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MORPHOMETRICS OF *TERRAPENE COAHUILA* (CHELONIA, EMYDIDAE), WITH COMMENTS ON ITS EVOLUTIONARY STATUS

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ABSTRACT. A sample of 164 *Terrapene coahuila* from marshes in the Cuatro Ciénegas basin, Coahuila, México, was analyzed for size and sexual dimorphism. Bivariate relations between seven carapace and plastron measures indicated strongest sexual dimorphism in the carapace height/length relationship (males 43%, females 46% in relative height). Males averaged 108.9 mm and females 100.9 mm in carapace length. Marsh-inhabiting *T. coahuila* are smaller than those from river or pool habitats. Dietary differences and/or greater competition in the more densely populated marshes may explain the inter-population differences in size. About 70% of adult turtles possess a vermiculated pattern of small, yellow markings on the carapace. Eleven (5%) of 218 *T. coahuila* had extra epidermal scutes or had less than the normal number.

The hypothesis that *T. coahuila* evolved as a Pleistocene relict produced by environmental isolation (championed by Milstead) is examined in the light of recent ecological observations coupled with a model of rapid evolutionary change proposed originally by Mosimann. These interpretations do not support the view that *T. coahuila* is a surviving remnant of an ancestral population of *Terrapene* but do support the idea of a relatively recent (mid-Pleistocene?) derivation for the species.

Unlike most turtles of the cosmopolitan family Emydidae, box turtles (genus *Terrapene*) have evolved adaptations for terrestrial existence. One species, *Terrapene coahuila*, is exceptional among living members of the genus, however, in that it alone is aquatic.

Of the four species of *Terrapene* currently recognized (*T. carolina*, *T. ornata*, *T. nelsoni*, and *T. coahuila*), all are represented in the herpetofauna of México. *T. coahuila* is endemic to a small intermontane basin in north-central México located near Cuatro Ciénegas, Coahuila. The turtle inhabits fresh-water marshes surrounded by Chihuahuan Desert grassland and shrub communities (Webb, et al., 1963; Brown, in press; Minckley, 1969).

Since its description by Schmidt and Owens (1944), published morphological data on *T. coahuila* have been few; moreover, the little existing information was not based on a large sample from one population. Size (carapace or plastron length—Schmidt and Owens, 1944;

Webb et al., 1963), shell proportions of 11 type specimens (Schmidt and Owens, 1944), and plastral scute ratios of 58 specimens (Milstead, 1969) account for the literature on the external shell morphology of *T. coahuila.*

This paper contributes the first statistical treatment of size and sexual dimorphism of *T. coahuila.* Measurements of 164 individuals from a single restricted area of the Cuatro Ciénegas basin were compiled. Notes on pattern and scute abnormalities are also included. Data were collected in the course of an ecological investigation of *T. coahuila* (Brown, in press) conducted between December 1964 and November 1967.

METHODS. All *T. coahuila* measured were obtained from a study area located approximately 9.5 km SW of Cuatro Ciénegas, Coahuila (grid location: NE¼, H-12 see Minckley [1969, Fig. 27]).

The following measurements were taken to the nearest tenth of a millimeter: *carapace length* (CL), the median straight-line distance (not along the curve of the back) from the most anterior to the most posterior part; *carapace height* (CH), the maximum straight-line height of the shell, measured as perpendicular to the plastron opposite the bridge; *carapace width at bridge* (BR-W), the straight-line width of the carapace across the anterior portion of the bridge at the pectoral-abdominal hinge (or, at about the contact between the fifth and sixth marginal scutes); *posterior carapace width* (POST-CW), the maximum straight-line width of the carapace at the widest point, usually at the eighth or ninth marginal scute; *plastron length* (PL), the median length of the plastron along a straight line; *anterior lobe of plastron length* (ANT-L), the mid-line length of the first three plastral scute pairs anterior to the hinge; *posterior lobe of plastron length* (POST-L), the mid-line length of the last three plastral scute pairs posterior to the hinge. Because all *T. coahuila* closed their shells tightly when handled, it was necessary to measure the anterior and posterior plastral lobes separately and to express total plastron length as the sum of these two components.

Best-fitting regression lines were calculated by the method of least squares. In all relations, CL and PL were used as the independent variables; in the relation PL/CL, carapace length was the independent variable. Only closely associated parts were related, such as CH vs. CL, or POST-L vs. PL.

Statistical methods and analysis are based mainly on the studies of Mosimann (1956, 1958a) and Mosimann and Bider (1960), who have pointed out that since there is no true independent (or fixed) variable in any of the cases as used here where regressions are run on body measurements of the same growing animal, the applications of regression are not strictly valid. These authors employed both X on Y and Y on X regressions (assuming each variable in turn as independent) to predict the value of one variable from another. Neither regression can give a single estimate of the joint relation between X and Y, except when high correlations exist. Only the Y on X regression was calculated in this study.

Preserved specimens examined are from the following collections: Arizona State University (ASU) 5853–5900, 8000; United States National Museum (USNM) 159578; University of Kansas Museum of Natural History (KU) 46917–46923, 51431, 51433–51436; and University of Utah (UU) 12555.

RESULTS AND DISCUSSION. *Size*—Males from the study area averaged 108.9 mm in carapace length (n=70) and females averaged 100.9 mm (n=94). In the field samples, most females fell in the size range 95–105 mm, while most males were between 105–115 mm. These values represent the approximate 95% confidence limits of sexual maturity (Brown, in press).

Carapace lengths in the *T. coahuila* population studied are notably smaller than *T. carolina*, *T. ornata*, and *T. nelsoni*. Nichols (1939) gives size distributions of 387 *T. c. carolina* from New York in which most females averaged about 133 mm and most males about 140 mm in plastron length. Specimens of *T. c. carolina* from Maryland that exceeded 118 mm in carapace length had well-developed secondary sex characters and were considered mature by Stickel (1950). Other subspecies of *T. carolina* (*bauri*, *major*, *triunguis*) in SE U.S. (Carr, 1952; Auffenberg, 1958; Milstead, 1967), *T. o. ornata* in Kansas (Legler, 1960), and *T. n. nelsoni* in western México (Milstead and Tinkle, 1967) surpass greatest sizes attained by nearly all female and most male *T. coahuila* in the population from the study area. However, *T. coahuila* elsewhere in the basin are larger. Mean plastron length of 26 adults (8 males, 18 females: 12 preserved, KU collection; 14 living, ASU collection) from scattered localities in the basin was 122.3 mm (range 100.1–153.2 mm), and mean carapace length of 10 adults (four males, six females) from a series of large marsh pools (Posos de la Becerra) was 121.5 mm (range 103.0–153.0 mm). Thirteen *T. coahuila* (including the type specimen) measured by Schmidt and Owens (1944) ranged from 135 to 155 mm in carapace length. Webb et al. (1963) gave plastral lengths of 164 mm for males and 159 mm for females as maximum sizes, and Milstead (1969) reported a maximum carapace length of 168 mm (mean 133 mm) in 58 specimens.

Population differences in size are indicated for *T. coahuila*. Turtles inhabiting marshes appear to be smaller than those from river or pool habitats in the Cuatro Ciénegas basin.

Inter-population differences in size and growth rates of *Chrysemys picta* were reported by Gibbons (1967). He postulated that difference in food quality between a marsh, lake, and river population (where turtles were mainly herbivorous, omnivorous, and carnivorous, respectively) was a likely factor responsible for the size differences observed: marsh *C. picta* were considerably small than lake or river turtles.

Such an explanation may be applicable for *T. coahuila* populations as well. *T. coahuila* in marshes are largely omnivorous, feeding in roughly equal amounts on aquatic invertebrates (chiefly insects) and plants (Brown, in press). Three of five turtles from a river (Río Mesquites) had eaten small fishes; these were the only cases of this dietary preference. Although not conclusive, food differences between marsh and river populations in the Cuatro Ciénegas basin may result in different growth rates and maximum sizes. Additional sampling of food habits of river or canal-inhabiting *T. coahuila* are needed to verify this possibility.

Another factor involved might be population densities. Marshes are densely populated by *T. coahuila* (see below), whereas rivers and canals appear to support smaller, more dispersed populations. If *T. coahuila* in marshes are simply more easily seen and collected than turtles in rivers and canals, a source of error in density comparisons between the two habitats is possible. However, much less shallow (<15 cm) water space (an optimal foraging requirement for *T. coahuila*) is available in rivers and canals and this fact by itself greatly reduces the chance of such an observational error. Effects of greater crowding and competition in marshes could cause a slower growth rate in marsh than in river populations. Unfortunately, no adequate population data for river-dwelling *T. coahuila* are as yet available to substantiate this possibility.

Sexual Dimorphism—Schmidt and Owens (1944) stressed difference in plastral indentation between male and female *T. coahuila*, and, along with Webb et al. (1963), noted a more prominently notched maxillary beak in males. Color or pattern differences between males and females are lacking. Most large males possessed flared marginals and often appeared flatter than females. The concave plastron of males was the most useful field character for sex determination, but it was frequently necessary to confirm the sex by inspecting the somewhat bulky tail of males and the more spacious cloaca of females. External traits that best distinguish the sexes in *T. coahuila* are as follow:

males	females
1. Posterior lobe of plastron indented (concave).	Posterior lobe of plastron flat or convex.
2. Tail longer, thicker at base.	Tail shorter, thinner at base.
3. Carapace relatively lower (average height/length ratio about 43%).	Carapace relatively higher (average height/length ratio about 46%).
4. Iris brownish, flecked with yellow.	Iris yellowish, flecked with brown.

To study sexual dimorphism in morphological characters involving the shell, six bi-variate relations between seven shell dimensions (see "Methods") were developed (Table 1, Fig. 1).

Correlation coefficients in all relations studied in *T. coahuila* are high, ranging from 0.82 to 0.99. Males and females are nearly identical in BR-W/CL, POST-CW/CL, ANT-L/PL, and POST-L/PL (Fig. 1 A-D). In all these relations, males show higher r values (Table 1) and a corresponding greater proportion of the variation in Y, as measured by sum of squares, due to linear regression of Y on X. Slight sexual dimorphism is seen in the PL vs CL regression (Fig. 1E), with the plastron length of females showing a relative increase greater than that of males as carapace length increases. The difference between regression coefficients was not significant, however ($P>0.05$).

The relationship showing strongest sexual difference in *T. coahuila* is CH/CL (Fig. 1F), although the regression coefficients do not differ significantly ($P>0.10$). Schmidt and Owens (1944:102) alluded to this difference when they described a female as having the shell "... a little more arched in lateral outline. . . ." In 70 males over the size range studied (carapace length 81.9–143.5 mm), carapace height ranged from 37.7 to 46.5% of carapace length, mean 42.9%; in 94 females (carapace length 88.5–114.1 mm) carapace height ranged

TABLE 1

Statistical data and regressions of linear relations for carapace and plastron measures (see text for abbreviations) in *T. coahuila*

Variables related	Sex	n	$\bar{x}$	$\bar{y}$	r	$Y = a + bX$	s^2YX
BR-W (Y)	♂	70	108.88	69.88	.931	$Y = 10.65 + 0.544X$	3.91
vs. CL (X)	♀	94	100.93	65.76	.876	$Y = 10.75 + 0.545X$	2.88
POST-CW (Y)	♂	70	108.88	73.94	.946	$Y = 8.61 + 0.600X$	3.69
vs. CL (X)	♀	94	100.93	69.27	.883	$Y = 7.60 + 0.611X$	3.37
CH (Y)	♂	70	108.88	46.69	.874	$Y = 12.94 + 0.310X$	2.57
vs. CL (X)	♀	94	100.93	46.06	.815	$Y = 10.33 + 0.354X$	2.03
ANT-L (Y)	♂	63	106.74	40.09	.967	$Y = -0.47 + 0.379X$	0.71
vs. PL (X)	♀	93	100.31	37.49	.927	$Y = -1.83 + 0.392X$	0.75
POST-L (Y)	♂	63	106.74	66.65	.987	$Y = 0.37 + 0.621X$	0.71
vs. PL (X)	♀	93	100.31	62.82	.966	$Y = 2.43 + 0.602X$	0.76
PL (Y)	♂	63	108.90	106.74	.978	$Y = 13.09 + 0.860X$	3.13
vs. CL (X)	♀	93	100.87	100.31	.961	$Y = 7.11 + 0.924X$	2.27

Symbols used: n = sample size; $\bar{x}$ = mean of X values; $\bar{y}$ = mean of Y values; r = correlation coefficient; a = Y intercept value; b = regression coefficient; s^2YX = sample variance from regression.

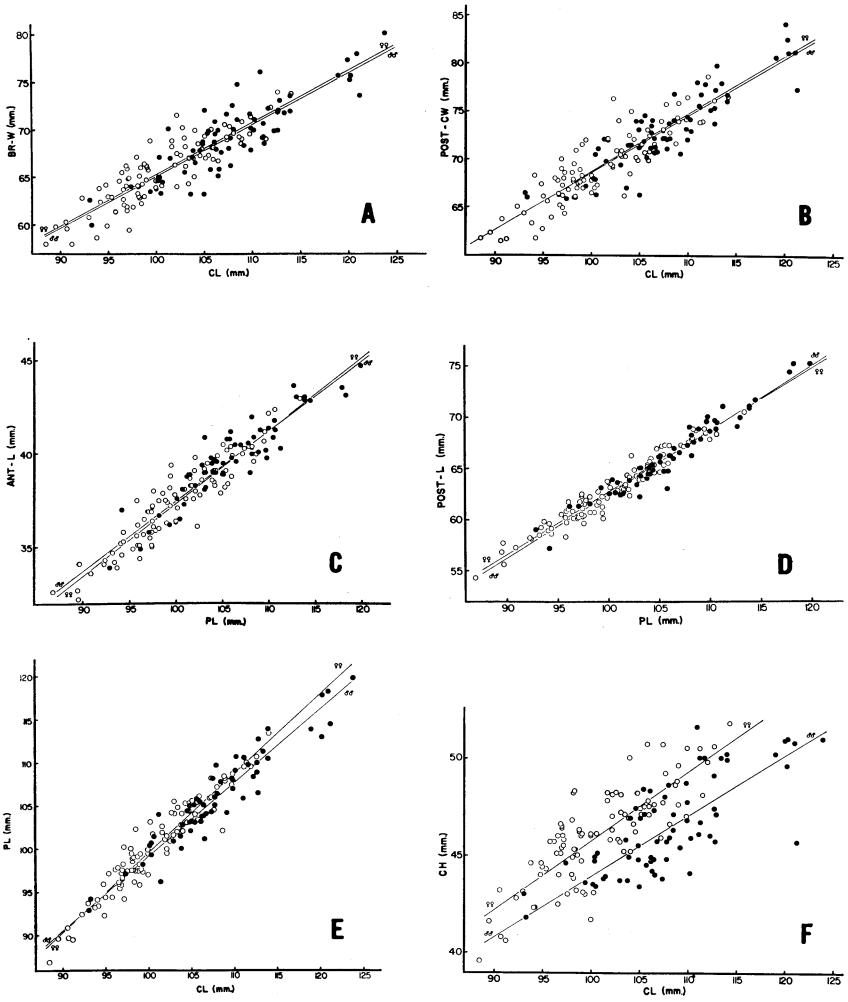

Fig. 1. Regressions of linear relations for carapace and plastron measures (see text for aabbreviations) in *T. coahuila*. Regression lines calculated by method of least squares. Solid circles, males; open circles, females. A, F, 66 males, 94 females; B, 65 males, 94 females; C, D, E, 59 males, 93 females.

from 41.7 to 49.1% of carapace length, mean 45.6%. The CH/CL ratio is significantly higher ($P<0.01$) in females than in males (Fig. 2).

The regression analysis shown here for *T. coahuila* indicates that the shell of females is relatively (but not significantly) higher than males,

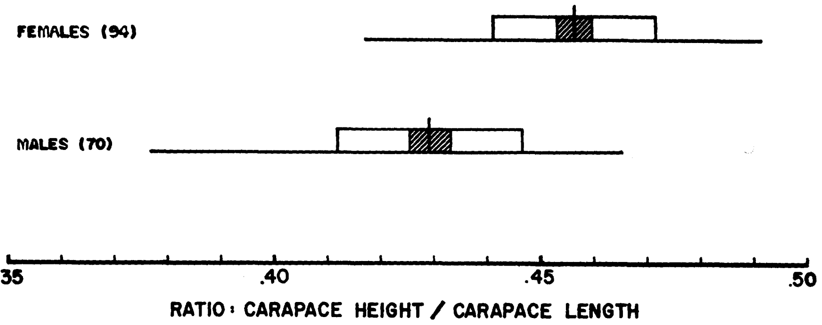

Fig. 2. Sexual dimorphism in ratio of carapace height to carapace length in 164 adult *T. coahuila*. Horizontal and vertical lines show range of variation and mean, respectively; hatched and open blocks represent 95% confidence limits (approximately two standard errors) and one standard deviation, respectively, on each side of the mean.

whereas reliance on the ratio plots alone tends to overstate the difference. In addition, a ratio provides no way to estimate the value of one variable from the known value of another as can easily be done using a least squares linear regression equation.

Color and Markings—Coloration and pattern of *T. coahuila* have been recorded by Schmidt and Owens (1944) and by Webb et al. (1963). The carapace has a uniform dark brown, brown, or olive-brown hue, which, in most specimens, is patterned with small, yellow, irregular lines, like worm tracks on the dark ground color (Fig. 3). These markings were called "fine yellowish vermiculations" by Schmidt and Owens (1944). Not all *T. coahuila* possess such a vermiculated pattern. It is often difficult to see unless the carapace is dampened and inspected closely. Note was made, however, of its presence or absence in 106 adult or subadult individuals in the field; 71% showed some extent of pattern. In the laboratory, 48 preserved specimens were examined more critically: 77% possessed some pattern. Vermiculations may be sparse, or may cover most of the central and upper portions of the lateral scutes. Whether a turtle possesses or lacks these markings is seemingly not correlated with body size.

The plastron of adults is plain dull yellow in color, but 13% of 48 preserved specimens had thin dark brown or black-rimmed seams of the plastral scutes. More males (29%) than females (6%) showed development of dark pigment on the plastron, and it was present only in smaller specimens of both sexes.

A recently-hatched juvenile (ASU 8000), caught 15 October 1966 (carapace 33.1, plastron 30.5 mm), had a carapace ground shade of

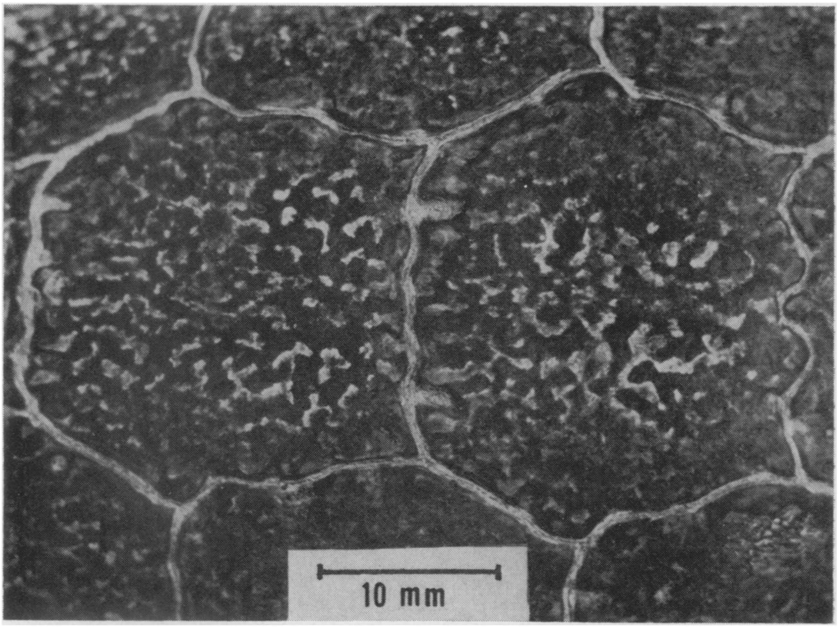

Fig. 3. Vermiculated pattern on carapace of *T. coahuila* (UU 12555, adult female). Second and third central scutes are shown (anterior toward left).

olive-brown overlain by a mottled pattern of darker brown or black spots, most noticeable on the first central and on the lateral scutes. The marginals were lighter (dull brownish-yellow) with dark brown posterior borders. A prominent dorsal keel was under the second, third, and fourth central scutes. The plastron was a light grayish-yellow, except at the seams where there were thin dark lines. Wider dark areas were present at the interhumeral, interabdominal, and interfemoral seams, and there was a dark blotch at the anterio-medial corner of both anal scutes. Ventrally, the marginal scutes had the same ground hue as the plastron and also possessed dark edges at the seams. Sides of the head were marked by a yellowish postocular stripe which widened to form a blotch. The antebrachial scales of the forelegs were light yellowish-gray, and the tail was marked by a distinct light stripe on the dorsal surface.

A juvenile (USNM 159578) collected and preserved on 20 August 1965 near the study area (carapace 51.4, plastron 49.8 mm) had solid yellow antebrachial scales on the forelegs, contrasting sharply with the dorsal brownish scales. A distinct, yellow, postocular stripe extended across the tympanum and graded into patches of brown, but continued posteriorly to the base of the skin fold of the neck. The throat was a marbled yellow as were the mandibular and maxillary beaks. The head was brown dorsally with a faint marbled pattern. Sides of the neck were predominantly yellow, with a brown mottled pattern. Carapace markings consisted of short, dark, enlarged lines radiating from the central portion to the periphery of the first four central and first three lateral scutes.

Both Cahn (1937) and Legler (1960) remarked that the carapace markings of *T. c. carolina* and *T. o. ornata*, respectively, tend to radiate from the central portion of a scute as growth proceeds. Legler (1960:654) states: "... the radial pattern is generalized and primitive for *Terraprene*. . . ." Webb et al. (1963:91) mentioned that juvenal *T. coahuila* have "... more contrasting patterns on the carapace and head than do adults. The carapace has a fine, yellowish-buff and blackish marbled, or reticulated, or radiating pattern. . . ." These authors also noted the presence of a postorbital stripe in the smallest specimen they examined (plastron 47 mm).

Scute Abnormalities—Of 218 *T. coahuila* examined (169 alive in the field, 49 preserved), 11 (5%) had either extra epidermal ("supernumerary") scutes or had less than the normal number, and five had incomplete or abnormal (usually crooked) interlaminal seams. Cagle (1950) recorded carapace scute abnormalities in 5.7% of 860 *Pseudemys scripta* from Illinois.

All scute anomalies occurred on the carapace, but distorted sutures were present on both carapace and plastron. Reduction of the normal number of all three series of carapace scutes was observed in four individuals, as follows: three laterals on both sides; three laterals and 11 marginals on both sides and four centrals; 11 marginals on both sides; and 11 marginals on right side only. Seven individuals possessed one additional scute (either seemingly inserted between existing normally-shaped scutes, or added by a mid-line seam in an existing normally-shaped scute) as follows: six centrals formed by a small accessory scute between the second and third centrals (two turtles); six centrals formed by a mid-sagittal division of the second central (three turtles); five right laterals formed by a divided (Y-shaped) first interlateral seam near the fifth marginal; and five right laterals formed by a median seam in the first lateral.

Some specimens of *T. coahuila* have shallow radiating furrows in the carapace, particularly on the lateral scutes. These furrows generally run down the sides (from the medial to peripheral border of the lateral scutes, irregularly on the centrals), giving a slightly corrugated appearance to the carapace. No mention of such carapacial corrugations has been seen in the literature for any turtle, and their significance (in *T. coahuila*) is unknown.

Evolutionary Status—Controversy over the phylogenetic position of *T. coahuila* has taken two views: (i) the species is generalized and primitive (Auffenberg, 1958; Legler, 1960; Williams, Smith and Chrapliwy, 1960); and (ii) the species is a Pleistocene relict produced by environmental isolation (Auffenberg and Milstead, 1965; Milstead, 1960, 1967).

It now appears, on the basis of data presented by Milstead (1969), that the case for *T. coahuila* being a primitive ancestral form has been damaged. In fact, no solid evidence, other than brief speculations occasioned by the ecological and morphological distinctness of *T. coahuila*, supports the "primitive" hypothesis.

The thesis of Milstead's argument is that *T. coahuila* evolved from a population of turtles inhabiting the broad eastern coastal plain of México during pluvial (i.e., glacial) periods of the Pleistocene. This coastal population was presumed to have been intermediate in morphology between an extinct subspecies, *Terrapene carolina putnami*, and the modern *T. c. triunguis*. Alternating north-south migrations of the Gulf Coast population with each interglacial and glacial stage of the Pleistocene left disjunct populations of *Terrapene* in the Yucatán peninsula (*T. c. yucatana*), along a small part of the east coast of México (*T. c. mexicana*), and in central Coahuila on the Mexican Plateau (*T. coahuila*). The final isolations of *T. c. yucatana* and *T. c. mexicana* presumably took place toward the end of the last (Wisconsin) glaciation.

Milstead (1967) first postulated that whereas *T. coahuila* may have been isolated earlier than the other two populations in eastern México, it seemed instead to have undergone rapid adaptations to an aquatic existence, possibly in as brief a time as only several thousand years. This rapid evolution was mediated through strong selective pressures to adapt to available aquatic habitats following the (post-Wisconsin?) invasion of arid conditions into the Cuatro Ciénegas basin. The founder population of box turtles was unable to withdraw during an interglacial period as coastal populations had done earlier. More recently, Milstead (1969) has concluded that the evolution of *T. coahuila* could have been initiated earlier in the Pleistocene, "in pre-Wisconsin times."

Milstead's argument would seem to be bolstered by the theoretical discussion of Mosimann (1958b). This paper has apparently been overlooked in discussions of the origins of *T. coahuila* and attention is called to it here because recent ecological observations of *T. coahuila* (Brown, in press) appear to lend strong support to Mosimann's discussion of instances in which an organism's choosing a habitat of limited area could increase the probability of mate-finding and lead to strong natural selection for certain traits in a population with initially small effective size. If this hypothesis is correct, the unique ecology (and morphology, see Milstead [1969]) of *T. coahuila* could have been produced relatively recently by natural selection from an earlier *Terrapene* ancestor.

For a population to maintain a sufficiently high adult density, preference for subareas within the geographic range (G) by habitat selection (ecological restriction to definite areas within G), and/or increasing the inter-individual detecting range (r), are two possible mechanisms considered by Mosimann (1958b) for effecting rapid evolutionary change. The crux of Mosimann's "habitat selection" hypothesis was stated as follows: "The effect of maintaining a favorable G/r ratio could produce some interesting evolutionary-ecological interactions. For example, in an area of two habitats, where one is of much less spatial extent than the other, there could be an accelerated natural selection for a character of specific adaptation for the smaller habitat, by virtue of the necessity of the sparse species to maintain itself above a critical density. This would be accelerated selection (by means of a density factor) for a physically adaptive genotype" (Mosimann 1958b: 256–257).

Preferred habitats of *T. coahuila* in much of the Cuatro Ciénegas basin today are small, spring-fed marshes of shallow water and dense emergent sedge cover (Brown, in press). No intermediate mesic habitat exists between the marshes and the surrounding arid terrain consisting of vast areas of halophytic grasses and shrubs. This ecological situation is seen to correspond remarkably well with that postulated by Mosimann as leading to high selection coefficients operating on characters "previously having only slight adaptive value in themselves." Characters strongly selected for in *T. coahuila* as the basin's environment became more arid, were (for the most part) those in the gene pool of the ancestral *T. carolina putnami* (Milstead, 1967). This form is believed to have been semiaquatic as is the modern *T. c. major* today. *T. coahuila* possesses certain characters present in both the extinct *T. c. putnami* (heavy postorbital bar, short anterior lobe of plastron, four hind toes) and the living *T. c. triunguis* (plastral seam ratios) (Milstead, 1969). Parallel evolution is invoked by Milstead (1969) as an explanation of the resemblance of plastral ratios in the earlier (pre-Wisconsin) *T. coahuila* to the later-derived *T. c. triunguis*.

Estimates of population densities of *T. coahuila* within marshes are about 60 adults per acre (Brown, in press). These densities are considerably higher than those reported for the terrestrial species, *T. o. ornata* and *T. c. carolina* (2–6 turtles per acre [Legler, 1960] and 4–5 turtles per acre [Stickel, 1950], respectively). Actually, the high population densities of *T. coahuila* do not detract from the plausibility of Mosimann's model in view of his statement that "populations which are by no means sparse today may show low-density adaptive traits inherited from their past" (Mosimann 1958b: 255).

The systematics of *Terrapene coahuila* is not complete. Further taxonomic studies employing multi-character analyses could elucidate whether certain characters in *Terrapene* may be confidently considered primitive or derived. Thus, whether the hypothesis of a recent derivation of *T. coahuila* (now supported by ecological facts) can stand will depend largely on future work by chelonian taxonomists. Nonetheless, conclusions reached by Milstead corroborate Mosimann's model of habitat selection rather well; the latter, in turn, appears to fit very nicely with what is known of the actual dispersion of *T. coahuila* in nature. The ecological evidence currently available tends to support the hypothesis of a pluvial Pleistocene evolutionary origin of *T. coahuila*.

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