rejecting them at present have been given more detailed consideration in discussions of *yucatana, coahuila,* and the Ornata Group.

Terrapene coahuila and the seven subspecies of *T. carolina* are discussed in greater detail below. The distribution of members of the Carolina Group are given in Figure 1, plastral ratios and other data on the group are given in Tables 1, 2, and 4, and representatives of the group are shown in Figures 4-14.

Terrapene carolina carolina (Linnaeus)

Figure 4; Table 2 (1-14)

Testudo carolina Linnaeus, 1758, Syst. Nat., ed. 10, 1:198.
Terrapene carolina Bell, 1825, Zool. Jour., 2:309.
Terrapene carolina carolina Stejneger and Barbour, 1917, Checklist N. Amer. Amphib. & Rep., ed. 1:115.
Testudo carinata Linnaeus, 1758, Syst. Nat., 1:198.
Testudo incarcerata Bonnaterre, 1789, Tabl. Encycl. Meth., Erp.: 29.
Testudo incarcerata-striata Bonnaterre, 1789. ibid.
Testudo clausa Gmelin, 1789, Syst. Nat., ed. 13, 1:1042.
Testudo virgulata Latreille, 1801, Hist. Nat. Rept., 4:100.
Emys schneideri Schweigger, 1814, Konigsberg. Arch. Naturg. Math., 1:317, 442.
Monoclida kentukensis Rafinesque. 1822, Kentucky Gazette, Lexington, 1 (21) :5.
Terrapene maculata Bell, 1825, Zool. Jour, 2:309.
Terrapene nebulosa Bell, 1825, ibid:310.
Emys kinosternoides Gray, 1831, Syn. Rept., pt. 1:32.
Cistudo virginea Aqassiz, 1857, Contrib. Nat. Hist. U.S., 1:441; 2:pl. 4, figs. 17-19, pl. 7, figs. 10-14.
Terrapene eurypygia Cope, 1860, Ext. Batrach., Reptilia, Aves, N. Amer.: 124.
Terrapene eurypygia Hay, 1902, Proc. Acad. Nat. Sci. Phila.: 385.
Terrapene formosa Hay, 1916, Florida State Geol. Surv., 8th ann. rept.: 39-76.

RECOGNITION FEATURES: — One or more of the plastral ratios of *T. c. carolina* shown in Tables 1 and 2 distinguish it from each of the other members of the species. The presence of four toes on each hind foot further distinguishes *carolina* from *bauri, mexicana,* and *triunguis,* and its relatively short carapace length further distinguishes it from *putnami, major, mexicana,* and *yucatana.* The deeply concave plastrons of male *carolina* separate them from males of *mexicana, triunguis,* and *yucatana.* The shape of *carolina* in lateral view (Figures 2, 4) distinguishes it from every other subspecies except *major* and *putnami.*

PRESENT DISTRIBUTION: — Cumberland and Allegheny plateaus eastward. North of the Ohio River it extends westward to Lake Michigan (Figure 1). Intergradation with *triunguis* occurs along the Ohio and Mississippi Rivers and south of the Appalachian Mountains east of the Mississippi. Intergradation with *bauri* occurs in eastern Georgia and northeastern Florida, and simultaneous intergradation with *major* and *triunguis* occurs in southwestern Georgia and southeastern Alabama. The intergrades are considered in the discussions of *bauri* and *triunguis.*

GENERAL DESCRIPTION: — A medium-sized box turtle (Table 2), which tends to be round in shape (Figures 2A, 4A-D) except in the northwestern part of its range (Figure 2, C; 4, E-H). In median sagittal section, *carolina* has a gently rounded carapace (Figures 2B, D, 4). The posterior lobe of the plastron of males has a deep concavity (Figure 4D, H) to harbor the carapace of the female during copulation. The postorbital bar is narrow, cartilaginous, or absent; toes number four on both hind feet of 131 out of 132 specimens on which the toes were counted; axillary scale usually absent (Table 2); 1st central scute infrequently straight-sided (Table 2). The posterior marginals have a large curvature radius, which means that the marginals are relatively straight rather than flaring outwards (Figure 4, A-D). Some variation exists in both the presence of an axillary scale and the flaring of the marginals, particularly in the northwestern part of the range. The plastral ratios of the various samples of *T. c. carolina* are given in Table 2 (1-14).

The color pattern of *T. c. carolina* is one of the most distinctive things about the subspecies, but unfortunately it also occurs in *major* and similar patterns occasionally occur in *bauri* and *triunguis.* The generic pattern of radiating lines that may be broken into a series of spots is present in *T. c. carolina* and consists of light yellow to orange or orange-red lines or spots on a dark ground color. In almost every case the lines or spots give the impression that they were painted on, and that the paint was smeared before it dried. This produces broad lines or spots with poorly defined borders, and at times lines run together to form broad blotches or configurations (Figure 4).

The largest *T. c. carolina* examined was a specimen from Michigan with a carapace length of 167 mm. A specimen from Pennsylvania and one from Indiana had lengths of 163 mm and 162 mm, respectively. A specimen (AMNH 74468) from Massachusetts with a length of 157 mm apparently had a life span of over 110 years. It died in the New York Zoological Gardens in 1954 with two dates carved in its shell, one for 1860 and the other for 1844. The average carapace lengths of the various samples of *T. c. carolina* are given in Table 2. The two most northern populations, Massachusetts (2C) and Michigan (10C), have the highest averages, but the samples show no definite north-south cline, and another northern sample (11C, Cincinnati) has one of the lowest averages.

The two samples of *T. c. carolina* from the northwestern part of the subspecies range (Table 1, 10C, and 11C; Figure 4 E-H) are so different from the other samples of *carolina* that it was thought during the early stages of the study that they might be very closely related to *T. c. major*. The differences are that individuals from the two northwestern populations are predominantly elongated in shape, while most individuals from other populations are rounded; the posterior marginals are flared rather than straight-sided in the northwestern specimens, and this flaring equals that of specimens of *major* in some individuals; the frequency of an enlarged axillary scale is greater in the two northwestern samples (especially in 10C) than in most of the other samples; and in at least one of the northwestern samples (10C) the average size is larger than in most samples. Compared with the degree and number of differences separating the subspecies of *Terrapene carolina*, the differences that separate the northwestern populations from the other populations of *T. c. carolina* fall far short of the trinomial level, but use of the tetranomial could be justified: *Terrapene carolina carolina michiganensis* for populations 10C and 11C, and *Terrapene carolina carolina carolina* for the other populations. On the basis of differences in frequencies of occurrence of the enlarged axillary scale and differences in size, the southern population (11C) of *T. c. c. michiganensis* could be further recognized as *Terrapene carolina carolina michiganensis ohioensis*. Further examinations of populations 10C and 11C could prabably justify the use of the sextanomial (compare for example, E, F, and G in Plate I). As previously noted, however, I do not see that the application of Latin names beyond the trinomial is very useful.

Two explanations are readily available for the differences between populations 10C and 11C and the other populations of *T. c. carolina*.

First, in reference to the suggested relationship of the northwestern populations to *major,* the characters of elongate body, flaring marginals, enlarged axillary scales, and large size are all characteristics of *putnami* and may be relics of a pre-Wisconsin influence of *putnami.* Second, the same characteristics are also associated to a lesser degree with *triunguis,* and a *triuguis* influence may be the better explanation. Populations 10C and 11C are not from the zone of intergradation between *carolina* and *triunguis.*

VERTICAL DISTRIBUTION: — I have examined only four fossil specimens of this subspecies. One, No. 1706 in the private collection of Phillip Kinsey, from Aftonian deposits in the Haile XV A site, Alachua County, Florida, is the oldest known representative of the subspecies. Another, AMNH 1484, from "Pleistocene" deposits in Talbot county, Maryland, is the holotype of Cope's (1869) *Cistudo eurypygia.* The other two, ANSP 157 and 162, from Yarmouth Interglacial deposits in Port Kennedy, Montgomery County, Maryland, were identified by Hay (1908) as *Terrapene eurypygia.* This species was described as differing from *T. carolina* primarily on the basis of what is now known to be an occasional scute aberration in the posterior carapace of *T. carolina,* and I have considered *T. eurypygia* a synonym of *T. c. carolina* (Milstead, 1965). Should additional specimens demonstrate that this aberration was the rule rather than the exception in early Pleistocene fossils related to *T. c. carolina,* it may be necessary to reconsider the relationships between the fossil and Recent specimens. If the high frequency of the aberration in the fossils can be supported by other differences, it may be desirable to recognize the early Pleistocene fossils as an extinct subspecies, *T. c. eurypygia,* from which *T. c. carolina* evolved. There is no need, to consider this possibility further at the present time. Other records of Pleistocene fossils related to *T. c. carolina* consist of one nearly complete carapace, two complete anterior plastral lobes, three complete posterior plastral lobes, and numerous carapacial and plastral fragments from Illinoian deposits near Coleman, Citrus County, Florida, which I have identified as *T. c. carolina x putnami* (Florida State Museum specimens). Auffenberg (1958, 1959, 1967) notes that much of the material from Sangamon and Wisconsin deposits in Florida displays an influence of *carolina,* but I have been unable to see this; perhaps, because of a slightly different interpretation of *bauri.*

Recent Specimens Examined. – Uuless otherwise noted all samples are from the Carolinian biotic province of Dice (1943).

1C. *T. c. carolina.* 15 specimens from the Long Island-New York City Area, New York: AMNH 4596, 7029, 7033, 7748, 8791, 44661-4, 44668-9, 66561; FMNH 92182; UF 3326; UCM 13798.

2C. *T. c. carolina.* Ecotone between Canadian and Carolinian biotic provinces of Dice (1943). 10 specimens from Connecticut, Massachusetts, and Rhode Island: AMNH 6406, 74468; BMNH 1889.9.18.1; UMMZ 99708-9, 113204-7, S443.

3C. *T. c. carolina.* 53 specimens from New Jersey: AMNH 22552, 38010, 64657, 66095, 71290-2, 85541, 86552; ANSP 14, 17602, no number; KU 15883, 15886-8, 15890-1, 16383-94, 16401-3, 18344, 51458-9; RC 72, 1214, 2288, 2691, 3206-7, 3409; TNW 2234-8; UMMZ 72489, 74468-71.

4C. *T. c. carolina.* 21 specimens from Allegheny, Frederick, and Washington counties, Maryland; Adams, Bedford, Cumberland, Huntingdon, and Perry counties, Pennsylvania; and Jefferson and Morgan counties, West Virginia: FMNH 83430; UF 12445-8; KU 3068, 48244-6, 48248; TNW 2021-2; UMMZ 74668, 99734-5, 113982-4, 113905, 113986-7.

5C. *T. c. carolina.* 45 specimens from Anne Arundel, Baltimore, Calvert, Cecil, Montgomery, Prince George's, and Queen Anne's counties, Maryland; and Accomac, Essex, Fairfax, Mt. Vernon, and Northhampton counties, Virginia: AMNH 46009, 66180; BMNH 1963, 1034; FMNH 42441, 42443; UF 261, 1231, 9689(1), 9689(3), 10607 (1-3), 12348-50; KU 2747, 2850, 2854, 2870-1, 3069-72, 15828-9, 15889, 48240-3; NMS 1120; UMMZ 52370-3, 52375-8, 94131, 96613-4, 99736.

6C. *T. c. carolina.* 7 specimens from Ohio, Roane, and Tyler counties, West Virginia: AMNH 69775; UMMZ 86032, 103001-5.

7C. *T. c. carolina.* 28 specimens from Floyd, Harlan, and Pike Counties Kentucky; Watauga County, North Carolina; Carter, Claiborne, Johnson, Sullivan, and Unicol counties, Tennessee; and Washington and Wythe counties, Virginia: AMNH 7584, 44590; FMNH 57445-6; UF 13155 (1-2); UF-RMJ 975, 976 (1-2), 977, 995-8; UMMZ 78978-81, 78983-4, 78986-9, 86225-6, 109555; USNM 86673.

8C. *T. c. carolina.* 56 specimens from Blount, Campbell, Knox, Loudon, McMinn, Meigs, Monroe, Polk, Rhea, Sevier, and Union counties, Tennessee: UF-RMJ 570, 591 (1-2), 592 (1-2), 600, 748 (1-3), 749 (1-2), 762, 789, 864, 903 (1-4), 903 (6-8), 916, 919, 923 (1-4), 924-5, 926 (1-2), 933, 934, (1-2), 935 (1-2), 936 (1-6), 994, 1036-7; UMMZ 86732-3, 96601-2, 102740-2; USNM 86668, 86696, 120111-2.

9C. *T. c. carolina.* 24 specimens from Habersham and Lumpkin counties, Georgia; Henderson, Macon, and Transylvania counties, North Carolina; and Greenville and Oconee counties, South Carolina; AMNH 8429; UF 4226, 4438, 7535; UMMZ 72836, 86142-3, 96603-10, 96612, 97553-60.

10C. *T. c. carolina.* 39 specimens from LaPorte, Porter, and St. Joseph counties, Indiana; Allegan, Barry, Berrien, Branch, Calhoun, Cass Hillsdale, Ingram, Kalamazoo, Kent, Lake, Mecosta, Monroe, Muskegon, Ottawa, Van Buren, and Washtenaw counties, Michigan; and Erie and Fulton counties, Ohio: UF 8268-9, 15447, 35430, 83393-5, 83403-4, 83442, 83444-5; UMMZ 32869, 34749, 36020, 40832-4, 52951, 53003, 53872, 54372-3, 70473-4, 70491, 72486, 74672-4, 78519, 81701, 83988, 86029-31, 99234, 103239, S1214.

11C. *T. c. carolina.* 19 specimens from Jefferson County, Indiana; Boone, Carroll, Carter, Fayette, Grant, Greenup, Lawrence, Nichols, and Wolfe counties, Kentucky; and Adams, Brown, Pike, and Scioto counties, Ohio: ANSP 311, UMMZ 78976, 78992, 79135-6, 86033-4, 96600, 102738-9, 103414-7, 103420, 103422-3, 109554, 109888-91.

12C(T). *T. c. carolina* (with some influence of *triunguis* as evidenced by coloration and shape of some specimens). 27 specimens from Coles County, Illinois; and Clay, Parke, Richland, and Vigo counties, Indiana: FMNH 18047, 18190, 18642-9, 19192-3, 22680, 31969-70, 39226-7; KU 46780-1, 46783-4, 46786-9; RMNH no number; SM 6166.

13C(T). *T. c. carolina* (with some influence of *triunguis* as evidenced by coloration, shape, and 3 hind toes of some individuals). Ecotone between Austroriparian and Carolinian biotic provinces of Dice (1943). 7 specimens from Lee, Montgomery, and Talladega counties, Alabama: UF 2377-80; UMMZ 89906, 92745, 99029.

14C(B) *T. c. carolina* (with some influence of *bauri* as evidenced by coloration, shape, and 3 hind toes of some individuals). Austroriparian biotic province of Dice (1943). 20 specimens from Burke, Candler, and Emanuel counties, Georgia; and Anderson, Bamberg, Berkeley, Charleston, Colleton, Edgefield, and Lexington counties, South Carolina: AMNH 69781; BMNH 1888.9.18.2; UF 4406-8, 4413, 4415, 4433, 7907, 10181; UMMZ 72835, 81147, 86035, 89874-5, 103252-4, 108843, 115738.

Terrapene carolina putnami Hay

Figures 5, 8

Terrapene putnami Hay, 1906, Bull. Amer. Mus. Nat. Hist., 22:30.
Terrapene carolina putnami Auffenberg, 1958, Bull. Florida State Mus., 3 (2): 53-92.
Cistudo marnocki Cope, 1878, Proc. Amer. Phil. Soc., 17:229, part.
Terrapene canaliculata Hay, 1907, Bull. Amer. Mus. Nat. Hist., 23:850.
Trachemys nuchocarinata Hay, 1916, Florida State Geol. Surv., 8th ann. rept.: 39-76.
Terrapene antipex Hay, 1916, ibid.
Terrapene singletoni Gilmore, 1927, Proc. U.S. Nat. Mus., 71 (15); 1-10.
Terrapene llanensis Oelrich, 1953, Copeia (1): 33-8, part.
Terrapene canaliculata Milstead, 1956, Copeia (3): 162-171, part.

Before describing *T. c. putnami* it is well to note that it is the most poorly known box turtle. Whereas the other subspecies of

T. carolina are represented by one or more good series of specimens, we know *putnami* at present only from a few fragments of Pliocene age, from isolated samples of a few specimens ranging rather continuously from Pliocene to Rancholabrean times, and from specimens intermediate between *putnami* and other subspecies. Thus, when a series of "pure" *putnami* is found, the characters of *putnami* may differ in some ways from those given below.

RECOGNITION FEATURES: – large size (around 300 mm), length of interhumeral seam equal to nearly one third of the total length of the anterior lobe of the plastron, marginals greatly flared outwards and upwards (Figure 5).

GENERAL DESCRIPTION: – largest of the box turtles. Some individuals attained a carapace length well in excess of 300 mm. The interhumeral seam in *putnami* is the longest of any form in the species except *T. c. yucatana.* In single specimens of *putnami* and in series of intermediate forms, the interhumeral seam is 30% or more of the length of the anterior lobe, and in individual specimens reaches a maximum of 36%. The long interhumeral seam is associated with a short intergular seam (40% or less of the anterior lobe length). The flaring of the marginals is the greatest found in the species. Auffenberg (1958) gives the angle of flare from the perpendicular as 50° to 70° in *putnami,* and the average curvature radius as 14.6 mm in *putnami* 15.8 mm in *major,* and 26.7 mm in *bauri.* The carapace of *putnami* is elongated and in median saggital section is gently rounded, but with a hump on the 5th central scute caused partially by the convexity of that scute and partially by the flaring and guttering of the marginal scutes. The posterior lobe of the plastron of males has a deep concavity to harbor the carapace of the female during copulation. The postorbital bar is thought to have been a broad, heavy span of bone (see Auffenberg, 1958, 1959, 1967); an enlarged axillary scale is present in both *putnami* and intermediate forms; and the 1st central scute is urn- or wedge-shaped in all specimens examined. In a number of specimens, the flare of the bony marginals indicates that the epidermal scutes must have been greatly recurved to form a deep gutter around the posterior half of the carapace. Anterior to the gutter, the flaring of the marginals is reduced to form a prominent lateral keel above the bridge. Anteriorly to the bridge, the marginals again flare outwards to produce a trace of guttering over the forelegs.

DISTRIBUTION: – The oldest specimens of *T. c. putnami* are from the middle Pliocene of Florida in the southeast; the Illinoian of Slaton, Texas, (near the Texas – New Mexico border in the southwest); and the Illinoian of Meade County, Kansas, in the midwest. Thus at times in the early Pleistocene *putnami* ranged from peninsular Florida west to New Mexico and north at least as far as Kansas. The *putnami* influence in modern turtles may have extended even farther: north to Michigan and south to Yucatan. The modern *T. c. major* is a palmetto-pine forest inhabitant, and remains of other animals found with *putnami* indicate that *putnami* occupied a similar habitat (Auffenberg, 1958, 1959, 1967; Auffenberg and Milstead 1965; Dalquest, 1967; Milstead, 1967). It was probably not exactly the same as that occupied today by *major*, because the early Pleistocene and modern climates are not identical, but presumedly the habitat was sufficiently similar to that of *major* to allow *putnami* to exist through the Pleistocene and finally emerge in the Recent epoch as *major*. It is also presumed that this habitat was extensive and constant enough over the eastern United States to permit *putnami* to range northwestward as far as Kansas and New Mexico, and that changes in climate that produced changes in habitat were responsible for the evolution of *triunguis* from *putnami* west of the Mississippi River. The weakest point in the story is the relationship of the early western box turtle remains. The size of the specimens is the only thing that relates them to *putnami*. No other characters are present. Thus, when more fossils from both the midwest and the southeast become available, they may show the presence of two subspecifically distinct giant box turtles at the close of the Pliocene, one which gave rise to *major* and one which gave rise to *triunguis*.

No late Pleistocene fossils of *putnami* have been found west of the Mississippi River. All the fossils from that area are identifiable as *triunguis* or as *putnami* x^t *triunguis*. These are considered under the discussions of *triunguis*.

SPECIMENS EXAMINED

Pliocene

Early Hemphillian: UF 9367, a single peripheral bone from deposits at the McGeehee site, Alachua County, Florida, tentatively identified as *T. c. putnami*.

Middle Hemphillian: several fragments in the UF from the Bone Valley Gravel, Polk County, Florida.

Late Hemphillian: fragments of two or more box turtles in the UF from the Withlacoochee River south of Ocala, Florida.

Pleistocene

Nebraskan: several fragments in the UF from the Santa Fe River north of Gainesville, Florida.

Kansan: UF 11152, 11155-58, and others in the same series. Numerous fragments from near Punta Gorda, Lee County, Florida.

Illinoian: MP 39442 and UT 882-315 from near Slaton, Lubbock County, Texas (erroneously cited by Milstead, 1967, as Yarmouthian deposits), and UMMP 43734 from Meade County, Kansas.

Sangamon and Wisconsin: all of the Florida specimens in the UF and USNM collections listed by Auffenberg (1958, 1959, 1967). These include the specimens from the Haile VIII A upper red zone (see discussion of *bauri* below).

Terrapene carolina major (Agassiz)

Figures 5, 6, Table 2 (23)

Cistudo major Agassiz, 1857, Contrib. Nat. Hist. U.S., 1:445.
Terrapene carolina major Carr, 1940, Univ. Fla. Publ., 3 (1): 101.

Recognition Features: – Two or more of the plastral ratios of *T. c. major* shown in Tables 1 and 2 distinguish it from each of the other members of the species. The large body size separates *major* from all living members of the species. The presence of four toes on each hind foot further distinguishes it from *bauri*, *mexicana*, and *triunguis*, and the concave plastron of males (Figure 6, D) from *mexicana*, *triunguis*, and *yucatana*.

Present Distribution: – northern ("panhandle") Florida west of the Aucilla River (Figure 1). Intergradation is with *bauri* in the western half of peninsular Florida; with *triunguis* in extreme northwestern Florida, southwestern Alabama, southern Mississippi, and southern Louisiana; and jointly with *carolina* and *triunguis* in southwestern Georgia and southeastern Alabama. The intergrades are considered in the discussions of *bauri* and *triunguis*.

General Description: – largest of the living box turtles (Table 2, 23M), with some individuals exceeding 200 mm in carapace length. The carapace is elongated and in median saggital section is either rugose or gently rounded (Figures 2 G, 5, 6), but with a hump on the 5th central scute caused partially by the convexity of that scute and partially by the flaring and guttering of the marginal scutes. The posterior lobe of the plastron of males has a deep concavity (Figure 6 D) to harbor the carapace of the female during copulation. The postorbital bar is a broad, heavy span of bone, toes number four on both hind feet on 9 of 10 specimens examined; enlarged axillary scale

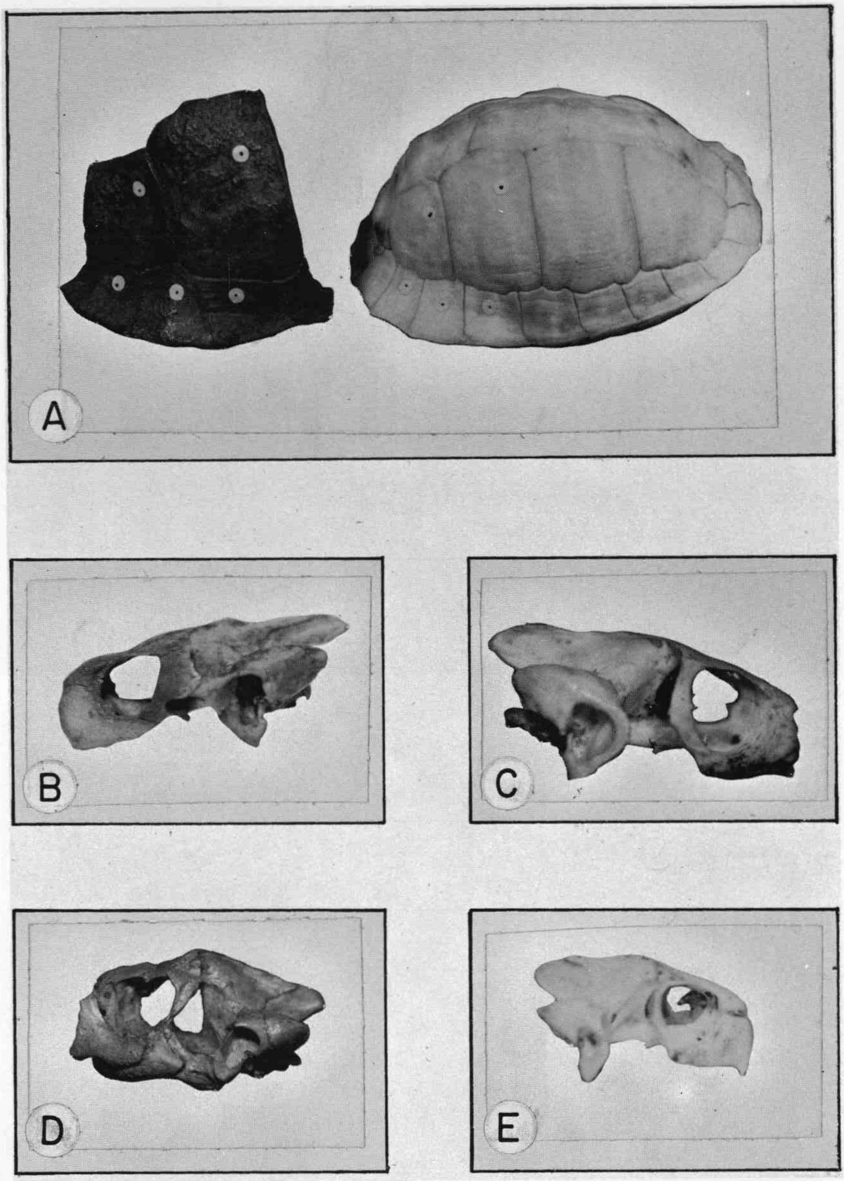


FIGURE 5. A, comparison of a carapacial fragment of *Terrapene carolina putnami* (UF 1616) with a carapace of a modern *T. c. major* (UMKC 0502). Spots on the shells indicate points of comparison. Both specimens are from Florida. B, skull of *T. c. major* (UMKC 0502). C, skull of *T. c. mexicana* (AMNH 7105). D, skull of *T. ornata longinsulae* (USNM 5983). E, skull of *T. nelsoni nelsoni* (UF 27138).

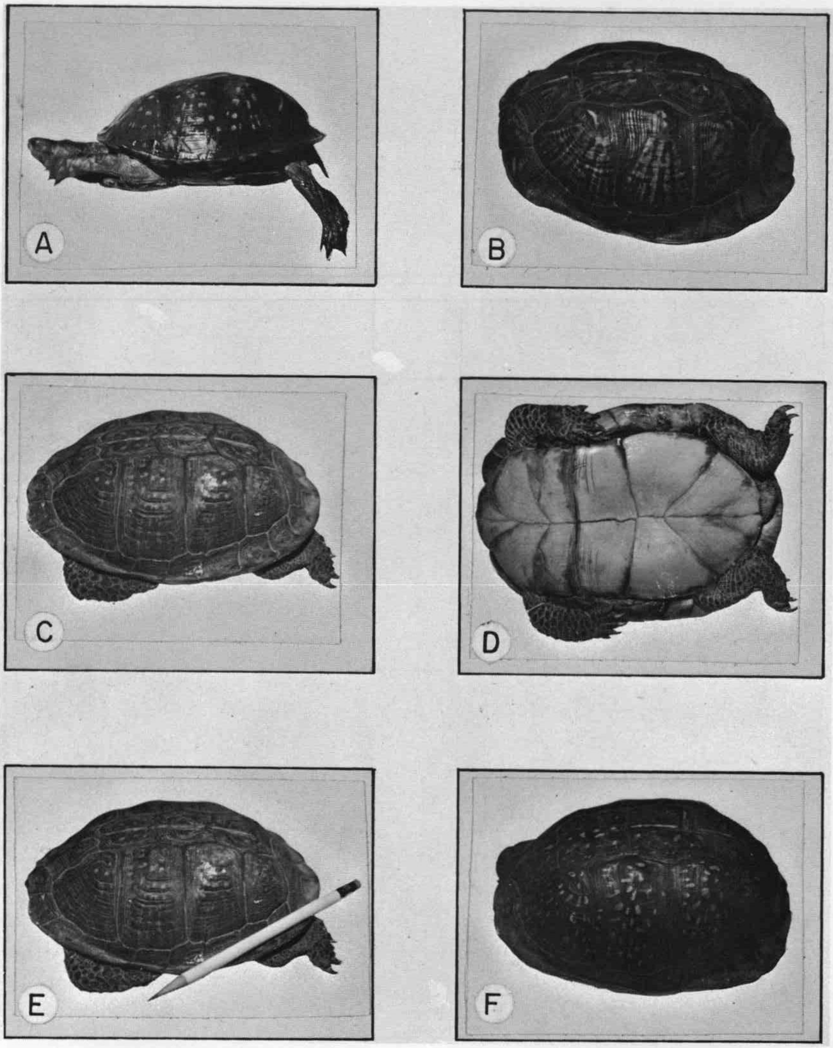


FIGURE 6. *Terrapene carolina major*. A, living specimen, Bay County, Florida. B, FMNH 83453, Leon County, Florida. C-E, FMNH 44990, Gulf County Florida. F, FMNH 83454, Calhoun County, Florida.

present in all (59) specimens examined; 1st central scute urn- or wedge-shaped in all the specimens examined. The posterior marginals have a small radius, and are thus greatly flared outwards. In many cases the marginal scutes are curved upwards to produce a distinct gutter (Figure 6 C, E) around the posterior half of the carapace. Anterior to the gutter, the flaring of the marginals is reduced to form a prominent lateral keel above the bridge. Anterior to this lateral keel, the marginals again flare outward to produce a trace of gutering over the forelegs. The plastral ratios of *T. c. major* are given in Table 2 (23M).

T. c. major has no distinct color pattern of its own, but instead has the color patterns of *bauri, carolina,* and *triunguis,* and mixtures of two or more of those patterns. Some adult specimens of *major* have a white or white-blotched head. This is also true of *yucatana* and in occasional specimens of *mexicana, T. c. bauri x major* and *T. c. major x triunguis.* The speckled head of *coahuila* is close to the white-blotching. All three of the forms *major, yucatana,* and *coahuila* are presumed close relatives of *putnami,* and I have suggested (Milstead, 1967) that the white markings may have been a *putnami* characteristic. Another color character of *putnami* may be the "fire-marked" examples of *major, mexicana,* and *yucatana.* All three subspecies live in areas subject to fire, usually by the deliberate burning of the habitat by man. Many specimens have fire scars on the scutes, and a number of these turtles have a color pattern of yellowish horn invaded to varying degrees by melanistic blotches. This color pattern has been generally attributed to fire, but I am not fully convinced of it. Some specimens that have the color have no other signs by fire, while others with fire scars on the scutes lack the color. Although my data are far from adequate, I have the impression that the "fire-marked" pattern may start, in young turtles having the proper genetic alleles, as horn or straw-colored scutes with dark borders and that the melanin increases with age. If this is so, the variation is considerable, because some specimens retain the light-colored scutes with dark borders throughout life, while others become partly to completely melanistic.

VERTICAL DISTRIBUTION: — As noted previously I interpret *major* as being a modified *putnami* extended into Recent times. This is essentially the interpretation first proposed by Auffenberg (1958). For the present epoch at least, this interpretation provides an absolute means of identification: if a turtle in question is fossil, it is either *putnami* or *putnami* x^t *major;* if it is not fossil, it is *major.* The distinction between *putnami* and *putnami* x^t *major* is, as noted above, a question that cannot be resolved on the basis of present material.

The range of *putnami* must have been greatly modified and remodified by the changing conditions of the Pleistocene. During each glacial stage *putnami* moved southward in the midwest because of cooler temperatures, westward across Texas because of additional territory made available by increasing humidity, and seaward around the Gulf Coast to take advantage of the coastal plain exposed by lower sea levels. Reversals in these movements took place with reversed physical conditions during the interglacial periods. Following the Wisconsin glaciation, rising sea levels and increasing aridity to the west gradually restricted *putnami* to the present range of *major*. The factors that caused the retreat of *putnami* also permitted the range extensions of *bauri* northwestward and *triunguis* eastward. Any relict populations left by *putnami* in suitable areas were swamped by the two advancing subspecies, and eventually the influences of *bauri* and *triunguis*, and also of *carolina*, modified the characters of *putnami* into those of *major*. If the climatic and biological factors that caused the extirpation of *putnami* continue in the same directions, it may be prophesied that *major* will be swamped at some future time leaving only three-way intergrade populations of *bauri*, *carolina*, and *triunguis*.

If the description of *major* is compared with that of *putnami*, it will be found that most of the characters of *major* are those of *putnami*, and that a number of them are unchanged (e.g., axillary scale and shape). The influence of *bauri*, *carolina*, and *triunguis* on the characters of *putnami* has produced in *major*: smaller size (300 mm to 200 mm), increased curvature radius of marginals (14.6 mm to 15.8 mm), increased intergular seam ratio (38% to 45%), decreased interhumeral seam ratio (30% to 29%), decreased interpectoral seam ratio (30% to 26%), possibly an increase in the length of the anterior lobe in relation to the length of the posterior lobe (? to 66%), and the expression of the color patterns of *bauri*, *carolina*, and *triunguis*. All the quantitative differences may become more emphasized when a series of "pure" *putnami* becomes available.

SPECIMENS EXAMINED

23. M. *T. c. major*. Austroriparian biotic province of Dice (1943): 59 specimens from Calhoun, Franklin, Gulf, Leon, Liberty, and Wakulla counties, Florida. Most of the specimens in this sample have been cited previously (Milstead, 1967, population H). The only additions to the sample were two untagged specimens at Florida State University and one specimen (1903.8.25.3) in the British Museum.

Terrapene carolina bauri Taylor

Figures 7, 8, Table 2 (16B, 17B)

Terrapene bauri Taylor, 1895. Proc. U.S. Nat. Mus., 17:576.
Terrapene carolina bauri Carr, 1940, Univ. Fla. Publ., 3 (1):100.
Terrapene innoxia Hay, 1916, Florida State Geol. Surv., 8th ann. rept. :39-76.

RECOGNITION FEATURES: — Two or more of the plastral ratios of *T. C. bauri* shown in Tables 1 and 2 (16B and 17B) distinguish it from each of the other members of the species. The shape of bauri in lateral view (Figure 2 F) also separates it from all other members of the species. The presence of three toes on each hind foot further distinguishes it from *carolina, major,* and *yucatana,* the concave plastron of males (Figure 7 D) from *mexicana, triunguis,* and *yucatana;* and its small size from *major, putnami, mexicana,* and *yucatana.*

PRESENT DISTRIBUTION: — eastern half of peninsular Florida (Figure 1). Intergradation (discussed below) occurs with *carolina* in eastern Georgia and northeastern Florida, and with *major* in the western half of the Florida peninsula.

GENERAL DESCRIPTION: — a small to medium-sized box turtle (Table 2) elongate in shape, and with a highly vaulted carapace posteriorly. In median saggital section the highest point of the carapace is seen on the posterior part of the third central scute (Figures 2 F; 7). The greatest width of the carapace also occurs at the third central (Figure 7 D). The greatest height and the greatest width occurring together well behind both the bridge and the mid-point of the carapace give an overall impression of a turtle with its bulk badly skewed to the rear. This is the most noticeable feature of the subspecies. Occasionally a hump appears on the 5th central scute (Figure 7 A, F) as in *major* (Figure 2 G). The posterior lobe of the plastron of males has a deep concavity (Figure 7, D) to harbor the carapace of the female during copulation. The postorbital bar is narrow, cartilaginous, or absent; toes number 3 on both hind feet of 10 out of 12 specimens on which the toes were counted; axillary scale usually absent (Table 2, 16B and 17B); 1st central scute infrequently straight-sided. Auffenberg (1958, 1967) has considered a straight-sided 1st central scute to be a characteristic of *bauri,* but this is due to a slightly different interpretation of the subspecies. As it emerges from this study, *bauri* is much more restricted in range than previously thought, and I interpret most of

Auffenberg's *bauri* as actually being *bauri x major*. Thus, the straight-sided 1st central becomes a character of *bauri* intergrades, particularly intergrades with *major* (Table 2, cf. *bauri* populations 16 and 17 with intergrade populations 15 and 18-22). The posterior marginals are more flared than in *carolina* and have developed to some extent the recurving or guttering of the greatly flared marginals of *major* (Figure 7). At times there may be a lateral keel above the bridge.

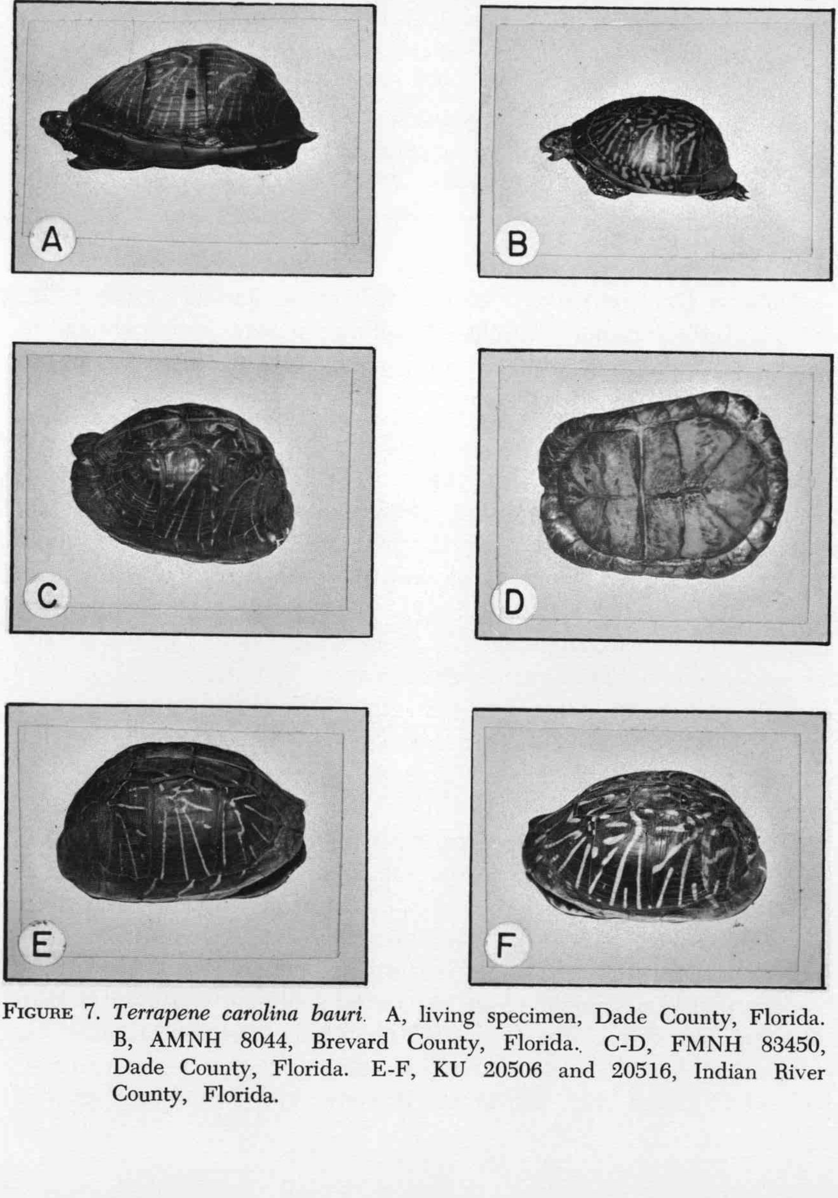


FIGURE 7. *Terrapene carolina bauri*. A, living specimen, Dade County, Florida. B, AMNH 8044, Brevard County, Florida. C-D, FMNH 83450, Dade County, Florida. E-F, KU 20506 and 20516, Indian River County, Florida.

The color pattern of *T. c. bauri* is another distinctive feature of the subspecies, but as in *carolina,* it cannot be relied upon. Some specimens of major and almost all of the *bauri* intergrades have the pattern, and very similar patterns occur infrequently in *carolina* and *triunguis.* The *T. c. bauri* pattern consists of long, thin, radiating, light (cream to yellow) lines on a dark (olive-drab to grayish or brownish black) ground color (Figure 7). The lines usually, but not always, have distinct borders and are rarely broken into spots.

VERTICAL DISTRIBUTION AND INTERGRADATION: — Auffenberg (1958, 1959, 1967) has advanced the thesis that *T. c. bauri* evolved from *carolina-putnami* intergrades that became isolated sometime in the Pleistocene. An alternative would be to consider *bauri* a third subspecies already existing in the Florida peninsula at the beginning of the Pleistocene. The only evidence to support the hypothesis of a third subspecies are a few morphological features of *bauri* not found in *carolina* or *putnami,* and differences in behavior patterns (L.T. Evans, pers. comm.). All of these can be attributed to the isolation necessary in Auffenberg's intergradation thesis, however, and Auffenberg's thesis also avoids the problem of defining the geographic range of a pre-Pleistocene *bauri.* As I understand it, sea levels at the end of the Pliocene were higher than they have been since, and most of Florida spent the Pliocene under water. The Florida peninsula first emerged during the Nebraskan glacial stage, was inundated again during the Aftonian interglacial, emerged again during the Kansan glacial, and was inudated for the last time during the Yarmouthian interglacial. Sangamon sea levels are presumed to have been only slightly higher than they are at present.

In Auffenberg's thesis, both *T. c. carolina* and *T. c. putnami* reached Florida about the same time and intergraded much as *bauri, carolina* and *major* do today. Rising sea levels following the first or second glacial stage isolated a population of these intergrades on one or more islands where the Florida peninsula is today. The *bauri* characteristics began to develop during this isolation. Lowering sea levels at a later date reunited the island(s) with the mainland and brought "*bauri*" into contact first with *putnami* and then with *carolina.* The order of contact is based on the reasoning that *putnami* occupied coastal marshes on the mainland, *carolina* occupied upland forests to the north, coastal marshes were the first box turtle habitats to move onto the emerging zone between the mainland and the old island, and the upland forest habitat (and *carolina*) did not appear until much later. The rising of the sea following the maximum extent of the glacier again brought the coastal marshes and *putnami* into contact with "*bauri*". Following this, there may have been a second isolation of "*bauri*" that brought a greater refining of the *bauri* characteristics. At present, we have no information on whether there were one or two isolations, but by the end of the Sangamon interglacial (approximate age of Haile VIII A), the characteristics of *bauri* had developed to the point that fossils from that time can be identified as *T. c. bauri* with only minor reservations (see below).

The modern *bauri* appears to be a mixture of *carolina*, *putnami*, and new (*bauri*) characteristics, and can be analyzed accordingly:

carolina characteristics: small size, lack of axillary scale, reduced postorbital bar.
putnami characteristics: elongate shape, flaring marginals.
bauri characteristics: "humping" of the shell, narrow skull, three toes on hind feet (number of toes in *putnami* unknown), plastral ratios intermediate between those of *carolina* and *putnami*, and straight-sided first central scute (although this is now gone from living *bauri*, it persists in intergrades with *carolina* and *major*).

The influence of *carolina* on the evolution of *bauri* was probably very slight after the initial intergradation with *putnami* and the first isolation. The influence of *putnami*, on the other hand, must have been much more significant because of the more frequent contact between *putnami* and *bauri*.

We have very little fossil evidence for the evolution of Florida box turtles during the first half of the Pleistocene. Like *putnami* and *carolina*, *bauri* first appears in the fossil record fully developed with no real clue to its origin. The pre-Rancholabrean fossils from Florida consist of one specimen of *carolina* and several specimens of *putnami*. An Illinoian site in Citrus County has yielded intergrades between *putnami* and *carolina* with no apparent traces of *bauri* characteristics. The lack of *bauri* evidence in these fossils, and the fact that *bauri* appeared fully developed in the next interglacial stage, seem to question Auffenberg's thesis on the origin of *bauri*. It should be noted, though, that Citrus County is located in the northern half of the west coast of Florida, and the turtles found there may not have been in contact with *bauri*-like turtles. That *bauri* was developing in southeastern Florida during Illinoian times as the result of an earlier intergradation between *putnami* and *carolina* does not exclude the possibility that *carolina* and *putnami* could continue to intergrade elsewhere independently of *bauri*.

Nothing presented in the preceding four paragraphs really eliminates the possibility that *bauri* was a third subspecies existing on an island in the Gulf of Mexico prior to the beginning of the Pliocene. It is hoped that fossil material that will provide a solution to the problem will be found eventually.

Most of the fossil finds from Rancholabrean deposits in Florida have consisted of one or a few specimens and are useful only in a limited way, with two notable exceptions: a large series of fossils from the Reddick IB site, Marion County, Florida (Auffenberg, 1958, 1959), which lend themselves to statistical analyses; and a smaller series of fossils continuous through three zones of deposition at the Haile VIII A site, Alachua County, Florida (Auffenberg, 1967).

The Reddick IB specimens originally presumed to be of Illinoian age (Auffenberg 1958, 1959), but now thought to be of Sangamon age (Auffenberg, 1967), are of turtles intermediate between *putnami* and *bauri*. In general the shape of the turtles is like that of *putnami*, but with a distinct skewing of the bulk posteriorly as in *bauri*. The intergular and interhumeral seam ratios are like those of *putnami*, and the carapace length is intermediate (Table 4, 85PB). Auffenberg (1958) gives the curvature radius of the marginals as intermediate (23.6mm) and notes that the axillary scale and first central scute are variable. The single skull found at the site is also considered intermediate (Auffenberg, 1959). At present I identify the Reddick IB specimens as horizontal intergrades, *T. c. putnami x bauri*. The obvious *putnami* characters in the Reddick IB turtles do not, however, demand the presence of *putnami*. The environment, presumed to have been a hibernaculum in a near-*putnami*-type habitat, may have been selecting for *putnami* traits in *T. c. bauri*. Should this prove to be the case, the specimens should be designated *T. c. bauri* x^{t} *putnami*.

The earliest record of *bauri* was found in Sangamon deposits at Haile VIII A in Alachua County, Florida. The site is of further interest in that it shows intergradation and replacement of *bauri* by *putnami* through successive stages of deposition. Auffenberg (1967) describes the site as an old sinkhole with four distinct zones of deposition above the rubble of the old cave roof. Turtle remains have been found in the top three zones. The lowermost of these, the sand zone, contains specimens that are almost identical to the modern *T. c. bauri*, the uppermost (upper red clay) zone contains specimens almost identical to *putnami*, and the middle (lower red clay) layer contains specimens of intermediate forms. Too few specimens are available for a statistical analysis of any of the characters, but by the

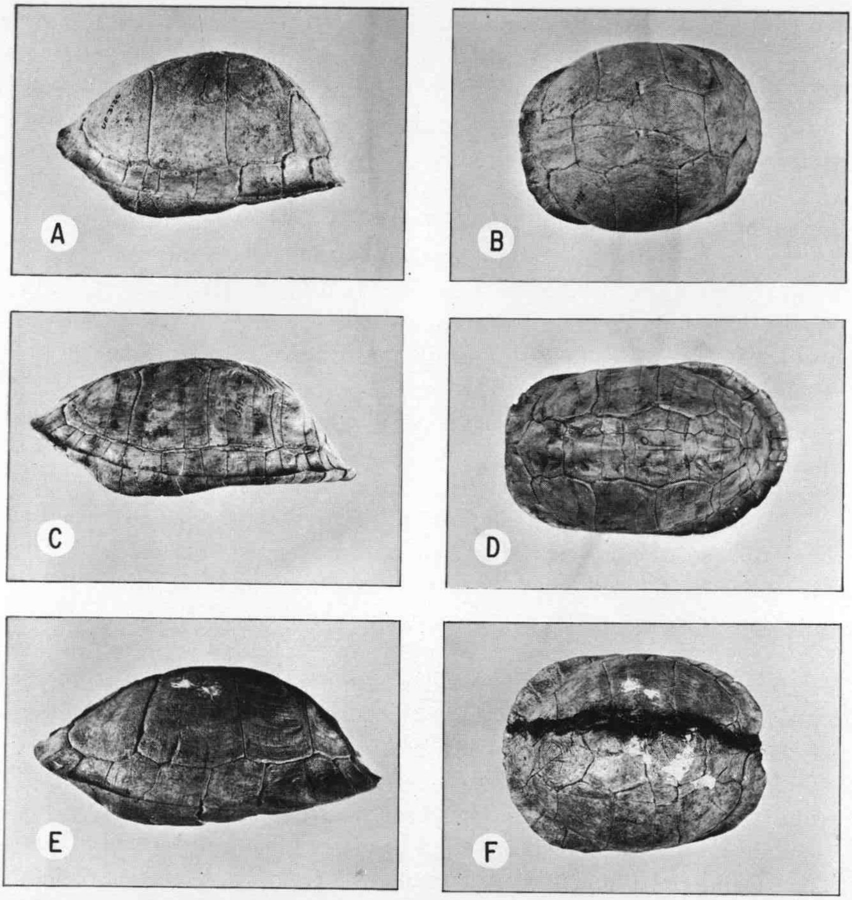


FIGURE 8. Fossils from Haile VIII A, Alachua County, Florida. A-B, *Terrapene carolina bauri* (with a *T. c. putnami* influence) UF 3136, Sand Zone. C-D, *T. c. putnami x bauri*, UF 3150, lower red zone. E-F, *T. c. putnami* (with a *T. c. bauri* influence), UF 3130, upper red zone. Courtesy of Florida State Museum.

size and shape of the carapaces and the degree of flare of the marginals, I tentatively identify the turtles as: sand zone, *T. c. bauri* with some influence of *putnami;* upper red zone, *T. c. putnami* with some influence of *bauri;* and lower red zone, *T. c. bauri x putnami.* Examples of all three forms are shown in Figure 8. Auffenberg interprets the sequence of events (rightly, I think) as a *bauri* habitat changing to a *putnami* habitat through the influence of rising sea levels prior to the Sangamon maximum. At the time the sand zone was deposited, the area was a *bauri*-type habitat occupied by *bauri.*

At the time the lower red zone was deposited, the habitat had changed to an ecotone between *bauri* and *putnami* habitats and had brought *putnami* in to intergrate with *bauri*. By the time the upper red zone was deposited, the habitat had changed to a *putnami* type, and *bauri* had retreated to higher ground, leaving the area to *putnami*. Auffenberg has long contended that *putnami* and *bauri* periodically replaced each other as habitats changed with rising and falling sea levels throughout the Pleistocene, and this idea is the basis for the suggested evolution of *bauri* given above. Other sequences of succession, both *putnami* to *bauri* and vice versa, have been given by Auffenberg (1958, 1967) for other fossil specimens from Sangamon and Wisconsin deposits in Florida. None of these is as good as the Haile VIII A example because the sequences are not complete and the ages of the deposits are not fully correlated.

Before leaving the Haile VIII A specimens, it should be pointed out, as it was for the Reddick IB specimens, that the presence of putnami is not mandatory. The change from *bauri* to *putnami* could have taken place through selection of *putnami* characteristics in the gene pool of *bauri*. In this case, the lower-red-zone intermediates should be designated *T. c. bauri* x^t *putnami*.

PRESENT INTERGRADATION: — Sample 15CB represents an intergrade population between *T. c. carolina* and *T. c. bauri*. Some specimens in the sample have the color pattern of *carolina*, some have the pattern of *bauri*, some have an intermediate pattern, and two specimens have patterns similar to *triunguis*. Shapes in the sample are *carolina*-like, *bauri*-like, or intermediate. The intergular and interhumeral seam ratios (Table 2) are intermediate. In 15 specimens 11 have three toes on each hind foot, and 4 have four toes. A straight-sided 1st central scute is more frequently present in the intergrade population than it is in either *carolina* or *bauri* (Table 2).

Samples 18BM-22BM represent intergrade populations between *T. c. bauri* and *T. c. major* (Figure 9 A-C, Table 2). All specimens in all these samples have the coloration of *bauri*. Sample 21BM has a shape intermediate between *bauri* and *major;* samples 18BM and 21BM have intermediate shapes, but are closer to *bauri*. Some specimens in each sample have three toes on each hind foot, while others have four. Occasional specimens have three toes on one foot and four on the other. In Sample 21BM the number of specimens with three toes and the number with four toes are about equal, but three toes predominates (greater than 70%) in all of the other

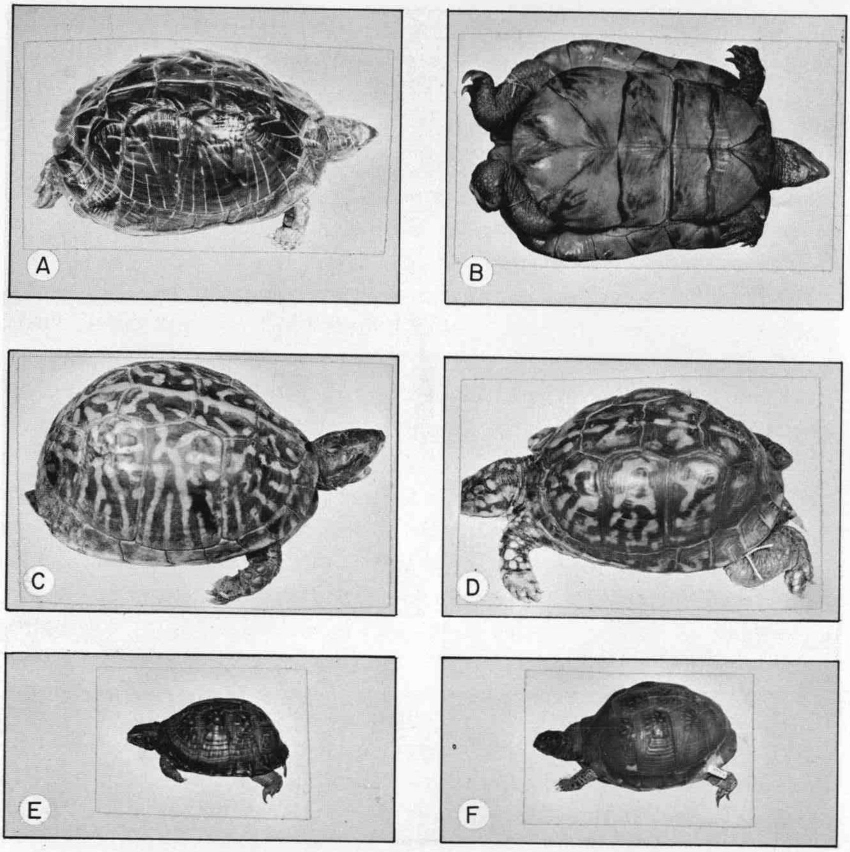


FIGURE 9. Some Recent *Terrapene carolina* intergrades. A-B, *T. c. bauri x major,* UF 8619, Big Pine Key, Monroe County, Florida. C, *T. c. bauri x major,* UF 972, Alachua County, Florida. D, *T. c. carolina x major x triunguis,* UF 4444, Bibb County, Georgia. E, *T. c. carolina x major x triunguis,* AMNH 29883, Thomas County, Georgia. F, *T. c. carolina x triunguis,* FMNH 83417, Crawford County, Indiana.

samples. The ratio between the anterior and posterior lobes (Table 2) is like *major* in sample 20BM, and like *bauri* in the other samples. The intergular ratio (Table 2) is intermediate between *bauri* and *major* in sample 20BM, like *bauri* in 21BM, and like *putnami* (as now known) in 18BM, 19BM, and 22BM. In samples 18BM, 19BM, and 21BM, an enlarged axillary scale is more frequently present than in *bauri* (Table 2). A straight-sided 1st central scute is more frequently present in all of the intergrade samples than it is in either *bauri* or *major* (Table 2).

RECENT SPECIMENS EXAMINED. — All are from the Austroriparian biotic province of Dice (1943).

15CB. *T. c. carolina x bauri.* 16 specimens from Atkinson, Charlton, and Ware Counties, Georgia, and Bradford, Clay, Duval, Flagler, Nassau, and St. John's counties, Florida: UF 4432, 7537, 9704, 9881-2, 10945, 12012, 14666-7, 14672, 41638, 47912; UCM 2193; UMMZ 67811, 81145, 106327.

16B. *T. c. bauri.* 27 specimens from Brevard, Indian River, Orange, and Osceola counties, Florida: AMNH 5928-30, 8044-5, 66094, 66107; UF 6822, 9000, 47143; KU 17367, 18348, 19738-9, 19741, 20506, 20508-18.

17B. *T. c. bauri.* 18 specimens from Dade, Martin, and Palm Beach counties, Florida: FMNH 83449-50; UF 390, 390 (A-E), 6604, 9575; KU 46814, 46827; TCW 8984; UMMZ 53231-2, 53294, 110682-3.

18BM. *T. c. bauri x major.* 11 specimens from Monroe County, Florida, mostly from the keys: UF 7101-3, 8619-20; MCZ 7393, 26768-9; UMMZ 107223-4, 111425.

19BM. *T. c. bauri x major.* 9 specimens from Charlotte, DeSoto, Glades, Highlands, Lee, and Sarasota counties, Florida: AMNH 65623; BMNH 1957.1.5.76, 1957.1.5.78; FMNH 83448; UF 586, 921, 4164, 8617, 11121.

20BM. *T. c. bauri x major.* 12 specimens from Hillsborough and Pinellas Counties, Florida: BMNH 1897.10.15.1-3; UF 6514-5; KU 48249; UMMZ 61738-42; and one unnumbered specimen at Florida State University.

21BM. *T. c. bauri x major.* There may be an influence of *T. c. carolina* in this sample. 36 specimens from Alachua and Marion counties, Florida: AMNH 8284-6; ANSP 21524; UF no number A-D, 537, 965, T972, 3328, 5210-11, 6512-13, 14117, 14266, 38050, 44264, 45400; KU 46811-13, 46815, 46817-18, 46820-1, 6824-6, 46828-30; UMMZ 52475.

22BM. *T. c. bauri x major.* There may be an influence of *T. c. carolina* in this sample. 7 specimens from Citrus, Dixie, Lafayette, and Levy counties, Florida; UF 7449, 9657, 11122, 14128, 14669; KU 46823, 46826.

FOSSIL SPECIMENS EXAMINED

85PB. *T. c. putnami x bauri.* 31 specimens of Sangamon Interglacial age from the Reddick IB site, Alachua County, Florida. The specimens examined consisted of 2 complete carapaces and fragments of others, 20 anterior plastral lobes, and 16 posterior plastral lobes. The average carapace length for this sample given in Table 4 (154 mm) is a repetition of Auffenberg's (1958) figure rather than an average of the lengths of the two carapaces seen (142 and 168 mm). The anterior lobe ratio (anterior plastral lobe/posterior plastral lobe) given in Table 4 is based on five complete plastra found intact. The other plastral ratios are based on N=20 for the anterior lobe and N=16 for the posterior lobe. The specimens include: UF 1462-3, 1476, 2060, 2060 A-C, 2061, 2063, 2179, 2333, 2339, 2913, 2915, 4266, 4747, 5697, 5699-700, 6101, 6137, 6600, 7041 A-E, 7041 G-I, 9972. Other specimens include those from the Haile VIII A site and all UF and USNM specimens from Sangamon and Wisconsin deposits of Florida cited by Auffenberg (1958, 1959, 1967).

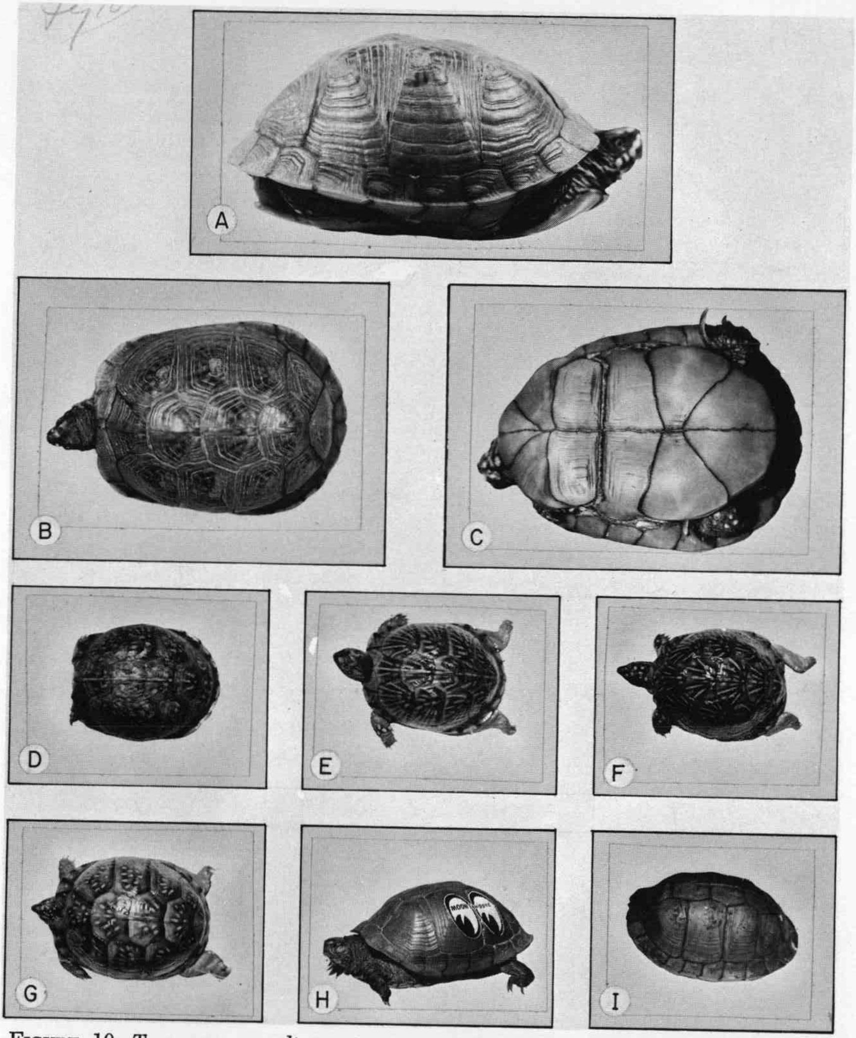


FIGURE 10. *Terrapene carolina triunguis*. A-C, living specimen, Bryan County, Oklahoma. D, UT 7456, Byran County, Oklahoma. E, UT 6539, Jefferson County, Texas. F, UT 8838, Angelina County, Texas. G, UT 8839, Robertson County, Texas. H, living specimen, Morgan County, Missouri, I, KU 23351, Cherokee County, Kansas.

Terrapene carolina triunguis (Agassiz)

Figures 10-11, Table 2 (31-44)

Cistudo triunguis Agassiz, 1857, Contrib. Nat. Hist. U.S., 1:445.
Terrapene carolina triunguis Strecker, 1910, Proc. Biol. Soc. Wash., 23:121.
Cistudo marnocki Cope, 1878, Proc. Am. Phil. Soc., 17:229, part.

Terrapene whitneyi Hay, 1916, Bull. Univ. Texas, 71:1-24.
Terrapene bulverda Hay, 1921, Proc. U.S. Natl. Mus., 58:83-146.
Terrapene impressa Hay, 1924, Publ. Carnegie Instit. Wash., (322A):245.
Terrapene llanensis Oelrich, 1953, Copeia, (1):33-8, part.
Terrapene canaliculata Milstead, 1956, Copeia, (3):162-171, part.

RECOGNITION FEATURES: – One or more of the plastral ratios of *T. c. triunguis* shown in Tables 1 and 2 distinguish it from each of the other members of the species. The shape of *triunguis* in lateral view (Figure 2H) separates it from all members of the species except *mexicana* and *yucatana*, and the shape in cross-section through the posterior part of the 4th central from *mexicana* and *yucatana* (Figure 2H, I, J). The presence of three toes on each hind foot further distinguishes *triunguis* from *carolina, major* and *yucatana;* the smooth or only slightly concave plastron of males from *bauri, carolina, major,* and *putnami;* and the small size from *major, mexicana, putnami,* and *yucatana.* Jackson and Legendre (1967) have shown a higher level of blood serum cholesterol in *major* than in *triunguis,* but additional studies are needed to determine the usefulness of this observation as a taxonomic character. The number of specimens they examined was very small, and there is some evidence that the differences may be dietary rather than hereditary. The carnivorous species they studied, for example, had higher cholesterol levels than the vegetarian or omnivorous species. Thus, the higher cholesterol level of *major* may be due simply to a higher percentage of animal foods in its diet.

PRESENT DISTRIBUTION: – West of the Mississippi River from central and southeast Texas northward into Wisconsin (Figure 1). Intergradation (discussed below) is with *carolina* along the Mississippi River roughly from central Mississippi northward to the Ohio River; with *major* along the Gulf coast from central Louisiana to Florida; and simultaneously with *carolina* and *major* in southeastern Alabama and southwestern Georgia.

GENERAL DESCRIPTION: – the smallest of the *carolina* box turtles in the southwestern part of its range, but increasing in size northeastward to attain the size of *carolina* and *bauri* (Table 2). The carapace is elongated and highly vaulted, both anteriorly and posteriorly, and with the 3rd central scute elevated to form a small hump (Figures 2H, I; 10A, H). The plastron of males is smooth or has only a shallow concavity in the posterior lobe (Figure 10C, cf. 4D). The postorbital bar is narrow, cartilaginous, or absent. Of 101 specimens on which the toes were counted, 94 had three toes on each hind foot, 3 had four toes, and 4 had three toes on one hind foot and four on the other. The presence of an enlarged axillary scale is variable. In some samples the frequency of occurrence of the enlarged axillary scale approaches that of *T. c. major* (e.g. Table 2, 36T-38T), but in most samples the frequency is intermediate between *T. c. major* and *T. c. carolina*. The first central scute is also variable, but is generally something other than straight-sided (Table 2). The posterior marginal scutes are similar to *T. c. bauri* in their degree of flaring (i.e., intermediate between *carolina* and *major*). A lateral keel above the bridge may be present. The plastral ratios of *T. c. triunguis* are given in Table 2 (31-44).

The coloration of *T. c. triunguis* is highly variable, but three types of pattern predominate throughout the geographic range. The generic pattern of radiating light lines is present in many individuals, although the lines may be broken into series of dashes or dots (Figure 10A, B, D-G). Frequently each light line is bordered by a dark line (Figure 10E, F), and in occasional individuals the light lines may be faint or lacking altogether. The latter situation results in a color pattern of radiating dark lines. This type of pattern is of more frequent occurrence in *mexicana* than in *triunguis*. The ground color of *triunguis* in both light-and-dark striped individuals is straw color to horn color, most frequently the latter. The third type of predominant color pattern in *triunguis* is the loss of both light and dark stripes to produce a turtle that is a uniform horn color (Figure 10H, I). The color pattern in *triunguis* appears to be genetically based and dependent upon several pairs of factors. Some turtles of all ages including yearlings have the uniform coloration, others of all ages have the lines, and still others have varying degrees of light lines, dark lines, and uniform coloration intermixed (Figure 10A, B).

The reduced concavity in the posterior lobe of the plastron in males of *T. c. triunguis* and the development of the hump on the 3rd central scute of the carapace are interesting in that they may provide an example of "complementarity of structure and function" as related to behavior. In observed matings of box turtles, a male of *T. carolina carolina, T. carolina major*, or *T. coahuila* mounts the female with the posterior part of her shell fitting into the concavity in his plastron, while in *T. carolina triunguis* the male has his main shell axis reclined away from the female and lies on the posterior part of his carapace supported by the hump on the third central scute. Legler (1960) in discussing mating in *T. ornata ornata*, which lacks both a plastral concavity and a carapacial hump, has noted that the male angles backwards away from the female supported by his hind legs, and that the stress on the legs is so great that the male may be incapable of walking following copulation. Auffenberg (pers. com.) has observed similar behavior in *T. c. bauri* and *T. c. major*.

Other noteworthy features of *triunguis* are the differences between the samples from the southern part of the range and those from the northern part. Although it does not form a consistent cline, an overall increase in size and bulk extends from Texas to Missouri. The carapace lengths that reflect these increases are shown in Table 2, but it should be noted that the increases are not directly proportionate to carapace length. The turtles from Missouri are much more massive and as a result are slightly differently shaped than turtles from central Texas (Figure 10, cf. A-G with H-I). The interhumeral seam ratios (Table 2) also show an inconsistent increase from south to north. Thus, as was the case in *T. c. carolina*, the turtles of one part of the range can be distinguished from those of another part of the range; but unlike *T. c. carolina*, the differences in *T. c. triunguis* can be related to the biotic provinces of Dice (1943). Nomenclatural recognition of the differences might be in order, but as in the case of *T. c. carolina*, I do not feel that the differences warrant recognition at the subspecific level. This again raises the question of the use of the tetranomial: *Terrapene carolina triunguis triunguis* for turtles from the Austrotiparian and Texan biotic provinces (Table 2, 30-37 and 39), and *T. c. triunguis kansensis* for turtles from the Carolinian and Illinoian provinces (Table 2, 38 and 40-44). For reasons previously given this is not proposed.

The differences between the samples of *T. c. carolina* from the northwestern part of its range, compared with these from the rest of the range were attributed to the possible influence of *triunguis* or *putnami*. In like manner the different morphology of *triunguis* in the northern part of its range may be attributed to the influence of *carolina* or of *putnami*, but the differences in size merit further consideration. Despite Lindsey's (1966) conclusion that nonmarine turtles show no latitudinal trend in size, both *T. c. carolina* and *T. c. triunguis* reach their greatest size in the northern parts of their range. This may be a lingering influence of *putnami*, but even so, it would have to be maintained by selection, and the end result is that both subspecies exhibit Bergman's rule for homoiothermic animals. Tinkle

(1961) has found similar north-south size relationships in *Sternothaerus.*

From these and other examples and from the simple experiment of placing turtles of different sizes in a refrigerator, it seems advantageous for a turtle to be large in the colder part of its range. But, if this is so, why did *triunguis* in the north become reduced in size from *putnami* by nearly two thirds, while *major* in the south became reduced by only one third? Apparently, a turtle must be large enough to survive winter cold, but small enough to recover rapidly in the spring and on warm days during the winter. The giant *putnami* developed in pre-Quaternary times under a warm maritime climate that had no extremes of cold or heat such as those found in the continental climates of today. Under those pre-Quaternary conditions, it might have been advantageous for a turtle to be large, because it would respond slowly to temperature changes between day and night, and this would produce a relatively constant body temperature for efficient metabolism.

In developing from *putnami, triunguis* had to reduce its body size to utilize heat better for recovery following modern winters. The average carapace length of *triunguis* is 127 mm in western Missouri and eastern Kansas, and 116-117 mm in southwestrn Louisiana and southeastern Texas. Winters in the northern area are severe with few warm days, and spring does not come until late April, while winters in the southern area are mild with frequent periods of warm days, and spring comes in late February or early March. I consider the larger size of the northern turtles to be advantageous for survival in the northern winters, while the smaller size of the southern turtles is advantageous for rapid recovery from cold in order to utilize the warm winter and early spring days.

The large size of *major,* which occupies a more southern and warmer area than *triunguis* in southern Texas and Louisiana, is the stumbling block in the theory: *major* should be smaller than *triunguis.* However *major* is a direct descendent of *putnami,* occupies the last *putnami*-type habitat available, and probably was not subjected at any time during the Pleistocene to such rigorous climatic changes as influenced the evolution of the box turtles in the midwest. The relatively large sizes of *mexicana* and *yucatana* support this argument in that they are closely related to both *triunguis* and *putnami* and are distributed to the south of *triunguis.* The reduction in size from *putnami* to *major* was attributed earlier (see discussion of *T. c. major*) to the influence of smaller subspecies, but may be due to selection for smaller size in response to the cooler modern climates and the need to recover following cold days.

A crude attempt to test some of the theories presented in the preceding paragraph was undertaken in the winters of 1962-63 and 1965-66. A dozen box turtles ranging in size from 80 mm to 180 mm carapace length were kept in an outside pen at the University of Missouri-Kansas City. The nine smallest turtles were *Terrapene carolina triunguis* and *Terrapene ornata ornata* from the Kansas City area, and the three largest ones were *Terrapene carolina major* from Bay County, Florida. In both tests the turtles were introduced into the pen during the fall and provided with food and water, and with piles of leaves to serve as shelters in the fall and hibernacula in the winter. At the outset it was predicted that (1) the Florida turtles would survive in spite of the severe winters because of their large size; (2) if any turtles should die, they would be the smaller, local turtles; and (3) the first turtles to appear in the spring or on warm days in winter would be the smaller, local turtles.

The first test in 1962-63 was something of a failure because of an unforeseen circumstance. The winter was severe and no turtles were seen on the surface after the middle of November. When no turtles had appeared on the surface by mid-May, the leaves were removed. All of the turtles were not only alive, but also active and fat, presumably from feeding on a rich aggregation of earthworms that had accumulated under the leaves. Apparently the turtles had not appeared on the surface because they had no physiological reason to do so.

The 1965-66 test produced better results. The winter was unusually mild with many warm, sunny days. On most of the warm days the smaller turtles, including the smallest *major* with a carapace length of 141 mm, appeared on the surface, but the two largest turtles were not seen until spring. With the onset of the first cold weather, all of the turtles maintained a body temperature (measured by a Yellow Springs Instrument Co. telethermometer through thermistor probes in the turtles' coeloms) several degrees higher than the environmental temperature (measured by thermistor probes taped to the turtles' carapace surfaces) for over a week. On two occasions measurements were taken through sequences of a cold day (0° C or below) one or two cool days, two or three warm days, a cool day, etc. In both cases the smaller turtles showed increases in body temperatures and became active on the warm days, while the two largest turtles showed no increase in temperatures and remained in-active. Thus although the data are too incomplete and are based on too small a sample both in numbers of turtles and in conditions, they indicate that predictions 1 and 3 above and the theories expressed in the preceding paragraph are worthy of further study.

Selection for size both during the Pleistocene and at the present time is probably not a single-factor selection, such as the ability both to survive and recover from cold. Tinkle (1961) in considering the larger average size of northern *Sternothaerus* populations suggests that it is advantageous for populations in cold regions to produce more offspring in order to insure that some of them survive, and that the only way a turtle can produce more eggs is by increasing the size of its encasing armor. I think this may be an important factor.

Auffenberg (1964) shows decreases in size of the tortoise genera *Geochelone* and *Gopherus* in North America through the Pleistocene, and suggests that the extirpation of *Geochelone* was due to the fact that it did not learn to dig holes as did *Gopherus*. Box turtles in the midwest are about the size of the smallest *Gopherus (G. berlandieri)*, and they either dig holes or hibernate in piles of leaves and debris, in caves, holes of other animals, or crevices. In this respect a smaller turtle would be expected to have a wider selection of hibernacula, and perhaps deeper and/or better insulated hibernacula than would a larger turtle.

Another important factor in the size-temperature relationship is availability of food and efficiency of metabolism, particularly in relation to warm days in winter. Townsend (1931) and Hibbard (1960) have discussed the plight of giant Galapagoes Island tortoises that survived cold winter nights in the United States from temperature as a direct effect, but died of gastritis from fermentation of foods eaten during the day and not properly digested during the cold-induced lower metabolism at night. In both this case and the case cited above where two large Florida turtles failed to show an increase in temperature on warm winter days, the effect of the cold is presumed to be cumulative in much the same way that an unheated building becomes progressively colder through the winter. Gastritis would most likely have occurred in the giant tortoises through an accumulation of food residues resulting from progressively poorer metabolism which in turn resulted from progressively lower body temperatures.

This provides another suggestion to account for the large size of *major* in northwestern Florida and the small size of *triunguis* in southeastern Texas. Selection in southeastern Texas may demand a small turtle that can reach activity temperature quickly on warm winter or spring days, obtain a small but sufficient quantity of food in a short time, and metabolize that food rapidly enough to avoid problems of fermentation. Among other considerations still to be made are those of physiological adjustments in response to temperature. We are just beginning to understand some of these responses in relation to heat gain (see papers by Norris, Dawson, and Tucker and discussions of these papers and others in Milstead, 1967b), but our knowledge of physiological responses of poikilotherms to cold is sadly inadequate.

VERTICAL DISTRIBUTION: — *T. c. triunguis* is presumed to have evolved from a western population of *T. c. putnami* that became isolated sometime in the Pleistocene, through some such factor as the opening of the Mississippi River embayment caused by rising seas following a glacial stage. The evolution of *triunguis* appears to have taken place in a rather straight-line fashion without the reversals that punctuated the evolution of *bauri* and *major*. This was, at least in part, a function of the amount and location of the area involved. The evolution of *bauri* and the later evolution of *major* took place in relatively small geographic areas under climatic conditions that were relatively uniform, while the evolution of *triunguis* took place over a much larger area with more variable climates.

Some evidence suggests climatic conditions favorable for *putnami* existed in the midwest at times during the Pleistocene (Hibbard, 1960; Auffenberg and Milstead, 1965; Milstead, 1967), but little evidence that these conditions either brought about a reversal to *putnami* characteristics or a reinvasion of southeastern *putnami* into the midwest, although they may have had a "braking" effect on the development of *triunguis* characteristics. The *putnami-triunguis* intermediate forms undoubtedly did come into contact with both southeastern *putnami* and *carolina*, but the influence of the southeastern *putnami* was probably most important along the Gulf Coast, and the influence of *carolina* cannot be detected in the limited fossil material from the midwest.

Most of the fossil turtle finds in the central United States are, like the Florida finds, limited to one or two specimens with two notable exceptions, Ingleside and the Friesenhahn Cave (Milstead, 1956, 1959, 1967). The Ingleside locality, near Ingleside, San Patricio County, Texas, was originally dated at about 20,000 years

B.P., but it is now thought to be about 50 to 80 thousand years B.P. Remains of at least 12 box turtles have been taken from the deposits. At the time the turtles died the area may have been a coastal bog. The Friesenhahn Cave, near San Antonio, Bexar County, Texas, dated at 10 to 14 thousand years B.P., has yielded remains of at least 122 box turtles when these turtles died they were probably using the cave as a hibernaculum. The age of the Friesenhahn deposits and the quantity of turtle remains seem to make a good case for the old idea that the Wisconsin glaciation sent killing cold waves southward in front of the advancing ice. A more likely explanation is that the assemblage of fossil remains in the Friesenhahn Cave was, like assemblages of nonfossil remains found in modern hibernacula, accumulated at the rate of one, two, or a few per winter over many winters. Always disturbing when studying fossils is the fact that we are working with the minority that did not survive a given situation rather than the majority that did. The same discomfort can be carried over to Recent specimens in museums. Our so-called random samples represent the minority that were indiscrete enough to encounter a collector, except in the rare cases where all or most of a population was available and the collector did sample randomly.

The oldest known turtles that show characteristics of *triunguis* are from the Sangamon deposits in Kansas and Texas (MP 26957, UMMP 38367, MCZ 2170, and UT 30907-19B) and are identified as *Terrapene carolina putnami* x^t *triunguis* (Milstead, 1967). When good specimens are available from early Pleistocene deposits west of the Mississippi River, they may show that the evolution of *triunguis* actually began in the early Pleistocene, as did the evolution of *bauri*. At the present time no evidence exists for or against this possibility. The specimens from the early Pleistocene of Kansas and Texas tentatively referred to *putnami* (above and Milstead, 1967) consist of one complete anterior lobe of a plastron (UT 882-315) and carapacial and plastral fragments of several turtles. The characters of carapace shape, which are the most useful characters in distinguishing individual specimens of *putnami* and *putnami* x^t *triunguis*, are not available in these early fragments. As noted above, the fragments are tentatively identified as *putnami* solely on the basis of their size, although size alone does not eliminate the possibility that the fragments could be *putnami* x^t *triunguis*. In the evolution of *bauri*, small size became a character early in the fossil record, but in *triunguis* selection for small size did not approach completion until after the Wisconsin glaciation. When maximum lengths (either actual or calculated) are compared (Table 5) for specimens from west of the Mississippi River, it becomes apparent that maximum lengths remained fairly stable throughout the Pleistocene, though average lengths may have progressively decreased. Averages based on 5 carapaces, 11 anterior lobes of plastron, and

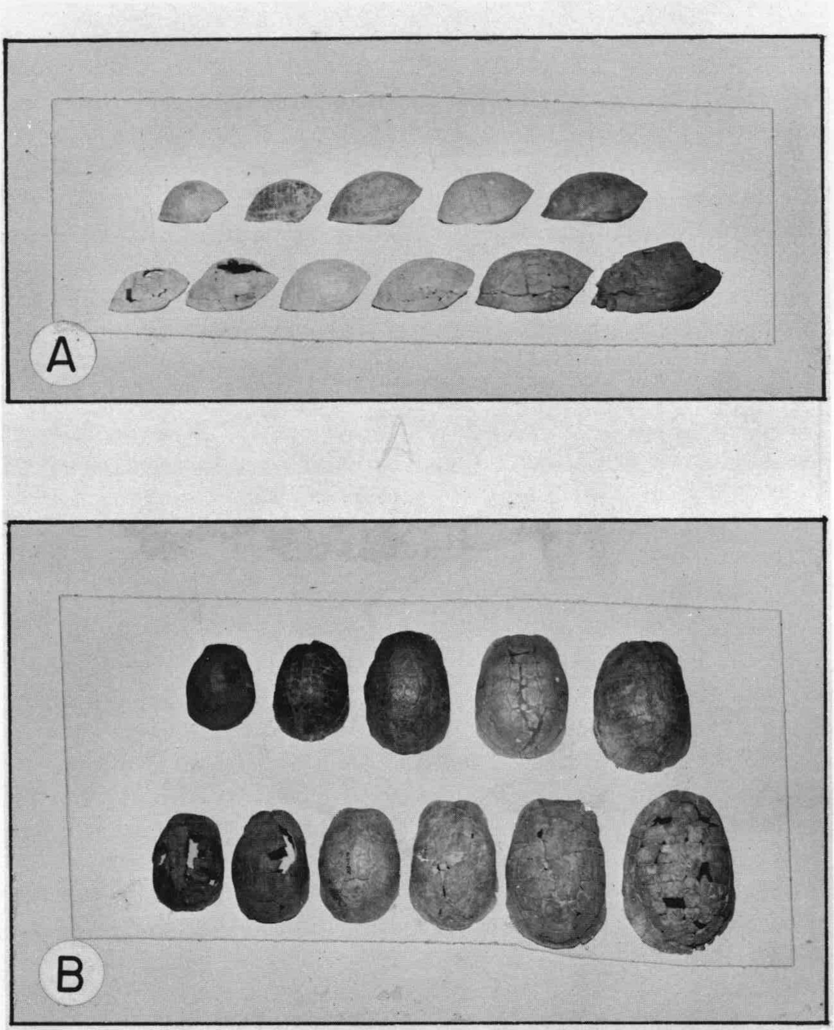


FIGURE 11. Fossils of *Terrapene carolina*. Upper row in both A and B, *T. c. putnami* x^{t} *triunguis*, Ingleside, San Patricio County, Texas. Lower row in both A and B, *T. c. triunguis* (with *T. c. putnami* influence), Friesenhahn Cave, Bexar County, Texas.

12 posterior lobes of plastron from the Ingleside locality (50-80 thousand years B.P.), and 25 carapaces, 122 anterior lobes, and 116 posterior lobes from the Friesenhahn Cave (10-14 thousand B.P.) show the following:

Ingleside:	174 mm	70 mm	95 mm
Friesenhahn:	163 mm	68 mm	92 mm

These measurements include all the turtles, both large and small from each locality. In Florida giant and small box turtles occur in different zones of deposition, particularly at Haile VIII A (above and Auffenberg, 1967), an important fact in the evolution of *bauri*. Of equal importance in the evolution of *triunguis* is the fact that no such size distinction is evident at either the Friesenhahn Cave or at Ingleside: giant and small turtles were found side by side in the various zones of deposition. The only evidence of possible *triunguis*-to-*putnami* reversals is the Spring Branch (Houston) specimen reported by McClure and Milstead (1967) taken near the Texas coast from deposits intermediate in age between the Ingleside and Friesenhahn deposits; it appears to be *triunguis* with no detectable influence of *putnami*. If additional Houston specimens indicate that "pure" *triunguis* existed prior to the Wisconsin maximum, at least a partial reversal would have been necessary to produce the Friesenhahn specimens. On the other hand, additional Houston specimens may show that most of the population now represented by one specimen did exhibit some *putnami* characteristics.

At the moment it seems best to suggest that three allelic combinations for size existed in Texas box turtles during the Wisconsin glaciation: one for "giants" the size of *putnami*, one for small turtles the size of modern Texas *triunguis*, and one for an intermediate form somewhat larger than modern Texas *triunguis*. All three existed at the time the Ingleside and Friesenhahn deposits were made (Figure 11), but in Recent times the giant form became extinct, the intermediate form became restricted to the northern part of the subspecies range (Kansas and Missouri), and the small form became restricted to the southern part (Arkansas, Louisiana, Oklahoma, Texas).

The fossil box turtles from the Friesenhahn Cave and from other late Wisconsin deposits are identified as *Terrapene carolina triunguis* (Milstead, 1967) in spite of the larger size of some of the fossils. Some differences in shape also exist in the fossils. Of the 28 carapaces from the Friesenhahn Cave, 9 closely approximate the shape of modern Texas *triunguis*, 6 closely approximate *putnami* from Florida, 10 are intermediate between the two, and 3 have the shape of *mexicana* and *yucatana*. Differences in shape still exist today; modern *triunguis* from Missouri are closer to *putnami* than modern *triunguis* from south-central Texas, and *mexicana* and *yucatana* are considered to be closely related to *triunguis* or *putnami* x^t *triunguis*. The plastral ratios of the Friesenhahn specimens are the same as modern *triunguis* in all but the interpectoral and interabdominal seam ratios (cf. Tables 2 and 4). The two exceptions are outside the observed ranges of the averages in modern *triunguis*, but the differences are not statistically significant. When the differences between the Friesenhahn fossils and the modern *triunguis* are compared with differences between any two living subspecies (e.g., *triunguis* and *major*), it is obvious tha the differences between Friesenhahn and modern *triunguis* are minor; that the only real difference is in the larger size of a very few of the fossils; that this difference may be due to allelic differences in a single pair of genes; that other differences are less than those existent between some samples of modern *triunguis;* and that all of the differences combined fall below the level for taxonomic recognition.

The fossils from Ingleside are more difficult to interpret than those from the Friesenhahn Cave. The shapes of the Ingleside turtles are either intermediate between *putnami* and *triunguis* (3 specimens), like *triunguis* (1 specimen), or like *mexicana* and *yucatana* (1 specimen). The plastral ratios place the Ingleside turtles intermediate between modern *major* and *modern triunguis*: the intergular ratio is like that of *major,* the interhumeral ratio is intermediate between that of *major,* and that of *triunguis,* and the interpectoral, inferfemoral, and interanal ratios fall within the ranges of *triunguis* (cf. Tables 2, 30-44, and 4, 86). The interabdominal ratio of the Ingleside turtles (29%) falls outside the observed averages for any living or fossil samples of the Carolina Group, but the Friesenhahn turtles have a ratio of 31% and modern *triunguis* in south-central Texas have a ratio of 32%.

Because of the apparent influence of both *putnami* (and/or *major*) and *triunguis,* I have identified the Ingleside fossils as *T. c. putnami* x^t *triunguis* (Milstead, 1967). This designation, which I still advocate, takes the position that the Ingleside turtles represent a stage on the chronocline from *putnami* to *triunguis,* although other interpretations are possible. If *triunguis,* like *bauri,* had evolved by the time the Ingleside deposits were made, the identification *T. c.*

triunguis or *T. c. putnami x triunguis* might be made. The coastal location of the Ingleside site could mean that the fossils found there were *T. c. triunguis* in which the environment had favored the expression of some *putnami* characteristics. Occasional specimens of modern *triunguis* from the Texas gulf coast exhibit some *major* characteristics, although samples from the area (Table 2, 32T) do not show this in their averages. The possibility of horizontal intergradation (*T. c. putnami x triunguis*) is also related to the coastal position of Ingleside. *T. c. putnami* and *T. c. triunguis* may have been intergrading on the Texas coast during the Wisconsin glaciation, much as *major* and *triunguis* intergrade on the Louisiana and Mississippi coasts today. Both the identification as *triunguis* or as *putnami x triunguis* must await the discovery of substantial fossil material contemporaneous with the Ingleside turtles, but located more inland and northeastward.

Another possibility is that the *mexicana-yucatana* shape exhibited by one of the Ingleside turtles and the *putnami*-like ratios may have come to Ingleside from *yucatana*, which I presume to have been isolated from the other members of the species at least once by Ingleside times. The difficulties with this hypothesis are (1) the uncertainty that the ranges of the Yucatan and Texas turtles were united during Ingleside times, and (2) lack of evidence that the *mexicana-yucatana* shape had its origin in *yucatana* rather than in *putnami* x^t *triunguis* or in early *triunguis*.

PRESENT INTERGRADATION: — Samples 45CT, 46CT, and 47CT (Figure 1 and Table 2) represent intergrade populations between *T. c. carolina* and *T. c. triunguis*. All three samples contain some individuals with the shape and color of *carolina*, some with the shape and color of *triunguis*, and some with intermediate shapes and colors. The interfemoral ratio is the only plastral ratio that will distinguish *carolina* and *triunguis*. All three of the intergrade samples have interfemoral ratios (11%) falling within the observed range of *carolina* (10%-12%) but outside the observed range of *triunguis* (12%-16%). The number of toes on each hind foot is intermediate in all three samples: 45CT, 3 toes 18%, 4 toes 82%, 46CT, 3 toes 29%, 4 toes 71%; 47CT, 3 toes 60%, 4 toes 40%.

Samples 27MT, 28MT, 29MT, and 30MT. (Figure 1 and Table 2) represent intergrade populations between *T. c. major* and *T. c. triunguis*. Some specimens in all four samples have the shape of *major*, some have the shape of *triunguis*, and some have intermediate shapes. The color of *major* (see discussion of *major*) except for the "fire-marked" pattern is the same as that of *bauri, carolina,* and *triunguis*. This influence of the other subspecies in *major* makes interpretation of color in intergrade populations difficult. Most of the specimens in all four samples of intergrades have the coloration of *triunguis,* but a few specimens in all four samples have the coloration of *carolina*, a few specimens in samples, 27MT, 28MT, and 29MT have the coloration of *bauri,* and one specimen in sample 27MT has the "fire-marked" pattern.

In three of the samples the ratio between the anterior and posterior plastral lobes and the interpectoral ratio are within the range of *triunguis* and outside the range of *major* (Table 2), but the ratios in all three samples are at the extreme of the *triunguis* range closest to *major.* The anterior lobe ratio of sample 30MT is close to *major* and the interpectoral ratio is well within the range of *triunguis.* The intergular and interhumeral ratios of samples 27MT, 29MT, and 39MT are intermediate between *major* and *triunguis,* while these ratios in sample 28MT are within the range of *triunguis* but close to *major.* The interfemoral ratio of sample 27MT is neither *major*-like nor *triunguis*-like, but is close to both. The interfemoral ratio is like both *major* and *triunguis* in sample 28MT, and like *triunguis* in samples 29MT and 30MT. Three toes on each hind foot occur in 67% of the individuals in sample 27MT, and in 100% of the individuals in samples 28MT, 29MT, and 30MT.

Samples 24CMT, 25CMT, and 26CMT (Figure 1 and Table 2) represent intergrade populations between *T. c. carolina, T. c. major,* and *T. c. triunguis.* Some specimens in all three samples have the shape of *carolina,* some have the shape of *major,* and some have the shape of *triunguis.* Some individuals in all three samples have the coloration of *carolina* and some have the coloration of *triunguis* (Figure 9, D-E). Two specimens in sample 24CMT have the coloration of *bauri,* but this is presumed to have come from *major.* The anterior lobe and interpectoral ratios of all three samples are like those of *carolina* and *triunguis.* The intergular ratios of all three samples are intermediate between the ratio of *major* and the minimum in both *carolina* and *triunguis.* The interhumeral ratio of sample 25CMT is intermediate between the ratio of *major* and the maxima of both *carolina* and *triunguis,* while the interhumeral ratios of samples 24CMT fall within the ranges of both *carolina* and *triunguis.* The interfemoral ratio of sample 24CMT falls within the range of *triunguis,* but outside the ranges of *carolina* and *major.* The interfemoral ratio of sample 25CMT fits all three subspecies, while the same ratio in sample 26CMT falls outside of the observed ratios in all three. The number of toes on each hind foot is three in 80% of the individuals in sample 24CMT, 17% in 25CMT, and 47% in 26CMT.

Recent Specimens Examined: — Unless otherwise noted all samples are from the Austroriparian biotic province of Dice (1943).

24CMT. *T. c. carolina x major x triunguis.* 31 specimens from Cook, Dekatur, Grady, Lanier, Lowndes, and Thomas counties, Georgia: AMNH 7525-7, 29883, 35466. 35469, 44657, 44737; FMNH 8074-7, 8212-4, 11282-3, 34743, 34907-8; UF 4247, 4411, 4414, 4416, 4418-9, 4430, 4443, 4450, 8592, 9711.

25CMT. *T. c. carolina x major x triunguis.* 34 specimens from Bibb and Jones counties, Georgia: UF 4225, 4227, 4229 (A-B), 4230-3, 4234 (A-B), 4236, 4237, 4240-1, 4410, 4412, 4420, 4427-30, 4435, 4437, 4440-2, 4444, 4446-8, 4452-3; KU 4608, 46807.

26CMT. *T. c. carolina x major x triunguis.* 16 specimens from Henry County, Alabama, and from Baker, Dougherty, Marion, Taylor, and Worth counties, Georgia: BMNH 1900.7.12.1-6; FMNH 2006 A-C; UF 4228, 4235, 4445, 9409, 9710; UMMZ 67812, 122273.

27MT. *T. c. major x triunguis.* 36 specimens from Harrison, Jackson, and Stone counties, Mississippi. Most of the specimens in this sample have been cited in Milstead (1967, population G). The only addition to the sample has been UF 11120.

28MT. *T. c. major x triunguis.* 25 specimens from Forest, Jones, and Lamar counties, Mississippi. All have been cited in Milstead (1967, population F).

29MT. *T. c. major x triunguis.* 27 specimens from East Baton Rouge, Livingstone, St. Bernard, St. Charles, St. Landry, St. Tammany, and Terrebonne parrishes, Louisiana. Most of the specimens have been cited in Milstead (1967, population E). The only additions to the sample were: KU 22818, USNM 86871-2 (cotypes of Agassiz's "*Cistudo triunguis*"), and USNM 100359.

30MT. *T. c. major x triunguis.* 5 specimens from Amite, Copiah, Rankin, Simpson, and Wilkinson counties, Mississippi: KU 46893, 47341-2, 47371; UMMZ 71755, 76459.

31T(M). *T. c. triunguis* (with some influence of *major,* as evidenced by an intermediate shape in several specimens, *carolina*-like coloration in one specimen, and the *major* "fire-marked" coloration in one specimen). 12 specimens from Calcasieu, Evangeline, Rapides, and Vernon parrishes, Louisiana: FMNH 29438; UMMZ 92732-5, 92738, 92741, 92744; USNM 64600, 95408, 138879, 138881.

32T. *T. c. triunguis.* Austroriparian biotic province of Dice (1943) and Blair (1950). 21 specimens from Brazoria, Chambers, Fort Bend, Galveston, Hardin, Harris, and Jefferson counties, Texas. Most of the specimens have been cited in Milstead (1967, population D). The only additions to the sample were: BM 1949.1.2.51 and UCM 20779.

33T. *T. c. triunguis.* Texan biotic province of Dice (1943) and Blair (1950). 55 specimens from Austin, Brazos, Grimes, Leon, Madison, Robertson, and

Walker counties, Texas. All of the specimens have been cited in Milstead (1967, population C).

34T. *T. c. triunguis*. Texan biotic province of Dice (1943) and Blair (1950). 15 specimens from Colorado, Fayette, Gonzales, Lavaca, Travis, and Victoria counties, Texas: ASU 58-206 (A-B); BMNH 1949.1.2.48, 1949.1.2.50; KU 3142-4; TCW 4662, 13975, 14957; UT 742, 6347, 9191, 10097-8.

35T. *T. c. triunguis*. Austroriparian biotic province of Dice (1943) and Blair (1950). 11 specimens from Angelina, Nacogdoches, Newton, Polk, Rusk, and Tyler counties, Texas: FMNH 2005; KU 51454; NMS 1882-3, 1885; TCW 460, 13974; UT 852, 8838, 17573-4.

36T. *T. c. triunguis*. Texan biotic province of Dice (1943) and Blair (1950). 11 specimens from Cooke and Dallas counties, Texas, and Bryan County, Oklahoma: FMNH 45311; USNM 45338; UT 7456, 7460, 8844-50.

37T. *T. c. triunguis*. Austroriparian biotic province of Dice (1943) and Blair (1950). 15 specimens from Howard County, Arkansas; Bossier and Caddo parishes, Louisiana; McCurtain County, Oklahoma; and Bowie and Rusk counties, Texas: FMNH 26283, 37454, 37461; UCM 11717; UMMZ 64062; USNM 45302-3, 45343; UT 8841, 8903, 9719-21, 9724-5.

38T. *T. c. triunguis*. Ecotone between Austroriparian, Carolinian, Illinoian, and Texan biotic provinces of Dice (1943). 14 specimens from Cleveland, Creek, Hughes, McIntosh, Muskogee, Payne, and Tulsa counties, Oklahoma: AMNH 7761, 16914-7; FMNH 6214, 8315, 8320, 8790; KU 3063; NMS 1317; UCM 11720-1, 11723.

39T. *T. c. triunguis*. 22 specimens from Garland, Montgomery, Pulaski, Sebastian, and Scott counties, Arkansas: FMNH 26284-6, 26288-90, 29158-9, 29439, 47469; UF 9731-41; KU 51453.

40T. *T. c. triunguis*. Carolinian biotic province of Dice (1943). 37 specimens from Benton, Franklin, Madison, and Washington counties, Arkansas; Barry, Newton, and Stone counties Missouri; and Ottawa county, Oklahoma: AMNH 35449, 64037-9; FMNH 31778-81, 45310, 55084; KU 17368, 18334, 18338, 18353-5, 19343, 19367, 19427-8, 19478, 46752-3, 46758, 46762-3, 46765, 48258; UCM 11718; UMMZ 60111, 79885-7, 81417; UT 8835-6, 26654.

41T. *T. c. triunguis*. Ecotone between Carolinian and Illinoian biotic provinces of Dice (1943). 47 specimens from Bourbon, Cherokee, Crawford, Greenwood, Labette, Linn, and Montgomery counties, Kansas: KU 3013-4, 3832, 19348, 20936-7, 21043-6, 23039, 23337-8, 23340-6, 23348-51, 46754-7, 46766-73, 46775-6, 48264-71.

42T. *T. c. triunguis*. Ecotone between Carolinian and Illinoian biotic provinces of Dice (1943). 15 specimens from Barton, Cedar, Dallas, Jasper, Lawrence, St. Clair, Vernon, and Webster counties, Missouri: AMNH 64040, 67276; FMNH 74778; KU 18387, 18390, 19344, 23040, 48272-4, 50752, 91350, 91356-7; UMMZ 112409.

43T. *T. c. triunguis.* Ecotone between Austroriparian and Carolinian biotic provinces of Dice (1943). 16 specimens from Craighead, Fulton and Lawrence counties, Arkansas; and Bollinger, Dunklin, Madison, and Wayne counties, Missouri: AMNH 36422; FMNH 8526-30, 8813-15, 33610-11, 33625, 38113; UMMZ 75823, 95292, 95295.

44T(C). *T. c. triunguis* (with some influence of *carolina* as evidenced by coloration of some individuals). Carolinian biotic province of Dice (1943). 12 specimens from Callaway, Crawford, Franklin, Iron, Phelps, Reynolds, St. Louis, and Texas counties, Missouri: FMNH 2667, 28600, 35393-4, 39487-8, 45309; UCM 11752; UMMZ 69098, 72501, 72503-4.

45CT. *T. c. carolina x triunguis.* Carolinian biotic province of Dice (1943). 16 specimens from Crawford, Orange, and Pike counties, Indiana; and Daviess, Edmonson, Henderson, Jefferson, and Meade counties, Kentucky: FMNH 2706, 2831, 83354, 83417, 83432; KU 19353, 47477-9, 47482-3, 48250; UMMZ 60983, 70746; USNM 79443-4.

46CT. *T. c. carolina x triunguis.* Ecotone between Austroriparian and Carolinian biotic provinces of Dice (1943). 24 specimens from Colbert County, Alabama; Alexander, Saline, and Union counties, Illinois; Graves County, Kentucky; Lafayette and Tippah counties, Mississippi; and Benton, Carroll, Dickson, Fayette, Henry, Madison, and Montgomery counties, Tennessee: FMNH 2219, 18635, 23738, 39228; KU 50505-7; UMMZ 52449, 53226, 53513, 53661-2, 70739, 70741, 72485, 74210, 98581, 99579, 113994-114000; USNM 45304, 95308.

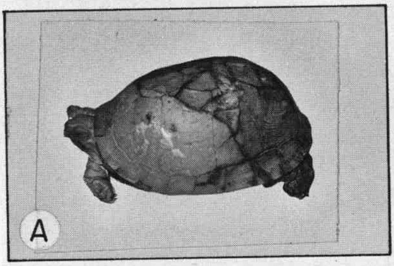
47CT. *T. c. carolina x triunguis.* Ecotone between Austroriparion and Carolinian biotic provinces of Dice (1943). 8 specimens from Choctaw and Wilcox counties, Alabama; and Lauderdale, Oktibbeha, and Webster counties, Mississippi: FMNH 48824-5; KU 47373; UMMZ 47374, 90133-4, 99581; USNM 62365.

FOSSIL SPECIMENS EXAMINED:

86PT. *T. c. putnami* x^t *triunguis.* Early Wisconsin glacial stage (50-80,000 B.P.). 5 carapaces, 11 anterior plastral lobes, and 12 posterior plastral lobes from Ingleside, San Patricio county, Texas. All are in University of Texas collection 30967. Other fossils of *T. c. putnami* x^t *triunguis* from Sangamon and early Wisconsin deposits which were examined in this study are cited in Milstead (1967).

87T(P). *T. c. triunguis* (with some influence of *putnami* as evidenced by large size). Late Wisconsin glacial stage (10-14,000 B.P.). 28 carapaces, 122 anterior plastral lobes, and 116 posterior plastral lobes from the Friesenhahn Cave, Bexar County, Texas. All are in University of Texas collection 933.

FIGURE 12. *Terrapene carolina yucatana.* A-B, UMMZ 76143, Merida, Yucatan. C-D, FMNH 27273, Chichen-Itza, Yucatan. E-F, UMMZ 83291, Chichen-Itza, Yucatan. G-H, UMMZ 73122, Chichen-Itza, Yucatan.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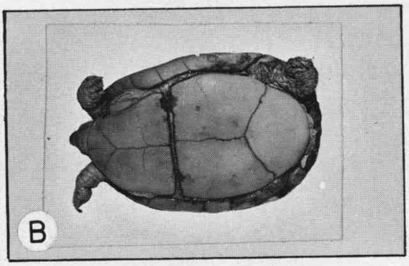
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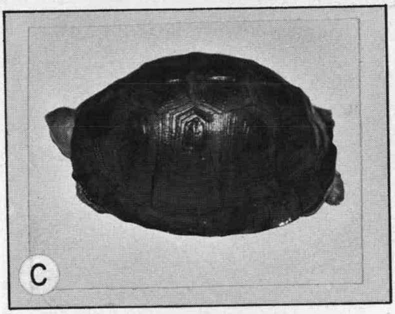
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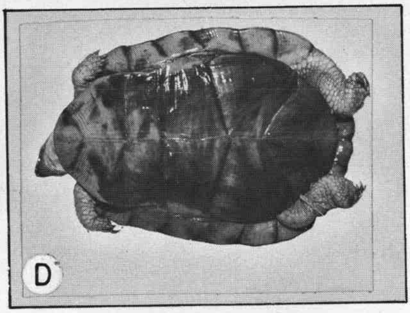
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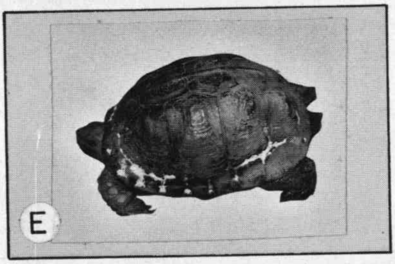
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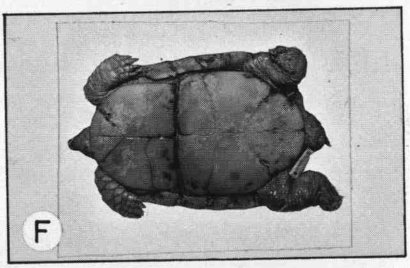
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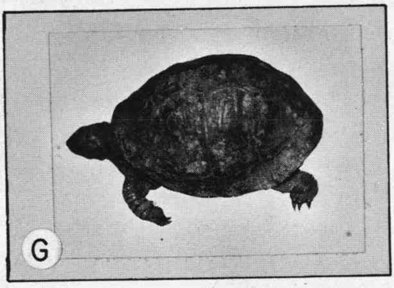
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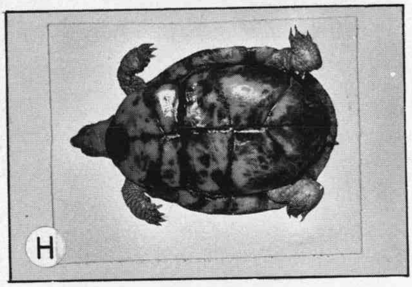
H

Other fossils of *T. c. triunguis* from Late Wisconsin and sub-Recent deposits which were examined in this study are cited in Milstead (1967) and McClure and Milstead (1967).

Terrapene carolina yucatana (Boulenger)

Figure 12, Table 2 (49)

Cistudo yucatana Boulenger, 1895, Ann. Mag. Nat. Hist., ser. 6, 15:330.
Terrapene yucatana Siebenrock, 1909, Zool, Jahrb. Suppl., 10:492.
Terrapene mexicana yucatana Smith, 1939, Publ. Field Mus. Nat. Hist., Zool. ser., 24:17-18.
Terrapene carolina yucatana Milstead, 1967, Copeia (1): 168-179.

RECOGNITION FEATURES: – Two or more of the plastral ratios of *T. c. yucatana* shown in Tables 1 and 2 distinguish it from each of the other members of the species. The shape of *yucatana* in lateral view and in cross-section through the 4th central scute (Figure 2 J) distinguishes it from all other members of the species except *T. c. mexicana*. The presence of four toes on each hind foot further separates *yucatana* from *bauri, mexicana,* and *triunguis;* the smooth or slightly concave plastron of males from *bauri, carolina, major,* and *putnami;* and the large size from *bauri, carolina,* and *triunguis.*

PRESENT DISTRIBUTION: – (Figure 1) limited to the Yucatan Peninsula in the Mexican states of Campeche, Quintana Roo, and Yucatan (Smith and Taylor, 1950).

GENERAL DESCRIPTION: – One of the largest of the living box turtles, with an average carapace length of 145 mm in 18 specimens examined and a maximum carapace length of 155 mm (UCM 16147a). The carapace is elongate and highly vaulted both anteriorly and posteriorly, and with the 3rd central scute elevated in a small hump (Figures 2 J, 12) as in *triunguis*. The hump is more emphasized in *yucatana* than in *triunguis* by indentations in the upper parts of the posterior pleural bones, which in cross-section give the carapace of *yucatana* (and of *mexicana*) a doubly-vaulted appearance (Figure 2, cf. H and J). The plastron of males is smooth or has only a shallow concavity in the posterior lobe (Figure 12 B, D, F, H; cf. 4 D). The postorbital bar is narrow, cartilaginous, or absent. Of 13 specimens on which the toes were counted 11 have four toes on each hind foot and 2 have three toes on one hind foot and four on the other. An enlarged axillary scale is present in 3 of 18 specimens examined, and all have urn- or wedge-shaped 1st central scutes. The posterior marginal scutes show little flaring, and are similar to those found in *T. c. carolina*. A lateral keel does not appear to be present in adult specimens. The plastral ratios of *T. c. yucatana* are given in Table 2 (49Y). These appear to be the best criteria for distinguishing *T. c. yucatana* and *T. c. mexicana.*

Two types of color pattern are present in *T. c. yucatana*: the horn-colored shell with dark radiating lines described for *triunguis* and the "fire-marked" pattern described for *major.* The latter pattern is the predominate one in the *yucatana* specimens examined. In *mexicana* the "fire-marked" pattern shows minimal melanism; i.e., horn or straw-colored scutes with black borders, but in *yucatana,* completely melanistic individuals are of frequent occurrence.

VERTICAL DISTRIBUTION: — No fossils of *T. c. yucatana* have yet been found. Remains of this subspecies found in an Indian site in Yucatan are quite recent.

The "fire-marked" coloration and white head of *yucatana* relate it to *major* and possibly to *putnami.* The ratio between the anterior and posterior plastral lobes and the intergular and interhumeral seam ratios of *yucatana* also place it close to *major* or to *bauri x major* in western Florida, but these ratios place it even closer to the Reddick IB *putnami x bauri* fossils from Florida (Tables 2 and 4). Because of these traits, I consider *yucatana* to be a descendent from a *putnami* or *putnami* x^{t} *triunguis* population that became isolated on the Yucatan Peninsula in pre-Sangamon or Sangamon times (Milstead, 1967). I suggest that during one of the glacial stages (possibly the Illinoian) when sea levels were low, a coastal plain existed around the gulf coast from Florida to Yucatan and that *putnami* ranged throughout the available habitat. With rising sea levels, the coastal plain became inundated in southeastern Mexico and the turtles on the Yucatan Peninsula became isolated from the rest of the species.

During the Wisconsin glaciation the coastal plain again became habitable and Yucatan turtles dispersing northward came into contact and intergraded with Texas turtles dispersing southward. At this time the *yucatana* shape may have been transmitted northward to the Ingleside turtles. Whether or not the range of *yucatana* was in contact with the range of the northern turtles by Ingleside times is questionable, as is the origin of the *yucatana* shape. The essential features of the *yucatana* shape are the "humping of the carapace posteriorly, as in *triunguis,* and indentation of the posterior pleural bones to produce the combined effect of a doubly-vaulted carapace

(Figure 2 J). Indentations of the posterior pleural bones occur rarely in fossil and Recent specimens of *bauri* and *carolina*. The shape has not been recorded in modern *triunguis*, but its presence in Texas fossils indicates that it could have originated in *putnami* x^t *triunguis* populations in southern Texas and northern Mexico, and could have been favored in southern populations (*mexicana* and *yucatana*), but not favored in northern populations (*triunguis*).

Other caracters in *yucatana* that may show a *triunguis* influence are the loss of the concave plastron of males, reduction of the post-orbital bar, and the color pattern of dark radiating lines, all of which could have developed independently. Two *yucatana* characters that apparently did develop independently are the high interfemoral seam ratio (21%), which falls well outside of the observed averages for all fossils and Recent samples of the Carolina group (Tables 1, 2, 4), and the non-flaring posterior marginal scutes. These open the way for an alternative suggestion on the evolution of *yucatana*: it may be a direct descendent of the proposed ancestor close to the base of both the Carolina and Ornata Groups (see the Genus *Terrapene*).

The oldest fossils of the Carolina Group show that *T. c. carolina* and *T. c. putnami* had already developed their characteristics by the beginning of the Pleistocene (see above), and no intermediate forms other than later day intergrades have been found. The characteristics of *yucatana* suggest such an intermediate, providing that the highly vaulted carapace of *yucatana* is considered to be a relatively recent development, with or without the influence of *triunguis*. Without this trait an early *yucatana* would be a flat turtle with a well-developed postorbital bar (although some individuals may have had it reduced), a size intermediate between *carolina* and *putnami*, frequency of axillary scale intermediate, plastral ratios similar to *putnami*, non-flaring marginals as in *carolina*, and an elongate shell as in *putnami* (although some individuals may have had a "round" shell as in *carolina*).

From this prototypic *yucatana* populations east of the Appalachians could have developed into *carolina* by decreasing in size, reducing the post-orbital bar (or favoring a reduced bar), developing (or favoring) a round shape, elevating the carapace and developing a concave plastron in males, and modifying some of the plastral ratios. West or south of the Appalachians, populations could have developed into *putnami* by increasing in size, developing flared marginal scutes, favoring development of the enlarged axillary scale, elevating the carapace and developing a concave plastron in males, and modifying (although only slightly) some of the plastral ratios. The highest interfemoral ratio in the non-Yucatan samples of the Carolina Group is 16% in two samples of *T. carolina triunguis* (Tables 1, 2), which shows a considerable reduction from the 21% of *yucatana*, but individual specimens of modern *carolina* and *triunguis* and one fossil of *putnami* (UF 7043, Haile XII B) have interfemoral ratios of 20% or over. Average interfemoral ratios of living *Terrapene ornata* are frequently 21% or over, and the Pliocene fossils (USNM 5983 and UMMP 45689) have ratios of 23% and 18%. Both living and fossil representatives of *T. ornata* are flat turtles with smooth posterior plastral lobes in males, as suggested for the *yucatana* prototype, and the size of the extinct *T. o. longinsulae* is comparable to that of modern *T. c. yucatana*. Thus *ornata* could have descended from the prototypic *yucatana* by loss of the postorbital bar, development (or favoring) of a round shape, and modification of some of the plastral ratios. Superficially at least, it seems that to make *ornata* out of the *yucatana* prototype would have involved fewer steps than to make *carolina* or *putnami*.

All that is needed to support this suggested evolution of the Carolina and Ornata groups is one specimen of the *yucatana* prototype, but it has not been found, and all the characteristics of modern *yucatana* can be attributed to evolution from *putnami* or *putnami* x^t *triunguis*. Most of the traits have already been considered in this sense (above), but the interfemoral seam ratio and the nonflaring marginals remain to be explained. Three explanations of the interfemoral seam ratio come quickly to mind: (1) as suggested above, the description of *putnami* based on individual specimens and intergrades from Florida may not be defining the characteristics of *putnami* exactly; (2) as noted above, the characteristics of *putnami* west of the Mississippi River are unknown and may not agree with eastern *putnami;* and (3) *yucatana* may have increased its interfemoral ratio in descending from *putnami* x^t *triunguis*, while *triunguis* decreased its interfemoral ratio. Reduction in flaring of the marginals from the condition found in *putnami* has already been demonstrated in the evolution of *bauri*, *major*, and *triunguis*, although *yucatana* has carried the reduction farther than any of the other modern subspecies.

Thus for the present no serious consideration need be given to the suggestion of a prototypic *yucatana* as the ancestor of both the Carolina and Ornata groups. If, however, someone someday discovers an early Pliocene fossil of a flat, *yucatana*-like *Terrapene*, the suggestion will have to be reconsidered.

SPECIMENS EXAMINED:

49Y. *T. c. yucatana*. Yucatan biotic province of Goldman and Moore (1945) and Goldman (1951). 18 specimens examined from the states of Campeche and Yucatan, Mexico. Ten of the specimen numbers are given in Milstead (1967, Population K). The eight additions to the sample are: BMNH 1974.3.5.45-7; KU 71773, 75657-9; and MCZ 9512. The three British Museum specimens are the cotypes of the subspecies (Boulenger's *Cistudo yucatana*).

Terrapene carolina mexicana (Gray)

Figure 13, Table 2 (48)

Cistudo (Onychotria) mexicana Gray, 1848 (1849), Proc. Zool. Soc. London, 16: 16-17.
Cistudo mexicana Gray, 1855, Cat. Shield reptiles Brit. Mus., pt. 1:40.
Onychotria mexicana, Duges, 1888, La Naturaleza, ser. 2, 1:107-108.
Cistudo carolina var. *mexicana* Boulenger, 1889, Cat. chelonians, rhyncocephalians, crocs Brit. Mus.: 118.
Terrapene mexicana Baur, 1893, Amer. Nat., 27:677.
Terrapene mexicana mexicana Smith, 1939, Publ. Field Mus. Nat. Hist., Zool. Ser., 24: 17-18.
Terrapene carolina mexicana Milstead, 1967, Copeia (1): 168-179.
Terrapene goldmani Stejneger, 1933, Proc. Biol. Soc. Wash., 46: 119-120.
Terrapene yucatana Ditmars (*nec* Boulenger), 1934, Zoologica, 17: 34-36.

RECOGNITION FEATURES: – Two or more of the plastral ratios of *T. c. mexicana* shown in Tables 1 and 2 distinguish it from each of the other members of the species. The shape of *mexicana* in lateral view and in cross-section through the 4th central scute (Figure 2 J) distinguishes it from all other members of the species except *T. c. yucatana*. The presence of three toes on each hind foot further separates *mexicana* from *carolina, major* and *yucatana;* the smooth or only slightly concave plastron of males from *bauri, carolina, major,* and *putnami;* and the large size from *bauri, carolina,* and *triunguis.*

PRESENT DISTRIBUTION: – (Figure 1) limited to a relatively small area in southwestern Tamaulipas, northeastern San Luis Potosi, and northern Vera Cruz (Smith and Taylor, 1950). The area is ecotonal between the Tamaulipan, Vera Cruz, and Sierra Madre Oriental biotic provinces of Goldman and Moore (1945) and Goldman (1951). For a detailed study on the herpetology of the area see Martin (1958).

GENERAL DESCRIPTION: – One of the largest of the living box turtles, with an average carapace length of 145 mm in 29 specimens examined, and a maximum carapace length of 173 mm (cotype

1947.3.5.48 in the British Museum). The carapace is elongated and highly vaulted, both anteriorly and posteriorly, and with the 3rd central scute elevated in a small hump (Figures 2J, 13) as in *triunguis*. The hump is more emphasized in *mexicana* than in *triunguis* by in-

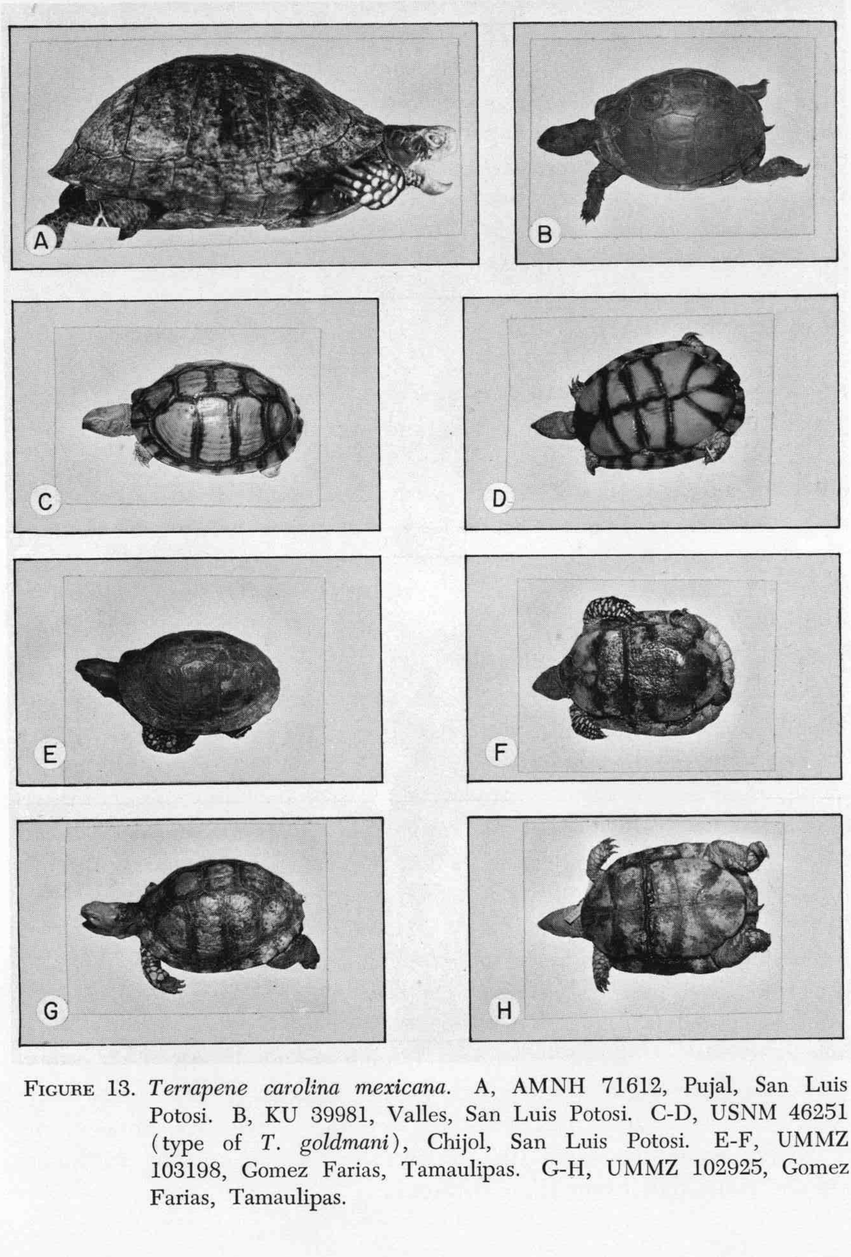

FIGURE 13. *Terrapene carolina mexicana.* A, AMNH 71612, Pujal, San Luis Potosi. B, KU 39981, Valles, San Luis Potosi. C-D, USNM 46251 (type of *T. goldmani*), Chijol, San Luis Potosi. E-F, UMMZ 103198, Gomez Farias, Tamaulipas. G-H, UMMZ 102925, Gomez Farias, Tamaulipas.

dentations in the upper parts of the posterior pleural bones which in cross-section give the carapace of *mexicana* (and of *yucatana*) a doubly-vaulted appearance (Figure 2 cf. H and J). The plastron of males is smooth or has only a shallow concavity in the posterior lobe (Figure 13 D, F, cf. 4 D). The postorbital bar is narrow, cartilaginous, or absent (Figure 5). In 17 specimens on which the toes were counted, 16 had three toes on each hind foot, and 1 had four. An enlarged axillary scale is present in 3 of 30 specimens examined, and all have urn- or wedge-shaped 1st central scutes. The posterior marginal scutes are similar to *T. c. triunguis* in their degree of flaring. A lateral keel above the bridge may be present. The plastral ratios of *T. c. mexicana* are given in Table 2 (48Mx). These appear to be the best criteria for distinguishing *T. c. mexicana* and *T. c. yucatana.*

Four types of color pattern are present in *T. c. mexicana*: the three patterns described for *T. c. triunguis*, and the "fire-marked" pattern described for *T. c. major* and *T. c. yucatana.* Of the three *triunguis* patterns, the horn-colored shell with dark radiating lines appears to be the one of most frequent occurrence in *T. c. mexicana.* The "fire-marked" pattern was described above as varying continuously from horn-colored scutes with dark borders to completely melanistic scutes. *T. c. mexicana* does not appear to become as melanistic as some individuals of *major* and *yucatana*, and the pattern of horn-colored scutes with dark borders (Figure 13, C-D) is most frequent. Occasional specimens of *mexicana* have the white or white-blotched head of *major* and *yucatana.*

VERTICAL DISTRIBUTION: — *T. c. mexicana* is another form for which no fossil representatives have been found. Earlier (Milstead, 1967), I suggested that *mexicana* may have evolved from *putnami* x^t *triunguis* in post-Wisconsin times because some of its characteristics appear to have come from *triunguis*, while others appear to have come from *major* or *putnami.* That the latter characteristics may have come from *yucatana* was somehow overlooked, but this seems to be a better explanation in view of the fact that *mexicana* has the same shape as *yucatana*, and *yucatana* is closer to *mexicana* in both time and space than is *putnami* or *major.* When *yucatana* is regarded as the contributor of the *major*-like characteristics, it becomes necessary to consider *mexicana* as having originated through intergradation between *triunguis* and *yucatana*, because the traits that distinguish *mexicana* from *triunguis* are the traits that came from *yucatana*, while the traits that distinguish *mexicana* from *yucatana* are the traits that came from *triunguis.*

I suggested above that *triunguis* and *yucatana* intergraded in Mexico during Wisconsin times, and *mexicana* fits the hypothetical intergrades in both morphology and geography. The isolation of *mexicana* may be assumed to have taken place in post-Wisconsin times, first from *yucatana* and later from *triunguis*. I suggest that separation from *yucatana* began shortly after the Wisconsin maximum glaciation when rising sea levels began to destroy the coastal plain that served as a dispersal route between Yucatan and northern Mexico, and that this separation was complete before the separation of *mexicana* from *triunguis* began. At present *triunguis* ranges no farther south or west than eastern Texas (Austroriparian and Texan biotic provinces of Dice, 1943; Blair, 1950) and is separated from *mexicana* by the arid Tamaulipan biotic province of Dice (1943), Goldman and Moore (1945), Blair (1950), and Goldman (1951). It is my contention that the present Tamaulipan province developed in relatively recent times following the period of humidity associated with the Wisconsin glaciation, and that *triunguis* withdrew northward as arid conditions progressed leaving the old intergrade population behind.

The suggestion that *mexicana* was in contact with *triunguis* after its separation from *yucatana* is supported by the fact that most of the characteristics of *mexicana* are *triunguis* characteristics. Aside from the *yucatana*-like shape and size, *mexicana* differs from *triunguis* only in (1) having intergular and interhumeral seam ratios intermediate between those of *triunguis* and *yucatana,* (2) having a high interpectoral seam ratio (Tables 1 & 2), and (3) having a white or white-blotched head and "fire-marked" pattern in some individuals. The *mexicana yucatana* shape can be ignored because of the possibility that it originated in *triunguis* or *putnami* x^t *triunguis,* and size can be ignored for the same reason. Although the average size of *mexicana* and *yucatana* (145 mm) is larger than in modern *triunguis,* it is smaller than in Friesenhahn *triunguis.*

In addition to fitting well with morphological characters and with the suggested relationships between *triunguis* and *yucatana,* the intergrade theory for the origin of *mexicana* also fits well with evolutionary patterns within the species. The four subspecies of *Terrapene carolina* in the United States are clearly distinct from each other in morphology, except in areas of intergradation. In discussing *mexicana* and *yucatana* previously (Milstead, 1967), I noted that, "The two subspecies now assigned to the species *T. mexicana* are not as distinct from each other or from *T. carolina* as the living subspecies of *carolina* (*bauri*, *carolina*, *major*, and *triunguis*) are from each other." When *mexicana* is removed from subspecific standing by considering it to be an intergrade between two other subspecies, *yucatana* becomes as clearly distinct as the other subspecies of *T. carolina*.

The problem of whether to call *mexicana* specimens *T. carolina mexicana* or *T. carolina triunguis x yucatana* remains to be resolved. Ordinarily, I do not think that intergrades should be accorded subspecific rank unless they have developed distinguishing traits of their own, and *mexicana* appears to have done this with only one character, the interpectoral seam ratio. I recognize it as a distinct subspecies on the basis of the interpectoral seam and three other rather weak reasons that I hope will not be readily accepted as criteria for naming other subspecies, either within or outside of the genus *Terrapene*. First, during its contact with *triunguis* following separation from *yucatana*, *mexicana* continued to maintain some *yucatana*-like traits, although triunguis in post-Friesenhahn times has definitely selected against two of those traits (size and shape). Second, since its separation from its northern relatives, *yucatana* has apparently selected against the *triunguis*-like traits which distinguish it from *mexicana*. Third, *mexicana* is presently isolated from both *triunguis* and *yucatana* in a habitat that is somewhat different from the habitats of *triunguis* and *yucatana*, and it may be the habitat of *mexicana* that is maintaining selection for a mixture of *triunguis* and *yucatana* traits.

SPECIMENS EXAMINED

48Mx. *T. c. mexicana*. Ecotone between the Tamaulipan, Vera Cruz, and Sierra Madre Oriental biotic province of Goldman and Moore (1945) and Goldman (1951). 30 specimens from the states of Tamaulipas and San Luis Potosi, Mexico. Most of the specimen numbers are given in Milstead (1967, population J). The only additions to the sample were Senkenberg Museum specimens 22262-3, 22289-90, and 22319, and British Museum specimens 1859.-5.11.4, 1947.3.5.48, and 1947.3.4.3. The last two specimens listed are the cotypes of the subspecies (Gray's *Cistudo mexicana*).

Terrapene coahuila Schmidt and Owens

Figure 14, Table 2 (50)

Terrapene coahuila Schmidt and Owens, 1944, Publ. Field Mus. Nat. Hist., Zool. ser., 29 (6): 101-103.

RECOGNITION FEATURES: – The flat carapace of *T. coahuila* (less that 40% of carapace length) distinguishes it from all other members of the Carolina Group. The relatively short anterior lobe of the plastron (63% of posterior lobe length) distinguishes *coahuila*

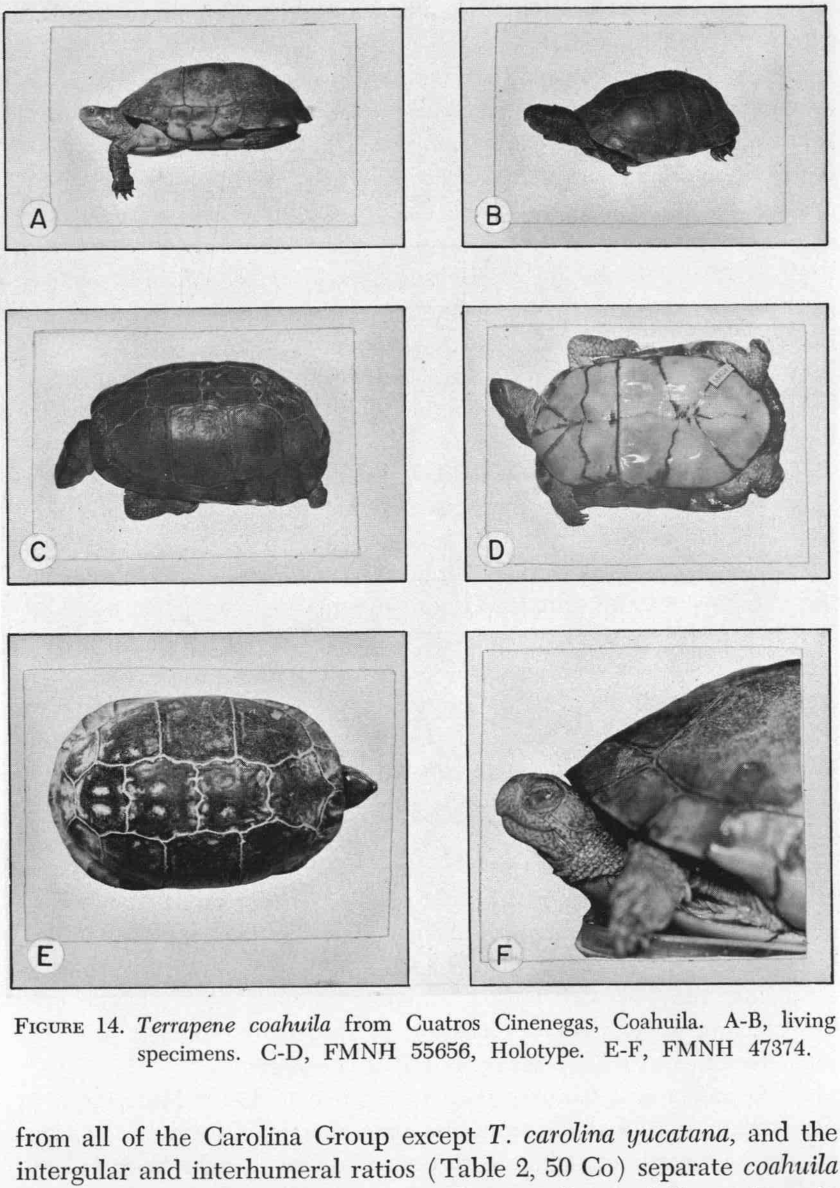

FIGURE 14. *Terrapene coahuila* from Cuatros Cinenegas, Coahuila. A-B, living specimens. C-D, FMNH 55656, Holotype. E-F, FMNH 47374.

from all of the Carolina Group except *T. carolina yucatana,* and the intergular and interhumeral ratios (Table 2, 50 Co) separate *coahuila* from all the Carolina Group except *T. c. carolina* and *T. c. triunguis.* The flat, elongate carapace of *T. coahuila* and its dark coloration give it the appearance of being intermediate between *Terrapene* and *Kinosternon* (Figure 14). This distinctive morphology provides a ready recognition feature for identifying *T. coahuila,* and I present it only as an identification tool, not as a suggestion of relationship between the two genera.

PRESENT DISTRIBUTION: – Known only from springs near the village of Cuatro Cienegas, Coahuila, Mexico (Figure 1). The aquatic or semiaquatic habitat and habits of this species have been described in detail by Webb, et al. (1963).

GENERAL DESCRIPTION: – A medium-sized box turtle with an average carapace length of 133 mm and a maximum length of 168 mm (KU 51432). The height of the carapace in *T. coahuila* is 34% to 37% of the carapace length when the height is measured from the bridge to the 3rd central scute along a line parallel with the seam between the 2nd and 3rd costal scutes. In other living members of the Carolina Group the height is over 40% of the carapace length (42%-45% in *T. c. bauri, T. c. carolina* and *T. c. major*, 46%-48% in *T. c. mexicana* and *T. c. yucatana*, and 48%-50% in *T. c. triunguis*). The carapace is elongate in *T. coahuila*, and may have a hump on the 5th central scute as described for *T. c. putnami*. The plastron of males has a deep concavity (Figure 1, D) to harbor the carapace of the female during copulation. The postorbital bar is a broad, heavy span of bone as in *T. c. major*. All 15 specimens on which the toes were counted had four toes on each hind foot. An enlarged axillary scale is present in 78% of 58 specimens examined. The posterior marginal scutes show about the same degree of flaring as in *T. c. triunguis*, i.e. intermediate between *T. c. carolina* and *T. c. major*. The plastral ratios of *T. coahuila* are shown in Table 2 (50 Co).

The color pattern of the *T. coahuila* carapace is usually a uniform dark gray (Figure 14), but occasional specimens have a light gray shell with dark lines somewhat like the dark radiating lines found in *T. c. triunguis*. The head is light to dark gray, and is frequently mottled with dark gray spots (Figure 14 F) which give the head an appearance reminescent of the white-blotched heads of some specimens of *T. c. major* and *T. c. yucatana*.

Two anatomical features that may prove to be of importance in distinguishing *T. coahuila* from other members of the Carolina Group are the presence of cloacal bursae and the penial morphology. Williams et al. (1960) report the presence of cloacal bursae in *T. coahuila*, but whether or not other living box turtles possess them is not certain. McDowell (1964) refers to cloacal bursae in *Terrapene* as very small or absent. In a study of penial morphology in cryptodiran turtles, Zug (1966) reports that the plicae internae are reduced in the penis of *T. coahuila,* while these folds or flaps are enlarged in *T. carolina* and *T. ornata.* He apparently examined only one specimen of *coahuila* and two each of *carolina* and *ornata.* In any case, such anatomical features as cloacal bursae and penial morphology are of only marginal use in this study because the nature of these characters cannot be determined in fossils.

VERTICAL DISTRIBUTION:—As with other box turtles from Mexico, no fossils of *T. coahuila* are known. This is particularly unfortunate because of the unsual morphotype of this species. Auffenberg (1958) and Legler (1960) take the position that *coahuila* is the most primitive known box turtle, and that its flat carapace, heavy postorbital bar, and semiaquatic habits are characteristics presumed to have occurred in the ancestor of both the Carolina and Ornata groups. I believe that *T. coahuila* is a descendent of *T. c. putnami* x *triunguis* (Milstead, 1960, 1967)[1], because some of its characteristics seem to indicate affinity with "advanced" members of the genus, rather than with "primitive" members. According to my interpretation of the evolution of *Terrapene* and *Emys* from *Clemmys,* for example, the more primitive members of both *Terrapene* and *Clemmys* must have had a solid contact between the jugal and the pterygoid. Such a contact is found in *T. c. major,* which I presume to be a modern descendent of *T. c. putnami. T. coahuila, T. c. bauri, T. c. triunguis,* and *T. c. yucatana,* all of which I presume to have evolved from *putnami,* lack the contact, although some specimens of all four have a mesially-directed flange on the jugal. Primitive forms of *Terrapene* must also have had a solid contact between the prefrontal and postorbital bones. Such a contact has been found in *T. c. carolina, T. c. major,* and *T. c. bauri,* but not in *T. coahuila.*

Certain morphological and physiological features of *coahuila* suggest that its semiaquatic adaptations are secondary rather than primary. Although it is a flat turtle, *T. coahuila* has the deeply concave plastron (in males) generally associated with an elevated carapace, and this indicates that it descended from ancestors with a high shell. The well-developed mid-dorsal keel of *coahuila* also suggests a high-shelled ancestor. A flat shell is generally associated with an aquatic habitat, and I contend that *coahuila* in assuming an aquatic habitat reproduced the flat shell of the hypothetical ancestral turtle by recombinations of genetic alleles. Reinvasion of the habitat

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[1] Auffenberg and Milstead (1965) also take this position, although the senior author was not as satisfied with the thesis as was the junior author.

is also indicated by the fact that *coahuila* is a clumsy swimmer and has buoyancy problems when in water more than a few inches deep. Hartweg (pers. comm.) observed that these problems were especially noticeable when *coahuila* was compared with mud turtles (*Kinosternon*) that have a shape and habitat similar to that of *coahuila.* It would seem that if *coahuila* had maintained a semiaquatic existence throughout its history, it would have solved these problems. Other characteristics of *coahuila* can be explained in terms of descent from *T. c. putnami* x^t *triunguis*: the heavy postorbital bar, short anterior lobe of the plastron, and four hind toes are *putnami* characteristics; while the intergular, interhumeral, interpectoral, and interfemoral seam ratios are *triunguis* characteristics. The size is intermediate between modern and Friesenhahn *triunguis,* and the frequency of the enlarged axillary scale could be either a *putnami* or a *triunguis* character.

I suggest that during some pluvial period of the Pleistocene *T. c. putnami* x^t *triunguis* invaded the Cuatros Cienegas bolson, that a population became isolated in the bolson with the retreat of the main population during an arid period, that increasing aridity eventually drove the turtles into the water, and that this initiated the evolution of *coahuila* (Milstead, 1967). Such a sequence of events could have taken place anytime in the Pleistocene, but the presence of deep concavity in the plastral lobe of males in *coahuila,* the presence of a heavy postorbital bar, and the absence of these traits in Wisconsin age fossils of *triunguis* indicate that the isolation took place in pre-Wisconsin times. The presence of plastral ratios similar to those of *triunguis* indicates either parallel development of *coahuila* and *triunguis* or a Wisconsin influence of *triunguis.* The latter possibility is somewhat supported by the knowledge that Cuatros Cienegas is less distant from the present day range of *triunguis* than is the Wisconsin site in Clovis, New Mexico, where *triunguis* fossils have been found, and that representatives of other eastern species have been recorded in northeastern Coahuila in modern times (Milstead, 1960).

In a previous paper (Milstead, 1967) I suggested that the evolution of *T. coahuila* required a much more rapid evolutionary rate than that found anywhere else in the genus, but reconsideration of the data does not show this to be true. Only one major morphological feature is involved, alternation (flattening) of the carapacial shape. In their evolution from *putnami, T. c. bauri* (by shifting its mass posteriorly and *T. c. triunguis* (by elevating its shell) changed their carapacial shapes in equivalently short, or perhaps shorter, periods of time.

SPECIMENS EXAMINED

50Co. *T. coahuila.* Chihuahuan biotic province of Blair (1940, 1950), Dice (1943), Goldman and Moore (1945), Goldman (1951) and Milstead (1960, 1961). 59 specimens from the Cuatros Cienegas bolson, Coahuila, Mexico. Most of the specimen numbers have been cited in Milstead (1967). Additions to the sample include: ASU (field numbers) ACE 321-2; BCB 9435-41; KU 46917-23, 51431, 51433-7, 92623; and UMKC 0496.

The number of specimens examined suggests that enough embalmed and skeletal specimens of *T. coahuila* are now available to satisfy the needs of almost any morphological study. It is hoped that future collectors at Cuatro Cienegas will keep this in mind. The *coahuila* habitat occupies a very small geographic area that may be threatened by climate and is definitely threatened by agricultural activities. Conservation plans for the area now being proposed by W. L. Minckley and others are badly needed.

THE ORNATA GROUP

The Ornata Group of box turtles includes two species: *Terrapene ornata* with one extinct and two living subspecies distributed over the Great Plains of North America, and *T. nelsoni* with two living subspecies distributed in the western foothills of the Sierra Madre Occidental in Mexico (Figure 1). The following characteristics of *T. nelsoni* distinguish it from *T. ornata*: (1) slightly larger size (Tables 2, 3), (2) higher interhumeral and interabdominal and lower interfemoral and interanal seam ratios (Tables 2, 3), (3) usually higher interpectoral ratios, (4) usually lower anterior lobe length and intergular ratios, (5) more frequent occurrence of a weak mid-dorsal keel on the carapace (60% in *nelsoni* vs. 8% in *ornata*), (6) more greatly flaring marginal scutes, and (7) an oval to elongate shell (vs. a round to oval shell in *ornata*). A flatter (scoop-shaped) 1st central scute further distinguishes *T. nelsoni* from the living subspecies of *T. ornata*, but it will not distinguish *T. nelsoni* from the extinct *T. o. longinsulae*.

All the living members of the Ornata Group are inhabitants of savannahs, and presumably the one extinct form was also. Although trees are sparse over most of the geographic range of the group, the turtles do enter forested areas where undergrowth consists of grass or of relatively open herbaceous vegetation. They avoid forests with dense undergrowth. The northermost member of the group, *T. o. ornata,* inhabits mesic to semiarid grasslands over most of the Great Plains in the central United States. *T. o. luteola* occurs in the arid grasslands of the southern Great Plains in the southwestern United States and north-central Mexico. Legler (1960) demonstrates that *luteola* is better adapted to arid grasslands than *ornata.* The wider distribution and greater abundance of *ornata* indicate that it is better-adapted to mesic grasslands than *luteola,* but the exclusion of *luteola* by *ornata* from mesic grasslands is probably due to competitive factors more complex than humidity tolerance. Legler (1960) found that *ornata* kept under arid conditions did not survive, but *luteola* did. The reverse situation does not appear to have the same results, although I have not kept *luteola* under humid conditions for as long as Legler kept *ornata* under arid conditions.

In parts of its range *luteola* occurs in oak-savannah habitats at altitudes above 4500 feet. This is the type of habitat in which *T. n. nelsoni,* the southernmost member of the Ornata Group occurs (Milstead and Tinkle, 1967). I presume that the habitat of *T. n. klauberi* in Sonora and Sinaloa is also an oak-savannah association (3500 feet and above), but the turtle may occur more frequently in desert scrub vegetation at lower altitudes.

Summary of Evolution in the Ornata Group

The oldest known fossils of the genus *Terrapene* are identified as *Terrapene ornata longinsulae.* Although all the fossils have been found within the present-day range of *T. o. ornata, longinsulae* appears to be most closely related to the living *T. o. luteola.* Distributional differences are attributed to changing conditions on the Great Plains during the Pleistocene. At times during the late Cenozoic, the Great Plains are presumed to have been more humid than they are today, and at other times more arid (Auffenberg and Milstead, 1965; and other papers there cited). Humid conditions are presumed to have driven the Ornata Group turtles southwestward, and arid conditions are presumed to have permitted them to expand (or driven them) northeastward. During these population shifts, the modern *T. o. luteola* is presumed to have evolved directly from *T. o. longinsulae* with only minor morphological changes. *T. o. ornata* may have evolved from a relict population of *longinsulae* or *luteola* left to the north or east during a southwestward population shift and *T. nelsoni* may have evolved from a relict population left to the southwest during a northeastward population shift. Subspeciation in *T. nelsoni* may have occurred (or may be occurring) through the facility of a partial or complete ecological or physiological barrier.

As in the Carolina Group, the known fossils of the Ornata Group have been found in the northern and central parts of the group range, which is one reason for assuming (above and in the following pages) that evolution proceeded from north to south. Were it not for the fossils, evolution in both groups of box turtles might be considered to have proceeded from south to north (see discussions under the Carolina Group). Within the Ornata Group the generalized clines in elevation of the 1st, 3rd, and 4th central scutes; in carapace length, in the anterior plastral lobe length ratio; and in the intergular, interhumeral, and interpectoral seam ratios, which I presume to have evolved from *luteola* to *ornata* in one direction and from *luteola* to *klauberi* to *nelsoni* in the other direction, may actually have evolved in a straight south-north line from *nelsoni* to *klauberi* to *luteola* to *ornata*. If this were the case, *nelsoni* would be closest of the living representatives to the base of the Ornata Group. This possibility is supported by a number of factors that relate *nelsoni* to the Carolina Group: elongate shell, frequency of a keeled carapace, and flaring marginals. Despite these arguments, the fossils do exist and give strong support for the suggested north-south direction of evolution in both groups. Futhermore *T. ornata luteola,* which is presumed to be the oldest living representative of the Ornata Group, and *T. carolina carolina*, presumed to be one of the oldest representatives of the Carolina Group, are similar in size, both are round and relatively flat in shape, their plastral ratios (Table 1) form a closer match than do the ratios of any other forms of the two species groups (Table 1), both have four toes on each hind foot, both lack flaring marginals, and both have a high number of radiating lines on each carapacial scute.

The three subspecies of *Terrapene ornata* and the two subspecies of *Terrapene nelsoni* are discussed in greater detail below. The distribution of members of the Ornata Group is given in Figure 1, plastral ratios and the other data on the group are given in Tables 1 and 3, and representatives of the group are shown in Figures 15-18.

Terrapene ornata longinsulae Hay

Figure 15

Terrapene longinsulae Hay, 1908, Proc. U.S. Natl. Mus., 35 (1640): 161-169.
Terrapene ornata longinsulae Milstead, 1967, Copeia (1): 168-179.

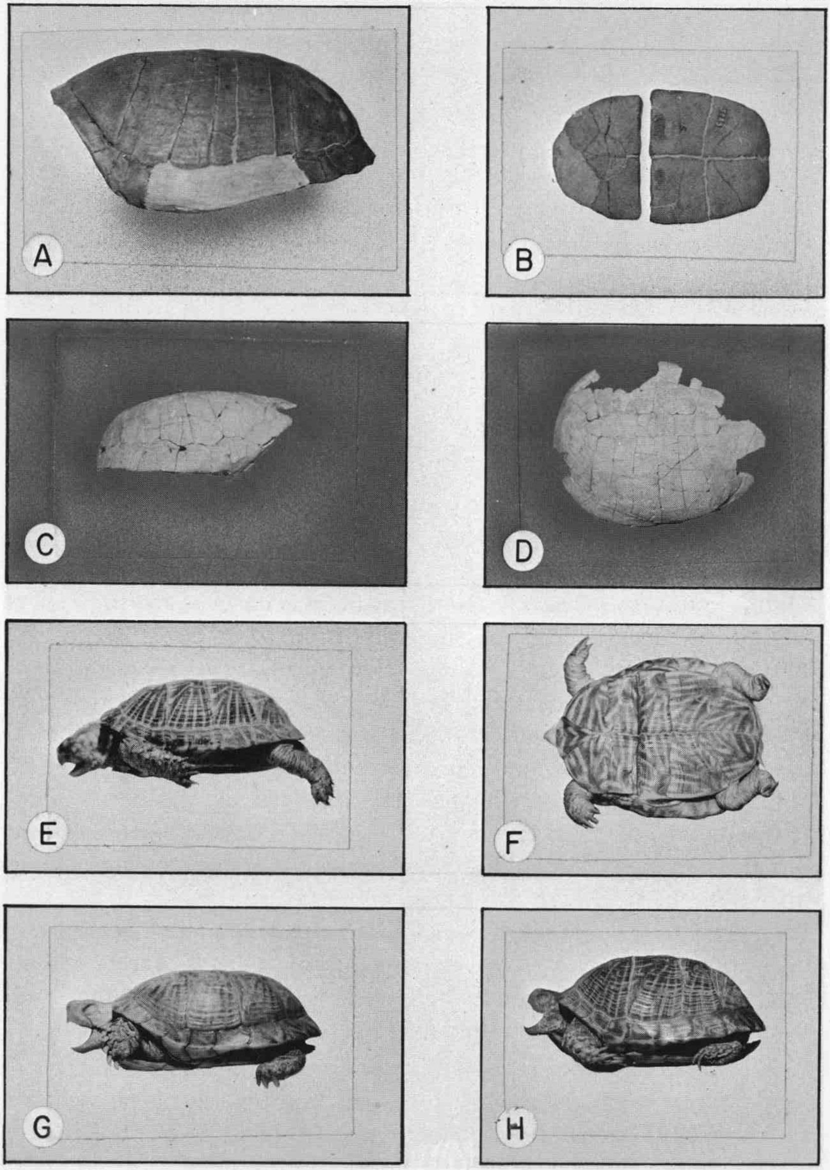

FIGURE 15. A-B, *Terrapene ornata longinsulae,* USNM 5983, Holotype, lower middle Pliocene of Long Island, Kansas. C-D, *T. o. longinsulae,* UMMP 37184, lower Pleistocene (Aftonian), Meade County, Kansas. E, *T. o. luteola,* UMKC 0501, Recent, Dona Ana County, New Mexico. F, *T. o. luteola,* UMKC 0500, Recent, Dona Ana County, New Mexico. G, *T. o. luteola,* UMKC 0499, Recent, Dona Ana County, New Mexico. H, *T. o. luteola,* Stanford University, unnumbered, Recent, Chihuahua-Sonora state line.

RECOGNITION FEATURES: — The low angle of elevation of the 1st central scute and the low elevation of the 3rd central scute distinguish *T. o. longinsulae* from both *T. o. luteola* and *T. o. ornata*. Lack of rugosity of the carapacial scutes and nonflaring and nonemarginate marginal scutes will further distinguish *longinsulae* from the other two.

PRESENT DISTRIBUTION: — *T. o. longinsulae* is a name given to a box turtle that is thought to be extinct, although its relationship with *T. o. luteola* prohibits arrival at a definite conclusion.

GENERAL DESCRIPTION: — A relatively small box turtle with a maximum carapace length (USNM 5983) of 125 mm in known specimens. The shell shape tends to be round in three specimens examined. The first central scute of the holotype rises at an angle of about 40° from a line connecting the anterior and posterior margins of the carapace, versus approximately 30° in *T. n. nelsoni*, 35-45° in *T. o. luteola*, 45° in *T. o. ornata*, and 50-55° in *T. c. triunguis*. The two other *longinsulae* carapaces have lower angles (28° in UMMP 37184) than the holotype. The low angles of elevation of the 1st central scute give the anterior margin of the carapace a flattened or scoop-shaped appearance in *longinsulae*. This appearance is perpetuated in living turtles by both subspecies of *T. nelsoni*, but is not so noticeable in *luteola* and *ornata*, except when they are compared with *T. carolina* (Figure 2, cf. B&K). The height of the holotypic *longinsulae* carapace in comparison with the length is 42% at the third central of the carapace versus 41% in another specimen (UMMP 37184), 35-41% in *luteola*, 48% in *ornata*, 40% in *klauberi*, and 45% in *nelsoni*. Height at the posterior half of the 4th central is 26% in the *longinsulae* holotype, 22-29% in *luteola*, and 30% in *ornata* and *nelsoni*. Thus, the slope from the 4th central to the posterior edge of the carapace in *longinsulae* is more gradual than in all members of the group except *luteola* (Figures 15-18). The marginal scutes of *longinsulae* show very little flaring, and thus are very much as they are in modern *T. c. carolina*. The posterioventral edge of each marginal in *longinsulae* unites smoothly with the anterioventral edge of the following marginal, so the carapace has no scalloped or emarginate posterior edge as in *ornata* (cf. Figure 15, A and Figure 16, A). The *longinsulae* fossils all have smooth shells rather than the rugose ones generally exhibited by *ornata*, but the validity of this feature as a character is questionable. Although living *luteola* is never as rugose as *ornata*, and this is a distinguishing feature between them, older specimens of *ornata* tend to lose their rugosity through abrasion of the shell, and abrasion might account for the smoothness of the *longinsulae* fossils.

VERTICAL DISTRIBUTION: – The holotype of *T. o. longinsulae* (USNM 5983 from the lower middle Pliocene of Long Island, Kansas) is the oldest known representative of the genus *Terrapene*. Other specimens of *longinsulae* consist of fragementary to almost complete shells of four turtles from late middle Pliocene (UMMP 45689, Beaver County, Oklahoma), early upper Pliocene (UMMP 37186 and 45689, Seward County, Kansas), and early (Aftonian) Pleistocene (UMMP 37184, Meade County, Kansas) deposits. The earliest fossils of any living representatives of *T. ornata* are from Wisconsin deposits in New Mexico and Texas. In spite of the age of the known fossils of *longinsulae* and of the hiatus in vertical range, the close similarity between *longinsulae* and the living members of the species, particularly *luteola*, make it inadvisable to consider *longinsulae* as a distinct species (Milstead, 1967; Milstead and Tinkle, 1967).

Terrapene ornata luteola Smith and Ramsey

Figure 15, Table 2 (51-54)

Terrapene ornata luteola Smith and Ramsey, 1952, Wasmann Jour. Biol., 10:45.

RECOGNITION FEATURES: – The high number of radiating lines on the carapace of *T. o. luteola* distinguishes it from the other living subspecies, *T. o. ornata*. Slightly larger size, a tendency toward horn or straw color, and a tendency to have the plastral hinge located opposite the 6th marginal scute also distinguish *luteola* from *ornata*. A more sharply elevated 1st central scute, a higher 3rd central scute and more flaring marginals distinguish *luteola* from the extinct *T. o. longinsulae*.

PRESENT DISTRIBUTION: – (Figure 1) Apparently limited to the northern portions of the Chihuahuan and Sonoran deserts in the states of Arizona, Chihuahua, New Mexico, Sonora, and Texas (Rocky Mountain Corridor of Auffenberg and Milstead, 1965). One specimen (AMNH 73720) has been recorded from Guaymas, Sonora, but additional specimens are needed before *T. o. luteola* can be said to range west of the Sierra Madre Occidental. Intergradation between *luteola* and *ornata* (discussed below) occurs in the extreme northern part of the Chihuahuan Desert in New Mexico and Texas and in southeastern Texas.

GENERAL DESCRIPTION: — a medium-sized box turtle (Table 3), larger than *T. o. ornata,* but about the same size as *T. o. longinsulae* and *T. nelsoni.* The largest specimen examined (UAZ 13092) is 149 mm in carapace length. The shell shape tends to be round or oval, but oval individuals are never as elongated as *T. nelsoni* and most of the members of the Carolina Group. The plastral hinge of *T. o. luteola* is usually (over 50% of individuals, see Table 3) located opposite the 6th marginal scute of the carapace. The degree of elevation of the 1st central scute is 35° to 45°. The elevation of the 3rd and 4th central scutes places *luteola* closer to *longinsulae* than to *ornata.* The degree of flaring and emargination of the marginal scutes and the rugosity of the carapace of *luteola* appear to be intermediate between *longinsulae* and *ornata.* The plastral ratios of *luteola* (Table 3, 51-54) do not clearly distinguish it from *ornata,* but in the cases of the anterior lobe, intergular, interpectoral, and interfemoral ratios, *luteola* exhibits extremes not found in *ornata.* The three specimens of *longinsulae* for which ratios can be calculated have interfemoral ratios 18, 23, and 25, which are close to the average interfemoral ratios exhibited by *luteola* but outside the observed averages of *ornata.*

The most distinguishing feature of *luteola* is the high number of radiating lines on the carapace, as Legler (1960) noted. When counted on the 2nd costal scute, the average number of lines is 12 to 14 in *luteola* versus 6 to 9 in *ornata.* Infrequently the radiating light lines may be broken up into spots. Another distinctive feature of *luteola* is the horn or straw-colored ground color. One-third of the specimens in some samples and up to 70% of the specimens in other samples display this coloration. Some individuals of *luteola* exhibit this coloration only in the ground color, while others carry it to the extreme of having a uniform greenish-horn or straw-colored shell. This uniform color of some individuals was the main basis on which *luteola* was named (Smith and Ramsey, 1952).

VERTICAL DISTRIBUTION: — No fossils of *T. o luteola* have yet been found, but *luteola* is virtually impossible to distinguish from *longinsulae.* The differences between the two are so slight that it may be presumed that *luteola* evolved from *longinsulae* by a simple rearrangement of existing alleles (Auffenberg and Milstead, 1965; Milstead, 1967; Milstead and Tinkle, 1967). Additional fossil specimens may show that the *luteola* phenotype was the most frequent phenotype within the range of variation of *longinsulae*. Should this be the case, *luteola* will have to be considered a synonym of *longinsulae*.

The known specimens of *longinsulae* are from Kansas and Oklahoma and are well outside of the present day range of *luteola*. I attribute this to displacement during Pleistocene times. It is suggested that during pluvial periods in the Pleistocene, forests extended into the present day Great Plains from both east and west and forced the ornate box turtles south and west (Auffenberg and Milstead, 1965; Milstead, 1967; Milstead and Tinkle, 1967). Reinvasion may have occurred during arid periods in the middle and late Pleistocene, but a post-Wisconsin return to habitats north and east of the modern Chihuahuan Desert was prohibited by the spread of *T. o. ornata* into those areas. The development of the Chihuahuan and Sonoran deserts in Recent times may have restricted the range of *T. o. luteola* and forced it northward (and possibly eastward). With its distribution restricted northward by *ornata* and southward by the deserts, *luteola* might be considered as a relict in danger of extinction in future times.

PRESENT INTERGRADATION: — The characteristics used to distinguish *luteola* and *ornata* make it exceedingly difficult to recognize intergrades between them. I identify samples 55 and 56 (Table 3) as *T. o. ornata x luteola* because they appear to be intermediate between the two subspecies in the characters of size, % with hinge opposite 5th marginal, % with hinge opposite 6th marginal, number of radiating lines, and % with some trace of horn-coloring. Sample 56 is from the extreme northern portion of the Chihuahuan Desert in the ecotone between the Chihuahuan, Kansan, and Navahonian biotic provinces of Dice (1943), and this is more or less where intergradation between *luteola* and *ornata* is expected. Sample 55, however, presents some problems because it is from the ecotone betwen the Tamaulipan and Texan biotic provinces (Dice, 1943; Blair, 1950), and is far removed from any known present day contact with *luteola*.

When we were both working in southeastern Texas and before either of us became seriously interested in box turtles, Auffenberg and I thought that ornate box turtles from the sample 55 area might represent an undescribed subspecies. But in discussing this with Legler about the time his book appeared (1960), he suggested that the turtles in question might be *ornata-luteola* intergrades. Now that the data are analyzed, this seems to be the best assumption. The only difficulty in accepting this view is the lack of contact between these turtles and the range of *luteola,* but this hiatus in range may be more apparent than real. Only a few specimens from southern Texas have reached collections (I have seen two from Kennedy County and one from LaSalle County), and no specimens are known from the Tamaulipan biotic province in northern Mexico. Additional specimens may show that these intergrades and *luteola* are contiguously distributed. The Chihuahuan and Tamaulipan biotic provinces are separated in Texas by the Balconian biotic province (of Blair, 1950), which is occupied by *T. o. ornata.* The Chihuahuan and Tamaulipan provinces have a broad zone of contact in northern Mexico, and there are, or have been, faunal exchanges between them (see Milstead, 1960, for examples of this).

Samples 57-59 appear to be *T. o. ornata,* but with a slight influence of *luteola,* as shown by some horn-colored individuals, high number of radiating lines, and relatively high percentage of individuals with the hinge located opposite the 6th marginal (Table 3). One or more of these traits are also shown by samples 62, 67, 72, and 77, but these samples are well-removed from *luteola* and are surrounded by "good" *ornata.*

RECENT SPECIMENS EXAMINED

51L. *T. o. luteola.* Apachian biotic province of Dice (1943). 30 specimens from Cochise, Pima, Pinal, and Santa Cruz counties, Arizona, and extreme northwestern Chihuahua: AMNH 64265-6; ASU 62021, 62368; UAZ 13092, 13093 (twice), 13094, 13101-2; UMMZ 13096, 69984, 71179-81, 75815, 114102-3; USNM 20556-61, 20989-93, 21707; Stanford University, one unnumbered specimen.

52L. *T. o. luteola.* Ecotone between Apachian and Chihuahuan biotic provinces of Dice (1943). 27 specimens from northern Chihuahua near El Paso; Dona Ana and Otero counties, New Mexico; and El Paso County, Texas: FMNH 2002 A-B, 4791; NMS 1876 and two unnumbered specimens; UCM 20780-1; UMMZ 60090-1, 64728-9, 72534-6, 85095, 101286-9; USNM 19061-2, 19394, 19410-2, 45771.

53L. *T. o. luteola.* Chihuahuan biotic province of Blair (1940, 1950), Dice (1943), Goldman and Moore (1945), Goldman (1951), and Milstead (1960, 1961). 14 specimens from near Gallezo and Ramos, Chihuahua: AMNH 82126; KU 45019, 45055, 51427; UCB 46651-54, 72844-49.

54L. *T. o. luteola.* Chihuahuan biotic province of Blair (1940-1950), Dice (1943), Goldman and Moore (1945), Goldman (1951), and Milstead (1960, 1961). 10 specimens from Brewster, Jeff Davis, and Presidio counties, Texas:

BUSM 6445; FMNH 27761; TCW 14897; UMMZ 50012, 100986, 101285, 114354-5; USNM 103676, 107755.

55RL. *T. o. ornata x luteola.* Ecotone between Tamaulipan and Texan biotic provinces of Dice (1943) and Blair (1950). 25 specimens from Arkansas, Calhoun, DeWitte, Jackson, Lavaca, Matagorda, Refugio, San Patricio, and Victoria counties, Teaxs: BCB 2628, 2631, 8797, 8800; BUSM 575, 2408, 2433-4, 2447, 2450, 7002; TCW 314, 4670, 13980, 14947, 14949; UMMZ 96571, 116266-70; USNM 20959.

56RL. *T. o. ornata x luteola.* Ecotone between Chihuahuan, Kansan, and Navahonian biotic provinces of Dice (1943) and Blair (1950). 38 specimens from Eddy and Lea counties, New Mexico; and Culberson, Gaines, Midland, Reeves, Ward, Winkler, and Yoakum counties, Texas: AMNH 71298-9, 71303; BCB 8888; FMNH 2003; NMS one unnumbered specimen; TT 379, 537 A-C; 976, 1767, 1835-6, 1845, 1870-1, 2002-3, 2007, 2017; UCM 6037-9; UMMZ 70199, 72499, 85094, 92746, 121905-6; USNM 19119, 92928; UT 17954-5, 20149-51.

Terrapene ornata ornata (Agassiz)

Figure 16, Table 3 (57-82)

Cistudo ornata Agassiz, 1857, Contrib. Nat. Hist. U.S., 1:445.
Terrapene ornata Baur, 1891, Science, 17:191.
Terrapene ornata ornata Smith and Ramsey, 1952, Wasmann Jour. Biol., 10:48.
Terrapene ornata var. *cimarronensis* Cragin, 1894, Colorado College Studies, 5:37.

RECOGNITION FEATURES: – The low number of radiating lines on the carapace of *T. o. ornata* distinguishes it from the other living subspecies, *T. o. luteola.* Slightly smaller size and a tendency to have the plastral hinge located opposite the contact betwen the 5th and 6th marginal scutes also separate *ornata* from *luteola.* Scalloped marginal scutes, a more sharply elevated 1st central scute, a higher 3rd central scute, more flaring marginal scutes and, a rugose shell distinguish *ornata* from both *luteola* and the extinct *longinsulae* (Figure 2, K).

PRESENT DISTRIBUTION: – (Figure 1) Between the Mississippi River and the Rocky Mountains from southern South Dakota to south central Texas. East of the Mississippi River, *T. o. ornata* extends into Illinois and Indiana in the "Prairie Peninsula" of Schmidt (1939) and Auffenberg and Milstead (1965). In the more heavily forested portions of the Austroriparian biotic province (of Dice, 1943) in southeastern Missouri, Arkansas, Louisiana, and eastern Texas, *T. o. ornata* appears to be extremely rare, although specimens

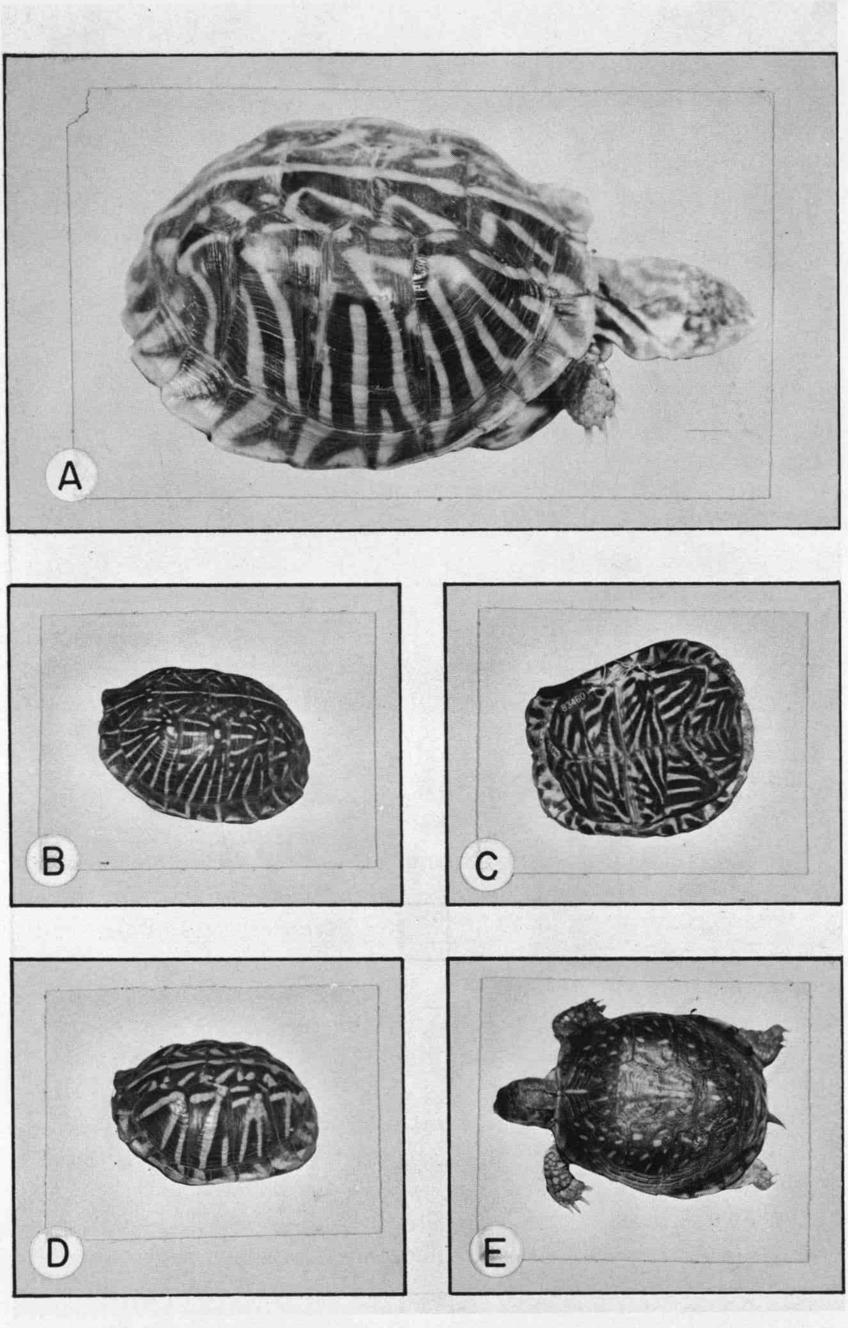

FIGURE 16. *Terrapene ornata ornata*. A, TT 105, Dickens County, Texas. B-C, FMNH 83460, Sapulpa, Oklahoma. D, FMNH 83346, Amarillo, Texas. E, UT 14001, Travis County, Texas.

have been recorded from cleared areas. The subspecies is abundant in the Austroriparian biotic province on the Texas coastal plain, but is rare on the coastal plain in southwestern Louisiana, and does not appear to reach the Mississippi in southeastern Louisiana. Intergradation with *luteola* (discussed above) occurs in the extreme northern part of the Chihuahuan Desert in New Mexico and Texas, and in southeastern Texas. One of the finest ecological studies ever performed on a reptile has recently been reported for *T. o. ornata* by Legler (1960).

GENERAL DESCRIPTION: – The smallest of the box turtles in both the Ornata and Carolina groups (Table 1). The largest specimen examined (KU 18358) is 134 mm in carapace length. The shell shape tends to be round in most cases, but occasional individuals are somewhat elongated (oval). The plastral hinge of *ornata* is usually (Table 3, 57-82) located opposite the contact between the 5th and 6th marginal scutes. Individuals with the plastral hinge located opposite the 5th marginal and those with it located opposite the 6th are about equally distributed in the samples. The maximum degree of elevation of the 1st central scute is about 45°, carapace height at the 3rd central is 48% of the carapace length in some specimens, and height at the 4th central reaches 30%. Thus *T. o. ornata* is the highest member of the Ornata Group. Flaring of the marginals in *T. o. ornata* (Figure 16) is the greatest in the species, and is approximately the same as in *T. carolina triunguis*. The posterioventral edge of each marginal scute in *T. o. ornata* projects outward beyond the anterioventral edge of the following scute, and this produces a scalloped or serrate posterior edge of the carapace (Figure 16). The carapacial scutes of many specimens of *ornata* tend to be quite rugose, a character not seen in *luteola* or *longinsulae*. This rugosity is not universally present even in medium-sized specimens of *ornata*, and older specimens tend to lose it through abrasion.

When counted on the 2nd costal scute, the number of radiating light lines averages 6 to 9 in *T. o. ornata*. In the 26 samples of *ornata* (Table 3, 57-82), 11 samples had an average of 8 lines, 8 samples had 7 lines, 6 samples 9, and 1 sample 6. Infrequently the lines are broken up into spots. Unlike *luteola*, *ornata* tends to retain its pattern throughout life.

VERTICAL DISTRIBUTION: – I have examined only two fossils specimens of *T. o. ornata*, ANSP 13780 and UT 937-201. Both are from deposits estimated to be of late or post-Wisconsin age (5000-10,000

B.P.), and both have the carapace elevated posteriorly and scalloped marginals posteriorly as in modern *ornata* (Milstead, 1967, Fig. 1 B). Holman (1963) records fragments of an ornate box turtle from the Sangamon of Denton County, Texas, but it now appears that the deposits may be of early Wisconsin age.

It has been suggested (Auffenberg and Milstead, 1965; Milstead 1967; Milstead and Tinkle, 1967) that *T. o. ornata* may have arisen from a relict population of *luteola* left to the north or east of the main population during one of the Pleistocene population shifts. This suggestion presumes that, during one of the pluvial periods of the Pleistocene when *luteola* (or *longinsulae*) shifted its range southward, a relict prairie area something like the modern prairie peninsula (Schmidt, 1939; Auffenberg and Milstead, 1965) in Illinois, Indiana, and Ohio permitted a population to remain in the otherwise vacated area. This isolated population evolved into the more mesically-adapted *ornata*[1], and with return of arid conditions following the Wisconsin glaciation it dispersed throughout the present day Great Plains.

RECENT SPECIMENS EXAMINED: — Kansan Biotic Province of Dice (1943).

57R(L). *T. o. ornata* (with some influence of *luteola* as noted above). 11 specimens from Chaves and Quay counties, New Mexico: FMNH 83355; NMS 267-8; UMMZ 69106-12, 69188.

58R(L). *T. o. ornata* (with some influence of *luteola* as noted above). 63 specimens from Baca and Prowers counties, Colorado; Morton County, Kansas; Union County, New Mexico; Cimarron County, Oklahoma; and Dallam, Hartely, and Sherman counties, Texas: FMNH 15470; TCW 4671-2; TT 2017-23, 2592, 2593 A-B, 2594, 2596-8, 2613, 2614 A-B, 2640; UAZ 13106; UCM 1179, 11708, 11710-1, 11729-32, and five unnumbered specimens; UMMZ 62470-4, 62476-9, 62480 (twice), 62481-4, 62486-90, 62493-8, 101322-3; USNM 87024.

59R(L). *T. o. ornata* (with some influence of *luteola* as noted above). 42 specimens from Logan, Phillips, Washington and Yuma counties, Colorado; and Dundy county, Nebraska: AMNH 64262-4, 68242-4; UCM 2560, 3379-80, 3385-8, 3390-1, 3393-6, 3398, 3401, 11688-90, 11692-6, 11712-4, 11716, 11740-1, 11747, 15173; UMMZ 62672-3, 112410; USNM 86907.

60R. *T. o. ornata.* 13 specimens from Adams, Arapahoe, Boulder, Larimer, and Weld counties, Colorado: UCM 2558-9, 11745, 11750, 13651-5; UMMZ 59843-4, 91911-2.

61R. *T. o. ornata.* 40 specimens from Barber, Barton, Edwards, Ellsworth, Ford, Kingman, Kiowa, Meade, Reno, Rice, and Stafford counties, Kansas; and Alfalfa and Harper counties, Oklahoma: ASU 60-121; ASU-ACE field number 62-050; FMNH 16890, 16899; UF 11026, 11027(1), 11028(1);

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[1] That is, more mesically-adapted than *longinsulae* or *luteola*.

KU 1877, 1917, 1936, 1938, 2767, 2856-7, 3214, 6862, 17220-1, 18358, 18369, 18374, 19347, 19485, 41563-65, 50305; UMMZ 62500-1, 64912-4, 96567; USNM 71531-2, 90427-8, 91031-2, 95273.

62R. *T. o. ornata.* 17 specimens from Armstrong, Gray, Hutchinson, Potter, and Randall counties, Texas: FMNH 83346; TT 311, 577-8, 1546, 1546 A; UMMZ 69100-5; UT 10540, 10598, 10694, 10701, 10742.

63R. *T. o. ornata.* 20 specimens from Andrews, Cochran, Hale, Hockley, Lamb, and Lubbock counties, Texas: TT 151, 171, 342, 346, 356, 378, 380, 539, 1060 A-E, 1531 A-C, 2006, 2008, 2010, 2015.

64R. *T. o. ornata.* 8 specimens from Hemphill and Lipscomb counties, Texas: TT 695, 1552 A-C, 1552 E-F, 2159; USNM 45340.

65R. *T. o. ornata.* 9 specimens from Briscoe, Childress, Dickens, and Motley counties, Texas: TT 105, 179, 317, 317.2, 544-5, 579, 694, 771, 1563; USNM 92654, 92690, 92732, 92759; UT 10276.

Mesquite Plains Biotic Province of Blair (1950).

66R. *T. o. ornata.* 8 specimens from Baylor, Clay, Knox, Throckmorton and Wichita counties, Texas; and Comanche County, Oklahoma: FMNH 13163, 47841; TT 187, 1424, 2400; UMMZ 70349; USNM 83689; UT 10275.

67R. *T. o. ornata.* 18 specimens from Brown, Callahan, Coleman, Comanche, Erath, Palo Pinto, and Taylor counties. Texas: AMNH 66108-10, 66116-7; ASU 326; BCB 6840-1; BUSM 0041, 0098; FMNH 45303-6; TCW 4678, 14898, UMMZ, 85093; UT 21737.

Austroriparian Biotic Province of Dice (1943) and Blair (1950).

68R. *T. o. ornata.* 12 specimens from Brazoria, Chambers, Galveston, Harris, Jefferson, and Waller counties, Texas: BUSM 236, 2337-8, 2340, 2407, 2437, 2442, 7004; FMNH 30588; TCW 313, 4677; USNM 100516; UT 21783-4.

Balconian Biotic Province of Blair (1950).

69R. *T. o. ornata.* 12 specimens from Burnet, Caldwell, Comal, Hays, and Travis counties, Texas: AMNH 32835, 36720, 67217; BCB 2236, 2787; BUSM 2406, 2658; UT 14000-02; 21652, 26829.

Texan Biotic Province of Dice (1943) and Blair (1950).

70R. *T. o. ornata.* 13 specimens from Bastrop, Brazos, Colorado, Fayette, Lee, and Walker counties, Texas: BCB 2021, 2109, 2627; TCW 297, 303, 4660, 4669, 14899, 15866, and four uncatalogued in student collections; UMMZ 118178.

71R. *T. o. ornata.* 17 specimens from Bell, Bosque, Coryell, Limestone, and McLennan counties, Texas: BMNH 1897.8.11.3-4, 1897.10.15.4; BUSM 0089-90, 2404, 2657, 3612-3, 5666, 7000-1; FMNH 46287-8; TCW 4676, 15423; USNM 100524.

72R. *T. o. ornata.* 12 specimens from Dallas, Denton, Hunt, Johnson, Navarro, Tarrant, and Wise counties, Texas; and Atoka and Carter counties, Oklahoma:

AMNH 7481; BCB 8799; BUSM 2336, 3482; FMNN 37464, 45302; UMMZ 70477-8; USNM 83861, 95402, 100532-3.

Ecotone between the Illinoian, Kansan, and Texan biotic provinces of Dice (1943).

73R. *T. o. ornata.* 19 specimens from Cleveland, Kingfisher, Major, and Oklahoma counties, Oklahoma: AMNH 37043; FMNH 8316; UCM 11725; UMMZ 81387-92, 81394-402; USNM 16263.

Ecotone between the Austroriparian, Carolinian, Illinoian, and Texan biotic provinces of Dice (1943).

74R. *T. o. ornata.* 32 specimens from Creek, Mayes, McIntosh, Muskogee, Okmulgee, Pawnee, Rogers, and Tulsa counties, Oklahoma: AMNH 7539, 16918, 16923; BCB 4361; FMNH 8490-1, 83460; UMMZ 64677-9, 69981, 81383, 81385, 81405, 81407-10, 81702-03, 81706-8, 81710-11, 85092, 96574-6, 96578, 96580, 96583.

Ecotone between the Illinoian and Kansan biotic provinces of Dice (1943).

75R. *T. o. ornata.* 9 specimens from Grove and Trego counties, Kansas: AMNH 15264; FMNH 22678; KU 2802, 3538, 3541, 3770-1; UCM 13795-6.

76R. *T. o. ornata.* 22 specimens from Boyd, Brown, Cherry, Custer, Grant, Halsey, and Holt counties, Nebraska; and Washabaugh county, South Dakota: AMNH 36724-5, 65435-6, 65441, 66198-9, 66201-2; FMNH 26048, 26050, 33723, 46156-7; UMMZ 19850, 67565, 76547, 78122, 79851-2; USNM 22304, 138875.

Illinoian Biotic Province of Dice (1943).

77R. *T. o. ornata.* 12 specimens from Clay, Pottanatomie, Riley, and Washington counties, Kansas: KU 20944, 41569, 48224-6; UMMZ 67560-64, 67660; USNM 7692.

78R. *T. o. ornata.* 19 specimens from Cook and Will counties, Illinois: FMNH 23006, 23010-6, 23018-9, 23022-3, 23025-7, 23030-2, 26400.

Ecotone between the Carolinian and Illinoian biotic provinces of Dice (1943).

79R. *T. o. ornata.* 38 specimens from Anderson, Bourbon, Chataqua, Cherokee, Cowley, Crawford, Elk, Linn, Montgomery, Sumner, and Wilson counties, Kansas; Barton, Jasper, Newton, and Vernon counties, Missouri and Craig and Kay counties, Oklahoma: FMNH 83347-8; KU 1172, 1370, 1911-2, 1919, 1937, 2753, 3309, 3332-3, 3830, 18371, 18381, 19342, 19346, 19352, 20941, 23353-4, 46856, 46860; UMMZ 70479, 71754, 72531, 81403; USNM 45306, 55660, 85493, 86422, 90433, 91028-9, 93765, 94369, 95302, 95410.

80R. *T. o. ornata.* 20 specimens from Douglas, Franklin, Miami, Shawnee, and Wabaunsee counties, Kansas; and Jackson and Osage counties, Missouri: KU 1105-6, 1920, 2745, 2748, 2769, 2847, 2861, 2901, 3160, 14113, 22073, 52161; UMMZ 59088, 79882; USNM 55663, 86425, 90429-31.

81R. *T. o. ornata.* 8 specimens from Richland and Wayne counties, Illinois: UMMZ 44352-3, 44356, 44593, 44596; USNM 9937, 9940, 13827.

Carolinian Biotic Province of Dice (1943).
82R. *T. o. ornata.* 5 specimens from Jasper, Pulaski, and White counties, Indiana: UMMZ 103406-8, 107928, 108075.

Terrapene nelsoni klauberi Bogert

Figure 17, Table 3 (83)

Terrapene klauberi Bogert, 1943, Amer. Mus. Nov. (1226): 1-4.
Terrapene nelsoni klauberi Milstead and Tinkle, 1967, Copeia (1): 180-187.

RECOGNITION FEATURES: – The interhumeral and interpectoral seam ratios (Table 3, cf. 83 and 84) appear to be the best means of distinguishing *T. n. klauberi* from *T. n. nelsoni,* although the round or oval *ornata*-like shell some individuals of *klauberi* exhibit readily distinguishes those individuals from *nelsoni.*

PRESENT DISTRIBUTION: – (Figure 1) known from several localities in southwestern Sonora and one locality in western Sinaloa, Mexico (Milstead and Tinkle, 1967).

GENERAL DESCRIPTION: – One of the largest of the Ornata Group box turtles with an average carapace length of 131 mm and a maximum of 151 mm. The carapace is round or oval (*ornata*-like) to elongate, and is quite flat (40% at the 3rd central and 27% at the 4th central). The angle of elevation of the 1st central scute is about 38°, and this gives *klauberi* a flatter anterior portion of the carapace than in *T. o. ornata* and *T. o. luteola,* but not so flat as in one specimen of *T. o. longinsulae* and in some specimens of *T. n. nelsoni.* The marginal scutes of male *klauberi* are flared to a much greater extent than they are in male *T. o. ornata,* but not to the extent that they are in some males of *T. n. nelsoni.* Female *klauberi* have the marginals flared to about the extent that they are in male *T. o. ornata.* A lateral keel may be present in both males and females of *T. n. klauberi.* The posterior margin of the carapace is smooth rather than emarginate as in *T. o. ornata.*

Coloration in most *klauberi* specimens consists of small, coffee-colored spots in the shell, head, neck, and forelimbs. Ground color of the shell is horn or greenish brown. Two of the specimens examined have a uniform horn-colored shell without spots and one specimen shows indistinct spots.

VERTICAL DISTRIBUTION: – No fossils of *T. n. klauberi* are known. A suggestion on its evolution is made under the discussion of *T. n. nelsoni.*

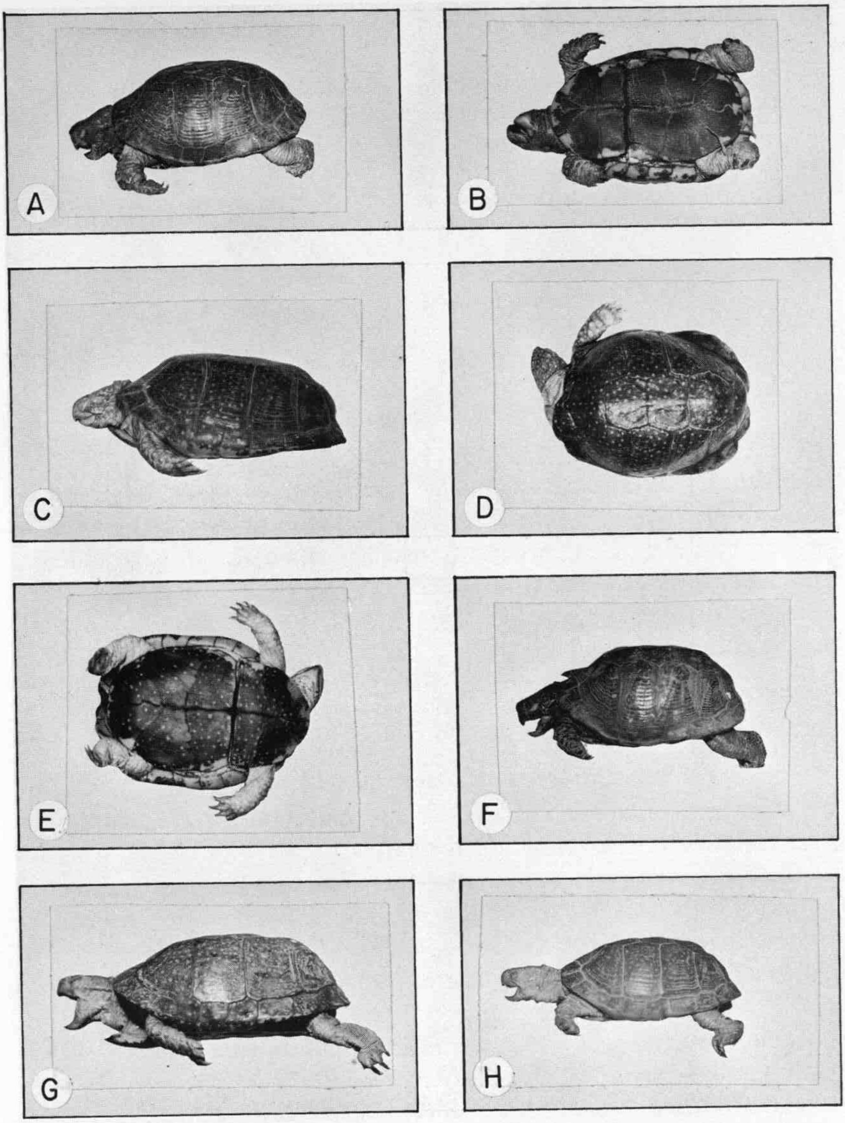

FIGURE 17. *Terrapene nelsoni klauberi*. A-B, AMNH 63763, Alamos, Sonora. C-E, FMNH 41269, near Alamos, Sonora. F, AMNH 63762, Alamos, Sonora. G, Stanford University 10770, Sierra de Batuc, Sonora. H, AMNH 63751, Holotype, Rancho Guricoba, near Alamos, Sonora.

RECENT SPECIMENS EXAMINED

83. *T. n. klauberi.* 15 specimens from southwestern Sonora, Mexico. Most of the specimens in this sample and the one known specimen from Sinaloa are cited in Milstead and Tinkle (1967). The only additions to the sample are MCZ 46855 and UMKC 0170 from Alamos, Sonora. As noted by Milstead and

Tinkle (1967), specimens labelled "Alamos" may be stray specimens that have wandered down out of the mountians, or they may have been collected at higher altitudes by local collectors. The Sierra de Alamos above the village of Alamos has an oak-savannah association above 3500 feet that may be the actual locality for the Alamos specimens. All the specimens of *T. n. nelsoni* have come from an oak-savannah association in Nayarit.

Terrapene nelsoni nelsoni Stejneger

Figure 18, Table 3 (84)

Terrapene nelsoni Stejneger, 1925, Jour. Wash. Acad. Sci., 15:463.
Terrapene nelsoni nelsoni Milstead and Tinkle, 1967, Copeia, (1): 180-187.

RECOGNITION FEATURES: — The interhumeral and interpectoral seam ratios (Table 3, cf. 83 and 84) appear to be the best means of distinguishing *T. n. nelsoni* from *T. n. klauberi*, although the flat carapace anteriorly and the widely flaring marginals exihibited by some *nelsoni* males (Figures 2L, 18 A-B) readily distinguish those individuals from *klauberi*.

PRESENT DISTRIBUTION: — (Figure 1) known only from the type locality at Pedro Pablo, Nayarit, Mexico (Milstead and Tinkle, 1967).

GENERAL DESCRIPTION: — A large Ornata Group box turtle with an average carapace length of 134 mm and a maximum of 146 mm. The carapace is elongate and relatively flat (45% of carapace length at the 3rd central and 30% at the 4th central). The most distinctive feature of the subspecies is the extremely flat anterior portion of the carapace exhibited by some males (Figures 2L, 18). This is produced jointly by widely flaring marginals over the forelimbs and a low angle of elevation (30°) of the first central scute. The posterior marginals of males are flared almost to the extent they are in *T. carolina major*. In females the marginals are flared as they are in males of *T. o. ornata*. A lateral keel may be present in both males and females of *T. n. nelsoni*. The posterior margin of the carapace is smooth rather than emarginate as in *T. o. ornata*. Differences of 3% and 2% respectively exist between the interhumeral and interpectoral seam ratios of *nelsoni* and those of *klauberi* (Table 3, cf. 83 and 84). These differences appear to be the best means of distinguishing between the two subspecies at the moment.

The known specimens of *T. n. nelsoni* have straw-colored to horn-colored or brownish-green ground color with small coffee-colored spots on the shell, head, neck, and forelimbs. The holotypes and two other specimens of *nelsoni* show a tendency toward a uniform horn color by having few and indistinct spots. I suggest that uniform horn-colored individuals do exist in the population at Pedro Pablo,

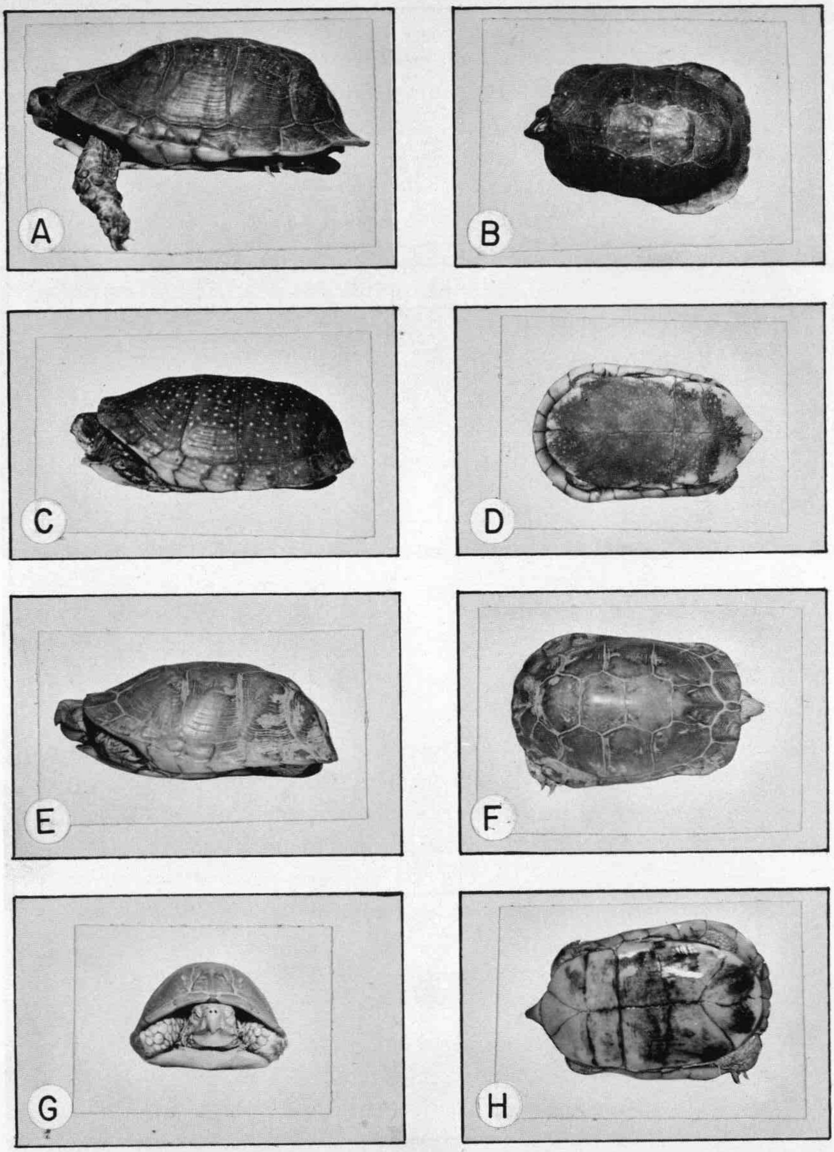

FIGURE 18. *Terrapene nelsoni* from Pedro Pablo, Nayarit. A-B, living male. C-D, living female. E-H, USNM 46252, Holotype.

and that their absence from the sample is a bias. Of 37 specimens recently collected at Pedro Pablo (Milstead and Tinkle, 1967) 36 were collected by the local residents of the area. The one turtle they did not collect, but which they used as a guide, had many distinct spots.

Some specimens of *T. o. ornata* and *T. o. luteola* have their patterns of radiating lines broken up into spots. In most cases these spots are very short dashes of variable length and width. In both subspecies of *nelsoni* the spots are small, almost round, and of fairly constant size. A pattern of radiating lines appears in all living forms of the genus except *nelsoni* and *klauberi*, so I presume that their spotted patterns arose through the interruption of radiating lines as in *T. ornata*. If lines are drawn through the spots of *T. nelsoni* in a radiating pattern, a high number of lines results: 10 to 14, as in *T. o. luteola*, to which I consider *T. nelsoni* to be closely related through *T. o. longinsulae*. However, almost any kind of pattern desired can be obtained by drawing lines through the spots.

VERTICAL DISTRIBUTION: – No fossils of *T. nelsoni* are known, although size and the flattened anterior portion of the carapace indicate relationship with the *T. o. longinsulae* fossils. It is suggested (Auffenberg and Milstead, 1965; Milstead and Tinkle, 1967) that *longinsulae* (or perhaps *luteola*) passed through the Rocky Mountains (Rocky Mountain Corridor of Auffenberg and Milstead, 1965) some time during the Pliocene or Pleistocene and reached the foothills of the Sierra Madre Occidental. Subsequently the route westward became closed, and the isolated western population began to diverge into *T. nelsoni*. Closing of the corridor to ornate box turtles could have occurred through either the return of arid conditions in the western portion of the corridor or development of more mesic conditions in the central portion of the corridor. Chance crossing of an ecological or physical barrier by some individuals, or development of such barriers, could have divided *T. nelsoni* turtles into northern and southern populations and set the stage for evolution of two subspecies. Although it is difficult to prove that the differences between *nelsoni* and *klauberi* are worthy of subspecific recognition (see Milstead and Tinkle, 1967), it is apparent that *klauberi* is both geographically and morphologically closer to *longinsulae* (and to *luteola*) than is *nelsoni*. The morphological basis for this statement is the round or oval *ornata*-like carapace of some individuals of *klauberi*, the flat carapace and the higher angle of elevation of the first central scute in *klauberi* (compared with *nelsoni*), and the lesser flaring of the marginal scutes of *klauberi.* As now known, the anterior plastral lobe ratios (Table 3) and the uniform coloration found in some individuals of *klauberi* place it somewhat closer to *luteola* than is *nelsoni.*

RECENT SPECIMENS EXAMINED

84N. *T. n. nelsoni.* 36 specimens which include the holotype (USNM 46252) and 35 of 37 topotypic specimens reported by Milstead and Tinkle (1967). Two specimens in the Milstead-Tinkle series now at Texas Technological College were not studied.

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TABLE 1. RANGES OF SAMPLE AVERAGES FOR CARAPACE LENGTHS AND PLASTRAL RATIOS FOR EXTANT TAXA OF TERRAPENE.

	Sample Number	Carapace Length (mm)	Anterior Lobe/ Posterior Lobe (%)	Intergular Seam/ Anterior Lobe (%)	Interhumeral Seam/ Anterior Lobe (%)	Interpectoral Seam/ Anterior Lobe (%)	Interabdominal Seam/ Posterior Lobe (%)	Interfemoral Seam/ Posterior Lobe (%)	Interanal Seam/ Posterior Lobe (%)
T. carolina carolina	1-11	122-140	68-72	47-52	18-23	29-31	34-35	9-12	53-56
T. carolina bauri	16-17	123-130	69-72	40-41	27-29	30-33	34-35	12-13	53
T. carolina major	23	162	66	45	29	26	35	12	53
T. carolina triunguis	32-43	116-127	68-72	47-52	18-22	29-34	32-36	12-16	52-55
T. carolina mexicana	48	145	72	41	23	36	33	15	52
T. carolina yucatana	49	145	64	37	33	33	32	21	47
T. coahuila	50	133	63	49	20	30	35	11	54
T. ornata luteola	51-54	122-131	69-72	46-56	12-15	32-36	29-30	19-22	48-51
T. ornata ornata	60-82	102-121	66-71	50-59	11-15	26-35	27-32	18-23	47-52
T. nelsoni klauberi	83	132	66	49	19	33	38	16	46
T. nelsoni nelsoni	84	134	65	50	16	35	39	16	46
Carolina Group	Above Combined	116-162	63-72	38-52	18-33	26-36	32-35	9-21	47-56
Ornata Group	Above Combined	102-134	65-72	46-59	11-19	26-36	27-39	16-23	46-52

TABLE 2. MORPHOLOGIC CHARACTERS OF EXTANT POPULATIONS, CAROLINA GROUP, GENUS *Terrapene*.

Sample Number	Number Specimens	Average Carapace Length	% with straight-sided 1st Central	% with enlarged axillary scale	Anterior Lobe/ Posterior Lobe	Intergular Seam/ Anterior Lobe	Interhumeral Seam/ Anterior Lobe	Interpectoral Seam/ Anterior Lobe	Interabdominal Seam/ Posterior Lobe	Interfemoral Seam/ Posterior Lobe	Interanal Seam/ Posterior Lobe
1C	14	131	0	13	69	48	21	31	34	11	55
2C	10	140	10	20	72	47	22	31	34	10	56
3C	53	125	4	32	70	47	22	31	34	12	54
4C	21	128	10	32	69	51	19	30	34	11	55
5C	45	126	12	22	69	49	21	31	34	11	55
6C	7	124	0	57	69	52	18	29	34	10	55
7C	28	125	3	44	70	48	20	31	34	10	56
8C	56	122	9	54	69	48	21	31	34	9	56
9C	24	125	4	50	68	49	19	31	34	10	55
10C	39	139	8	80	72	47	20	31	35	11	53
11C	21	122	10	48	71	48	23	29	35	10	55
12C(T)	27	133	4	60	70	47	21	31	34	12	54
13C(T)	7	114	0	14	71	44	23	33	35	12	52
14C(B)	20	128	15	95	69	46	22	32	34	11	55
15CB	16	120	38	12	70	44	25	31	35	10	54
16B	27	130	7	4	69	40	27	33	34	13	53
17B	18	123	9	6	72	41	29	30	35	12	53
18BM	11	143	36	18	69	38	29	31	35	11	54
19BM	9	139	56	22	69	37	29	32	34	13	53
20BM	12	138	50	0	67	43	28	31	34	11	54
21BM	36	128	36	16	69	40	26	33	35	12	53
22BM	7	134	71	0	69	37	30	33	34	12	54
23M	59	162	0	100	66	45	29	26	35	12	53
24CMT	31	128	3	30	70	46	22	32	33	13	54
25CMT	34	125	4	21	69	46	24	30	34	12	54
26CMT	16	121	6	25	68	46	22	32	35	10	55
27MT	36	137	0	94	68	46	24	29	34	11	54
28MT	25	121	4	72	68	48	21	30	35	12	53
29MT	27	123	9	74	68	46	23	30	34	14	53

TABLE 2. MORPHOLOGIC CHARACTERS OF EXTANT POPULATIONS, CAROLINA GROUP, GENUS *Terrapene*. (Continued)

Sample Number	Number Specimens	Carapace Lg.	1st. Central	Axillary	AL/PL	IG/AL	IH/AL	IP/AL	IA/PL	IF/PL	IA/PL
30MT	6	119	20	50	70	44	24	32	33	14	53
31T(M)	12	116	0	58	72	48	19	32	34	12	54
32T	14	117	14	80	72	50	19	30	32	15	52
33T	55	118	4	55	71	49	18	32	33	14	53
34T	15	120	0	53	72	50	19	31	33	14	53
35T	11	116	9	64	72	49	18	33	34	13	52
36T	11	120	9	91	70	47	20	33	36	13	52
37T	15	119	0	87	69	49	18	32	34	13	53
38T	14	131	0	86	68	47	22	31	33	15	52
39T	22	116	0	41	68	50	20	30	34	12	54
40T	37	124	6	70	71	50	20	30	36	16	54
41T	47	127	2	49	70	51	20	29	36	16	55
42T	15	127	0	60	70	50	21	29	34	13	52
43T	16	123	0	56	70	52	18	34	34	14	52
44T(C)	12	125	0	67	69	49	20	31	35	13	52
45CT	16	127	6	50	72	48	21	27	34	11	54
46CT	24	126	17	50	69	48	20	32	35	11	55
47CT	8	120	12	25	69	47	21	32	35	11	55
48Mx	30	145	0	10	72	41	23	36	33	15	52
49Y	18	145	0	17	64	37	33	30	32	21	47
50Co	58	133	0	78	63	49	20	30	35	11	54

Table 3. Morphological Characters of Extant Populations of *Ornata* Group, Genus *Terrapene*.

Sample Number	Number Specimens	Carapace Length	% with hinge at 5th Marginal	% with hinge at 6th Marginal	Anterior Lobe/ Posterior Lobe	Intergular Seam/ Anterior Lobe	Interhumeral Seam/ Anterior Lobe	Interpectoral Seam/ Anterior Lobe	Interabdominal Seam/ Posterior Lobe	Interfemoral Seam Posterior Lobe	Interanal Seam Posterior Lobe	Radiating Lines	% with Horn Color
51L	30	124	3	76	71	53	15	32	29	21	50	14	70
52L	27	122	0	56	70	54	13	33	30	19	51	13	54
53L	14	128	0	85	72	49	15	36	29	21	50	13	43
54L	10	131	10	70	69	56	12	32	29	22	48	12	33
55RL	25	111	9	35	69	56	12	32	30	21	50	9	20
56RL	38	114	4	28	68	57	12	30	29	20	50	10	17
57R(L)	11	109	30	20	69	56	11	33	27	20	52	9	11
58R(L)	63	118	12	23	68	58	13	30	29	20	52	8	11
59R(L)	42	110	29	29	69	56	14	30	27	20	53	8	10
60R	13	109	23	15	70	56	13	31	27	19	53	8	0
61R	40	113	12	12	70	54	14	32	29	21	49	8	0
62R	17	112	10	30	69	54	14	31	29	21	50	8	0
63R	20	112	0	0	70	55	12	32	30	20	49	....	....
64R	8	110	0	0	69	52	14	32	29	22	49	7	0
65R	18	110	0	18	66	55	12	33	29	20	50	7	0
66R	8	112	20	0	70	50	14	35	29	21	49	7	0
67R	18	116	24	29	68	56	12	31	30	20	50	7	0
68R	12	114	30	20	68	57	14	29	30	22	49	8	0
69R	12	116	40	20	70	55	11	34	30	23	47	8	0
70R	13	108	15	15	69	57	11	31	32	18	50	8	0
71R	17	115	29	24	69	56	13	31	30	21	49	9	0
72R	12	109	17	33	68	55	13	32	29	21	50	8	0
73R	19	111	11	28	70	54	15	31	29	21	50	7	0
74R	32	106	10	23	69	55	13	32	31	22	48	7	0
75R	9	121	33	11	69	53	13	33	30	21	49	9	0
76R	22	114	32	4	69	57	13	30	29	21	51	8	0
77R	12	117	25	8	71	55	12	33	29	22	49	9	8
78R	19	105	21	21	69	55	13	31	30	21	48	6	0
79R	38	109	11	17	69	55	13	32	30	21	49	7	0
80R	20	112	15	0	71	56	15	29	30	22	48	8	0
81R	8	106	12	12	70	55	16	29	30	21	49	9	0
82R	5	102	20	20	68	59	15	26	27	21	52	7	0
83K	15	131	55	0	66	49	19	33	38	16	46	....	....
84N	36	134	34	23	65	50	16	35	39	16	46	....	....

Table 4. Morphologic Characters of Fossils of the *Carolina* Group, Genus *Terrapene*.

Sample Number	Average Carapace Length	% with straight-sided 1st central	% with enlarged axillary scale	Anterior Lobe/ Posterior Lobe	Intergular Seam/ Anterior Lobe	Interhumeral Seam/ Anterior Lobe	Interpectoral Seam/ Anterior Lobe	Interabdominal Seam/ Posterior Lobe	Interfemoral Seam/ Posterior Lobe	Interanal Seam/ Posterior Lobe
85PB	155	....	....	69	37	30	32	35	13	52
86PT	174	0	75	....	45	23	33	29	16	15
87T(P)	163	0	0	....	47	18	35	31	16	53

Table 5. Maximum Length Comparisons (in mm) of Fossil and Recent *Terrapene Carolina* from West of the Mississippi River.

Number	Locality	Age	Carapace Length	Anterior Lobe Lg.	Posterior Lobe Lg.
UT882-315	Slaton, Lubbock Co., Texas	Illinoian	230[1]	90	136[1]
UMMP26957	Meade Co., Kansas	Sangamon	230[1]	90[1]	137
UT30907-19B	Henderson Co., Texas	Sangamon	184[1]	72	109[1]
MCZ2170	Archer Co., Texas	Sangamon	235	89	139
UT30967-617	Ingleside (San Patricio Co., Texas)	50-80,000 B.P.	203	80[1]	121[1]
UT30967-270	Ingleside	50-80,000 B.P.	220[1]	86	130[1]
UT30967-615	Ingleside	50-80,000 B.P.	198[1]	78[1]	118
SMU (RKH 55)	Denton Co., Texas	35,000 B.P.	253-281[1]	102	168
UT908-2367	Uvalde Co., Texas	Late Wisconsin	246[1]	96[1]	146
UT903-3687	Friesenhahn Cave (Bexar Co., Texas)	10-14,000 B.P.	233	88	141
UT903-2104	Friesenhahn Cave	10-14,000 B.P.	229[1]	89	139
UT40450-138	Kendall Co., Texas	10,900 B.P.	156[1]	61[1]	93
USNM8617	Travis Co., Texas	5-10,000 B.P.	153	60	91
KU46768	Cherokee Co., Kansas	Present	150	63	85
TCW4666	Brazos Co., Texas	Present	134	53	80
BMNH1947.3.5.48	"Mexico"	Present	173	69	96

[1] Estimates based on proportions of USNM 8617.

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