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APPENDIX II

Continued

Branch	Character	CI	Change
	22	0.333	0 → 1
	25	0.500	0 → 1

APPENDIX III

Scute Landmarks Depicted in Figure 1

1, midline of cervical at shell edge; 2, seam between marginals 1 and 2 at the shell edge; 3, seam between marginals 2 and 3 at the shell edge; 4, seam between marginals 3 and 4 at the shell edge; 5, seam between marginals 4 and 5 at the shell edge; 6, seam between

marginals 5 and 6 at the shell edge; 7, seam between marginals 6 and 7 at the shell edge; 8, seam between marginals 7 and 8 at the shell edge; 9, seam between marginals 8 and 9 at the shell edge; 10, seam between marginals 9 and 10 at the shell edge; 11, seam between marginals 10 and 11 at the shell edge; 12, seam between marginals 11 and 12 at the shell edge; 13, seam between marginals 12 and 13 at the shell edge; 14, intersection of marginals 1 and 2 and pleural 1; 15, intersection of marginal 5 and pleurals 1 and 2; 16, intersection of marginal 7 and pleurals 2 and 3; 17, intersection of marginal 9 and pleurals 3 and 4; 18, intersection of marginal 11, pleural 4, and vertebral 5; 19, intersection of marginals 12 and 13 and vertebral 5; 20, intersection of vertebrae 4 and 5 at the midline; 21, intersection of vertebrae 1 and 2 at the midline; 22, intersection of vertebrae 2 and 3 at the midline; 23, intersection of vertebrae 3 and 4 at the midline.

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PHYLOGENETIC RELATIONSHIPS AMONG THE BOX TURTLES, GENUS *TERRAPENE*

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ABSTRACT: The North American box turtles belong to a taxonomically diverse assemblage adapted to a wide variety of habitats. Relationships within the genus are complex, and variation within *T. carolina* is especially problematic. I analyzed 32 morphological characters phylogenetically to deduce the most parsimonious relationships among the 11 currently recognized taxa. Two species groups, the *ornata* and *carolina* groups, are recognized. The *ornata* group includes *T. ornata* and *T. nelsoni*, the *carolina* group includes *T. carolina* and *T. coahuila*. *Terrapene coahuila* is the basal clade of the *carolina* group. Within *T. carolina*, *T. c. major* is the most basal subspecies with the rest comprising two monophyletic groups: (1) *T. c. yucatanana*, *T. c. mexicana*, and *T. c. triunguis* and (2) *T. c. carolina* and *T. c. bauri*. Within the *ornata* group, *T. ornata* is the sister taxon of *T. nelsoni*.

Key words: Systematics; Turtles; *Terrapene*; Morphology

THE North American box turtles comprise four ecologically diverse species. Monotypic *Terrapene coahuila* (Schmidt and Owens) is an aquatic form endemic to the Cuatro Ciénegas region of northern

Mexico (Iverson, 1982a). The six subspecies of *Terrapene carolina* (Linnaeus) are primarily terrestrial turtles that inhabit temperate forests in the eastern and southeastern United States and the eastern thornscrub forests of Mexico. The two subspecies of *Terrapene nelsoni* (Stejneger) occur in the Pacific versant of the foothills of the Sierra Madre Occidental in Mexico

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(Iverson, 1982*b*), and the two subspecies of the xeric-adapted *Terrapene ornata* (Agassiz) occur in the Great Plains of the United States, and in the Chihuahuan and Sonoran deserts of the United States and Mexico (Ward, 1978).

Relationships within the genus *Terrapene* are unclear (Ditmars, 1934; Milstead, 1969; Pope, 1939) and the included taxa have undergone several nomenclatural revisions (Boulenger, 1889, 1895; Carr, 1940; Milstead, 1967; Smith, 1939; Stejneger and Barbour, 1933). The intergrading (or possibly parapatric) subspecies of *T. carolina* (*T. c. bauri*, *T. c. carolina*, *T. c. major*, and *T. c. triunguis*) have been especially problematic. Previous investigators (Carr, 1940, 1952; Conant and Collins, 1991; Milstead, 1969; Mount, 1975) have variously identified intergradation zones by using different combinations of diagnostic characters. *Terrapene c. major* is the least understood of the subspecies, and considerable disagreement exists concerning its status. Auffenberg (1958) suggested that *T. c. major* is not a subspecies but is a population of intergrades (e.g., *T. c. putnami* (extinct) × *T. c. triunguis* or *T. c. carolina* or *T. c. bauri*). Later, Milstead (1967, 1969) concluded that the Appalachian population is the only non-intergrading "pure" population of *T. c. major*. Dundee and Rossman (1989) considered some populations of that subspecies from Louisiana as non-intergrading. Conversely, Ward (1980) concluded that *T. c. major* is a full species, ecologically isolated from *T. carolina*.

The genus exhibits considerable intraspecific variation in morphology (Barbour and Stetson, 1931), and phylogenetically informative characters are difficult to establish. Nevertheless, Milstead (1969) proposed a phylogeny of the genus using paleontologic data and morphometrics of interplastral scute ratios. On the basis of 16 characters, he subdivided the genus into two species groups: the *ornata* group (*T. ornata* and *T. nelsoni*) and the *carolina* group (*T. carolina* and *T. coahuila*). In this study, I examined 32 morphological characters phylogenetically to resolve relationships among the 11 currently recognized taxa of *Terrapene*.

METHODS

The characters used in this study (Table 1) have been arranged into three categories: skeletal, head and limbs, and carapace and plastron, respectively. Both discrete and continuously varying characters with appropriate character distributions are included (autapomorphies are included only if previously undescribed in the literature). I used two methods alternately to code discrete data. In the first, discrete characters were treated as in Cartmill (1978). When two character states occurred in a taxon, only the derived state, rather than an intermediate, was recognized (intermediate states were only those that were morphologically intermediate in form between two other states). In the second method, discrete characters were treated as in Meylan (1988), wherein a taxon was recorded as having the intermediate state if it had both apomorphic and plesiomorphic conditions, or if it had only the morphologically intermediate condition. I did not formulate a priori hypotheses concerning the direction of evolution in a transformation series by ordering multi-state characters. Continuously varying traits were divided into states by the occurrence of natural breaks along a continuum of plotted averages (Meylan, 1988). The 32 characters are given equal weight in all analyses.

Phylogenies were rooted using a composite of outgroups to make a hypothetical ancestor, because the closest relative of *Terrapene* is not well established. *Clemmys* (McDowell, 1964) and *Emys* (Milstead, 1969) have each been suggested to be the sister taxon of *Terrapene*. The relationship of *Emydoidea* to *Terrapene* has also been debated. Tinkle (1962), McDowell (1964), Zug (1966), and Dryden (1985) supported a close relationship between *Emydoidea* and *Deirochelys*, whereas Bramble (1974), Jackson (1978), and Seidel and Adkins (1990) have shown that *Emydoidea* share affinities with *Terrapene*. Therefore, polarization of characters was determined using *Clemmys insculpta*, *Emydoidea blandingi*, and *Emys orbicularis* as a composite outgroup. Several stud-

TABLE 1.—The data matrix for character states of *Terrapene*, including that for a hypothetical ancestor, Hypanc. Sample sizes are in parentheses, question marks are undetermined or missing data, and zeros indicate the primitive state. Specimens were examined for characters CC, BS, NG, IC, IM, IB, and WP, but no specific records were kept for these characters. The character abbreviations here are the same as in the text. For some characters, a second state (separated by a backslash) is the alternative state by using Cartmill's (1978) method (Fig. 2).

	PO	ZA	PF1	PF2	CO	NC	SP	TP	SC	HC	CC	BS	NG	PR	IC	MK
Hypanc	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
<i>T. c. yucatanana</i>	1	1	0	1	1	0	0	1	1	0	0	0	0	0	?	1
	[1]	[1]	[7]	[10]	[2]	[1]	[1]	[1]	[1]	[9]				[10]		[10]
<i>T. c. mexicana</i>	1	1\2	1\2	2\1	1	0	0	1	1	1	0	0	0	0\1	0	1
	[3]	[2]	[8]	[9]	[3]	[1]	[1]	[1]	[1]	[13]				[16]		[24]
<i>T. c. triunguis</i>	1	1\2	1\2	2\1	1	0\1	0	1	1	1	0	0	0	0\1	0	1
	[5]	[27]	[28]	[11]	[35]	[19]	[6]	[2]	[2]	[69]				[64]		[27]
<i>T. c. carolina</i>	1	1\2	2	1	1	0\1	0	1	1	0	0	0	0	1	0	1
	[6]	[22]	[21]	[14]	[26]	[10]	[3]	[1]	[7]	[31]				[29]		[12]
<i>T. c. bauri</i>	1	1	2	1	1	0	0	1	1	1	0	0	0	2\1	2	1
	[5]	[12]	[24]	[24]	[22]	[8]	[2]	[2]	[14]	[39]				[34]		[27]
<i>T. c. major</i>	0	0	0	1	1	0	0	1	1	0\1	0	0	0	3\2	0	1
	[4]	[4]	[5]	[6]	[8]	[3]	[2]	[1]	[6]	[31]				[30]		[17]
<i>T. coahuila</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	3\2	1	0
	[6]	[4]	[5]	[7]	[6]	[5]	[3]	[2]	[5]	[14]				[14]		[15]
<i>T. o. ornata</i>	2	2	3\1	2\1	0	1	1	0	0	0	1	0	1	0\1	0	2
	[6]	[14]	[5]	[2]	[20]	[17]	[14]	[2]	[7]	[14]				[22]		[39]
<i>T. o. luteola</i>	2	2	?	2\1	0	1	1	0	0	0	1	0	1	0	0	2
	[1]	[1]	[0]	[1]	[12]	[2]	[2]	[1]	[3]	[8]				[17]		[17]
<i>T. n. klauberi</i>	?	?	3\1	1	?	?	?	?	?	0	1	1	0	0	0	0
	[0]	[0]	[2]	[3]	[1]	[0]	[0]	[0]	[0]	[7]				[7]		[8]
<i>T. n. nelsoni</i>	2	2	3\1	2\1	0	2\1	1	0	0	0\1	1	1	0	0	0	0
	[3]	[3]	[2]	[2]	[4]	[4]	[4]	[1]	[3]	[30]				[21]		[34]

ies (Forbes, 1966; Frair, 1982; Merkle, 1975; Parsons, 1968) suggest that *C. insculpta* has retained more plesiomorphic characters than other species of *Clemmys*. When outgroup analysis was inconclusive, polarity was based on commonality and embryologic states (Wiley, 1981).

I used Phylogenetic Analysis Parsimony (PAUP, version 1990) by Swofford (1990) to formulate the most parsimonious hypotheses of hierarchical relationships among the included taxa. I used the branch and bound, mulpars, and global swap options to find all equally parsimonious trees.

CHARACTER ANALYSIS

Skeletal

Postorbital bone (PO).—Skull terminology follows Zangerl (1948), unless otherwise stated. The postorbital bone or postorbital arch (Cahn, 1937; Taylor, 1895) is reduced in *Terrapene*, and this condition is presumably correlated with a terrestrial

existence (Legler, 1960). The relative width of the bone is its shortest width divided by its longest width along the suture with parietal. The postorbital is wide in *T. coahuila* and *T. c. major*, and narrow in *T. c. bauri*, *T. c. carolina*, *T. c. mexicana*, *T. c. triunguis*, and *T. c. yucatanana*. A third state, an extremely thin postorbital bone, occurs in *T. ornata* and *T. n. nelsoni*. A wide postorbital is the condition of outgroup members and is considered the plesiomorphic state. A skull of *T. n. klauberi* was not available for observation.

Zygomatic arch (ZA).—The zygomatic arch in *Terrapene* is composed of the quadratojugal and jugal bones. The arch is sutured anteriorly to the postorbital and maxilla and posteriorly to the quadrate. Reduction of the zygomatic arch is also correlated with a terrestrial existence (Legler, 1960). The arch is present in *T. coahuila*, *T. c. major*, and in most *T. c. bauri*. In most *T. c. carolina*, *T. c. mexi-*

TABLE 1.—Extended.

DS	PB	MS	HP	IM	AN	EC	AP	AS	IS	IB	WP	LR	IL	CS	CP
0	0	0	?	0	0	0	0	?	0	0	0	0	0	0	0
1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	1
[11]	[11]	[6]	[10]			[10]	[10]	[10]	[8]			[8]	[10]	[8]	[1]
1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	1
[14]	[24]	[25]	[14]			[14]	[13]	[24]	[11]			[13]	[22]	[13]	[1]
1	0	0	1	0	1	0	0	2	1	1	1	0	1	1	1
[65]	[60]	[42]	[64]			[65]	[60]	[70]	[21]			[73]	[62]	[25]	[8]
0	0	0	1	0	1	0	0	1	1	1	1	0	1	1	2
[29]	[21]	[12]	[26]			[25]	[30]	[29]	[13]			[21]	[20]	[13]	[8]
0	0	0	1	0	1	0	0	1	1	1	1	0	1	1	2
[33]	[33]	[19]	[21]			[24]	[20]	[38]	[33]			[49]	[36]	[32]	[5]
0	0	0	1	0	1	0	0	2	1	1	1	0	0	1	2
[29]	[29]	[17]	[47]			[31]	[29]	[29]	[23]			[30]	[31]	[33]	[10]
0	0	0	0	0	0	1	0	2	1	1	1	0	0	0	2
[11]	[11]	[8]	[13]			[13]	[8]	[8]	[11]			[15]	[15]	[11]	[6]
0	0	1	2	0	1	2	1	3	0	0	0	1	0	0	0
[43]	[43]	[41]	[46]			[45]	[43]	[16]	[88]			[42]	[41]	[61]	[16]
0	0	1	2	0	1	2	1	3	0	0	0	1	0	0	0
[15]	[13]	[16]	[15]			[16]	[14]	[9]	[15]			[14]	[14]	[17]	[5]
0	0	0	0	1	1	0	1	0	0	1	1	0	0	1	0
[10]	[10]	[7]	[10]			[10]	[7]	[8]	[3]			[8]	[8]	[4]	[2]
0	0	0	0	1	1	1	1	0	0	1	1	0	0	1	0
[29]	[27]	[27]	[30]			[24]	[29]	[29]	[7]			[31]	[38]	[8]	[4]

cana, *T. c. triunguis*, *T. c. yucatana*, and some *T. c. bauri*, the arch is cartilaginous with anteriorly directed jugal processes and/or posteriorly directed postorbital processes. Rarely in *T. c. mexicana*, *T. c. triunguis*, and *T. c. carolina* are the processes absent. In *T. ornata* and *T. n. nelsoni*, the arch is absent, as are the processes. The arch is well developed in the outgroup members and thus considered plesiomorphic. A skull of *T. n. klauberi* was not available for observation.

Phalangeal formula of forefeet (PF1).—The phalangeal formulae of the forefeet are variable in some taxa of *Terrapene* but not in others (Minx, 1992; Taylor, 1895). *Terrapene coahuila*, *T. c. yucatana*, and *T. c. major* have the forefoot formula of 2-3-3-3-2, which is considered the plesiomorphic condition of the forefeet and hindfeet in *Terrapene* (Minx, 1992). A formula of 2-3-3-2-2 is typical for *T. c. triunguis* and *T. c. mexicana*. *Terrapene c. car-*

olina and *T. c. bauri* have both states, but the plesiomorphic state is typical. The condition of these two taxa is coded as a third state by the Meylan (1988) method, but the condition is considered derived by the Cartmill (1978) method (Table 1). The most reduced formula, 2-2-2-2-2, is shared by *T. o. ornata* and *T. nelsoni*. The phalangeal formula of the forefoot in *T. o. luteola* was not observed.

Phalangeal formula of the hindfeet (PF2).—The phalangeal formulae of the hindfeet are even more variable than the forefeet in some taxa (Minx, 1992). *T. coahuila* has the plesiomorphic hindfoot formula of 2-3-3-3-2 (Minx, 1992). *Terrapene ornata*, *T. n. nelsoni*, *T. c. triunguis*, and *T. c. mexicana* have the derived formula of 2-3-3-3-1. Both states were observed in the two specimens of *T. n. klauberi* that were examined, which is considered a third state by Meylan (1988). *Terrapene c. major*, *T. c. yucatana*, *T. c. carolina*, and *T.*

c. bauri are also variable, but the plesiomorphic state is typical in the former two subspecies and the derived state is typical of the latter two.

Co-ossification of carapace bones (CO).—Co-ossification, an apomorphic state in *Terrapene*, occurs between neural bones, neural and peripheral bones, and occasionally between the suprapygal and peripheral bones. Co-ossification of some or all of these bones was observed in specimens of *T. carolina* and *T. coahuila*. Ankylosis of carapacial bones in the *carolina* group appeared to be correlated with shell wear (presumably age), so subadults were not utilized. Co-ossification was not observed in *T. ornata*, or *T. n. nelsoni*, or the outgroups. The shell of the one specimen of *T. n. klauberi* examined in the study showed some signs of co-ossification, but the character state of that taxon was considered inconclusive. The shell of this specimen also did not provide data for the two following characters.

Neural configuration (NC).—The typical and plesiomorphic configuration of the neural bones in emydids is hexagonal (Pritchard, 1988). In *Terrapene*, the shape of the neurals varies considerably. The seven neurals of *T. carolina* and *T. coahuila* are typically hexagonal with the exception of the first and seventh neurals, which are typically tetragonal and heptagonal, respectively. Usually, the first three neurals of *T. n. nelsoni* and *T. ornata* are alternately tetragonal and octagonal. Though a trend is evident, the first three neurals appear to be too variable to characterize the *ornata* and *carolina* groups. The most distinguishing neurals are the fourth and fifth. *Terrapene n. nelsoni* has derived states, in which the fourth neural is either octagonal or heptagonal, and the fifth neural is tetragonal or pentagonal. *Terrapene ornata* has both the plesiomorphic and derived states. Rarely, *T. c. triunguis* and *T. c. carolina* have an octagonal fourth neural and a tetragonal or pentagonal fifth neural. The last two neurals of *T. n. nelsoni* and *T. ornata* are hexagonal and heptagonal, respectively, as in *T. carolina*. The typical neural formula of *T. n. nelsoni*, 4-8-4-(7,8)-(4,5)-6-7 is considered derived and the 4-6-

6-6-6-7 formula of the *carolina* group is considered plesiomorphic. The neural configuration in *T. n. klauberi* was not observed.

Suprapygal configuration (SP).—The suprapygal in *T. carolina* and *T. coahuila* is spade-shaped. The eleventh pair of peripherals has a relatively broad region of contact with the suprapygal. In *T. ornata* and *T. n. nelsoni*, the suprapygal is triangular and the area of contact with the eleventh pair of peripherals is comparatively small. Polarity as determined by outgroup analysis was inconclusive, and a question mark was used for the character state of the hypothetical ancestor. The shape of the suprapygal was not observed in *T. n. klauberi*.

Thickened peripherals (TP).—North American box turtles are noted for their well developed anterior plastral hinge. In *Terrapene*, the peripherals posterior to the hinge may be thin and outwardly expanded as in *T. ornata* and *T. n. nelsoni*. Only a slight lip is formed by the posterior peripherals, into which the posterior plastral lobe roughly fits. In the *carolina* group, the peripherals are thick and form a distinct lip into which the posterior plastral lobe tightly fits. Outgroup members, with or without a hinge, have the plesiomorphic condition of a thin posterior plastral peripheral, with no lip. The peripherals were not observed in *T. n. klauberi*.

Scapular processes (SC).—The length of the scapula (upper branch) is longer than the acromial process (inner branch or endoscapula) in *T. carolina* and *T. coahuila* but is approximately equal in length to the acromial process in *T. ornata* and *T. nelsoni* (Baur, 1891; Taylor, 1895). The length of the scapula may simply reflect the height of the carapace, and by itself may not be of phylogenetic significance. For instance, the carapaces of *T. c. mexicana*, *T. c. yucatanana*, and *T. c. bauri* are highly arched and their scapular processes are correspondingly long. A scapular process of *T. n. klauberi* was not available for observation. The lengths of the scapula and acromial process are approximately equal in *Emys* and *Emydoidea*, but not *Clemmys*. The state of the former two outgroup

taxa and the *ornata* group is considered plesiomorphic.

Head and Limbs

Hind claws (HC).—The number of hind claws, often referred to as the number of hindtoes, varies between three and four in *Terrapene*. Three-clawed forms, such as *T. c. triunguis*, *T. c. bauri*, and *T. c. mexicana*, are more variable than four-clawed taxa. All taxa that are scored here as derived are actually intermediate, because no taxon is invariably three-clawed. For example, some specimens of *T. c. mexicana* have three claws on one hindfoot and four on the other. In addition, three-clawed specimens appear as rare variants in *T. c. major* and *T. n. nelsoni*. Reduction of the number of hind claws is apparently a terrestrial adaptation, and the character's phylogenetic significance is questionable. The reduced state of three hind claws is derived as indicated by the lack of the state in outgroup members.

Clasping claw (CC).—The ability of males to rotate the first hindtoe abruptly forward (clasping claw) was observed in *T. ornata* (Cahn, 1937) and *T. nelsoni* (Legler, 1960). The claw is typically thick and recurved in males of all species of *Terrapene*, but *T. coahuila* and *T. carolina* lack the ability to rotate the claw forward. The rotating claw is the derived state by outgroup analysis.

Bulbous shields (BS).—The scales or shields of the forelegs of *T. nelsoni* are convex, protruding outward, and appear bulbous or rugose. The bulbous shields, typically occurring in males of *T. nelsoni*, were not observed in other taxa of *Terrapene* or in outgroups.

Narial gap (NG).—The snout of *T. ornata* is soft, bulbous, and rounded in dorsal view. The nostrils are widely separated and are horizontally to diagonally oval. All other species of *Terrapene* have a flat, hard, and squared snout. The nostrils are narrowly separated and round or vertically oval. A few males of *T. n. klauberi* observed in the study had rounded and widely separated nostrils, similar to *T. ornata*. Outgroup members possess squared snouts and narrowly separated, round nostrils.

Premaxilla or maxillary shield (PR).—The maxillary beak and premaxilla is notched in *Terrapene*, except in most individuals of *T. c. carolina*, many individuals of *T. c. bauri*, and rarely in *T. c. triunguis*, *T. c. mexicana*, and *T. o. ornata*. In *T. c. carolina*, the beak is pointed. The character is variable and is considered an intermediate state in *T. c. bauri* (Ditmars, 1934). Besides the intermediate condition of *T. c. bauri*, three character states were identified. A single and sharp tomiodont (in *T. c. carolina*), two tomiodonts with a shallow cusp (in *T. nelsoni*, *T. ornata*, *T. c. triunguis*, *T. c. mexicana*, and *T. c. yucatanana*), and two large tomiodonts with a deep cusp (in some individuals of *T. coahuila* and *T. c. major*, most noticeably in males). The median notch may be worn smooth or rounded in adult specimens; therefore, juveniles are useful to evaluate the character. When visible, the premaxilla underlying the maxillary shield is useful, because it is not exposed to wear. A smooth or slightly rounded beak was observed in all taxa of *Terrapene*, presumably the result of wear. None of the outgroups have a down-turned beak as in *Terrapene*. The common condition among species of *Terrapene*, a shallowly-cusped beak, is considered plesiomorphic.

Iris coloration (IC).—The color of the iris has been frequently described (Carr, 1952; Conant and Collins, 1991) as a means of diagnosing sex in box turtles, although the trait is known to vary within taxa. Typically, the iris of the male is bright red and that of the female is brown-red, brown or yellow-green. The trait is not diagnostic for the genus. Brown (1971) reported that although some sexual dichromatism is evident in the iris of *T. coahuila*, bright red eyes are not found in this species. Apparently, red-eyed males also do not occur in *T. c. bauri*. The iris of males of *T. coahuila* is dark brown with darker flecks, and in males of *T. c. bauri* the iris is typically yellow or light brown, commonly with black stripes. Live specimens were examined for this trait, except for *T. c. yucatanana*, for which live specimens were not available. Reddish eyes in males occur to some extent in *Clemmys insculpta*, *Emy-*

doidea, and *Emys*. Red eyes are considered plesiomorphic in *Terrapene*.

Carapace and Plastron

Middorsal keel (MK).—A prominent middorsal keel occurs on the second, third, and fourth vertebral scutes of *T. carolina*. In *T. ornata*, the keel is absent, except a weak keel rarely occurs on the fourth vertebral scute. A moderately developed keel is usually present on the second, third, and fourth vertebrae in *T. coahuila* and *T. nelsoni*, except in specimens with considerable shell wear (presumably old specimens). The keel in all groups is susceptible to wear and, thus, immature specimens are most useful for observation. *Clemmys insculpta* has a very prominent keel, but a moderate keel, as in *Emys*, *T. coahuila*, and *T. nelsoni*, is presumed to be the plesiomorphic condition, because most aquatic emydines have a weak to moderate keel (my personal observation). *Emydoidea* has a weak keel when present.

Dark seams (DS).—The carapace of many specimens of *T. c. mexicana* and *T. c. yucatanana*, and some specimens of *T. c. triunguis* (Strecker, 1910), is dark olive brown, light brown, or horn-colored with black seams bordering each scute. Overall, carapace color patterns in box turtles are typically unique to taxa and thus phylogenetically uninformative. The dark seam pattern may be useful in that it is shared by three taxa, and thus distinctive from other taxa (and easily recognized). The pattern does not occur in the outgroups and is considered a derived trait.

Posterior pleural bone depression (PB).—Milstead (1967, 1969) regarded the presence of depressions in the upper parts of the posterior pleural bones as a synapomorphy for *T. c. mexicana*, and for *T. c. yucatanana*. This qualitative character is somewhat variable and does not appear to be as distinct as Milstead (1969) implied. The depressions are uncommon in *T. c. mexicana*, but most individuals of *T. c. yucatanana* possess them to some degree. Depressions in the pleurals are rarely observed in *T. carolina* in the United States, but when present, the depressions typically occur in the posterior half of the

fourth costals, instead of the anterior half as in *T. c. mexicana*, and in *T. c. yucatanana*. This trait appears to coincide with the highly vaulted, tectiform carapace (Taylor, 1895) of most individuals of *T. c. yucatanana*, and some individuals of *T. c. mexicana*. Outgroups do not have the depressions and their presence is considered apomorphic.

First marginal shape (MS).—In *T. carolina*, *T. coahuila*, and *T. nelsoni*, the first marginal scute is short in width (nuchal to the second marginal), long in length (anterior-most edge near the second marginal to where the first marginal, the first central, and the first costal meet) and long at the first marginal to first costal seam. In *T. carolina*, *T. coahuila*, and *T. nelsoni*, the sum of the length of the marginal and the length of first costal seam is greater than the width of the first marginal (nuchal to the second marginal). In *T. ornata*, the scute is long in width, short in length, and the first costal seam is short. Milstead (1969) reported that the marginal is oval in the *ornata* group and square in the *carolina* group; however, the first marginal of *T. nelsoni* is also square. Outgroups were variable and so the more common condition of the *carolina* group is presumed to be ancestral.

Location of the highest point of the carapace (HP).—The highest point of the carapace is anterior to, posterior to, or at the plastral hinge in *Terrapene*. In *T. carolina*, except in some males of *T. c. major*, the highest point is at the posterior end of the second costal, which is posterior to the hinge. In *T. coahuila* and *T. nelsoni*, the highest point is approximately at the middle of the second costal, and the angle of the scute is low, indicating that the highest point is only slightly higher than at the hinge, and thus typically posterior to the hinge. In most individuals of *T. ornata*, especially *T. o. luteola*, the highest point is at the posterior end of the first costal, which is anterior to the hinge. In outgroup members that have a hinge, the second costal is angled low and the highest point is variable, but it typically occurs at the hinge. Polarization by outgroup analysis was inconclusive and was coded as such,

but the condition in *T. nelsoni* and *T. coahuila* appears closest to what may have been the ancestral state.

Depression between the twelfth pair of marginals (IM).—Commonly, *T. nelsoni* (especially *T. n. klauberi*) possesses a depression in the seam between the twelfth pair of marginals (Bogert and Oliver, 1945: their Fig. 11). In many specimens of *T. ornata* and *T. carolina*, the distal end of the seam between the twelfth marginals is split by a gap, but a depression is lacking. The depression does not occur among the three outgroups and is considered the derived state.

Pronounced growth annuli on carapace scutes (AN).—Schmidt and Owens (1944) and Brown (1974) reported that the carapace scutes of *T. coahuila* were smooth and without evident growth rings in adults and subadults. Sculpturing of the shell in the form of annuli is typical in *T. nelsoni*, *T. ornata*, and *T. carolina*, but it usually wears with age (Leuck and Carpenter, 1981; Nichols, 1939; Stickel, 1978). Sculpturing in juvenile *T. coahuila* is indistinct and similar to aquatic emydids (e.g., *Chrysemys*) and not rugose as in other juvenile *Terrapene*. In *Emydoidea* and *Emys*, the annuli are indistinct, as in *T. coahuila*, and this state is considered plesiomorphic. The carapace of *Clemmys insculpta* is deeply sculptured and is considered a derived condition.

Elongated carapace (EC).—The carapace in most individuals of *Terrapene* is oval in dorsal view. In *T. ornata*, the shell is noticeably circular. In *T. coahuila* and *T. n. nelsoni*, the shell is elongated. The extreme variability of shell shape in box turtles indicates that shell shape is a relatively plastic character (Barbour and Stetson, 1931). However, the shell outline of these three taxa distinguishes them from other box turtles. The outgroups are variably round to elongate and thus the more common condition, the oval shape, is considered plesiomorphic.

Apical scale (AP).—The apical scales (Legler, 1960) are located at the lateral edges of the plastral hinge. In *T. ornata* and *T. nelsoni*, the scale is round or oval in shape and domed ventrally. The scale

is cornified, hard, and commonly has growth rings. The scale is not common in most individuals of *T. carolina*, but when present the scale is small, elongate, soft, not cornified, and is without growth rings. The scale is absent in *T. coahuila* and in the outgroups. Presence of the scale (as it occurs in *T. ornata* and *T. nelsoni*) is considered the derived state.

Axillary scale (AS).—These scales are interiorly located on the ventral surface between the fifth and third marginal scutes (Auffenberg, 1958; Cahn, 1937; Milstead, 1969). A long scale centered at the fourth marginal occurs in *T. coahuila*, *T. c. major*, and *T. c. triunguis*. Commonly, the scale is split in *T. c. triunguis*, and part of the additional scale extends to the fifth marginal. The split axillary scale might be coded as a different character state, but is not in this analysis. The scale is absent or rudimentary at the fourth marginal in *T. c. bauri*, *T. c. carolina*, *T. c. mexicana*, and *T. c. yucatanana*. In *T. nelsoni*, the scale is centered between the fourth and fifth marginals, and in *T. ornata*, the scale is centered at the fifth marginal. The scale is at the fourth marginal in *Emydoidea* and *Clemmys insculpta*, but in *Emys* and most hatchlings of *T. ornata* and *T. carolina*, the scale is centered between the fourth and fifth marginals. The character state of the hypothetical ancestor was coded as undetermined.

Inguinal scale (IS).—The inguinal scales are located along the seams of the posterior plastral hinges between the sixth and seventh marginal scutes near the buttress of the pectoral scutes. The scale is elongate, cornified, and has growth annuli when present in *T. ornata* and *T. nelsoni*. The scale is not present in *T. coahuila*, and it is uncommon in *T. carolina*. When present in *T. carolina*, the scale is small, not well cornified, and lacks growth rings. In most emydids, the inguinal scale is present and composes part of the bridge (my personal observation), but in *Emys*, the scale appears identical in size and location to the scale in *T. nelsoni* and *T. ornata*. Presence of a large, cornified inguinal scale is considered plesiomorphic.

Inguinal buttress (IB).—The inguinal

buttress is the portion of the hypoplastron that in *Terrapene* articulates with the fifth and sixth peripheral bones of the carapace. The buttress does not make solid contact with the carapace, and the suture between the bones contains ligamentous tissue. In *T. ornata*, there is an expansion of the hypoplastron that extends posteriorly from the buttress and is vertically oriented to form a distinct inguinal bridge (Cahn, 1937). In all other box turtles, there is a small, horizontally oriented extension of the hypoplastron that does not contact the marginals, and a bridge is absent. In *Emys*, the buttress forms a narrow bridge, similar to *T. ornata*. The presence of a bridge, as in *Emys* and *T. ornata*, is considered the plesiomorphic condition.

Posterior plastron width (WP).—In *T. ornata*, the posterior plastron is widest anteriorly, toward the hinge. In all other taxa, the posterior plastron is widest at the femoral scutes or the femoral scutes are as wide as at the hinge. In outgroup members, the plastron is widest at the hinge as in *T. ornata*, and the generalized condition of other *Terrapene* is considered derived.

Shape of the posterior plastron (LR).—In *T. ornata*, the anal scutes are extended beyond the underlying xiphiplastron to form a squared posterior plastral margin. The squared shape may become rounded in old specimens of *T. ornata* with worn shells. The extension of the anal scutes occurs in some specimens of *T. c. major*, but the extended region is rounded, not squared. The anal scutes in outgroups are indented medially and not rounded or squared. The generalized condition of a rounded lobe is considered plesiomorphic.

Indented posterior plastral lobe (IL).—The lateral margins of the posterior plastral lobe may be entire or indented at and posterior to the femoro-anal seam. The indented character state is not common in any taxon except *T. c. carolina*, and it is not always distinct. An indented lobe may allow for a tighter fit of the carapace to the plastron, and thus may provide complete shell closure. The posterior lobe is entire in *T. ornata*, *T. nelsoni*, *T. coahuila*, and *T. c. major*. The indented posterior plastron is present to various extents in *T.*

c. yucatanana, *T. c. mexicana*, *T. c. triunguis*, *T. c. bauri*, and *T. c. carolina*. The posterior lobe in outgroups is entire, which is the assumed plesiomorphic state.

Femoro-anal seam curvature (CS).—The distal end of the femoro-anal seam is anteriorly curved in many specimens of *T. nelsoni*, *T. c. major*, *T. c. bauri*, *T. c. carolina*, *T. c. triunguis*, *T. c. mexicana*, and *T. c. yucatanana*. In *T. ornata*, the seam is straight or slightly curved along the mid-point, but it is not curved distally. In *T. coahuila* and in the outgroups, the seam is also straight, which is considered the plesiomorphic condition.

Concavity of the posterior plastron (CP).—In *Terrapene*, the males (and sometimes the females: J. P. Ward, personal communication) may have a depression, or concavity, in the posterior plastral lobe. The depression is more common among taxa with the deepest depression. The depression is very deep, and round in *T. c. bauri* and *T. c. carolina*. In *T. coahuila* and *T. c. major*, the depression is deep, but slightly shallower and more elongate than it is in *T. c. bauri* or *T. c. carolina*. The deep and elongate depression of *T. coahuila* and *T. c. major* may represent a shared state, but the condition is not always obvious. In this study, all four taxa were coded the same. The depression is commonly absent in *T. c. triunguis*, *T. c. mexicana*, and *T. c. yucatanana*, and when present, it is shallow, round, and more posteriorly located than in other taxa. The depression is centered on the interfemoral seam in these three taxa, and it is centered on the interabdominal seam, or at the junction of the interabdominal seam and the femoro-abdominal seam in other taxa. The depression in *T. ornata* and *T. nelsoni* is very narrow and shallow when present. In *Emys*, the depression is often absent, but when present it is similar to that in *T. ornata* and *T. nelsoni*, but more rounded in shape. The state of *T. ornata* and *T. nelsoni* is assumed to be plesiomorphic.

RESULTS

Computer-assisted phylogenetic analysis of *Terrapene* using 32 characters rooted with a hypothetical ancestor, and using

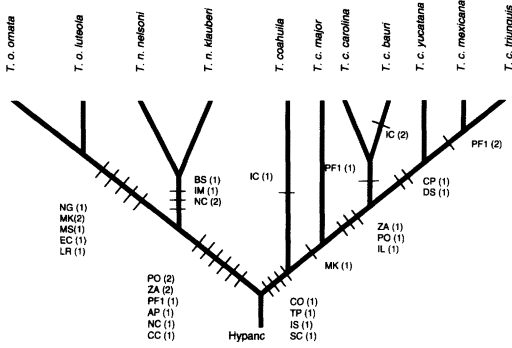


FIG. 1.—A cladogram of *Terrapene* using intermediate states. The cladogram has a consistency index of 0.81 and is 58 steps long. Apomorphies are indicated by bars and the character abbreviation and the state are included. Character abbreviations are the same as in the text. Hypanc is the hypothetical ancestor.

intermediate states to code discrete characters, resulted in a single most parsimonious cladogram (Fig. 1) for interpreting the distribution of characters (Table 1). This method provided a shorter, single tree with lower homoplasy and greater consistency than the three trees generated by Cartmill's (1978) method (Table 1, alternative characters, and Fig. 2).

DISCUSSION

The cladograms (Figs. 1, 2) substantiate the basal bifurcation that Milstead (1969) proposed in dividing the genus into two species groups. However, 14 of the 16 characters that Milstead (1969) used were either re-interpreted or were found to be too variable to be useful. The clasping claw (CC) and the postorbital bar (PO) were the only characters used in both Milstead (1969) and in this study.

Several synapomorphies were identified that clearly defined the *ornata* group from the *carolina* group (Fig. 1). There is one autapomorphy (MK) that defines *T. carolina*, and the single autapomorphy that defines *T. coahuila*, the absence of red eyes (IC), has similarly been lost in *T. c. bauri*. The distribution of apomorphies within the *carolina* group may reflect greater character evolution among the subspecies of *T. carolina* than previously recognized and/or a closer relationship between *T. coa-*

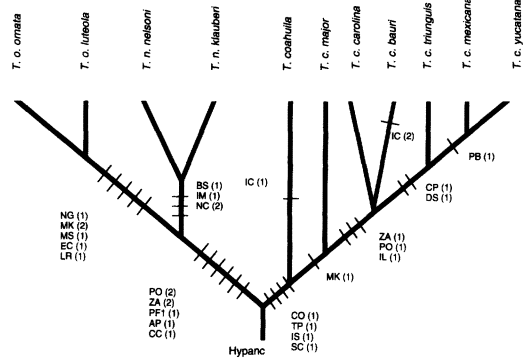


FIG. 2.—A consensus tree of three equally parsimonious trees of *Terrapene* derived by using Cartmill's method for variable characters. The tree has a consistency index of 0.717 and is 60 steps long. Apomorphies are indicated by bars and the character abbreviation and the state are included. Character abbreviations are the same as in the text. Hypanc is the hypothetical ancestor.

huila and *T. carolina* than previously described.

The few divergent characters found between *T. coahuila* and *T. carolina* become particularly evident when compared to the number of characters that distinguish *T. ornata* and *T. nelsoni*, such as the synapomorphies for the subspecies of *T. nelsoni* [bulbous shields (BS), an octagonal or heptagonal fourth and a tetragonal or pentagonal fifth neural (NC), and a depression between the twelfth pair of marginals (IM)], and of *T. ornata* [a wide narial gap (NG), middorsal keel is absent (MK), elongated carapace (EC), first marginal shape (MS), and the shape of the posterior plastron (LR)].

The cladograms agree with the sister relationship of *T. ornata* and *T. nelsoni* proposed by Milstead and Tinkle (1967), but the numerous plesiomorphies retained by *T. nelsoni*, and the numerous autapomorphies of *T. ornata*, put considerable doubt on Milstead's contention that *T. nelsoni* was derived from *T. ornata* (*T. o. luteola* or extinct *T. o. longinsulae* according to Milstead, 1969).

The most significant divergence of my cladograms from the evolutionary scheme of Milstead (1969) is the relationship of *T. coahuila* to the other members of the *car-*

olina group. Milstead (1969) suggested that *T. coahuila* is a relatively recent form that was derived from intergradation between *T. c. triunguis* and now extinct *T. c. putnami*, and later modified through anagenic events. In my analysis, *T. coahuila* appears as an early derivative of the *carolina* group as hypothesized by Auffenberg (1958) and Legler (1960), but it does not indicate that *T. coahuila* is basal to the entire genus as suggested by Williams et al. (1960) and Bramble (1974). *Terrapene coahuila* may have originated from a terrestrial box turtle and then differentiated through a recent retreat into the springs at Cuatro Ciénegas. Alternatively, *T. coahuila* may have originated from a completely aquatic box turtle that went extinct, except in Cuatro Ciénegas. Regardless of its derivation, a close relationship with *T. c. triunguis* is not indicated in the cladograms.

A closer relationship between *T. c. yucatanana*, *T. c. mexicana*, and *T. c. triunguis* was found in this study than was implied by Milstead (1969). The *T. c. mexicana-triunguis-yucatanana* clade is supported by the synapomorphies dark seams (DS) and concavity of the posterior plastron (CP). Rosen (1978) used the posterior pleural bone depressions (PB) to show that there is a closer relationship between *T. c. yucatanana* and *T. c. mexicana* than to the other subspecies of *T. carolina*. This relationship is corroborated in the consensus tree (Fig. 2) but not in the single cladogram (Fig. 1) in which *T. c. mexicana* and *T. c. triunguis* are linked by phalangeal formula on the forefeet (PF1). The close monophyletic relationship among the three taxa warrants their recognition as a subspecies group.

The cladograms (Figs. 1, 2) do not support Milstead's (1969) view that *T. carolina* is a basal lineage of the genus. The intermediate condition of the phalangeal formula of the forefeet (PF1) in *T. c. carolina* and *T. c. bauri* weakly supports a sister relationship for these two subspecies. *Terrapene c. bauri* was previously thought to have originated from intergradation between *T. c. carolina* and *T. c. major* (Auffenberg, 1958; Milstead, 1969). In the phy-

letic analysis using intermediate character states (Fig. 1), *Terrapene c. carolina* and *T. c. bauri* form a sister clade with the *T. c. yucatanana-mexicana-triunguis* clade. In the other phyletic analysis (Fig. 2), *Terrapene c. carolina*, *T. c. bauri*, and the *T. c. yucatanana-mexicana-triunguis* clade form an unresolved trichotomy. This clade of five taxa is supported by three relatively weak characters. The zygomatic arch (ZA) and the indented lobe (IL) are variable characters. Furthermore, the zygomatic arch (ZA) and the postorbital bar (PO) have been independently reduced in both the *ornata* group and in the members of the clade mentioned above. The existence of this clade of five taxa is considered a tentative arrangement in need of further testing.

The basal position of *T. c. major* relative to the other subspecies of *T. carolina* concurs with earlier conceptions of the taxon (Auffenberg, 1958; Milstead, 1969). There is general agreement that *T. c. major* is a plesiomorphic member of the *carolina* group. Nevertheless, *T. c. major* remains an enigmatic taxon. Throughout its range, it retains most of its distinctive morphological traits, but in size and coloration, it is more variable than all other species or subspecies of *Terrapene*. The subspecies generally occurs in three color morphs that are somewhat regionally distributed. In southern Louisiana, it is light brown as is the intergrading (or parapatric) subspecies *T. c. triunguis*. In southern Alabama, southwestern Georgia, and the Florida panhandle, it is black or dark brown with yellow to orange blotches, which is similar to the nearest intergrading/parapatric subspecies, *T. c. carolina*. In the Appalachian region of the Florida panhandle, including St. Vincent Island, St. George Island, and the St. Joseph Peninsula, *T. c. major* is black with dull yellow stripes and is most similar to the proximate *T. c. bauri*. Throughout the range of *T. c. major*, some male specimens have a blotched white or completely white head, but this coloration does not occur in any of the intergrading/parapatric subspecies.

Milstead (1969) interpreted the variability of *T. c. major* to represent recent

and complete intergradation (except possibly in the Appalachian region) with the surrounding subspecies, but he did not take into consideration the morphological traits that persist despite supposed intergradation [i.e., thick zygomatic arch, and sexual dimorphism (with males larger and having a deeply cusped maxillary beak, often with a white head, and with the shields of the forelegs in males not brightly colored)]. Joseph P. Ward (personal communication) suggested that the distinctive traits of *T. c. major* indicate that it is reproductively isolated and that variability in color is the result of the retention of plesiomorphic colorations in varying environments. Regardless of their origins, these three color morphs appear to represent three distinct populations with unique histories within *T. c. major*. A study of microgeographic variation is needed that will focus on divergence within *T. c. major*, and on evidence of introgression between it and intergrading/parapatric subspecies.

By overlaying the proposed cladogram with the current distribution of *Terrapene* (Fig. 3), the early east-west vicariant episode separating the *carolina* and *ornata* groups becomes apparent (Milstead and Tinkle, 1967). The two most basal and aquatic taxa in the *carolina* group, *T. coahuila* and *T. c. major*, are widely separated in distribution. Fossil remains of *T. c. putnami*, a form similar to these two basal taxa (and possibly identical to *T. c. major*), have been found in New Mexico, Texas, Kansas, and Florida (Milstead, 1969). The distributions of the *T. c. mexicana-triunguis-yucatanana* and the *T. c. bauri-carolina* clades suggest another vicariant episode (roughly east-west) within *Terrapene*.

In comparison to a cladistic interpretation of Milstead's (1969) evolution of box turtles (Minx, 1992), my proposed phylogeny deviates from his by the terminal location of *T. c. carolina*, the sister relationship between *T. c. carolina* and *T. c. bauri*, the arrangement of *T. c. triunguis*, *T. c. mexicana*, and *T. c. yucatanana* into a clade, and the basal position of *T. coahuila*. I suggest that a closer relationship exists be-

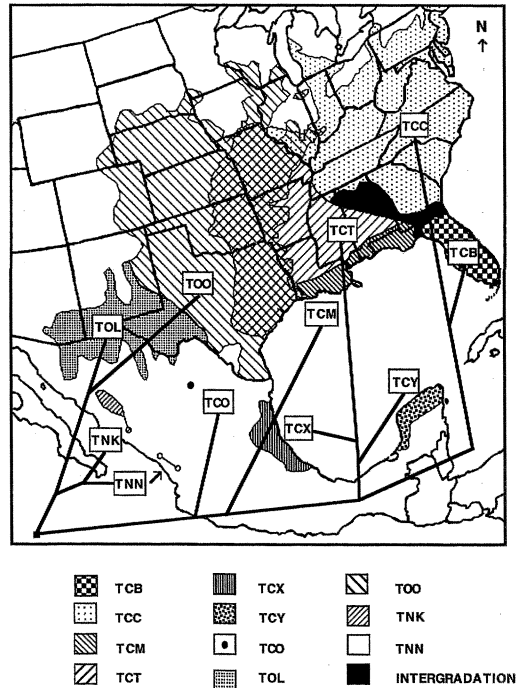


FIG. 3.—Area cladogram of *Terrapene*. Distributions were arranged in part from Carr (1952), Conant and Collins (1991), Iverson (1992), and Mount (1975). The lettering corresponds to the distributions of the following taxa: TCB = *T. c. bauri*; TCC = *T. c. carolina*; TCM = *T. c. major*; TCT = *T. c. triunguis*; TCX = *T. c. mexicana*; TCY = *T. c. yucatanana*; TCO = *T. c. coahuila*; TOL = *T. o. luteola*; TOO = *T. o. ornata*; TNK = *T. n. klauberi*; TNN = *T. n. nelsoni*. The blackened area is a presumed region of intergradation of *T. carolina* subspecies TCB, TCC, TCM, and TCT.

tween *T. carolina* and *T. coahuila* than previously considered. Further studies of the genus are needed to examine genetic divergence and gene flow between supposed intergrading taxa to address questions of species' status within the *carolina* group and to test the proposed phylogeny.

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APPENDIX I

Material Examined

Institutional abbreviations are listed in Leviton et al. (1985), except GLPZ (Gladys Porter Zoo), ASDM (Arizona Sonoran Desert Museum), and SLZP (St. Louis Zoological Park).

T. c. bauri: KU 17367, 19738-9, 19741, 46810-5, 46817-8, 46820-1, 46823-30, 46854, 48249 UF 6604, 8614, 47869-70, 47873, 47876, 47878, 47882, 47884-5, 47891, 47895, 47897, 47899, 47911-2, 66424, 66594, 66598 (live specimens—1 Alachua Co., Florida) Skeletons: KU 18348, 20506-18, 177211-3 UF 10946-8, 14088, 14117, 14664, 27601. *T. c. bauri* × *T. c. carolina* (presumed intergrades): UF 4247, 4411, 4414, 4416, 4419, 4443, 4450, 8592, 9711. *T. c. carolina*: KU 3068, 3070, 3072, 15883, 15886-90, 19353, 46871,