

# Relationships among turtles of the genus *Clemmys* (Reptilia, Testudines, Emydidae) as suggested by plastron scute morphology

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Accepted 7 May 1991

Lovich, J. E., Laemmerzahl, 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. — *Zool. Scr.* 20: 425–429.

The conservative morphology of hardshelled turtles has fostered the use of size relationships between epidermal scutes (scales) on the shell to differentiate between species and subspecies of many taxa. The size relationships of the six major pairs of plastral scutes were used to compare the four currently recognized species of the genus *Clemmys* with each other, as well as with the distantly related *Graptemys barbouri* using Jaccard Coefficients, Shannon–Weiner diversity indices, and multivariate analysis. Results were concordant among the three techniques used and confirm our prediction that plastral morphology varies little among closely related species and widely among distantly related taxa. *Clemmys muhlenbergii* appears to be more different from *Clemmys guttata* than previously suggested. Analysis of plastral morphology shows promise as a taxonomic tool for turtle systematists.

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## Introduction

Advances in turtle taxonomy, based on external morphology, are hindered by a conservative turtle shell architecture with few meristically variable characters. Whereas in some groups of reptiles the number and arrangement of scales varies widely among taxa, in turtles these characters are remarkably consistent and rarely of taxonomic value below the family level. This condition has fostered the use of size relationships and the position of contact zones between two or more shell scutes (scales) to differentiate between turtle species and subspecies (Lyons 1969; McDowell 1964; Tinkle 1962; Zangerl 1969; Zangerl & Johnson 1957). One relationship that has gained widespread acceptance as a diagnostic character involves the relative ranking of midseam contact lengths formed by pairs of plastral scutes (Fig. 1). Numerous authors have used this relationship, or 'plastral formula', to characterize a given species of turtle. In a recent review of the technique, Lovich & Ernst (1989) reported that plastral formulae vary considerably within taxa due to the effects of sampling variability, sex, and body size. They concluded that although a given species cannot be represented by a single immutable plastral formula, taxa often exhibit mutually exclusive suites of plastral formulae.

Our objective in this study was to determine if analysis of plastral morphology can be used as a taxonomic tool to show patterns of relatedness concordant with those

based on other accepted techniques. Our prediction was that plastral morphology varies little among closely related species and widely among distantly related taxa.

To test this hypothesis we chose the turtle genus *Clemmys* (Emydidae: Emydinae). As currently recog-

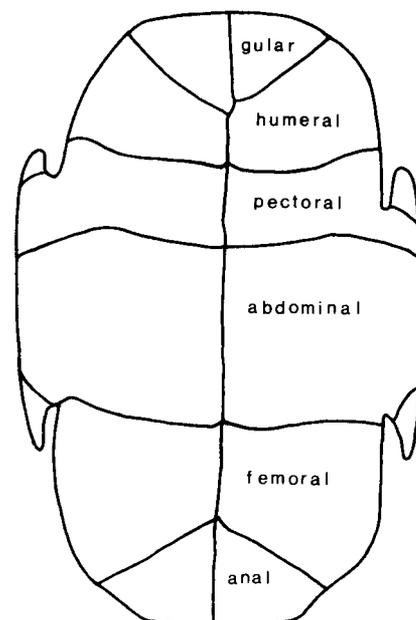


Fig. 1. Ventral view of a typical freshwater turtle shell (plastron) showing the six major paired scutes. Drawing modified from Ernst and Barbour (1972).

Table I. Measures of variation in plastral formulae (PF) of five species of turtles. M = males, F = females. Sample sizes are given in parentheses. H' is not based on condensed data as discussed elsewhere in text. Refer to text for computational details

Diversity measure	Species/category									
	<i>Clemmys guttata</i>		<i>Clemmys insculpta</i>		<i>Clemmys marmorata</i>		<i>Clemmys muhlenbergii</i>		<i>Graptemys barbouri</i>	
	M	F	M	F	M	F	M	F	M	F
Number of PF	16 (92)	17 (107)	30 (49)	25 (44)	24 (77)	17 (44)	37 (83)	30 (74)	11 (38)	15 (55)
MPV	0.17	0.16	0.61	0.57	0.31	0.39	0.45	0.41	0.29	0.27
H'	0.915	0.793	1.393	1.344	1.177	1.117	1.414	1.323	0.777	0.884

nized (McDowell 1964), this genus contains four species: *C. guttata*, *C. insculpta*, *C. marmorata* and *C. muhlenbergii*. Relationships within this genus have been studied using a wide variety of characters and techniques including electrophoresis (Merkle 1975), cytosystematics (Bickham 1975; Stock 1972), penial morphology (Zug 1966), choanal structure (Parsons 1968), carapacial seam contacts (Tinkle 1962), presence or absence of rostral pores (Winokur and Legler 1974), and presence or absence of mental glands (Winokur & Legler 1975). In addition, Holman (1966) described dramatic differences in plastral architecture between *C. insculpta* and *C. guttata*. Collectively, these data suggest the existence of an eastern North American species assemblage comprised of *C. guttata*, *C. insculpta* and *C. muhlenbergii*. Of these *C. guttata* and *C. muhlenbergii* are thought to be most closely related. *Clemmys marmorata*, which lives along the Pacific Coast of North America, appears to be distinct from this group. We contrasted results for this group with data for *Graptemys barbouri*; a related species in the subfamily Deirochelynae (Gaffney & Meylan 1988) with similar plastral morphology (no hinge or other structural specializations). Relationships among these species are explored in this paper using an analysis of plastral morphology.

## Material and methods

Midseam contact lengths of the six paired plastron scutes of live or museum specimens were measured with dial calipers accurate to the nearest 0.1 mm. Lists of specimens examined can be obtained from the senior author upon request. Measurements were ranked from largest to smallest to form plastral formulae (Lovich & Ernst 1989). Although turtles of the genus *Clemmys* do not exhibit marked sexual size dimorphism (Gibbons & Lovich 1990), we tested for differences in scute proportions between sexes. Since we did not measure midline plastron length (MPL), it was estimated by summing the values for all six plastron scute midline lengths. Each of the six scute midline lengths was then divided by MPL to determine the proportion of MPL that it occupied. All proportions were arcsine square-root transformed to meet assumptions of parametric analysis. Multivariate analysis of variance (MANOVA), testing all six transformed scute proportions simultaneously, revealed significant differences ( $P < 0.001$ ) between the sexes in *C. guttata*, *C. muhlenbergii*, *C. marmorata* and *G. barbouri*. Scute proportions did not differ significantly ( $P > 0.05$ ) between males and females of *C. insculpta*. However, this species is known to exhibit sexual size dimorphism (Lovich et al. 1990). Based on these results we chose to analyze data for males and females separately. Specimens that did not exhibit secondary sexual characters were not included in any of the analyses.

Variation in plastral formulae (PF) within species was quantified using two techniques. The first is the Measure of Plastral Variation (MPV) used by Lovich and Ernst (1989), where  $MPV = \frac{\text{number of plastral formulae observed}}{\text{sample size}}$ . Second, measures of diversity were calculated using the Shannon-Weiner index

$$H' = \frac{n \log n - \sum_{i=1}^k f_i \log f_i}{n}$$

where  $n$  is sample size,  $k$  is the number of PF, and  $f_i$  is the number of observations per PF. This index increases with the number of PF observed in a sample, and also with more even distributions of PF within a sample.

We employed three techniques to compare plastral morphology between species. The first was to calculate similarity coefficients for PF. A large number of binary similarity coefficients have been proposed and their properties are reviewed in detail by Cheetham & Hazel (1969). We employed the simple ratio of shared plastral formulae between two taxa divided by the total number of unique formulae. This value, also known as the Jaccard Coefficient (Cheetham & Hazel 1969), is represented as

$$\frac{C}{N_1 + N_2 + C}$$

where  $C$  is the number of shared plastral formulae and  $N_1$  and  $N_2$  are the number of plastral formulae represented in each taxon. The values range from 0 to 1 with 1 representing the case where there is perfect correspondence between taxa.

The second technique we used compared 'condensed' Shannon-Weiner diversity indices for PF between all pairwise combinations of species using the 't-test' proposed by Zar (1984). Diversity indices were condensed in the sense that each was calculated using all shared PF for each species pair (one category per shared PF) plus an additional category where all unshared PF were combined. This ensured that each species in a pair had the same number of categories even though they had different numbers of PF. This is important for two reasons. First, Lovich & Ernst (1989) demonstrated that the number of PF observed in a species was a partial function of sample size. In this study sample sizes among species were unequal. Second,  $H'$  varies not only as a function of 'evenness' among categories, but also as a function of 'richness' or total number of categories. By ensuring that richness was the same between pairwise comparisons of  $H'$ , we ensured that differences between species were due only to differences in the evenness of plastral formulae observed among categories. It is important to note that this technique is unable to measure the strict degree of association between taxa. Instead, it compares the degree of variation exhibited by each. Our assumption here is that closely related taxa will exhibit similar levels of variation. Alpha was adjusted to 0.005 in order to maintain a conservative experimentwise error rate of  $\alpha = 0.05$  for the 10 pairwise comparisons (Sokal & Rohlf 1981).

We also employed multivariate statistical techniques to compare all six transformed scute proportions simultaneously among taxa. After transformation the six transformed scute proportions were compared among taxa simultaneously using MANOVA. Since statistically significant differences were demonstrated among taxa we executed a discriminant function analysis to classify specimens according to predicted taxon using transformed scute proportions. Statistical techniques were executed using SYSTAT (Wilkinson 1986) and STATGRAPHICS (STSC 1986).

## Results

All five species exhibited substantial variation in plastral formulae (Table I). Variation was greatest in *C. insculpta* and *C. muhlenbergii* as indicated by large numbers of PF and high values of MPV and  $H'$ . Similarly coefficients for males ranged from 0.052 to 0.290 for comparisons within

Table II. Jaccard Coefficients for all pairwise comparisons using males. The number in parentheses represents the number of plastral formulae shared between the species

Species	<i>C. muhlenbergii</i>	<i>C. marmorata</i>	<i>C. insculpta</i>	<i>C. guttata</i>	<i>G. barbouri</i>
<i>Clemmys muhlenbergii</i>	—	—	—	—	—
<i>C. marmorata</i>	0.052 (3)	—	—	—	—
<i>C. insculpta</i>	0.136 (8)	0.200 (9)	—	—	—
<i>C. guttata</i>	0.060 (3)	0.290 (9)	0.150 (6)	—	—
<i>Graptemys barbouri</i>	0.000 (0)	0.000 (0)	0.108 (4)	0.000 (0)	—

Table III. Jaccard Coefficients for all pairwise comparisons using females. The number in parentheses represents the number of plastral formulae shared between the species

Species	<i>C. muhlenbergii</i>	<i>C. marmorata</i>	<i>C. insculpta</i>	<i>C. guttata</i>	<i>G. barbouri</i>
<i>Clemmys muhlenbergii</i>	—	—	—	—	—
<i>C. marmorata</i>	0.068 (3)	—	—	—	—
<i>C. insculpta</i>	0.170 (8)	0.235 (8)	—	—	—
<i>C. guttata</i>	0.068 (3)	0.308 (8)	0.167 (6)	—	—
<i>Graptemys barbouri</i>	0.047 (2)	0.000 (0)	0.081 (3)	0.032 (1)	—

Table IV. Condensed Shannon–Weiner indices for all pairwise comparisons of males. The top index in each pair is associated with the species shown in that column. The lower index is associated with the species shown in that row. Pairwise comparisons of indices that are significantly different at the experimentwise error rate of 0.005 are designated with an asterisk. NS designates those pairs of species with no shared plastral formulae. Refer to text for computational details

Species	<i>C. muhlenbergii</i>	<i>C. marmorata</i>	<i>C. insculpta</i>	<i>C. guttata</i>	<i>G. barbouri</i>
<i>Clemmys muhlenbergii</i>	—	—	—	—	—
<i>C. marmorata</i>	0.0848*	—	—	—	—
	0.3999				
<i>C. insculpta</i>	0.3900	0.8179	—	—	—
	0.6138	0.6691			
<i>C. guttata</i>	0.0848*	0.8101	0.5352	—	—
	0.2556	0.8505	0.6520		
<i>Graptemys barbouri</i>	NS	NS	0.2275*	NS	—
			0.5123		

Table V. Condensed Shannon–Weiner indices for all pairwise comparisons of females. The top index in each pair is associated with the species shown in that column. The lower index is associated with the species shown in that row. Pairwise comparisons of indices that are significantly different at the experimentwise error rate of 0.005 are designated with an asterisk. NS designates those pairs of species with no shared plastral formulae. Refer to text for computational details

Species	<i>C. muhlenbergii</i>	<i>C. marmorata</i>	<i>C. insculpta</i>	<i>C. guttata</i>	<i>G. barbouri</i>
<i>Clemmys muhlenbergii</i>	—	—	—	—	—
<i>C. marmorata</i>	0.1578	—	—	—	—
	0.3522				
<i>C. insculpta</i>	0.4817	0.7831	—	—	—
	0.6498	0.6465			
<i>C. guttata</i>	0.1578*	0.8339	0.5324	—	—
	0.3663	0.7051	0.6619		
<i>Graptemys barbouri</i>	0.0849	NS	0.2007	0.0230*	—
	0.0777		0.1882	0.2038	

the genus *Clemmys*, and 0–0.108 for comparisons between the two genera examined (Table II). The mean similarity among *Clemmys* was higher ( $\bar{X} = 0.148$ ) than the mean similarity between the two genera ( $\bar{X} = 0.027$ ). Within the genus *Clemmys*, high similarity was observed between *C. marmorata* and *C. guttata* and between *C. marmorata* and *C. insculpta*. Low similarity was exhibited between *C. muhlenbergii* and *C. marmorata* and also between *C. muhlenbergii* and *C. guttata*. Females exhibit comparable relationships (Table III) with similarity coefficients ranging from 0.068 to 0.308 for comparisons within the genus *Clemmys* and 0–0.081 for comparisons between the two genera. The mean similarity among *Clemmys* was higher ( $\bar{X} = 0.169$ ) than the mean similarity between genera ( $\bar{X} = 0.040$ ). High similarity was observed between *C. marmorata* and both *C. insculpta* and

*C. guttata*. *Clemmys muhlenbergii* and *C. guttata* exhibited low similarity.

Pairwise comparisons of condensed diversity indices for males revealed significant differences between *C. muhlenbergii* and *C. guttata* and also between *C. muhlenbergii* and *C. marmorata* (Table IV). Only one species pair (*C. insculpta* vs *G. barbouri*) exhibited shared PF in between-genera comparisons, and their diversity indices were significantly different. Pairwise comparisons within the genus *Clemmys* using female data revealed a significant difference in the diversity indices of *C. muhlenbergii* and *C. guttata* (Table V). Between-genera comparisons were not significantly different in two out of four species pairs.

The six transformed scute proportions differed significantly among the five species (MANOVA,  $P < 0.001$  for

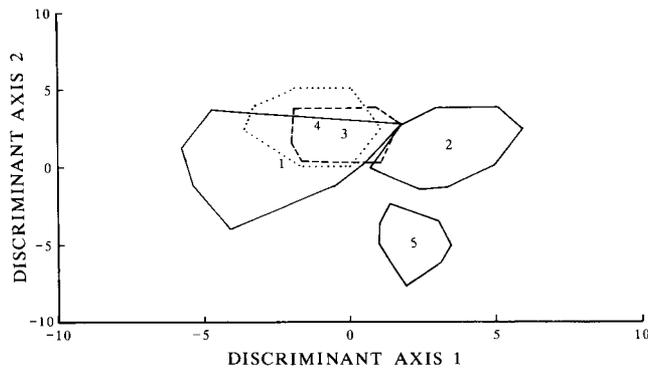


Fig. 2. Discriminant function plot of taxa examined, based on six transformed scute proportions of males. Polygons define extreme values of each cluster. Centroids are designated with numerals representing each species as follows: 1 = *Clemmys guttata*, 2 = *C. muhlenbergii*, 3 = *C. marmorata* (dotted polygon), 4 = *C. insculpta* (dashed polygon), and 5 = *Graptemys barbouri*.

both sexes). A discriminant function analysis based on the transformed scute proportions of males correctly classified 92 per cent ( $n = 327$ ) of the specimens examined. The plot of discriminant scores on the first two axes shows complete separation between *G. barbouri* and the clusters associated with each species of *Clemmys* (Fig. 2). Clusters for *C. muhlenbergii* and *C. guttata* are almost completely separated from each other. Clusters for *C. insculpta* and *C. marmorata* show high overlap. Discriminant function analysis for females correctly classified 94 per cent ( $n = 300$ ) of the specimens examined. Complete separation is again demonstrated between *G. barbouri* and all four species of *Clemmys* (Fig. 3). Cluster overlap and separation among the four species of *Clemmys* is similar to that exhibited by males.

## Discussion

In a recent review of variation of plastral formulae, Lovich & Ernst (1989) noted that although a given species may be represented by numerous *PF*, the proportion of shared formulae can vary considerably between species. In that paper we reported that no *PF* were shared between two distantly related taxa, but that similar *PF* were observed among closely related taxa. The results of this present analysis support our previous contention; a higher number of *PF* were shared among four species of

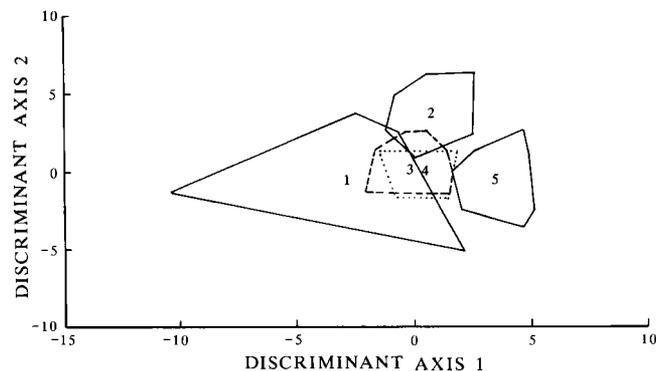


Fig. 3. Discriminant function plot of taxa examined, based on transformed scute proportions of females. Polygons define extreme values of each cluster. Symbols as in Fig. 2.

the genus *Clemmys* than were shared between the genera *Clemmys* and *Graptemys*. Similar results were obtained for males and females in spite of significant sexual size dimorphism and the associated effect of allometry. Results based on binary similarity coefficients and pairwise comparisons of diversity indices were concordant with those based on multivariate analysis. Collectively these observations support our prediction that plastral morphology does not differ greatly among closely related taxa. In this case, differences were greater between genera, as expected. However, minor differences were also detected within the genus *Clemmys*.

Electrophoretic studies by Merkle (1975) have shown that *C. muhlenbergii* is apparently most closely related to *C. guttata* (14 protein systems with shared bands), and is more similar to *C. marmorata* (13 systems) than is *C. guttata* (12 systems). Since *C. muhlenbergii* shared many bands with *C. marmorata* including one not shared with *C. guttata*, Merkle thought *C. muhlenbergii* may be less derived than *C. guttata* and closer to a common ancestor of all three species. This was previously suggested by Hay (1908) on the basis of comparison with fossil species of *Clemmys*. *Clemmys insculpta* may be the least-derived member of the genus. Parsons (1968) reported it possessed a different choanal structural than the other three species of *Clemmys*, and Merkle (1975) demonstrated it contained a distinct electrophoretic band not found in the other three. Forbes (1966) reported that *C. insculpta* had a more primitive karyotype than *C. guttata*, but Bickham (1975) could not substantiate this.

Our results, based on plastral morphology, challenge previously proposed relationships. *Clemmys marmorata* appears to be more similar to other members of the genus than we expected. Mean Jaccard Coefficient values were higher between comparisons of *C. marmorata* and the other three species (males  $\bar{X} = 0.181$ , females  $\bar{X} = 0.204$ ) than for comparisons between *Clemmys* species other than *C. marmorata* (males  $\bar{X} = 0.115$ , females  $\bar{X} = 0.135$ ). Condensed Shannon-Weiner indices were not significantly different between *C. marmorata* and other congenics except for male *C. muhlenbergii* (Tables IV and V). Discriminant function plots confirm the similarity between *C. marmorata* and other *Clemmys* species exclusive of *C. muhlenbergii* (Figs 2 and 3).

All three techniques suggest that *C. guttata*, *C. insculpta* and *C. marmorata* form a group separate from *C. muhlenbergii*. This relationship provides support for the hypothesis proposed by Merkle (1975) that *C. muhlenbergii* is less derived than other members of the genus and thus closer to the common ancestor. The relative dissimilarity observed between *C. muhlenbergii* and *C. guttata* in this study is somewhat surprising given that the two are known to hybridize (Ernst 1983) and that other researchers found them to be closely related (Zug 1966; Parsons 1968; Merkle 1975). Whether the disagreement between results from our analysis and previous studies is significant or not will require additional study.

The concordance among the three techniques we used to quantify variation in plastral morphology is significant in the light of their differences in diagnostic sensitivity. For example, Jaccard Coefficients are useful for describing diversity of form when categorical morphotypes such

as *PF* are assembled from suites of mensural characters. However, this measure does not take into consideration the relative proportion of the total sample represented in each *PF*. Another limitation of this technique is that it requires a relatively large sample size (Lovich & Ernst 1989).

Calculation of the Shannon–Weiner index,  $H'$ , simultaneously considers both richness (number of *PF*) and evenness (number of specimens per *PF*). This presents a problem when comparing samples with different numbers of *PF*, since the number of *PF* observed in a species is a function of sample size (Lovich & Ernst 1989). We obtained a partial solution to this dilemma by using 'condensed' measures of  $H'$  (see Material and Methods). Unfortunately, by combining all unshared *PF* in a taxon into a single category, some information on variation is lost. Additionally, unlike Jaccard Coefficients, this technique is unable to measure the strict degree of association between taxa.

The multivariate approach we used is capable of simultaneously comparing the relationships among all six scute proportions for the taxa investigated. While it does not necessarily provide discrete measures of richness or evenness, it does allow the projection of canonical scores that are of use in determining phenetic relationships.

All three techniques suggest the same conclusion; based on plastral scute relationships, turtles of the genus *Clemmys* are more similar to each other than to specimens of another turtle genus. Because of this concordance we recommend the multivariate approach for future studies, since it is not subject to the limitations of the other two techniques. We conclude that multivariate analysis of plastral morphology shows promise as a taxonomic tool for researchers interested in turtle systematics. The technique appears to be especially sensitive to intergeneric differences. Intrageneric differences reported in our study do not support previous hypotheses about relations among the four recognized species of *Clemmys*. Further studies will be required to determine the significance of this contradiction.

### Acknowledgements

We are grateful to Dan Holland for providing us with data for *Clemmys marmorata*. The following museum curators (in alphabetical order) provided generous access to specimens: James Dobie (Auburn University), Harold Dundee (Tulane University), George Foley (American Museum of Natural History), Joshua Laerm (University of Georgia Museum of Natural History), Robert Mount (Auburn University), Clarence McCoy (Carnegie Museum), and George Zug (U.S. National Museum). The Nature Conservancy kindly allowed JFM to capture and measure wood turtles at a nature preserve that they administer in Virginia. Earlier versions of this manuscript benefited from comments offered by John Bickham. Manuscript preparation was supported by

Contract DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia, Savannah River Ecology Laboratory.

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