

**A Comparison of Plastral Scute Lengths
Among Members of the Box Turtle Genera
Cuora and *Terrapene***

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The turtle shell is one of the most conservative derived vertebrate structures known, having remained substantially unchanged since the Triassic (Romer, 1956, 1966). The arrangement of the epidermal scutes on the shell of turtles belonging to the families Bataguridae and Emydidae is particularly uniform, especially those of the plastron (Cherepanov, 1989), and provides few systematically important variants. However, research by Lovich and Ernst (1989) demonstrated that a great deal of variability occurs in the relative lengths of plastral scutes and plastral formulae in several emydid species. Later research indicated that closely related species could be differentiated from each other, as well as more distant relatives, by using the length relationships of plastral scutes (Lovich et al., 1991).

Several genera of "box turtles" belonging to the families Bataguridae (*Cuora*, *Cyclemys*, *Notochelys*, *Pyxidea*,

etc.) and Emydidae (*Emydoidea*, *Emys*, *Terrapene*) occur in different parts of the world; these turtles have a more or less vaulted carapace and a single moveable hinge on the plastron situated between the pectoral and abdominal scutes that allows the two plastral lobes to close the shell. We have chosen to concentrate our studies on two genera of "box turtles" that contain species which are the most superficially similar and that occupy ranges on opposite sides of the globe: the Asian genus *Cuora* (Bataguridae; Gaffney and Meylan, 1988) ranges marginally from the Indian subcontinent and southeastern Asia through Indonesia to Sulawesi and the Philippine Islands, while the North American genus *Terrapene* (family Emydidae) occurs from the northeastern USA southwestward to southern Mexico (Ernst and Barbour, 1989; Ernst and McBrean, 1991). Our objective was to compare the relative lengths of those scutes positioned along the plastral midline and their corresponding plastral formulae of selected species in *Cuora* and *Terrapene*. Similarity of these genera at one time led to confusion and erroneous placement of some relatively vaulted *Cuora* in the genus *Terrapene* (McCoy and Richmond, 1966). The shells of *Terrapene carolina*, *T. ornata*, *Cuora amboinensis*, *C. evelynae*, *C. flavomarginata*, and *C. galbinifrons* in particular, are morphologically very similar. Our hypothesis was that the above species of the two genera would be morphometrically distinguishable using the technique of Lovich et al. (1991) to analyze plastral scute formulae in spite of other superficial anatomical similarities.

Materials and Methods. — A total of 783 specimens was examined from various museum collections (BMNH, CAS, HMCZ, CMNH, FMNH, GMU, MNHN, USNM, a list of specimens examined is available upon request from CHE), including the species *Terrapene carolina*, *T. ornata*, *Cuora amboinensis*, *C. evelynae*, *C. flavomarginata*, and *C. galbinifrons*. Island and mainland populations of *C. amboinensis* (corresponding to the subspecies *C. a. kamaroma*, *C. a. amboinensis*, and *C. a. couro* of Rummeler and Fritz, 1991) were analyzed as separate taxonomic entities since unpublished studies by Ernst et al. (in prep.) indicate that *C. a. couro* is synonymous with *C. a. amboinensis*. Straight-line measurements were taken along the midline contacts of the six paired plastral scutes (gular [G], humeral

[H], pectoral [P], abdominal [Ab], femoral [F], and anal [An]) with dial calipers to the nearest 0.1 mm (Table 1).

The plastral scute length data were standardized for carapace length and analyzed separately for males and females. Multivariate normality was verified using chi-square quantile plots (Johnson and Wichern, 1992). A MANOVA was used to determine significant differences between species. The specimens were then classified to predicted taxa using quadratic discriminant function analysis with crossvalidation. Techniques generally followed those of Lovich et al. (1991). The first two canonical variables of a canonical discriminant function were used to generate graphs showing separation of the genera. All statistical analyses were done with SAS software (SAS Institute, 1989). Plastral formulae were also derived from these data and analyzed separately for males and females.

Results and Discussion. — Multivariate analysis of variance on females confirmed the difference among the species examined using all six plastral scute measurements simultaneously (Wilks' lambda = 0.036; $F = 62.97$; $p < 0.0001$). The discriminant function correctly classified 80% of the female sample to species (Table 1). Perfect classification was achieved between the species examined within the two genera, as misclassifications occurred only within genera. Within the genus *Terrapene* just over 3% were misclassified, within *Cuora* 43% were misclassified. Separation of genera on the first two canonical discriminant axes is shown in Fig. 1.

Multivariate analysis of variance on males also showed the difference among species using all six plastral scute measurements simultaneously (Wilks' lambda = 0.036; $F = 42.16$; $p < 0.0001$). The discriminant function correctly classified 89% of the male sample to species (Table 2). With one exception, perfect classification was achieved between genera; only a single *T. ornata* was incorrectly classified with the island group of *C. amboinensis*. Slightly fewer than 3% of the male *Terrapene* were misclassified, while 22% of the male *Cuora* were misclassified. Separation of taxa on the first two discriminant axes is shown in Fig. 2.

The fact that the analysis resulted in almost perfect separation of these members of the two genera is interesting given their apparently similar plastral morphology. We conclude that in spite of the influence of plastral anatomy,

Table 1. Classification of female turtles, based on plastral scute dimensions. Correctly classified individuals in bold numbers.

Actual Taxon	Classified as							Total
	<i>Terrapene</i>		<i>Cuora</i>					
	<i>carolina</i>	<i>ornata</i>	<i>amboinensis</i> (mainland)	<i>amboinensis</i> (island)	<i>evelynae</i>	<i>flavomarginata</i>	<i>galbinifrons</i>	
<i>T. carolina</i>	191	4	0	0	0	0	0	195
<i>T. ornata</i>	5	69	0	0	0	0	0	74
<i>C. amboinensis</i> (mainland)	0	0	0	11	1	0	0	12
<i>C. amboinensis</i> (island)	0	0	5	90	6	10	2	113
<i>C. evelynae</i>	0	0	0	10	6	2	0	18
<i>C. flavomarginata</i>	0	0	2	24	1	15	1	43
<i>C. galbinifrons</i>	0	0	0	7	0	2	2	11
Total	196	73	7	142	14	29	5	466

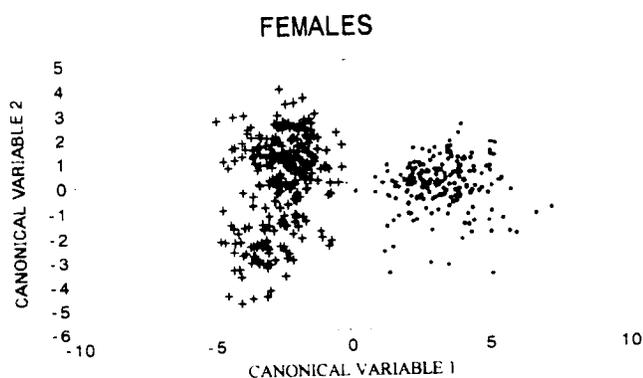


Figure 1. Plot of first two canonical variables for females of species groups representing *Cuora* (•) and *Terrapene* (+).

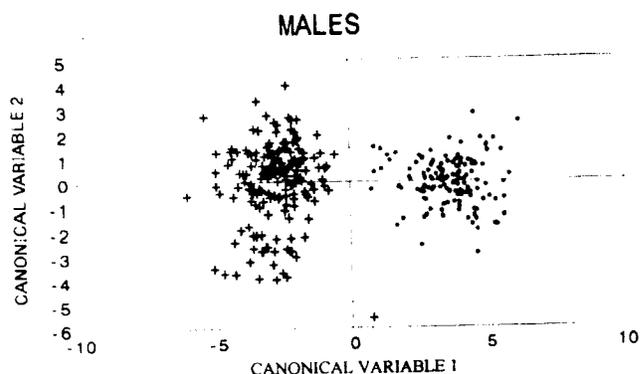


Figure 2. Plot of first two canonical variables for males of species groups representing *Cuora* (•) and *Terrapene* (+).

the two genera have significant morphometric differences in their relative plastral scute lengths.

Examination of the corresponding plastral formulae generated by the differences in plastron scute lengths also revealed major differences between the compared species of *Cuora* and *Terrapene* (Tables 3 and 4). Thirty-nine formulae were recorded from the plastra of female *Cuora* and *Terrapene*, of which 34 (87.2%) were not shared across genera. Thirty-six plastral scute formulae were recorded from males of these genera; 33 (91.7%) did not overlap between genera. When combining the plastron formulae of female and male *Terrapene*, 86.8% of the individuals (388 of 447) had one of six formulae: An>Ab>G>P>H>F (146), An>G>Ab>P>F>H (97), An>G>Ab>P>H>F (48), An>Ab>G>P>F>H (40), An>G>Ab>F>P>H (29), and An>Ab>G>H>P>F (28). Similarly, 66.4% of the individual *Cuora* (223 of 336) had one of only four formulae: Ab>An>P>G>F>H (79), An>Ab>P>G>F>H (68), Ab>An>P>G>H>F (44), and An>Ab>P>G>H>F (32). Rummeler and Fritz (1991) reported variation in plastral formulae among populations of *Cuora amboinensis* which they believed to be associated with subspecific variation. This may be correct (see above comment regarding *C. a. couro*), but they did not compare the various island populations of the currently recognized *C. a. amboinensis*. Such comparisons are necessary to assess total subspecific or other variation in this complex. This has been done by Ernst et al. and will be presented in a later paper.

The major differences between the two genera lie in the relative lengths of the gular and pectoral scutes and their positions in the formulae (Tables 3 and 4; Fig. 3). The gular is always one of the three longest scutes in *Terrapene*, but one of the shortest three in *Cuora*; the reverse is true regarding the pectoral (Ernst and Barbour, 1989). Observed intraspecific variation in plastral formulae within *Cuora* may influence current taxonomic designations, and will be addressed in a later paper.

Cuora and *Terrapene* are not ecological equivalents in habitat requirements or behavior (CHE, pers. obs.). Neither subspecies of *Terrapene ornata* enter water for extended periods of time, possibly due to a scarcity of water in much of their habitat, and should be considered terrestrial. Individuals of *T. carolina* more readily enter water; however, the subspecies *carolina*, *triunguis*, *mexicana*, and *yucatanana* should probably be regarded as primarily semiterrestrial. On the other hand, the subspecies *bauri* and *major* require more water than the former four and could be considered semi-aquatic. In fact, *T. c. major* spends considerable time in water, often feeding and mating there (Ernst, 1981), and is the most aquatic *Terrapene* next to the fully aquatic, specialized, Mexican species *T. coahuila* (Ernst and Barbour, 1989).

Of the *Cuora* examined in this study, *C. galbinifrons* and *C. flavomarginata*, and probably also the latter's sister species *C. evelynae* (Ernst and Lovich, 1990), are highly terrestrial (Ernst and Barbour, 1989), usually entering water only to drink or occasionally to soak in extremely hot

Table 2. Classification of male turtles, based on plastral scute dimensions. Correctly classified individuals in bold numbers.

Actual Taxon	Classified as						Total	
	<i>Terrapene</i>		<i>Cuora</i>					
	<i>carolina</i>	<i>ornata</i>	<i>amboinensis</i> (mainland)	<i>amboinensis</i> (island)	<i>evelynae</i>	<i>flavomarginata</i>		<i>galbinifrons</i>
<i>T. carolina</i>	146	2	0	0	0	0	0	148
<i>T. ornata</i>	3	26	0	1	0	0	0	30
<i>C. amboinensis</i> (mainland)	0	0	0	4	1	0	0	5
<i>C. amboinensis</i> (island)	0	0	0	104	1	2	0	107
<i>C. evelynae</i>	0	0	0	9	1	0	0	10
<i>C. flavomarginata</i>	0	0	0	9	0	4	0	4
<i>C. galbinifrons</i>	0	0	0	3	0	1	0	4
Total	149	28	0	130	3	7	0	317

Table 3. Ratio of plastral scutes to plastron length for females of the taxa examined.

Taxa	Plastral Scute					
	G	H	P	Ab	F	An
<i>T. carolina</i>	0.186	0.089	0.127	0.203	0.068	0.328
<i>T. ornata</i>	0.222	0.055	0.134	0.172	0.120	0.297
<i>C. amboinensis</i> (mainland)	0.173	0.054	0.193	0.261	0.069	0.251
<i>C. amboinensis</i> (island)	0.170	0.053	0.206	0.260	0.061	0.249
<i>C. evelynae</i>	0.160	0.049	0.207	0.273	0.051	0.260
<i>C. flavomarginata</i>	0.160	0.060	0.205	0.251	0.065	0.258
<i>C. galbinifrons</i>	0.160	0.078	0.201	0.253	0.072	0.236

Table 4. Ratio of plastral scutes to plastron length for males of the taxa examined.

Taxa	Plastral Scute					
	G	H	P	Ab	F	An
<i>T. carolina</i>	0.187	0.088	0.129	0.196	0.072	0.326
<i>T. ornata</i>	0.220	0.060	0.131	0.174	0.131	0.284
<i>C. amboinensis</i> (mainland)	0.187	0.048	0.194	0.241	0.065	0.264
<i>C. amboinensis</i> (island)	0.175	0.054	0.213	0.245	0.067	0.246
<i>C. evelynae</i>	0.170	0.049	0.203	0.271	0.056	0.251
<i>C. flavomarginata</i>	0.163	0.069	0.196	0.240	0.071	0.261
<i>C. galbinifrons</i>	0.148	0.070	0.212	0.252	0.083	0.236

weather (CHE, pers. obs.). *Cuora amboinensis*, however, is much more aquatic and spends considerable time in water, particularly to feed, sleep, or migrate, and possibly to mate. In this respect it more closely resembles the North American wood turtle, *Clemmys insculpta*, in its behavior (Ronald I. Crombie, pers. comm.). Another major difference between the two genera is the period of daily activity. *Terrapene* species are almost exclusively diurnal except for nesting females, while *Cuora amboinensis*, *C. flavomarginata*, and *C. galbinifrons* are often active at night (CHE, pers. obs.).

Plastral kinesis, or the ability to flex the plastron, has evolved independently in several lineages apart from the two

genera examined (Bramble, 1974; Ernst and Barbour, 1989). In Asian *Cuora*, closure of the anterior plastral lobe is controlled by the hypertrophied testoscularis muscle. The scapulo-carapacial articulation is modified to allow dislocation of the joint during shell closure, thus accommodating displacement of the pectoral girdle as the shell is closed (Bramble, 1974). In contrast, in American *Terrapene* a portion of the main cervical retractor muscle raises the anterior end of the plastron and a segmented scapula permits effective accommodation of the pectoral girdle (Bramble, 1974). These architectural differences are reflected in the bony structure of the plastron and may be translated into the lengths of the epidermal scutes.

John B. Iverson (pers. comm.) has suggested an interpretation of the differences in the plastral formulae in relation to the hinge-closing arrangement in the two species. His interpretation of the long interpectoral seam is as follows. In *Cuora* the force (i.e., the pull) generated to close the plastral forelobe is exerted via the acromion process which is connected by a ligament to the entoplastron. In *Terrapene*, a significant part of the force (pull) generated to close the plastral forelobe is exerted via the cervico-plastral ligament, which is attached to the epiplastra (much farther anterior on the forelobe). Thus in *Cuora*, the tug is on the entoplastron, whereas in *Terrapene* it is on the epiplastra. Under this arrangement, it would be logical to expect a strengthening of the ento-hyo-plastral suture in *Cuora* to prevent the chance of buckling of that suture during closing, but to expect a strengthening of the interepi-plastral suture and the anterior epi-entoplastral suture in *Terrapene* to prevent buckling in the more anterior part of the plastral forelobe during closing. The functional, or adaptive, significance of the large pectoral scutes in *Cuora* may thus simply be to strengthen the ento-hyo-plastral connection in that genus, whereas the larger gular scutes of *Terrapene* may simply strengthen the sutures among the epiplastra and the entoplastron.

In conclusion, the results of analysis of variation in the relative plastral scute lengths and plastral formulae of turtles of the genera *Cuora* and *Terrapene* are congruent with phylogenetic hypotheses based on the separate evolution of other characters (Bramble, 1974; Gaffney and Meylan, 1988) in the presence of superficially striking morphological similarities. Although the two genera may have converged in several ways, they have not done so in plastral formulae.

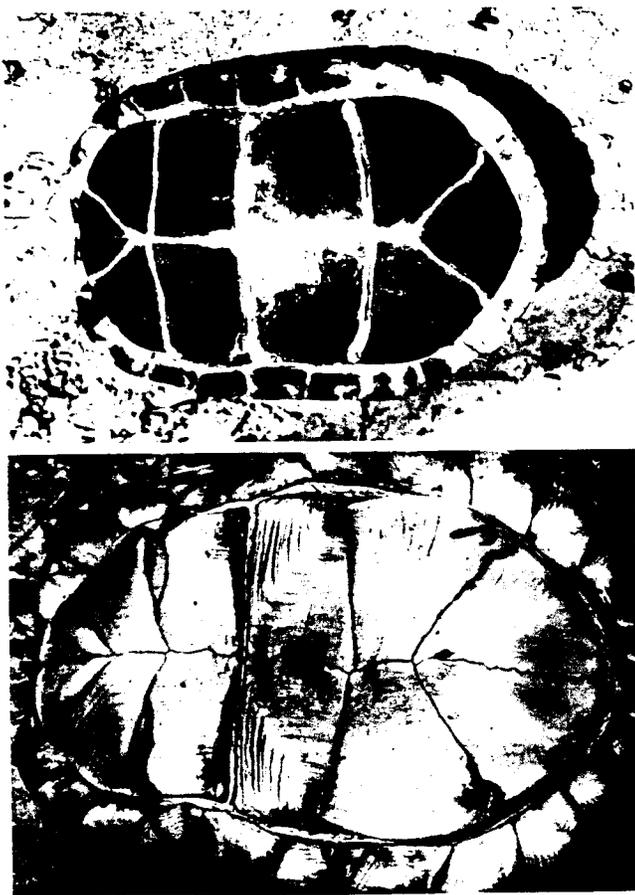


Figure 3. Plastra of *Cuora galbinifrons* (top) and *Terrapene carolina* (bottom).

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Literature Cited

- BRAMBLE, D.M. 1974. Emydid shell kinesis: biomechanics and evolution. *Copeia* 1974:707-727.
- CHEREPANOV, G.O. 1989. New morphogenetic data on the turtle shell: discussion on the origin of the horny and bony parts. *Studia Palaeocheloniologica* 3:9-24.
- ERNST, C.H. 1981. Courtship behavior of male *Terrapene carolina major* (Reptilia, Testudines, Emydidae). *Herp. Rev.* 12:7-8.
- ERNST, C.H., AND BARBOUR, R.W. 1989. *Turtles of the World*. Washington: Smithsonian Inst. Press. 313 pp.
- ERNST, C.H., AND LOVICH, J.E. 1990. A new species of *Cuora* (Reptilia: Testudines: Emydidae) from the Ryukyu Islands. *Proc. Biol. Soc. Wash.* 103:26-34.
- ERNST, C.H., AND MCBREEN, J.F. 1991. *Terrapene*. *Cat. Amer. Amph. Rept.* 511:1-6.
- GAFFNEY, E.S., AND MEYLAN, P.A. 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). *The Phylogeny and Classification of the Tetrapods, Volume I. Syst. Assoc. Spec. Vol 35A:157-219.*
- JOHNSON, R.A., AND WICHERN, D.W. 1992. *Applied multivariate statistical analysis*. 3rd Ed. Englewood Cliffs, NJ: Prentice Hall. 642 pp.
- LOVICH, J.E., AND ERNST, C.H. 1989. Variation in the plastral formulae of selected turtles with comments on taxonomic utility. *Copeia* 1989:304-318.
- LOVICH, J.E., LAEMMERZAHN, A.F., ERNST, C.H., AND MCBREEN, J.F. 1991. Relationships among turtles of the genus *Clemmys* (Reptilia: Testudines: Emydidae) as suggested by plastron scute morphology. *Zoologica Scripta* 20:425-429.
- MCCOY, C.J., AND RICHMOND, N.D. 1966. The identity of the Chinese box turtle, *Terrapene culturalia*. *Copeia* 1966:886.
- RÖMER, A.S. 1956. *Osteology of the Reptiles*. Chicago: Univ. Chicago Press. 772 pp.
- RÖMER, A.S. 1966. *Vertebrate Paleontology*. Chicago: Univ. Chicago Press. 468 pp.
- RÜMMLER, H.J., AND FRITZ, U. 1991. Geographische Variabilität der Amboina-Schamierschildkröte *Cuora amboinensis* (Daudin, 1802), mit Beschreibung einer neuen Unterart, *C. a. kamaroma* subsp. nov. *Salamandra* 27:17-45.
- SAS INSTITUTE. 1989. *SAS/STAT User's Guide*. Version 6. Fourth Edition. 2 vols. Cary, NC: SAS Institute, Inc.

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