Acknowledgments.—We wish to thank E. Kelly for access to the study area, R. Vogt for suggestions during the course of the study, C. Jefferson and W. Smith for plant identification, M. Ross for completing the figure, and especially J. Congdon for help with statistics and use of computer facilities at SREL. Data analysis and figure preparation was supported by contract DE-AC09-76SROO-819 between the University of Georgia and the United States Department of Energy. R. Buech, J. Congdon, M. Davis, C. J. McCoy, J. Moriarty, and two anonymous reviewers improved earlier drafts of this paper.

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Accepted: 27 January 1992.

Journal of Herpetology, Vol. 26, No. 2, pp. 234–238, 1992

Variation in Phalangeal Formulae in the Turtle Genus *Terrapene*

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Baur (1891, 1893) employed phalangeal formulae to distinguish five taxa of American box turtles. Later, Taylor (1895) used the number of phalanges to distinguish among *Terrapene carolina major* (Agassiz), *T. c. bauri* (Taylor), *T. c. carolina* (Linnaeus), *T. c. triunguis* (Agassiz), *T. c. mexicana* (Gray), and *T. ornata* (Agassiz). His study stands as the most extensive investigation of box turtle phalangeal formulae to date. Since those studies, phalangeal formulae have been used only in descriptions and diagnoses of previously undescribed taxa. Stejneger (1925) and Smith (1939) described the formulae of the forefeet of a single specimen each of *T. n. nelsoni* and *T. c. yucatana*, respectively. The phalangeal formulae of the forefeet and hindfeet in one specimen of *T. n. klauberi* were reported by Bogert and Oliver (1945).

In this study, I examine the phalangeal formulae of the eleven extant taxa of *Terrapene*, compare them with the accounts in Taylor (1895), and discuss their utility as diagnostic and phylogenetic characters.

I made counts of box turtle phalanges from 38 skeletal specimens of *Terrapene* as well as from radiographs of the feet (either left or right depending on accessibility) of 95 preserved specimens (Appendix 1). Although radiographs are generally superior to skeletal material for determining formulae, joints between phalanges are sometimes (though rarely) difficult to resolve.

Three character states of the forefeet and two states of the hindfeet are predominant (Tables 1, 2; Fig. 1a–e). Usually, *T. carolina major*, *T. c. yucatana*, *T. c bauri* (Fig. 1e), and *T. coahuila* (Fig. 1a, d) have forefeet formulae of 2-3-3-3-2 (digits I to V). In the forefeet of *T. c. carolina*, 71.4% have the plesiomorphic condition. The phalangeal formula 2-3-3-3-2 appears to be the plesiomorphic state for both the forefoot and the hindfoot of box turtles. The primitive condition of cryptodires is 2-3-3-3-3 (Zug, 1971), and the formula of *Emydoidea blandingi*, an apparent close relative of the box turtles (Bramble, 1974; Seidel and Adkins, 1989), is 2-3-3-3-2 (Zug, 1971). A forefoot formula of 2-3-3-2-2 is common for both *T. c. mexicana* (100%; Fig. 1b) and *T. c. triunguis* (82.1%), and is found in 23.8% of *T. c. carolina*. Both subspecies of *T. nelsoni* (Fig. 1c) and *T. ornata* have a reduced forefoot formula of 2-2-2-2-2. Most specimens of *T. coahuila*, *T. carolina major*, and *T. c. yucatana* have the plesiomorphic hindfoot formula, while most specimens of *T. c. bauri*, *T. c. mexicana*, *T. c. triunguis*, *T. ornata*, and *T. n. nelsoni* have a hindfoot formula of 2-3-3-3-1. *Terrapene n. klauberi* and *T. c. carolina* may have either condition; 50% and 41.7%, respectively, have the derived state.

Terrapene c. major, *T. c. yucatana*, and *T. coahuila* exhibit no to modest phalangeal variation in the forefoot and hindfoot. Although the sample sizes are small, *T. o. ornata*, and *T. n. nelsoni* do not appear to demonstrate variability. *Terrapene c. triunguis* and *T. c. carolina* appear to be the most variable taxa in phalangeal formulae.

Discrepancies between these findings and those of Taylor (1895) may be due to incorrect localities or misidentification. For instance, Taylor listed the localities of two *T. c. major* from Galveston, Texas, and Nashville, Tennessee, both of which are outside their presently known range; this suggests the identification or provenience of the specimens is incorrect. He also reported on two specimens of *T. ornata* allegedly from the Yellowstone River, which is several hundred kilometers outside the species' known range. Three specimens of Taylor's *T. ornata* are probably *T. o. luteola*, since two are from Las Cruces, New Mexico, and one is from El Paso, Texas. Most of the formulae in

TABLE 1. Distribution of forefoot phalangeal formulae in the genus *Terrapene*. Phalangeal formulae of forefeet: (A) 2-3-3-3-2; (B) 2-2-2-2-2; (C) 2-3-3-2-2; (D) 2-3-2-2-2; (E) 2-3-3-2-1; and (F) 2-3-3-3-3. On the far right is one possible arrangement of forefoot phalangeal formulae into character states (CS). The coding method is that of Cartmill (1978) for variable characters.

	Forefeet						
	A	B	C	D	E	F	CS
Terrapene carolina bauri	23	0	1	0	0	0	0
Terrapene carolina carolina	15	0	5	0	0	1	1
Terrapene carolina major	5	0	0	0	0	0	0
Terrapene carolina mexicana	0	0	8	0	0	0	1
Terrapene carolina triunguis	0	1	23	3	1	0	1
Terrapene carolina yucatana	7	0	0	0	0	0	0
Totals	50	1	37	3	1	1	
Terrapene coahuila	5	0	0	0	0	0	0
Terrapene nelsoni klauberi	0	2	0	0	0	0	2
Terrapene nelsoni nelsoni	0	2	0	0	0	0	2
Totals	0	4	0	0	0	0	
Terrapene ornata luteola	0	0	0	0	0	0	?
Terrapene ornata ornata	0	6	0	0	0	0	2
Totals	0	6	0	0	0	0	

this study, which differ from those of Taylor and other workers, are from single specimen reports, and may be attributed to variation demonstrated by larger samples. However, differences between studies in the hindfeet of *T. c. carolina* and *T. c. triunguis* are not easily accounted for. In this study no correlation was observed between the number of claws on the hindfoot and phalangeal formulae. Some four-clawed forms, such as specimens of *T. c. carolina*, had reduced formulae, and some three-clawed forms, such as some *T. c. bauri*, had the primitive formula.

Loss of phalanges in amphibians and reptiles usually occurs in the lateral toes or toe IV (i.e., Alberch and Gale, 1985; Greer, 1991). The pattern of phalangeal reduction in box turtles typically occurs in the last two toes (IV and V), except in the manus of *T. ornata* and *T. nelsoni*. In these two species phalanges on toes II, III, and IV are lost and their formula, 2-2-2-2-2, is the same as that of the forefeet of testudinines, which are also terrestrially adapted (Auffenberg, 1961).

Phalangeal characters of the forefeet have utility in distinguishing among the box turtles. *Terrapene c. major*, *T. c. bauri*, *T. c. yucatana*, and *T. coahuila* share

TABLE 2. Distribution of hindfoot phalangeal formulae in the genus *Terrapene*. Phalangeal formulae of hindfeet are: (G) 2-3-3-3-2; (H) 2-3-3-3-1; (I) 2-3-3-2-2; (J) 2-3-3-2-1; (K) 2-3-3-3-0; and (L) 2-3-3-4-2. On the far right is one possible arrangement of hindfoot phalangeal formulae into character states (CS). The coding method is that of Cartmill (1978) for variable characters.

	Hindfeet						
	G	H	I	J	K	L	CS
Terrapene carolina bauri	6	17	1	0	0	0	1
Terrapene carolina carolina	5	7	1	1	0	0	1
Terrapene carolina major	5	1	0	0	0	0	1
Terrapene carolina mexicana	0	8	0	0	1	0	1
Terrapene carolina triunguis	0	9	1	0	0	1	1
Terrapene carolina yucatana	8	1	0	0	0	0	1
Totals	24	43	3	1	1	1	
Terrapene coahuila	7	0	0	0	0	0	0
Terrapene nelsoni klauberi	1	1	0	0	0	0	1
Terrapene nelsoni nelsoni	0	2	0	0	0	0	1
Totals	1	3	0	0	0	0	
Terrapene ornata luteola	0	1	0	0	0	0	1
Terrapene ornata ornata	0	3	0	0	0	0	1
Totals	0	4	0	0	0	0	

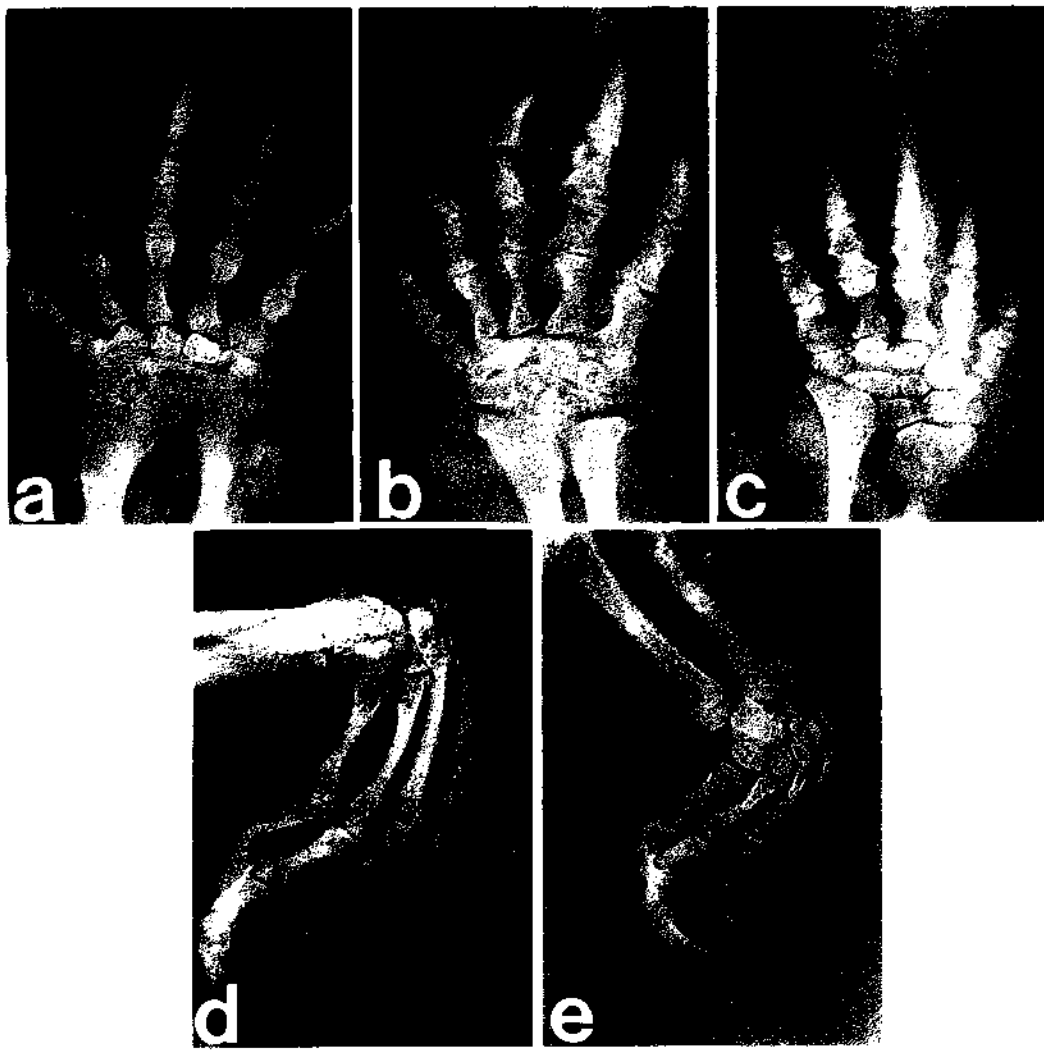

FIG. 1. Illustrations of the predominant phalangeal formulae in the genus *Terrapene*: (a) forefoot 2-3-3-3-2 of *T. coahuila*, KU 46918; (b) forefoot 2-3-3-2-2 of *T. carolina mexicana*, IUMNH 60999; (c) forefoot 2-2-2-2-2 of *T. nelsoni nelsoni*, KU 211192; (d) hindfoot 2-3-3-3-2 of *T. coahuila*, KU 46918; and (e) hindfoot 2-3-3-3-1 of *T. carolina bauri*, KU 17367.

the presumed primitive formula. *Terrapene c. mexicana* and *T. c. triunguis* share the derived formula 2-3-3-2-2. *Terrapene c. carolina* is variable, possessing either the primitive or the derived condition. The number of phalanges in the forefeet, 2-2-2-2-2, distinguishes *T. ornata* and *T. nelsoni* (*ornata* group of Milstead and Tinkle, 1967) from the other taxa of *Terrapene*. The hindfeet are not as diagnostically useful in distinguishing the box turtles as the forefeet, since most taxa show the derived condition, 2-3-3-3-1. *Terrapene c. major*, *T. c. yucatana*, and *T. coahuila* share the primitive state, but *T. c. carolina*, *T. c. bauri*, and at least some *T. n. klauberi*, have either the primitive state or the derived condition.

The considerable variation observed in the phalangeal formulae of *Terrapene* may render them impractical for phylogenetic inference, since variation within taxa is as great as variation between taxa. Nevertheless, the phalangeal formulae could be treated as in Cartmill (1978; a coding method for variable characters). The forefoot could be coded as a three state character, and the hindfoot as a two state character (Tables 1, 2). The distribution of character states of the forefoot and hindfoot among taxa does not conflict with a phylogeny of box turtles (Fig. 2) proposed by Milstead (1969), with the possible exception of *T. c. mexicana* and *T. coahuila*. From the formula of *T. c. mexicana* a relationship with *T. c. triunguis* is inferred, but a relationship with *T. c. yucatana* is not apparent. Specimens of *T. coahuila* invariably show

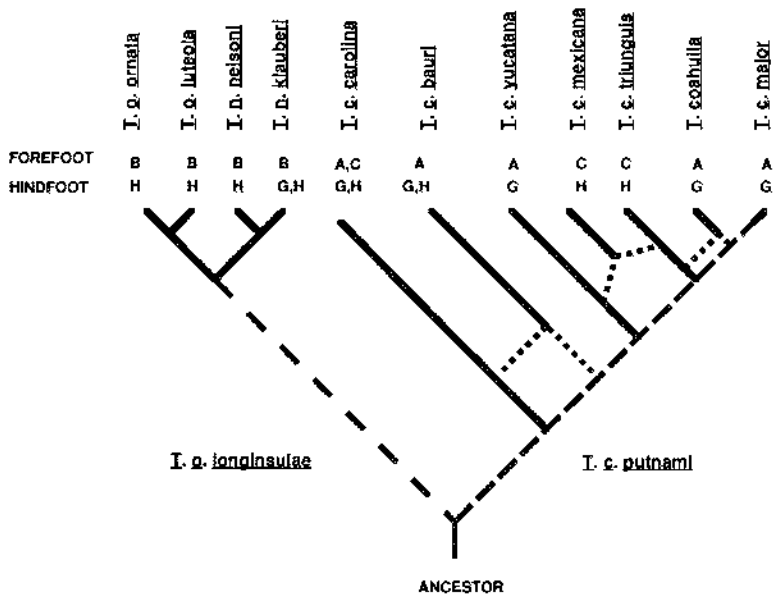

Fig. 2. Cladistic representation of the phylogeny of *Terrapene* adapted from Milstead (1969), with forefoot and hindfoot phalangeal formulae superimposed. Dashed lines are extinct lineages and stippled lines indicate reticulate evolution. Depicting the proposed relationship of *T. c. major* to other *Terrapene* on a cladogram is problematic: Milstead viewed *T. c. major* as a form identical to *T. c. putnami*, but modified by recent intergradation with *T. c. carolina*, *T. c. triunguis*, and possibly *T. c. bauri* (not indicated here). He did not imply a sister relationship between *T. coahuila* and *T. c. major*. The same alphabetical representation of phalangeal formulae is followed here as in Tables 1 and 2, except that only the predominant states are indicated.

the plesiomorphic state in both fore- and hindfeet. The phalangeal formula of *T. coahuila* does not appear consistent with the hypothesis that *T. coahuila* is recently derived, or that it is closely related to *T. c. triunguis* (Milstead, 1969; Brown, 1971), which has derived formulae in fore- and hindfeet. The formulae of *T. coahuila* are consistent with the view that it is more closely related to primitive *Terrapene* than to extant members of *T. carolina* (Legler, 1960; Williams et al., 1960; Bramble, 1974). *Terrapene coahuila* may be closely related to the extinct *T. c. putnami* as suggested by Milstead (1967, 1969), but the phalangeal formulae observed in *T. coahuila* do not suggest a recent relationship with *T. c. triunguis*.

Forefoot and hindfoot phalangeal formulae will be used in a phylogenetic analysis of the genus along with other morphological characters to discern homoplasies within the phalangeal characters and to test the phylogeny of Milstead.

Acknowledgments.—This study was financially supported by the St. Louis Herpetological Society. I wish to thank the following institutions for providing specimens: University of Kansas (KU); Field Museum of Natural History (FMNH); Florida State Museum, University of Florida (UF); University of Michigan Museum of Zoology (UMMZ); University of Illinois Museum of Natural History (UIMNH); and University of Utah (UU). Special thanks to Bradford Russell and Wesley Russell for radiographic expertise, and Michael Newmann for photographic work. Arnold Grobman, John Iverson, and Allan Larson reviewed the manuscript.

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Accepted: 27 January 1992.

APPENDIX 1

Specimens Examined (*denotes skeletal specimens).—*Terrapene carolina bauri*: KU 17367, 19739, 19741, 20506*, 20510*-3*, 46829–30; UF 3617, 6604, 47869–70, 47873, 47876, 47878, 47882, 47884–5, 47891, 47895, 47897, 47899, 47911–2, 66424, 66594, 66598. *Terrapene c. carolina*: KU 2850*, 15890, 16383*, 16387*-9*, 16392*, 16401*-2*, 18307*, 19353, 46807, 47479, 48241, 48245, 48247, 50505, 51456, 51458, 143855, 144569, 153637, 177214, 197234. *Terrapene c. major*: KU 39743*, 46778, 46791, 46797, 46801, 47362, 47364. *Terrapene c. mexicana*: KU 24075*–6, 39981, 70969; IUMNH 9994, 48532–3, 60999; UMMZ 100128, 100925–6. *Terrapene c. triunguis*: KU 3142, 18338*, 18354*–5*, 19427*-8*, 21043*, 21045*, 23040, 23337, 46752–3, 46762–3, 46766, 46775, 47341, 48258, 48264*-8*, 48270*-4*, 51453, 91350, 177217. *Terrapene c. yucatana*: KU 70970-2, 75657–9; FMNH 27273; UMMZ 73122, 76143. *Terrapene coahuila*: KU 46917–9, 46921–2, 51433, 51435–6. *Terrapene nelsoni klauberi*: KU 51430; UU 3846. *Terrapene n. nelsoni*: KU 211192–3. *Terrapene ornata luteola*: KU 51155. *Terrapene o. ornata*: KU 1106*, 2232*, 2901*, 14113*, 21041*, 46878, 51424, 211176–7.

Journal of Herpetology, Vol. 26, No. 2, pp. 238–241, 1992

Defensive Hemipenis Display in the Kukri Snake *Oligodon cyclurus*

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Oligodon cyclurus is a widespread and common Asian colubrid species. In Thailand, it is frequently found in most of the center and the north-east of the country (Taylor, 1965; Cox, 1991). Like many other species of the genus, *O. cyclurus* exhibits a defensive caudal display (Greene, 1973, 1988). In addition, it is an extremely irascible snake which will strike repeatedly at anything within or near its striking range at the slightest provocation (Smith, 1943; Taylor, 1965). We report on an unusual defensive behavior pattern observed in four specimens of this species.

A young male specimen of *O. cyclurus* (SVL 265 mm, TL 305 mm, weight 10.0 g) was captured on 27 July 1990 in Bangkok. It was maintained in a 40 × 20 × 20 cm cage in an open, well-ventilated garage exposed to normal Bangkok climatic conditions.

On 13 August 1990, the specimen was taken into the open for photographic purposes. As usual, the snake tried to escape, and thrashed and struck wildly whenever it was restrained or its escape path was blocked. Simultaneously, it raised the tail and the rear part of the trunk. The tail was rolled into a spiral, exposing the immaculate white underside of the tail and of the posterior part of the trunk. During this display, the bright, pinkish red hemipenes were repeatedly extruded to a varying degree for a few seconds (Fig. 1A). The tail-up position and hemipenis extrusion were never maintained for more than a few seconds at a time. Hemipenis extrusion and withdrawal was generally slow. This behavior was observed repeatedly, whenever the snake was provoked. Due to the immaturity of the specimen, the hemipenes were small (approximately 3 mm), but because of the color contrast between them and the white ventral surface, their extrusion was conspicuous.

Two adult males were captured in Bangkok in December 1990. During capture, the first of these two snakes (SVL 460 mm, TL 560 mm, weight 68.2 g) exhibited the usual spiraling of the tail, and the hemipenes were extruded, the behavior being similar to that of the juvenile specimen. The hemipenes of this specimen measured approximately 10 mm, and their color was crimson. The increased size and darker color made their extrusion more conspicuous against the immaculate white ventral color. However, this specimen was less prone to extruding its hemipenis when restrained than was the juvenile specimen. This snake did not strike wildly, but bit a gloved hand when picked up.

The second adult male, measuring approximately 600 mm in total length, was captured at night in Bangkok. In the poor light available, the white underside of the tail was clearly visible, but hemipenis extrusion

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