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Terrapene of Western Mexico, with Comments on the Species Groups in the Genus

WILLIAM W. MILSTEAD AND DONALD W. TINKLE

Two species of box turtles occur in western Mexico: *Terrapene ornata* and *Terrapene nelsoni*. *Terrapene ornata luteola* is regarded as a possibly relict form occurring in Chihuahua and Sonora. Two subspecies of *Terrapene nelsoni* occur in Mexico: *T. n. nelsoni* and *T. n. klauberi*. *T. n. nelsoni* is known only from the type locality at Pedro Pablo, Nayarit. *T. n. klauberi* is known from a number of localities in Sonora and one locality in Sinaloa. It was formerly considered a distinct species, but new material from Nayarit indicates that *klauberi* is conspecific with *nelsoni*. It seems likely that the reproductive potential of *T. nelsoni* is lower than that of either *T. ornata* or *T. carolina*. This is attributed to the southern distribution of *T. nelsoni*.

On the basis of twelve morphological characteristics the fossil and Recent box turtles are divided into two species groups: the Ornata Group including the forms *T. nelsoni klauberi*, *T. nelsoni nelsoni*, *T. ornata longinsulae* (extinct), *T. ornata luteola*, and *T. ornata ornata*, and the Carolina Group including the forms *T. carolina bauri*, *T. carolina carolina*, *T. carolina major*, *T. carolina mexicana*, *T. carolina putnami* (extinct), *T. carolina triunguis*, *T. carolina yucatana*, and *T. coahuila*. Evolution in the Ornata Group is correlated with climatic fluctuations in the Great Plains during the Pliocene and Pleistocene. It is suggested that *ornata* evolved from *longinsulae* during humidity shifts on the Great Plains and that *nelsoni* evolved either from *ornata* or from *longinsulae* after having crossed over a mesic corridor to the west coast of Mexico in the Pliocene or Pleistocene. Speciation was initiated through isolation at a later date by the closing of the corridor.

THE box turtles of Mexico have long been an enigma in studies of evolution in the genus *Terrapene*. Aside from *T. ornata*, which is better known from the United States (see Legler, 1960), the Mexican box turtles consist of one species (*T. carolina*) along the eastern coast, one aquatic species (*T. coahuila*) in a bolson in central Mexico, and one or two species (*T. nelsoni* and *T. klauberi*) located west of the Sierra Madre. In describing *T. coahuila* Schmidt and Owens (1944) expressed the frustrations of all reviewers of the genus when they said (p. 102), "Not evidently more closely related to any one of the known species than to others."

In the past decade, through the collection of new fossil material and new Mexican material, a much better understanding of the relationships of the various species of *Terrapene* is beginning to emerge. The primary purpose of this paper is to consider the box turtles of western Mexico, particularly the relationships between *T. nelsoni* and *T. klauberi* and between those turtles and the other forms of the genus.

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), Field Museum of Natural History (FMNH), San Diego Natural History Museum (SDM), Stanford University (SU), United States National Museum (USNM), University of Arizona (UAZ), University of California at Berkeley (UCB), University of Kansas (KU), University of Michigan (MP and MZ), and University of Southern California.

Terrapene ornata luteola Smith and Ramsey

Only the western subspecies of the ornate box turtle has actually been recorded from Mexico, although *T. o. ornata* is to be expected in northeastern Mexico (Legler, 1960). *T. o. luteola* appears to be limited in its distribution to the northern parts of the Chihuahuan and Sonoran deserts in western Texas, southern New Mexico, southern Arizona, northern Chihuahua, and northern Sonora (see map in Legler, 1960, p. 533). From our own experience and the reports of others who have worked in the Chihuahuan and Sonoran deserts (Gloyd, 1937; Bogert and Oliver, 1945; Jameson and Flury, 1949; and others), the western ornate box turtle appears to be uncommon in most of its range, and it rarely reaches the density that *T. o. ornata* does in many parts of its range. *T. o. ornata* appears to inhabit the most mesic grasslands, and this may be the explanation for the differences in population densities. Many areas in the range of *T. o. luteola* are either too arid or physiographically unsuitable for box turtle habitation, and areas that are suitable usually do not have the dense plant cover found north and east of the deserts. For these reasons and others mentioned below, we suggest that *T. o. luteola* is a relict form of a mesically-adapted and formerly more widespread box turtle. If this is true, and the southwest continues to become more arid as it has in recent millenia, then the continued existence of the western ornate box turtle may be in some peril.

SPECIMENS EXAMINED

CHIHUAHUA: 9 miles SSW Arados, KU 52160; 17 miles N Chihuahua, AMNH 82116; near Gallezo, UCB 72844–9; dry flat S Laguna de Santa Maria, FMNH 2002A–B; 5 miles W El Paso (Texas); USNM 19061–2, 19394, 19410–12; NW Chihuahua, USNM 46275; Ramos, UCB 46651–4; Samalayuca, AMNH 68604, UCB 72850; 8 miles E Chihuahua-Sonora state line, SU; near Villa Ahumada KU 45019, 45055, 51427–8, no specific locality, USNM 30808–12, 86422. SONORA: Arispe, UAZ 13097–9; Guaymas, AMNH 73720; Inuris, KU 51151, UAZ 13100; 3 miles N Magdalena, AMNH 75131; northern Sonora, AMNH 4602; Pilares, MZ 78467. The Guaymas record is apparently the only one from west of the Sierra Madre, and therefore, the natural occurrence of the ornate box turtle west of the Sierra remains to be proved.

Terrapene nelsoni nelsoni Stejneger

T. nelsoni was described from one specimen collected by Goldman and Nelson in Pedro Pablo, Nayarit, in 1897. No additional specimens of the Sierra box turtle were found until 1963 when we reached the type locality. During our brief stay at Pedro Pablo in June 1963, we collected one specimen. In the following month, the people of the village collected 36 adult specimens for us.

In 1943 Bogert described *Terrapene klauberi* from the Rancho Guirocoba near Alamos, Sonora. At that time, the holotype of *T. nelsoni* (USNM 46252) was not available for study. Thus, the only comparison Bogert could make between his turtles and *T. nelsoni* was through use of the pictures published by Ditmars (1934). It was later discovered by Bogert and reported by Shaw (1952) that the figures of *T. nelsoni* and *T. goldmani* (= *T. carolina mexicana*) were reversed in Ditmars' paper. Thus, Bogert's (1943) comparison of *T. klauberi* and *T. nelsoni* was actually between *T. klauberi* and *T. carolina*. Bogert (pers. comm.) has since remarked that he would not have described *T. klauberi* had he seen the type of *T. nelsoni* beforehand. Upon comparison of a small series of *T. klauberi* with the type of *T. nelsoni*, Shaw (1952) concluded that *T. klauberi* should be considered a distinct species at least until more specimens were available. Our series of *T. nelsoni* shows that there is very little difference between the two forms.

In general, the descriptions of *T. klauberi* given by Bogert (1943), Bogert and Oliver (1945), and Shaw (1952) will suffice for *T. nelsoni*. Two characteristics used by Bogert (1943) and reemphasized by Shaw (1952) to distinguish the two species are not valid differentiators when applied to the larger series of *nelsoni*. These are the notching of the upper jaw and the relative length of the first central scute compared with the width of the third. The upper jaw is notched in 15 *nelsoni* specimens and entire in 10. The length of the first central is equal to the width of the third central in 7 and less in 18.

The most distinguishing feature of our specimens of *nelsoni* is the concave or scoop-shaped first central. In *klauberi* the first central is somewhat scoop-shaped but not to the extent that it is in some of the males of *T. nelsoni* (Fig. 1B). The males of *nelsoni* are more rugose and have more flaring posterior marginal scutes than those of the *T. klauberi* males, although this may be a bias in the few specimens of the latter sample. Comparisons of the plastral ratios of *nelsoni* and *klauberi* (Table 1) reveal differences that may prove to be the best distinguishing characters, particularly the intergular, interhumeral, and interpectoral ratios. This is suggested because the plastral ratios in series of other box turtles appear to be among the least variable characters. All of our specimens of *T. nelsoni* are elongated turtles (reminiscent of *T. carolina*), while *T. klauberi* varies from elongate to round (reminiscent of *T. ornata*). Thus, for the present, a "round" *ornata*-like turtle of the *nelsoni* complex may be identified as *klauberi*. Most of the specimens of *klauberi* have coffee-colored spots on the head, neck, forelimbs, and shell. The exceptions are a few males that have uniform straw or horn-colored shells. All of our specimens of *nelsoni* have the spots, although two of them and the holotype show a tendency toward the uniform horn color. The spotting in all specimens of *nelsoni* as opposed to some uniform-colored specimens of *klauberi* may be due to a biased sample of the *nelsoni* population, however.

There is very little sexual dimorphism in *T. n. nelsoni*. The most pronounced feature is the medially turned inner toe of the males, as described for *Terrapene ornata* by Legler (1960). Other dimorphic characters are the more scoop-shaped first central, the more rugose shell, and the more flared marginals present in some of the males (Fig. 1, *cf*. A, B).

Of the 20 females in our series of *T. n. nelsoni*, 19 yielded some information on reproduction. Reproductive potential in reptiles can usually be estimated accurately by counts of oviducal eggs, corpora lutea, or yolked follicles (Tinkle, 1961a). A mean clutch size of 2.7 ($N = 26$) was calculated using all three techniques. Essentially the same results were obtained with each method individually:

Yolked follicles	2.8 ($N = 8$)
Oviducal eggs	2.9 ($N = 8$)
Corpora lutea	2.6 ($N = 10$)

The actual number of eggs varied from 1 to 4, but 3 may be taken as the usual size of a clutch. There was no significant relationship between size of female and either number or size of eggs. The mean size of 17 eggs (47 × 27 mm) is considerably larger than the mean of eggs in the larger clutches of *T. ornata* (36 × 22 mm) reported by Legler (1960), but this difference is not unexpected when turtle size and clutch size are compared.

The data give no indication of multiple clutches in *T. n. nelsoni*. Females that have already produced one clutch often have small yolked follicles (5–10 mm), but it is unlikely that these will mature and be ovulated the same season, although this possibility cannot be excluded after examination of a single sample. It is not unusual for turtles to produce yolked follicles in the late summer and fall after laying and to hold the follicles in the ovary through the winter (Tinkle, 1961b). This phenomenon has been demonstrated in box turtles of two species by Altland (1951) and by Legler (1960).

Allard (1935) reported an average of 4.2 eggs in 60 clutches of *Terrapene carolina* from the vicinity of Washington, D. C. Legler (1960) found an average of 4.7 eggs in 28 clutches of *Terrapene ornata* from Kansas. Both authors reported that 4 eggs was the most frequent clutch size. Legler (1960) further stated that one-third of the females may lay more than one clutch per year. This idea was based upon findings of fresh and old corpora lutea in the ovary of the same female or large ovarian follicles and corpora lutea in the same female. In our sample neither condition existed. Two females did have 1 or 2 large ovarian eggs and also eggs in the oviduct, but we believe that these ovarian eggs would have become atretic rather than have contributed to a second clutch. This prediction is based on two females in the sample with recent corpora lutea in which the remaining large ovarian follicles were undergoing atresia. However, our females were not opened for a considerable time after capture, which might account for the atresia.

It seems likely that the reproductive potential of *nelsoni* is lower than that of either *carolina* or *ornata*. This would be expected if the latter two species exceeded it in size for there is a tendency for larger females within a species or species group to lay more eggs (Tinkle, 1961b). However, this is not the case; the mean plastron length of our series of female *T. nelsoni* (142 mm) exceeds the maximum of *T. ornata* studied by Legler (1960) and of 25 adult female *T. carolina* examined by us from the vicinity of Washington, D. C.

The clutch size does correspond with figures reported by Tinkle (1961b) for the turtle *Sternothaerus odoratus* in which it was shown that the average clutch size is much greater in this species in the northern than in the southern parts of the range. This same phenomenon apparently applies to southern species of *Terrapene* as opposed to northern. If true, lower reproductive potential should be found in *T. carolina*

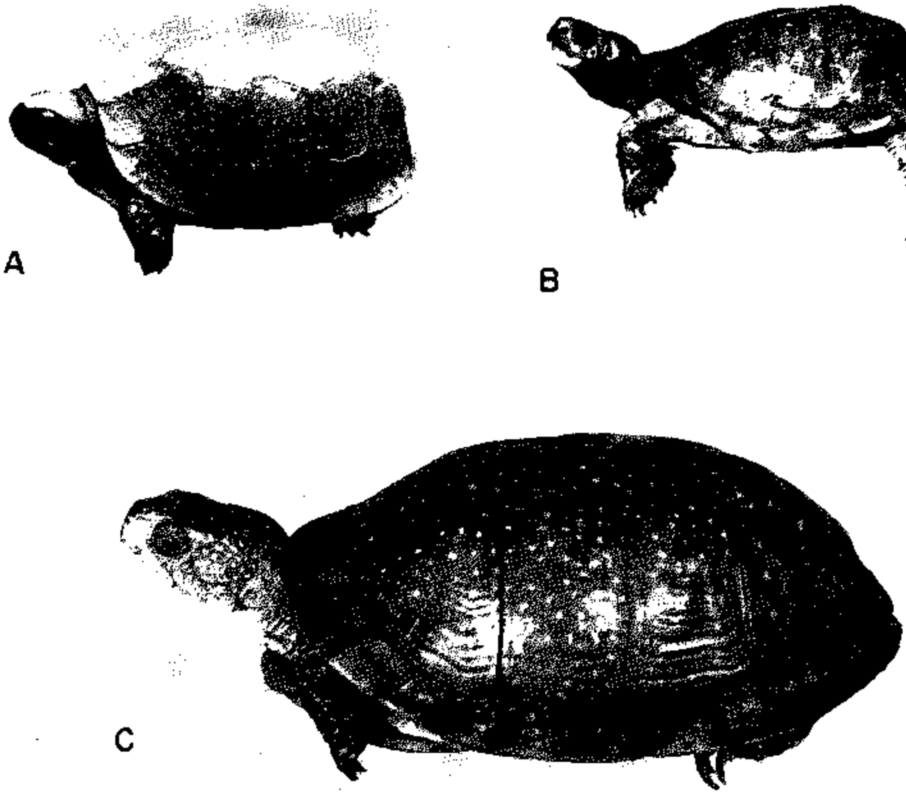

Fig. 1. A–B. *Terrapene nelsoni nelsoni* from Pedro Pablo, Nayarit. A,♀; B, ♂. C. *T. n. klauberi,* ♀ from near Alamos, Sonora. After Bogert, 1943 (courtesy American Museum of Natural History).

yucatana when a sufficiently large series becomes available for comparison with northern *T. carolina.* Again, it must be admitted that the southern turtles may produce more than one clutch per year, a possibility that can be determined only from seasonal sampling of the populations.

All of the females of *T. nelsoni* were at approximately the same reproductive stage. They had either just laid (as indicated by recent corpora lutea), contained oviducal eggs, or contained ovarian eggs nearing ovulatory size. This suggests rather precise timing of the beginning of reproduction and of ovulation in this species. Evidently eggs are deposited in June at the onset of the rainy season and hatching probably occurs near the end of it when food for the young turtles is undoubtedly abundant. The nearest accurate rainfall records (in inches) are from Tepic, Nayarit, about 100 miles SW of Pedro Pablo at an altitude of 3027 ft:

Jan.	1.2	July	13.7
Feb.	0.8	Aug.	11.5
Mar.	neg.	Sept.	8.1
Apr.	neg.	Oct.	3.0
May	0.1	Nov.	0.3
June	6.8	Dec.	2.6

On our trip from Acaponeta, Nayarit, to Pedro Pablo, we found very little to question in Goldman's (1951) description of the physiography, vegetation, and ecology of the area. Acaponeta is located in the Nayarit-Guerrero biotic province of Goldman and Moore (1945) and Goldman (1951). The region consists of a "scrub forest" with many thorny bushes, cacti, and low trees (25–30 ft height). The foothills and low mountain chains are ecotonal between the Nayarit-Guerrero, Sinaloan, and Sierra Madre Occidental biotic provinces. The mountain range where Pedro Pablo is located was referred to by Goldman (1951) as the Sierra de Teponahuasta, but the people of the region did not recognize that name.

The village of Pedro Pablo is located on a horseshoe-shaped ridge slightly higher than the main mountain mass. The center of the horseshoe lies on one side of the village and is a valley we estimated to be 500 ft deep. On the opposite side of town is a steep hill which Goldman (1951) called the summit of the Sierra de Teponahuasta. Goldman estimated the altitude of the village as 3500 ft and its location as 22 miles E of Acaponeta. These estimates appeared correct to us.

The people of Pedro Pablo told us that the spotted turtle we sought lived on the little hill above town. We were in the village for a day and a half and spent most of the time collecting in the luxuriant vegetation on the valley floor. Although the area closely resembles the habitat of box turtles in the southeastern U. S., the only turtles we found were *Kinosternon integrum.* The hill has an entirely different type of habitat. The summit is an open savannah with many small oak trees. We collected a specimen of *T. nelsoni* near the summit on a rocky trail at the foot of a bluff.

It is doubtful that all of the specimens collected for us by the villagers came from the one small hill. If the villagers are correct in their observations of the turtle's habits, however, then it must be largely limited to the oak-savannah association which Goldman (1951) records as occurring above 4000 ft. The people at nearby El Oro (elevation about 1500 ft) did not know the turtle.

Our topotypic series has been distributed as follows: American Museum of Natural History (6), Field Museum of Natural History (6), Texas Technological College (2), U. S. National Museum (6), University of Kansas (8), University of Michigan (7), and University of Missouri at Kansas City (2). Two of the specimens at Kansas, one at Michigan, and one at Kansas City have been skeletonized.

Terrapene nelsoni klauberi Bogert
(Fig. 1, C)

Other than the information given above and in Table 1, very little can be added to the accounts of Bogert (1943), Bogert and Oliver (1945), and Shaw (1952) on the morphology of *T. n. klauberi.* The males of *T. n. klauberi* have the medially turned inner toe of *T. ornata,* as noted by Legler (1960).

The habitat of *T. n. klauberi* is largely unknown. Myers (1945) recorded that a Sierra de Batuc specimen was collected, "on the western slope, among granitic hills, with volcanic intrusions, covered with desert scrub." A specimen (UAZ 13105) collected by C. H. Lowe was caught on the northeast slope of the Sierra de los Alamos near Alamos. R. L. McDiarmid (pers. comm.) reported that a specimen from Sinaloa was collected on a southeast facing slope behind a farm. So far as is known, all of the specimens have been collected below 3500 ft altitude. If the "usual" habitat of *T. n. klauberi* is below 3500 ft, then a strong ecological difference may exist between *klauberi* and *T. n. nelsoni.* The former may be considered a turtle of the forests and scrub forests below 3500 ft, while the latter may be considered a turtle of the oak-savannahs above 3500 ft. There are, however, reasons for believing that this distinction in habitat does not exist. The specimens of *klauberi* that have been collected may be specimens that occasionally come down onto the lower slopes. The "usual" habitat of *klauberi* may be above 3500 ft.

Specimens Examined

Sonora: Alamos, AMNH 63762–3, KU 51430, UAZ 13105; Rancho Guricoba (type locality), 18 miles SE Alamos, AMNH 63751 (holotype) and 63753, FMNH 41269; Rio Chuchujagui, 7 miles SE Alamos, SDM 42413; Sierra de Batuc, SU 10770; Tepustate, 8 miles NW Alamos, SDM 42411–2; 17 miles N Tonichi, UAZ 13103–4. Sinaloa: 3 miles W Terreros (44 miles N Culiacan), University Southern California specimen. The Sinaloa specimen is not included in Table 1. The specimen consists of a carapace and a posterior lobe of the plastron. The carapace length is 135 mm. The plastral posterior lobe ratios are: interabdominal 34%, interpelvic 17%, and interanal 48%.

Species Groups in the Genus *Terrapene*

It has been suggested that the modern *Terrapene carolina* and *Terrapene ornata* may be living representatives of two species groups that have been distinct since the close of the Miocene (Milstead, 1956, 1959). The suggestion was made contingent upon demonstrated relationships between *T. carolina* and *T. putnami* and between *T. ornata* and *T. longinsulae.* Auffenberg (1958) has shown that *T. putnami* is an extinct subspecies of *T. carolina*. After studies of the holotype (USNM 5983) and two additional specimens of *T. longinsulae* (MP 37184, 44648), Milstead (1967) concluded that *T. longinsulae* is an extinct subspecies of *T. ornata* which may have been ancestral to both of the living subspecies. It has been shown that *putnami* is of early Pleistocene age (Auffenberg, pers. comm.) and that *longinsulae* is of Pliocene and early Pleistocene (Aftonian) age (Milstead, 1967). Comparisons of many box turtles with respect to morphological traits, ecology, and geographic distribution indicate that recognition of two species groups is not unreasonable. The two groups, Carolina and Ornata, have been distinct at least since the late Blancan of the Pleistocene.

The morphological traits that distinguish the two species groups are as follows:

	Ornata Group	Carolina Group
1.	Postorbital bar[1] absent; posterior border of orbit smooth.	Postorbital bar[1] usually present although the central portion (squamosal) may be cartilaginous; when postorbital bar is absent the postorbital bone has a posteriorly directed process.
2.	Interfemoral suture long (see Table 1).	Interfemoral suture short.
3.	First central scute concave or straight along midline (Fig. 1).	First central scute convex along midline.
4.	Highest vaulting of carapace anterior to bridge; carapace flat in both sagittal and cross section.	Highest vaulting of carapace posterior to bridge; carapace rather high in both sagittal and cross section.
5.	First marginal scute irregularly oval or triangular in shape.	First marginal scute usually rectangular in shape.
6.	Dorsal keel usually absent, but a weak keel may be present on the fourth central scute.	Dorsal keel usually present and prominent; rarely absent.
7.	Inner toe of male capable of being turned inward at sharp angle to foot to serve as clasper.	Inner toe of male similar to other toes.
8.	Posterior lobe of plastron not or only shallowly concave (bowed dorsally) in males.	Posterior lobe of plastron deeply concave (bowed dorsally) in males.
9.	Posterior margin of plastron usually straight.	Posterior margin of plastron rounded.
10.	Bridge opposite the contact between the 5th and 6th marginals or opposite the 6th marginal when viewed laterally; infrequently opposite the 5th marginal.	Bridge opposite the 5th marginal or, infrequently, opposite the contact between the 5th and 6th marginals when viewed laterally.
11.	Margin of plastron entire.	Margin of plastron frequently indented at the pelvic-anal seam.
12.	Carapace generally round in overall appearance, except in *T. nelsoni nelsoni*.	Carapace elongate except in some *T. carolina carolina*.

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[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."

TABLE 1. COMPARISONS OF THE PLASTRAL RATIOS (PERCENTAGES) OF 32 SPECIMENS OF *Terrapene nelsoni nelsoni* FROM PEDRO PABLO, NAYARIT, AND 13 SPECIMENS OF *Terrapene nelsoni klauberi* FROM SEVERAL LOCALITIES IN SONORA. The ratios are based on lengths of elements measured on the midline of the plastron.

Ratio	*T. n. nelsoni* Range ($\bar{X}$)	*T. n. klauberi* Range ($\bar{X}$)
Anterior lobe/posterior lobe	59–70 (65)	66–70 (66)
Intergular seam/anterior lobe	45–56 (50)	45–56 (48)
Interhumeral/anterior lobe	9–20 (16)	13–23 (18)
Interpectoral/anterior lobe	31–40 (35)	29–38 (33)
Interabdominal/posterior lobe	34–43 (39)	34–40 (38)
Interfemoral/posterior lobe	10–20 (16)	12–19 (16)
Interanal/posterior lobe	41–51 (46)	42–50 (46)

Application of these characteristics to the known forms of *Terrapene* yields the following arrangement of species and subspecies:

Ornata Group	Carolina Group
T. nelsoni klauberi	*T. carolina bauri*
T. n. nelsoni	*T. c. carolina*
T. ornata longinsulae (extinct)	*T. c. major*
	T. c. mexicana
T. o. luteola	*T. c. putnami* (extinct)
T. o. ornata	
	T. c. triunguis
	T. c. yucatana
	T. coahuila

Reasons for the omission of *T. culturalia*, *T. eurypygia*, *T. marnocki*, and *T. whitneyi* were given by Milstead (1965).

In the midwestern United States where the ranges of *T. ornata* and *T. carolina* are contiguous, there are persistent rumors of hybridization. Legler (1960) after considering the rumors and the specimens concluded (p. 533), ". . . I find no convincing evidence that hybridization occurs under natural conditions." We concur with Legler's statement. The few "hybrids" that we have seen prove to be examples of one species (usually *ornata*) that superficially resemble the other. Furthermore, we attach little significance to the numerous records of laboratory matings. We have seen attempted matings in the laboratory between *T. ornata* and *T. carolina*, *T. ornata* and *Testudo hermani*, *T. carolina* and *Pseudemys scripta*, and *T. coahuila* and *T. carolina*.

EVOLUTION IN THE ORNATA GROUP

During both the Pliocene and Pleistocene, there were extensive fluctuations in humidity so that the Great Plains were at times more mesic and at other times more arid than they are today (Hibbard, 1960; Auffenberg and Milstead, 1965). *T. o. longinsulae* is known from a few specimens found in Kansas in Pliocene and early Pleistocene deposits that correspond to arid periods. It is suggested that *T. o. longinsulae* was a grassland form as *T. ornata* is today, and that it was forced to shift its distribution to the south and west during pluvial periods in the Pliocene and Pleistocene and that it reinvaded the Great Plains during arid periods. Sometime between the Aftonian of the early Pleistocene and the Sangamon of the late Pleistocene it evolved into the modern *T. ornata*. Of the two subspecies of *T. ornata*, *T. o. luteola* more closely resembles the ancestral *T. o. longinsulae* than does *T. o. ornata*. Thus, *T. o. luteola* may represent the older stock. *T. o. ornata* may have arisen from a relict population left to the north or east of the main population during one of the Pleistocene pluvial periods.

One of the important effects of the fluctuating humidity conditions in the Pliocene and Pleistocene was the opening and closing of a Rocky Mountain corridor across the continental divide in southern New Mexico and Arizona (Auffenberg and Milstead, 1965). During pluvial periods, the humid conditions resulted in the expansion of woodlands on the Great Plains and the extension of open grassy forests over the Rocky Mountain corridor. Over this route either *longinsulae* or *luteola* migrated to the western foothills of the Sierra Madre Occidental. Decreasing humidity during arid periods closed the corridor. The southwestern population isolated by the closing of the corridor ultimately evolved into *T. nelsoni*. The oak-savannah association where *T. n. nelsoni* occurs is at approximately the same altitude as the old Rocky Mountain corridor. Most of the present-day geographic range of *T. o. luteola* overlies the old corridor and essentially marks the route westward. Thus, *T. o. luteola* may be one of the few survivors of the various forms that used the corridor during its last (post-Wisconsin) opening. The geographic range of the turtle, coupled with its resemblance to older stock of the Ornata Group and its apparent low population density, have led to our suggestion that *T. o. luteola* may be a relict form now diminishing in numbers.

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