Fossil Box Turtles (*Terrapene*) from Central North America, and Box Turtles of Eastern Mexico

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A large amount of fossil box turtle material has now been recovered from deposits in the central states of Illinois, Missouri, Kansas, Arkansas, Oklahoma, Texas, and New Mexico. The fossil material has been identified as two species: *Terrapene ornata* of the middle Pliocene to Recent and *Terrapene carolina* of the Pleistocene and Recent. *Terrapene ornata longinsulae* (formerly *T. longinsulae*) is an extinct subspecies known on the basis of five specimens from the middle and late Pliocene and the Aftonian of the Pleistocene in Kansas. Only two fossil specimens of *Terrapene ornata ornata* were examined. Both were from New Mexico, one from a Wisconsin and one from a post-Wisconsin deposit.

Most of the fossil box turtles from the central United States are referred to *Terrapene carolina*. The oldest specimens are from pre-Sangamon deposits of Texas and Kansas and are identified as *T. carolina putnami*. A number of the fossils are of Sangamon and early Wisconsin age and are identified as *Terrapene carolina putnami* × *triunguis*. The majority of the fossils are of late Wisconsin age and are identified as *T. carolina triunguis*, which occupies most of the central U. S. today. It is suggested that at times during the Pliocene and Pleistocene conditions comparable to those of the modern Gulf Coastal Plain extended as far inland as Kansas, New Mexico, and eastern Mexico, and that this broad coastal plain area was occupied by a single subspecies, *T. carolina putnami*. Climatic fluctuations and associated environmental changes during the Pleistocene ultimately led to the differentiation of *putnami* into *T. carolina major* in the southeast and *T. carolina triunguis* in the west.

In Mexico, *T. carolina putnami*, or forms intermediate between *putnami* and *triunguis*, gave rise to *T. carolina mexicana* (formerly *T. m. mexicana*), *T. carolina yucatana* (formerly *T. m. yucatana*), and *T. coahuila*. *T. carolina mexicana* has a restricted distribution in southeastern Mexico and it is morphologically close to *T. carolina triunguis*. Texas fossils of late Wisconsin times indicate that the isolation of *mexicana* and *triunguis* is a relatively recent occurrence. *T. carolina yucatana* is restricted in distribution to the Yucatan Peninsula and it is morphologically close to *T. carolina major*. It is suggested that *yucatana* reached the Yucatan Peninsula during a glacial state of the Pleistocene when sea levels were low and a coastal plain was exposed between the present gulf coast and the mountains. The isolation of *yucatana* occurred prior to that of *mexicana*, and *yucatana* is somewhat closer to the older *putnami* stock than is *mexicana*. *T. coahuila* is restricted in distribution to a bolson in central Coahuila where it maintains an aquatic existence. Its distinct morphology may be attributed either to isolation from *putnami* at a time earlier than the other turtles were isolated or to a higher evolutionary rate as a result of rigorous selective pressure.

A variety of names has been applied to fossil remains of box turtles (*Terrapene*) found in the United States in the last century. In general these names have been given without consideration to comparative morphology from an evolutionary standpoint. The first comparative study was that of Barbour and Stetson (1931). They compared fossil material from Florida with a series of Recent box turtles from the same state and concluded that larger size of the fossils was the only significant difference. They referred all of their fossils to *Terrapene canaliculata* Hay. In 1956 I reported that Texas fossils differed only in larger size when compared with examples of living box turtles (*Terrapene carolina* Linnaeus). Hence, the Texas material also was identified as *T. canaliculata*. After examining a quantity of new material from Florida, Auffenberg (1958) placed *T. canaliculata* in the synonymy of *T. carolina*.

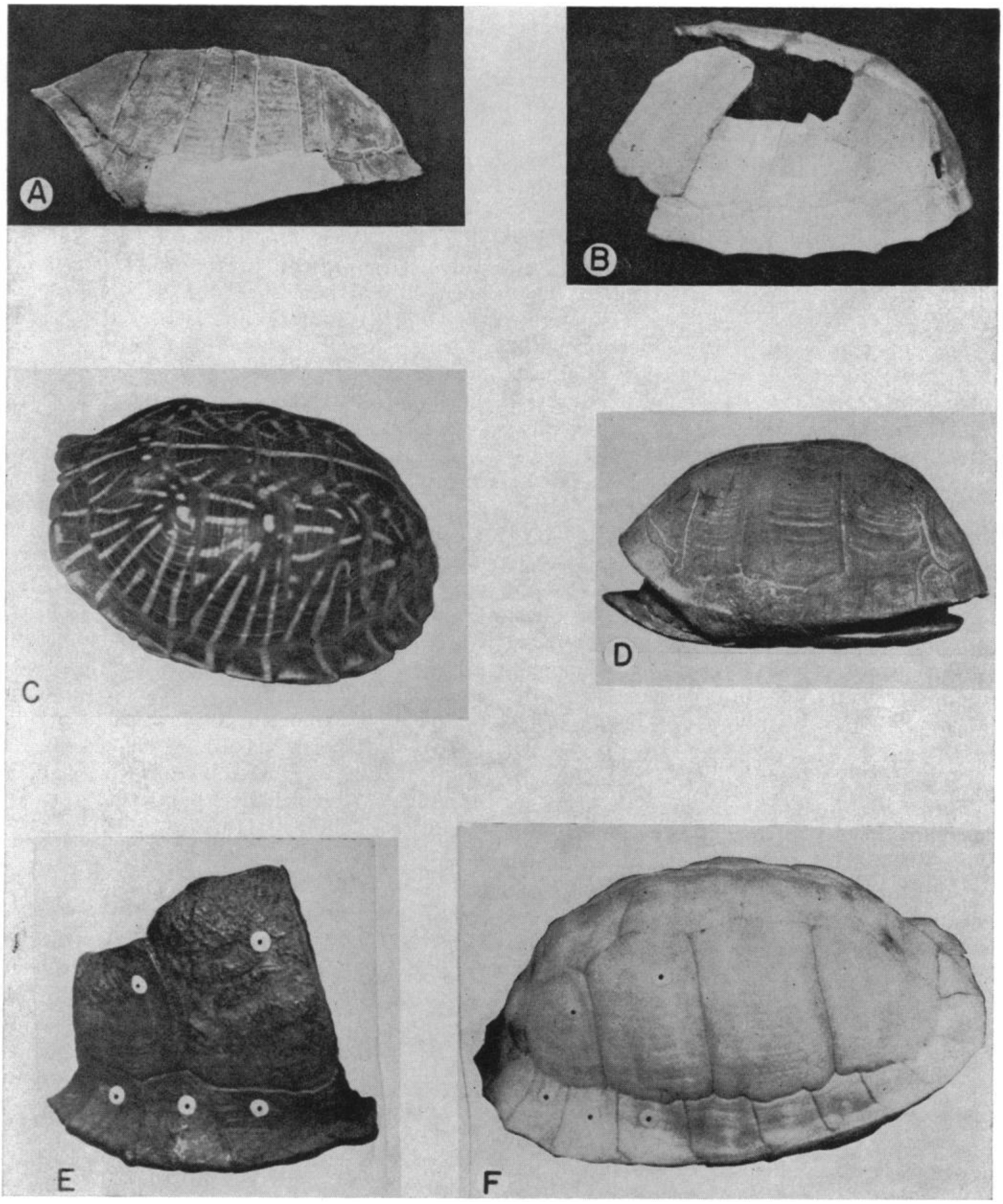

Fig. 1. A. Holotype of *Terrapene ornata longinsulae* (USNM 5983) from lower middle Pliocene of Long Island, Kansas B. *T. o. ornata* (UT 937-201). Fossil remains from post-Wisconsin deposits near Clovis, New Mexico. C. *T. o. ornata* (FMNH 83460). Recent specimen from Sapulpa, Oklahoma. D. *T. carolina triunguis* (USNM 8616—holotype of *Terrapene whitneyi*) from post-Wisconsin gravels in Austin, Texas. E. *T. c. putnami* (UF 1616). Fragment of fossil from Illinoian deposits in Florida. F. *T. c. major* (UMKC—see Auffenberg, 1958:Fig. 4). Recent specimen from Gulf County, Florida. Photographs E and F were made simultaneously from the same negative and are, thus, to the same scale. The specimen of *major* is 190 mm in length. Spots on the shells indicate areas of comparison.

In making his decision Auffenberg pointed out (1) that some modern box turtles are larger than most of the fossils, (2) that in Florida the largest fossils are from different stratigraphic groups than the smaller fossils, and (3) that the smaller fossils from Florida include the modern Florida subspecies of *Terrapene carolina* and intergrades between these subspecies and the larger fossils. Auffenberg applied the name *Terrapene carolina putnami* (Hay) to the large fossil box turtles from Florida (an earlier name in the literature than *canaliculata* by page priority: see Hay, 1907). Auffenberg's work left the subspecific relationships of the western fossils in doubt pending re-analysis of the material.

The collections visited in connection with this report and the initials used to identify them in the text are: Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), Central Missouri State College (CMSC), Field Museum of Natural History (FMNH), Mike Sabbath (MS), Southern Methodist University (SMU), Texas A & M University (TCW), Texas Technological College (TT), Tulane University (TUL), United States National Museum (USNM), University of Colorado (UC), University of Florida (UF), University of Kansas (KU), University of Michigan (MP and MZ), and University of Texas (UT).

Terrapene ornata longinsulae Hay

Terrapene longinsulae (Fig. 1, A) was described as an extinct species from the lower Middle Pliocene of Long Island, Kansas on the basis of a complete carapace, plastron, and skull and some limb bones from a single individual (Hay, 1908a). The holotype (USNM 5983) is close to the modern *T. ornata*, a point on which Auffenberg (1958), Legler (1960), and I (1956, 1959) have agreed. The differences between *longinsulae* and *ornata* are minor, and I now consider the two forms conspecific.

The carapace of the *longinsulae* holotype slopes more ventrad posteriorly than it does in *ornata* (Fig. 1, *cf.* A, B). However, other fossils of *longinsulae* are intermediate in this character. The proneural and first neurals of the holotype are flared outward rather than curved downward, and this interrupts the normal curvature of the shell causing a flattened area anteriorly. This character is more pronounced in other fossils of *longinsulae* than it is in the holotype. The character is present in *ornata*, especially noticeable in comparison with *carolina*, but it is not nearly so strongly developed as in *longinsulae* (Fig. 1, *cf.* A, C, D, F). The fossils also appear to be somewhat more flattened and also more rounded than *ornata* and *luteola* although the condition of their preservation does not permit an accurate comparison. The carapaces of *ornata* and *luteola* are more rugose in some examples than those of the fossils and the marginals are decidedly more emarginate (Fig. 1, *cf.* A, B, C). These are not features universally present in living *ornata*, however. One of the specimens of *longinsulae* (MP 37184) has a faint keel on the fourth central scute and there is an indication of a keel on one of the other specimens (MP 44648). A weak keel posteriorly also occurs in some specimens of *ornata* and *luteola*.

The other fossil material that I am assigning to *T. ornata longinsulae* consists of four specimens in the collection of the University of Michigan Museum of Paleontology. They are: 37184—an almost complete carapace and parts of the plastron from the Ballard Formation (Aftonian) of Meade County, Kansas (Hibbard, 1958); 44648—complete carapace and plastron, but badly distorted; and 37186—fragment of plastron, both from early upper Pliocene of Seward County, Kansas (Hibbard, 1963b); 45689—fragments of a carapace and plastron from the Ogallala Formation (late middle Pliocene) of Beaver County, Oklahoma (Hibbard, 1954).

Terrapene ornata ornata (Agassiz)

I have seen only two fossil specimens which are clearly referable to *T. o. ornata* (Fig. 1, B): ANSP 13780 from the Wisconsin of Clovis, New Mexico, and UT 937-201 from the post-Wisconsin of Clovis, New Mexico. Holman (1963) referred fragments of a box turtle from the Sangamon of Denton County, Texas, to this species.

T. o. longinsulae is known from the middle and late Pliocene and from the early Pleistocene. *T. o. ornata* is known from the late Pleistocene and the Recent, and *T. o. luteola* is known from the Recent. Of the two living subspecies, *luteola* appears to be closer to *longinsulae* than does *ornata*. It is suggested that fluctuating conditions of humidity on the Great Plains during the Pleistocene (discussed below) and accompanying changes in vegetation produced shifts in the ranges of *T. ornata* which brought about the evolution of *luteola* from *longinsulae* by genetic recombinations. *T. o. ornata* may have arisen from a relict population of *luteola* left north or east of the main population during one of the population shifts.

Terrapene carolina (Linnaeus)

Most of the fossil box turtles from the central United States have been recovered from late Pleistocene deposits. Most are representative of *T. carolina.* Today the greater part of the area between the Appalachians and the Great Plains and between the Great Lakes and the Gulf of Mexico is occupied by one subspecies, *T. c. triunguis,* which appears to have evolved during the Pleistocene. The sequence of events, as I picture them, involved the gradual replacement of an older, more widespread subspecies, *T. c. putnami,* by two modern subspecies, *T. c. triunguis* in the midwest and *T. c. major* in the southeast.

The distinguishing characteristics of *T. c. putnami* (Fig. 1, E) are: (1) large size (over 200 mm in adults); (2) a broad, elongated shell; (3) gently rounded in sagittal section as in *T. c. carolina;* (4) a broad heavy postorbital bar[1] in the skull (see Auffenberg, 1958, 1959); (5) a long interhumeral suture; (6) a large axillary scale (occupying at least half of the ventral side of the 4th marginal scute); and (7) extreme flaring of the marginal scutes (see Auffenberg, 1958). Unfortunately not enough specimens of *putnami* exist from any one locality to perform statistical analyses of these or other traits.

On the basis of Recent specimens, *T. c. major* (Fig. 1, F) may be described as a large box turtle (carapace length averages 165 mm in 55 specimens from the vicinity of Tallahassee) with a broad, elongated shell that is gently rounded in sagittal section (Fig. 1, F); a broad and heavy postorbital bar is usually present; the interhumeral suture is long in most specimens (Fig. 2, H); axillary scales usually large (Table 1, H) usually with greatly flared marginal scutes (but never to the extreme that characterizes *putnami;* see Auffenberg, 1958); hind foot usually with four toes. The color pattern is like that of *bauri, carolina,* or *triunguis.* The only color distinction of *major* that has not been observed in the other subspecies in the United States is the white, or white-blotched, head that occurs in some large specimens of *major.*

The modern *T. c. triunguis* (Fig. 1, D) may be described as a small box turtle (carapace length averaging 118 mm in 55 specimens from central Texas) with a narrow, elongated shell, highly vaulted in sagittal section, and usually raised in a hump just behind the bridge on the third central (Fig. 1, D); postorbital bar reduced, cartilaginous, or absent; interhumeral suture short (Fig. 2, C); axillary scales reduced or absent (Table 1, C); marginals flared more than in *carolina* or *bauri,* but not so much as in *major* or *putnami;* hind foot usually with three toes. The color pattern consists of dark or straw-colored radiating markings on a ground color of horn. Occasionally the shell may be of a uniform horn color or the markings may be broken up into spots.

The oldest known examples of *T. carolina* are from the late Blancan of Florida (UF 11152, 11155–58, and others), the Yarmouth of Pennsylvania (ANSP 157 and 162) and Texas (MP 39442, UT 882-315) and the late Illinoian of Kansas (MP 43734). The Pennsylvania specimens are identifiable as *T. c. carolina* (Milstead, 1965) and the Florida specimens are identifiable as *T. c. putnami* (Auffenberg, pers. comm.). The Texas and Kansas specimens consist of fragments of giant box turtles comparable in size to *T. c. putnami,* and I tentatively assign them to that subspecies.

All other fossil specimens of *T. carolina* from the central United States examined are intermediate between *T. c. putnami* and *T. c. triunguis.* The oldest of these fossils are of Sangamon age and appear to be morphologically as close to *triunguis* as to *putnami.* The most recent fossils are from post-Pleistocene deposits in Texas and Oklahoma, and they clearly approximate living *T. c. triunguis,* with the exception of their slightly larger maximum size. Greater size is the most clearly recognizable of the *putnami* features and it appears to have been the last one eliminated in the evolution of *triunguis.* Other traces of *putnami* can be found, however, in shell shape and in some of the

[1] The postorbital bar (zygomatic arch) is composed of the squamosal bone and parts of the postorbital, jugal, and quadrate bones. Some authors refer to the bar as the quadratojugal, a term which identifies the span of the bar. McDowell (1964), however, prefers to use the term "squamosal."

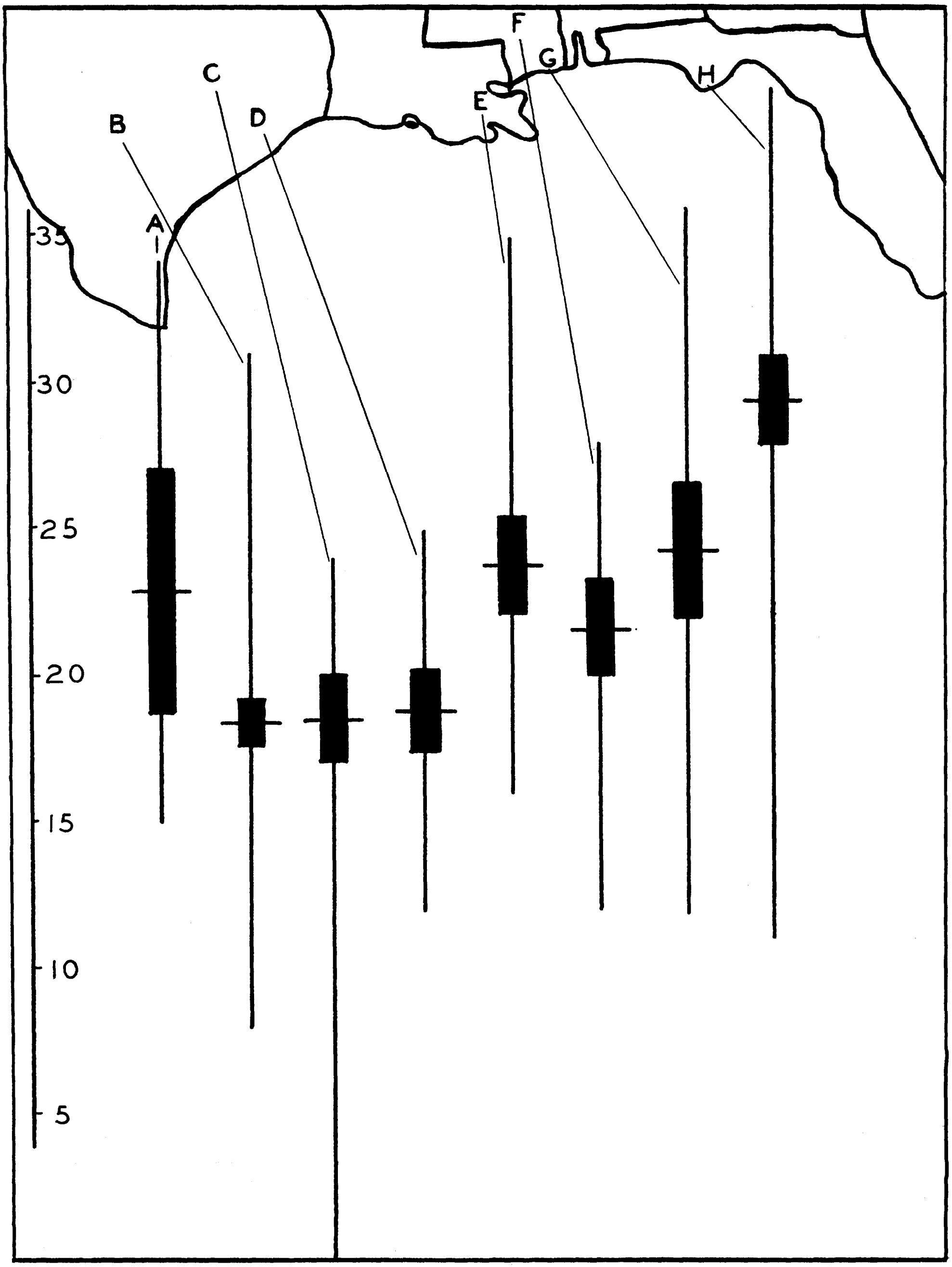

Fig. 2. Percentage of anterior lobe length occupied by the interhumeral suture in some coastal populations of *Terrapene carolina*. Vertical lines = ranges, horizontal lines = means, black rectangles = twice the standard error of the means added to each side of the means. See text for localities and other information.

plastral ratios. Most of the fossil finds have supplied only a single specimen, but two beds have produced enough material for statistical analyses: the Friesenhahn Cave and the Ingleside localities reported previously (Milstead, 1956).

A comparison of the relative lengths of the interhumeral seams in the Friesenhahn and Ingleside turtles with the same character in *T. c. triunguis* and *T. c. major* and intermediate forms is shown in Fig. 2. There is a cline in this character on the northern Gulf Coast from *T. c. major* in Florida to *T. c. triunguis* in Texas. The difference between the two terminal forms is statistically significant. In this character the Friesenhahn turtles approximate the modern *triunguis* from Central Texas (Fig. 2, C). The Ingleside turtles, which are somewhat older in age than the Friesenhahn fossils and are from the Texas coast, are intermediate between *major* and the modern coastal form of *triunguis*. Thus, the relative length of the interhumeral seam forms a cline both in space and time from *putnami* of the Pleistocene and *major* of the Recent to modern *triunguis*. The same geographic clines and chronoclines are evident in the character of the axillary scale in Table 1 and in other features shown in Table 2.

The specimens from which data were taken for Fig. 2 and for Tables 1 and 2 are over 99 mm in carapace length. Data from smaller specimens have been omitted to reduce the possible influence of ontogenetic factors. The data for females and males are combined in Fig. 2 and in Tables 1 and 2. This was done after it was determined that there is no significant sexual dimorphism in the characters used. The localities and specimen numbers are given at the end of this section and the section on Mexican forms.

A chronocline also appears to exist in sizes of turtles. In the Ingleside fossils (40,000 to 50,000 B.P.) for example, the average length of the posterior lobe of the plastron in 11 specimens is 104 mm, in 115 Friesenhahn specimens (10,000–14,000 B.P.) the average length is 93 mm, and in 55 Recent specimens from central Texas (Fig. 2, C) the average length is 69 mm. In shape, 9 of the 28 carapaces from the Friesenhahn site closely approximate *triunguis*, 6 closely approximate *putnami*, 10 appear intermediate between *triunguis* and *putnami*, and 3 have the shape of *mexicana* and *yucatana*.

TABLE 1. SIZE OF AXILLARY SCALE IN SOME POPULATIONS OF *Terrapene*. The term "large" is used to designate an axillary scale that occupies at least half of the ventral side of the fourth marginal scute. The term "reduced" is used for axillary scales that occupy less than half of the scute. See text for localities and other information.

Population	No. Having Axillary Scale: Large	Reduced	Absent
A. *T. carolina putnami* ×[t] *triunguis* (fossil)	3	0	1
B. *T. c. triunguis* (fossil)	0	0	26
C. *T. c. triunguis*	3	28	25
D. *T. c. triunguis*	2	12	5
E. *T. c. major* × *triunguis*	17	4	6
F. *T. c. major* × *triunguis*	0	18	7
G. *T. c. major* × *triunguis*	10	23	2
H. *T. c. major*	50	2	0
J. *T. c. mexicana*	0	1	21
K. *T. c. yucatana*	0	3	7
L. *T. coahuila*	29	1	4

Auffenberg (1958) presumed that *T. c. putnami* was a marsh-inhabiting turtle as *T. c. major* is today. The southern part of the range of the modern *T. c. triunguis* and additional areas to the west may have been occupied by *T. c. putnami* during parts of the early and middle Pleistocene. One fossil close to *putnami* from the Illinoian of southwestern Kansas (MP 43734) was associated with a rice rat (*Oryzomys fossilis*; see Hibbard, 1963a; Hibbard, *et al.*, 1965) which indicates conditions similar to modern conditions on the Gulf Coastal Plain. Throughout the Pliocene and the Pleistocene there were shifting humidity conditions in the midwestern U. S. which at times brought more mesic environments and at other times more arid environments than at present. Futhermore, the Pleistocene was marked by changing temperatures and sea levels, and by an overall progressive change in the southern and middle United States from the subtropical climates of the Pliocene to the temperate climates of today. These changes had pronounced effects on the reptilian faunas in producing distributional shifts that set the stage for isolation of populations and subsequent speciation (for greater detail see Auffenberg and Milstead, 1965; Hibbard, 1955, 1960, 1963a; Hibbard and Taylor, 1960;

TABLE 2. AVERAGE PLASTRAL RATIOS IN SOME POPULATIONS OF *Terrapene*. Ratios based on lengths of elements measured on midline of plastron. See text for localities and other information.

	Population										
Ratio	A	B	C	D	E	F	G	H	J	K	L
Anterior lobe/posterior lobe			71	72	69	68	68	66	73	63	64
Intergular seam/anterior lobe	45	47	49	50	47	48	46	44	41	36	49
Interhumeral seam/anterior lobe	23	18	18	19	24	22	24	29	23	31	20
Interpectoral seam/anterior lobe	33	35	32	31	29	30	29	26	36	29	30
Interabdominal seam/posterior lobe	29	31	33	32	33	35	34	35	33	32	35
Interfemoral seam/posterior lobe	16	16	14	15	14	12	11	12	15	21	10
Interanal seam/posterior lobe	55	53	54	52	54	53	54	53	52	47	54

Hibbard, *et al.*, 1965; Milstead and Tinkle, 1967; Slaughter, 1964; and others). These are the changes suggested above as producing the evolution of *T. ornata ornata* and *T. o. luteola* from *T. o. longinsulae.* I am assuming from the available evidence that these changes also brought about the evolution of *T. c. putnami* into *T. c. major* in the southeast and *T. c. triunguis* in the midwest. One of the openings of the Mississippi River embayment during the Pleistocene may have been the actual physical barrier that isolated the populations which ultimately diverged into *triunguis* and *major,* but increasing aridity and subsequent changes in vegetation undoubtedly played an important role in the evolution.

Whatever the forces are that favor *triunguis* characteristics for inland turtles and *putnami —major* charactersitics for coastal turtles, they seem to be highly selective. This can be illustrated in the three populations that show intergradation (Fig. 2, E, F, G and Tables 1, 2). Population G (Mississippi, Boot Heel) is from a coastal area that is characterized by a palmetto-pine forest much like that in which *major* occurs in Florida. Although they are intergrades, all of the turtles superficially look like *major.* Six miles north of Population G, Population F occurs in an area that is only a few feet higher in elevation. Here the forests are of mixed pine and hardwoods (called "flatwoods" by Florida botanists) and the turtles, although intergrades, superficially resemble *triunguis.* Population E is from a coastal grasslands near New Orleans. The overall habitat is neither typically *major* nor *triunguis* in character, but contains some of the elements of both types of habitats. The superficial morphological characteristics of the intergrades from this area are not as rigidly selected as in the other two areas. Some turtles (including the cotypes of *triunguis,* USNM 86871–2) look like *triunguis* and some look like *major,* but most of them look like intermediate forms.

Of the many fossil box turtles that have been found, only three or four have had skulls with them, and only one (CMSC), preserved in good condition, suggests that the postorbital bar was represented by a thin bridge of cartilage, as in modern *triunguis.* The skull appears to be identical with *triunguis,* save for larger size.

SPECIMENS EXAMINED

A total of 326 shells or shell fragments were examined in the study.

Terrapene carolina putnami—3 specimens, MP 39442 and UT 882-315 from the Yarmouth of Lubbock Co., Texas, and MP 43734 from the Illinoian of Meade Co., Kans.

Terrapene carolina putnami ×t *triunguis*—36 specimens from Sangamon and early to middle Wisconsin deposits. I am adding a superscript "t" to the usual designation of an intermediate form to indicate that these are intermediate vertically (i.e., in time) rather than geographically. Sangamon Deposits. Kansas (3 specimens). Meade Co. MP 26957 (holotype of *T. llanensis,* see Milstead, 1956, 1959) and MP 38637 (fragments of 2 or 3 turtles). Texas (2 specimens). Archer Co., Mt. Berry (Bear Mt.), Harvard Univ. 2170; and Henderson Co., UT 30907–19B. Wisconsin. Texas (31 specimens). Denton Co. Lewisville, SMU (2 specimens, see Holman, 1966); Duval Co., San Diego, AMNH 3936 (referred to *T. marnocki* by Hay, 1908b; see Milstead, 1965); San Patricio Co., Ingleside (Population A in Fig. 2 and Tables 1 and 2), 5 carapaces, 11 anterior lobes of plastron, and 12 posterior lobes of plastron, all in UT collection 30967.

Terrapene carolina triunguis—287 specimens from late Wisconsin deposits. All of the following specimens are intermediate between *T. c. putnami* and *T. c. triunguis,* but they are much nearer *T. c. triunguis* than *putnami.* Ark. (1 specimen). Marion Co., Yellville, FMNH-PRI. Ill. (1 specimen). Colec Co., Polecat Gravel Pit, FMNH-P15213. Mo. (2 specimens). Central Missouri State College specimens from Franklin Co. and Enon Sink. N. Mex. (4 specimens). Curry Co., Clovis, ANSP 13474, UT 937-202, UT 937-206, and UT 937-241. Okla. (2 specimens). Logan Co., Marshall, FMNH-P15377; Domebo Locality, 65.145 in Museum of the Great Plains (Lawton, Okla.). Texas (277 specimens). Bee Co., UT 31034–119 and UT 31186; Bexar Co., Friesenhahn Cave (Population B in Fig. 2 and Tables 1 and 2), 28 carapaces, 122 anterior lobes of plastron, and 116 posterior lobes of plastron, all in UT collection 933; Brazos Co., Pitts Bridge on Brazos River, UT 40099-1; Burnet Co., Longhorn Caverns, UT 40279-75 and UT 40279-139; Dallas Co., Dallas Pits, FMNH-P 12871; Kendall Co., Cave without a name, UT 40450-138; Travis Co., Austin, USNM 8617 (type of *T. whitneyi*, see Milstead, 1965), Cave X on Foster Ranch, UT 40448-2, 1 mile N of Pilot Knob, UT 266-T-I; Uvalde Co., Kincaid Site, UT 908-2367.

The Recent specimens from the U. S. used in Fig. 2 and Tables 1 and 2 are as follows:

Population C—*Terrapene carolina triunguis*, 55 specimens from Austin, Brazos, Grimes, Leon, Madison, Robertson, and Walker counties, Texas (Texan Biotic Province of Blair, 1950)—FMNH 31798, FMNH 37455–7, FMNH 37460, FMNH 37462–3, FMNH 46284–6, KU 61854, TCW 43, TCW 83–4, TCW 92, TCW 304–8, TCW 462–3, TCW 4658–61, TCW 4663, TCW 4666–7, TCW 13747–48, TCW 13973, TCW 13976, TCW 15424, TCW 15867–69, TCW No Numbers A–J, UT 8839–40, UT 13998–9, UT 20916, UT 21392, UT 22587–8.

Population D—*Terrapene carolina triunguis*, 19 specimens from Brasoria, Chambers, Fort Bend, Galveston, Hardin, Harris, and Jefferson counties, Texas (Austroriparian Biotic Province of Dice, 1943; Blair, 1950)—FMNH 37459, TCW 310–1, TCW 4665, TCW 14956, UT 6539–40, UT 8837, UT 8843, UT 8853–7, UT 20453, UT 21374, UT 21378–9, UT 21785.

Population E—*Terrapene carolina major* × *triunguis*, 23 specimens from New Orleans and vicinity, La.—AMNH 7097, AMNH 7101–2, AMNH 7108, KU 22970, MZ 92739–40, TUL 3456, TUL 5856, TUL 7678, TUL 10004, TUL 11129, TUL 11141, TUL 11216, TUL 11916–7, TUL 12485, TUL 13466, TUL 13804, TUL 14013, TUL 14501, TUL 15348, TUL 17271.

Population F—*Terrapene carolina major* × *triunguis*, 25 specimens from Forest, Jones, and Lamar counties, Miss.—KU 46796, KU 46800, KU 46802–6, KU 47347–4, KU 47346–7, KU 47349–50, KU 47352, KU 47354–5, KU 47357–61, KU 47367–70, MZ 90132.

Population G—*Terrapene carolina major* × *triunguis*, 35 specimens from Harrison, Jackson, and Stone counties, Miss.—AMNH 46771, FMNH 21606, KU 46791–5, KU 46797–9, KU 46801, KU 47353, KU 47362–6, KU 47372, KU 51460, MZ 76887, MZ 92536–43, MZ 92545–7, MZ 93872–4, MZ 94544.

Population H—*Terrapene carolina major*, 55 specimens from Calhoun, Franklin, Gulf, Leon, Liberty, and Wakulla counties, Fla.—FMNH 44986–90, FMNH 44992–5, FMNH 83453–4, KU 46778, KU 46790, KU 46816, KU 46819, KU 46822, KU 46851–3, KU 51461, UF 383, UF 383A–C, UF 431, UF 431A, UF 443, UF 443A, UF 451, UF 451A–B, UF 7443–44, UF 7446, UF 8590–91, UF 9390–92, UF 9492–1 & 2, UF 9493–95, UF 9497–502, UF 45338–39, UF 45339A, UF 47427–29.

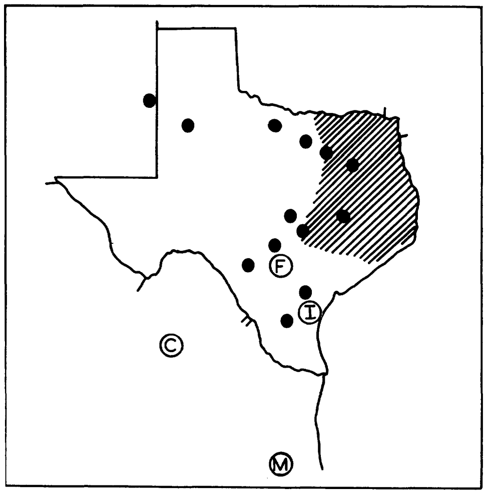

Fig. 3. Distribution of *Terrapene carolina* in Texas, New Mexico and Mexico and type locality of *Terrapene coahuila*. Slanted lines = present distribution of *T. carolina* in Texas. Black circles = localities of fossil *T. carolina* in Texas and New Mexico. In the open circles: C is type locality of *T. coahuila*, F is the Freisenhahn Cave, I is the Ingleside locality, M is the northernmost record of *T. carolina mexicana*. Circles F and I = localities of B and A, respectively, in Fig. 2 and Tables 1 and 2.

Box Turtles of Eastern Mexico

Three forms of box turtles live in Mexico east of the Sierra Madre Occidental. These are known as *Terrapene mexicana mexicana* (Gray) in southeastern Mexico, *Terrapene mexicana yucatana* (Boulenger) in the Yucatan Peninsula, and *Terrapene coahuila* Schmidt and Owens in central Mexico. Each is isolated from all other relatives. *T. carolina* and *T. mexicana* today are separated by the Tamaulipan biotic province (of Dice, 1943; Goldman and Moore, 1945; Blair, 1950), but the Ingleside locality and several other localities (Fig. 3) place *T. carolina* in what is now the Tamaulipan province near the end of the Pleistocene. *T. coahuila* is isolated from *T. carolina* today by a large part of the states of Coahuila and Texas, but fossils found in central and southern Texas indicate that *T. carolina* could have easily reached the *T. coahuila* locality from the Balconian or Tamaulipan biotic provinces during pluvial periods (Fig. 3). The patterns of distribution suggest that at times in the past the distribution of these box turtles was continuous across eastern Mexico and southern Texas.

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. In fact, some specimens of *T. m. mexicana* are difficult to distinguish from *T. c. triunguis* and some specimens of *T. m. yucatana* are difficult to distinguish from *T. c. major.* In some specimens of *mexicana* and *yucatana* there is what might be described as a doubly-vaulted carapace. That is, in cross-section the shell appears to have an exaggeration of the hump found in *triunguis,* produced in *yucatana* by indentations in the posterior pleural bones. This extreme in humping of the shell also occurs in a few specimens from both the Ingleside and Friesenhahn deposits. An analysis of plastral ratios (Table 2) shows that *mexicana* is more closely related to both fossil and living *triunguis* than to other forms included in the table. Two of the ratios are intermediate between those of *triunguis* and *major,* however, and occasional specimens of *mexicana* have the white or white-blotched head of *major.* Most *mexicana* have three toes on the hind feet and some have the shell and skin markings and shape of *triunguis.* Most specimens of *yucatana* have the white or white-blotched head and the four hind toes of *major.* The plastral ratios in *yucatana* are different in most cases from any others shown in Table 2. Although the number of specimens of *yucatana* is small, a reverse in the clines of the first three ratios is indicated. In these characters, *yucatana* agrees with *bauri* × *major* intergrades from western Florida on the opposite end of the cline. The femoral ratio of *yucatana* appears to be the termination of a cline from Florida around the coast to Yucatan. Although *yucatana* diverges in this cline more sharply from *mexicana* than *mexicana* diverges from *triunguis* or *major,* the Friesenhahn and Ingleside turtles indicate that the steps of the cline may have been more pronounced at times in the past.

The strong morphological resemblances seen in the Recent specimens of *mexicana* and *carolina* leave the present distribution as the main reason for considering *mexicana* a distinct species. The Texas fossils of *carolina* indicate that the geographic isolation is of relatively recent occurrence. *T. mexicana* is best treated as conspecific with *T. carolina.* The two subspecies should then be known as *T. carolina mexicana* and *T. carolina yucatana.*

The separation of *T. c. mexicana* and *T. c. yucatana* from the larger portion of the species and from each other may be related to the same climatic and sea level changes suggested for the evolution of *triunguis* and *major* from *putnami.* Box turtles intermediate between *putnami* and *triunguis* probably spread over all of Texas and eastern Mexico during each pluvial period of the Pleistocene, and retreated northeastward along the gulf during each arid period. Each retreat may have left populations wherever suitable habitats remained. This appears to be the case for *mexicana.* It lives in a relatively small austroriparian-like habitat bounded by mountains on the west and south, by coastal marshes on the east, and by the arid Tamaulipan biotic province on the north. The presence of *triunguis* characters in *mexicana* and of *mexicana* characters in some of the Texas fossils suggests that the last separation of *mexicana* and its northern relatives took place since the time of the Ingleside and Friesenhahn deposits; i.e., with the return of arid conditions in northern Tamaulipas during the waning stages of the Wisconsin glaciation. The presence of *major* characters in *mexicana* may mean environmental selection for those characters from the gene pool of turtles of the Friesenhahn and Ingleside types, or they may have been retained by *mexicana* from an earlier isolation that took place before *triunguis* characters had become fully developed.

The isolation of *yucatana* is more closely related to sea level changes and took place before the last isolation of *mexicana.* Today there is no connection between the ranges of *yucatana* and *mexicana,* presumably because of unsuitable habitats. In the Isthmus of Tehuantepec and contiguous areas today, the coastal marshes are close to the central mountain mass and exclude habitats favored by any living form of *T. carolina.* The Gulf of Mexico in that area is very shallow, however, and lowered sea levels during glacial periods would have exposed a coastal plain suitable for the occupancy of *putnami–triunguis* type box turtles. Rising sea levels as the glaciers melted would sever this dispersal route during each interglacial and isolate the turtles that had reached Yucatan. The last contact that *yucatana* had with *mexicana* must have been near the maximum extent of the Wisconsin glaciation. The nearness of the Ingleside locality to the sea shows that the isolation of *yucatana* took place several thousand years before the separation of *mexicana* and the Texas turtles.

The evolution of *T. coahuila* is associated with the events that resulted in the differentiation of *T. c. mexicana* and *T. c. yucatana*, but no doubt its history is more complex. Auffenberg (1958) and Legler (1960) both considered *coahuila* to be the most primitive of the living box turtles, a relict of the ancient past. In 1960, I suggested *coahuila* might have a close relationship with the more advanced *carolina*, but considered *coahuila* something of an enigma because some of its characters are *putnami*-like and some are *triunguis*-like. Examination of *coahuila* and *carolina* and re-examination of the Texas fossils gives a new basis for resolving some of the questions which have confused the relationships of *coahuila* in the past. On the basis of these interpretations, *coahuila* would seem to be descended from one of the intermediate forms between *putnami* and *triunguis*, as suggested above for the origin of *mexicana* and *yucatana*, although the isolation of *coahuila* very likely took place at an earlier date than the isolations of either *mexicana* or *yucatana*.

T. coahuila is the only aquatic box turtle. It is restricted in distribution to a well-watered bolson in central Mexico near the village of Cuatro Cienegas (see Webb *et al.*, 1963). The restricted distribution suggests that it is a relict of a more widely distributed species. The major characters of *coahuila* indicate that it is closely allied to *carolina* (Milstead and Tinkle, 1967), and most of the features of *coahuila* can also be found in both modern examples of *carolina* and fossils from the Friesenhahn and Ingleside sites. It is suggested that when this relict of *carolina* was first isolated at Cuatro Cienegas sometime in the Pleistocene the initial selection was from the *putnami* features in the gene pool. Later, as the environment became more arid, selection favored those mutations and new gene combinations leading to the distinct morphotype characteristic of the aquatic adaptation of the living species. The degree of divergence of *coahuila* from *carolina* in but a few thousand years suggests that the evolutionary rate of the form has been much more rapid than that of any other population relegated to this genus. As I have pointed out elsewhere (1960), however, the relicts at Cuatro Cienegas were probably subjected to more rigorous selective pressure than were any other members of the genus at any time in their history. Cuatro Cienegas, as in most desert oases, has no intermediate habitat between the water of the swales and ponds and the surrounding arid terrain. As the Chihuahuan Desert formed, the Cuatro Cienegas bolson, because of its water supply, probably remained mesic much longer than the surrounding country. Then, as arid conditions began to invade the bolson, the box turtles were not able to withdraw eastward as the box turtles outside of the basin had done earlier. Those trapped in the basin were forced to move into the water. Adaptation to an aquatic existence took place in a relatively short time when one considers that it took nearly a million years to transform the marsh-inhabiting *putnami* into *triunguis*.

Evidence of *triunguis* characteristics in *coahuila* are found in the head and plastron. The head in both forms is small and narrow in comparison with other members of the genus. Some of the plastral ratios of *coahuila* (Table 2) are close to those of fossil and Recent *triunguis* and some are intermediate between *triunguis* and *major*.

Characteristics of *coahuila* that seem to be *putnami*-like are the broad postorbital bar, the broad and elongate carapace which is also gently rounded as seen in sagittal section, the greatly flared marginal scutes of most specimens, and the usually enlarged axillary scales (Table 1). In these characteristics, *coahuila* is closer to *major* than to any other of the modern subspecies of *carolina*. In addition, the throat of *coahuila* is often mottled with gray and white and this is reminiscent of the white-blotched head and neck of some specimens of *major*. The maximum size of *coahuila* is not as great as that of *major* or *putnami*, but it is greater than in most living box turtles.

T. c. major and *T. c. putnami* have been presumed to be the most aquatic *T. carolina*. *T. coahuila* is certainly more aquatic in its habits than is *major*. The shell of *T.*

coahuila is flatter and more streamlined than the shell of *major, putnami*, or any of the Texas fossils, and this type of shell is more often associated with aquatic turtles than with terrestrial ones.

Aside from the difficulty of determining primitive and advanced traits, three things seem to question the hypothesis of *coahuila* being a primitive relict. First, the males have a deeply indented posterior lobe of the plastron. This indicates that, even though *coahuila* is the flattest of the living box turtles, it evolved from a terrestrial turtle with a high, vaulted carapace (such as the *putnami-triunguis* fossils). Second, *coahuila* is an awkward swimmer when compared with other emydid turtles. Third, most of the plastral ratios of *coahuila* are closer to one of the advanced forms (*triunguis*) than to one of the more primitive forms. It seems best, therefore, to consider *coahuila* as a highly adapted member of the genus specialized for its aquatic habitat.

Another characteristic of *coahuila* is the presence of cloacal bursae. No other modern box turtle seems to possess them. Cloacal bursae are apparently advantageous for an aquatic turtle, and it would seem to be another trait relating *coahuila* to primitive ancestors which are presumed to have been aquatic. Actually, however, this characteristic is of little use in studying the relationships of *coahuila* because it cannot be determined whether or not *putnami* and the Texas fossils had cloacal bursae; nor can it be determined when the more terrestrial members of the genus lost them.

Specimens Examined

Terrapene carolina mexicana (Population J in Tables 1 and 2)—22 specimens from San Luis Potosi and Tamaulipas—AMNH 7105, AMNH 71612, AMNH 79909, KU 24075–6, KU 39981, KU 47902, KU 70969, MZ 51774, MZ 100128–9, MZ 102925–6, MZ 103198, MZ 104966, MZ 105478–9, MZ 112861, MZ 119485, USNM 46251 (type of *T. goldmani*), USNM 107302, USNM 108639.

Terrapene carolina yucatana (Population K in Tables 1 and 2)—10 specimens from Chichen-Itza, Merida, and Piste, Yucatan—AMNH 38847, FMNH 27273, KU 70970–2, MZ 73122, MZ 76143, MZ 83291, UC 16147a–b.

Terrapene coahuila (Population L in Tables 1 and 2)—35 specimens from near Cuarto Cienegas, Coahuila—AMNH 64815, FMNH 41234–5, FMNH 41258–61, FMNH 47373–4, FMNH 47376, FMNH 55656, KU 46924–7, KU 46929, KU 51432, MZ 52638, MZ 120405, MS 2–6, MS 327, TT 2274.0–.9.

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