Copeia, 1989(2), pp. 304–318

Variation in the Plastral Formulae of Selected Turtles with Comments on Taxonomic Utility

JEFFREY E. LOVICH AND CARL H. ERNST

The relative ranking of midseam scute lengths on the plastron to form a "plastral formula" has often been used by turtle taxonomists to characterize species. However, the results of this study demonstrate that a given species may be represented by as many as 35 plastral formulae. In addition, the relative frequency of these formulae may differ dramatically among sexes and size classes. Some variation may also be due to sampling techniques, or genetic and environmental factors. Preliminary results suggest that distantly related taxa may not share any plastral formulae, while closely related forms may exhibit a high degree of overlap.

IN some groups of reptiles the number and arrangement of scales on the body may vary widely between different taxa. In contrast, the number and arrangement of scutes on the turtle shell is remarkably consistent throughout most of the order and is rarely of taxonomic importance below the family level. Because of this, the size relationships and position of contact zones between two or more scutes have often been used to differentiate between species or subspecies (Boulenger, 1889; de Rooij, 1915; Zangerl and Johnson, 1957; Legler, 1960; Tinkle, 1962; McDowell, 1964; Lyons, 1969; Zangerl, 1969; Pritchard, 1979; Smith and Smith, 1980). One relationship that has gained widespread acceptance as a diagnostic character involves the relative ranking of the midseam contact lengths formed by pairs of plastral scutes. Many authors have used this relationship, or "plastral formula" to characterize a given species of turtle (Table 1) (see also Ernst and Barbour, 1989). However, we report here that the plastral formula of a turtle species can vary considerably among individuals. Our main objective in this paper is to quantify the extent of variation in the plastral formulae (PF) of three species of turtles: *Chinemys reevesii, Graptemys pulchra* and *Platemys platycephala.* In addition, we discuss factors which may influence the levels of variation observed.

METHODS AND MATERIALS

A total of 117 *Platemys platycephala* (Ernst, 1983), 252 *Chinemys reevesii* (Lovich et al., 1985), and 132 *Graptemys pulchra* (see Material Examined) were examined from various museums. Institutional abbreviations follow Leviton et al. (1985). Specimens were examined from throughout the respective ranges of each species. Midseam contact lengths for gular (G), humeral (H), pectoral (P), abdominal (Ab), femoral (F), and anal (An) scutes as well as greatest straight-line plastron lengths (PL) were measured with dial calipers accurate to the nearest 0.1 mm. When one of the paired scutes extended farther posteriorly along the midline than its twin, measurements were taken at a point midway between their extremities. The measurement for the next pair of scutes began at this point. In the case of pleurodiran turtles, the G are partly or completely separated by a single intergular scute (IG). The gular variable for *P. platycephala* (a pleurodiran turtle) was measured along one of the contact seams between the gulars and the intergular. The unpaired latter variable was measured along the long axis of the plastron. Consistency was maintained between investigators by carefully defining each dimension a priori. PF were then determined for individual specimens by ranking the midseam contact lengths from largest to smallest. Turtles were sexed on the basis of precloacal tail length and degree of plastral concavity. Specimens that did not exhibit clearly defined secondary sexual characters were classified as juveniles. The amount of variation in the observed PF within species and sexes was measured using a variety of techniques. A simple measure is given as:

$$\frac{\text{number of plastral formulae observed}}{\text{sample size}}$$

These values are referred to in this paper as Measures of Plastral Variation (MPV). An additional measure of diversity in PF was calcu-

TABLE 1. SELECTED LIST OF PLASTRAL FORMULAE PREVIOUSLY RECORDED IN THE LITERATURE. Formulae are quoted directly from references or calculated from tables, figures or descriptions. Abbreviations refer to plastral scutes (see Methods and Materials).

Family/species	Formula	Comments	Reference
Chelidae			
Chelus fimbriatus	F > all others	—	Pritchard and Trebbau (1984)
Elseya dentata	F > P > Ab	Modal formula	Legler and Cann (1980)
Elseya latisternum	An > P > IG	Modal formula	Legler and Cann (1980)
Emydura krefftii	P > F > Ab	Modal formula	Legler and Cann (1980)
Phrynops geoffroanus	(IG, F, An) > (G, H, P, Ab)	Venezuela	Pritchard and Trebbau (1984)
Phrynops gibbus	IG > (Ab, F, An) > H, P	—	Pritchard and Trebbau (1984)
Phrynops nasutus	IG > F (P = Ab) > (H, An)	—	Pritchard and Trebbau (1984)
Phrynops williamsi	F > IG ≥ An > Ab ≥ P ≥ H	—	Rhodin and Mittermeier (1983)
Phrynops zuliae	F > IG > (G, H, Ab, F) > (P > < An)	—	Pritchard and Trebbau (1984)
Platemys macrocephala	IG > F > Ab > H ≥ An > P	—	Rhodin et al. (1984)
Platemys platycephala	IG > Ab > F > An > G > H > P	—	Ernst (1983)
	(IG, Ab, F) > (H = P = An)	—	Pritchard and Trebbau (1984)
Rheodytes leukops	F > An > Ab	Modal formula of 3 largest scutes	Legler and Cann (1980)
Cheloniidae			
Caretta caretta	An > (H > < F) > (G, Ab) > P	—	Pritchard and Trebbau (1984)
Eretmochelys imbricata	An > (P, Ab, F, H) > G	—	Pritchard and Trebbau (1984)
Lepidochelys olivacea	(F, An) > G > Ab > (H = P, G)	—	Pritchard and Trebbau (1984)
Emydidae			
Chinemys kwangtungensis	Ab > (P = F) > G > An > H	—	Pope (1935)
Chinemys reevesii	Ab > F > P > G > An > H	—	Mao (1971)
	Ab ≥ < (P, F) > (An, G) > H	"Very variable"	Pope (1935)
Chrysemys picta	Ab > An > G > P > F > H	—	Ward (1984)
Cuora chriskarannarum	An > Ab > P > G > F > H	—	Ernst and McCord (1987)
Cuora flavomarginata	Ab > An > P > G > H > F	"Coalesced portion (of An) included"	Mao (1971)
	Ab > P > G > (H, F)	—	Pope (1935)
Cuora pani	An > P > Ab > G > F > H	Based on mean of scute measurements	Ernst (1988)
Cuora trifasciata	(Ab, P) > (An, F, G) > H	—	Pope (1935)
Cuora yunnanensis	G > (P, F, An) > (Ab, H)	—	Pope (1935)
	Ab > P > An > G > F > H	Based on mean of scute measurements	Ernst (1988)
Emys orbicularis	An > (G, P, Ab subequal) > F > H	—	Loveridge and Williams (1957)
Geoemyda spengleri	Ab > (P, F, An, H) > G	—	Pope (1935)
	Ab > H = P = F > An > G	—	Walbaum (1785) in Pope (1935)

Table 1. Continued.

Family/species	Formula	Comments	Reference
Graptemys spp.	G < H < P < Ab > F < An (89%)	—	Dobie (1981)
Heosemys silvatica	Ab > G > < An	—	Moll et al. (1986)
Kachuga dhongoka	Ab > F > H > < P > An > < G	—	Moll (1986)
Kachuga kachuga	Ab > F > H > P > An > G	—	Moll (1986)
Malaclemys terrapin	G, H < P < Ab > F < An (76%)	—	Dobie (1981)
Mauremys caspica rivulata	Ab > F > P > G > An > H	—	Busack and Ernst (1980)
Mauremys caspica caspica	F > Ab > P > G > H > An	Male	Busack and Ernst (1980)
	Ab > F > P > G > H > An	Female	Busack and Ernst (1980)
Mauremys leprosa	Ab ≥ (P ≥ or < F) > (An ≥ or < G) > H	—	Loveridge and Williams (1957)
	Ab > F > P > G > An > H	Male	Busack and Ernst (1980)
	Ab > P > F > G > An > H	Female	Busack and Ernst (1980)
Mauremys mutica	F > Ab > P > H > An > G	—	Mao (1971)
	(Ab, F) > (H, P) : An < G	—	Pope (1935)
Ocadia sinensis	Ab > P > F > G > An > H	—	Mao (1971)
	Ab > (An, P, F, G) > H	—	Pope (1935)
Pseudemys concinna	Ab > An > G = P > F > H	—	Ward (1984)
Pseudemys floridana	Ab > An > P > G > F > H	—	Ward (1984)
Pseudemys nelsoni	Ab > An > G > P > H > F	—	Ward (1984)
Pseudemys texana	Ab > An > P > G > F > H	—	Ward (1984)
Pyxidea mouhotii	Ab > (F, An, P, H) > G	—	Pope (1935)
Rhinoclemmys annulata	Ab > P > F > An > H > G	—	Ernst (1978a)
Rhinoclemmys areolata	Ab > P > F > An > G > H	—	Ernst (1978b)
Rhinoclemmys diademata	(P, Ab) > (G, F, An) > H	—	Pritchard and Trebbau (1984)
Rhinoclemmys funerea	Ab > P > F > G > An > H	—	Ernst (1978c)
Rhinoclemmys nasuta	Ab > P > F > An > G > H	—	Ernst (1978d)
Rhinoclemmys punctularia	Ab > P > F > An > G > H	—	Ernst (1978e)
	Ab > P > (F = An) > G > H	—	Pritchard and Trebbau (1984)
	Ab > P > An > G > F > H	—	Paolillo O. (1985)
Rhinoclemmys pulcherrima	Ab > P > F > An > G > H	—	Ernst (1978f)
Rhinoclemmys rubida	Ab > P > An > G > F > H	—	Ernst (1978g)
Sacalia bealei	Ab > (P, F, An) > G = H	—	Pope (1935)
Trachemys scripta	Ab > An > G > P > F > H	—	Ward (1984)
Trachemys scripta callirostris	Ab > (An, F, G) > (H > < P)	—	Pritchard and Trebbau (1984)
Trachemys scripta chichiriviche	Ab > (P, F, An, G) > H	—	Pritchard and Trebbau (1984)
Trachemys scripta taylori	Ab > An > P > G > F > H	—	Legler (1960)

TABLE 1. CONTINUED.

Family/species	Formula	Comments	Reference
Trachemys scripta yaquia	Ab > An > F > P > G > H	—	Legler and Webb (1970)
Kinosternidae			
Kinosternon alamosae	Ab > An > G > H > F > P	—	Berry and Legler (1980)
Kinosternon angustipons	Ab > An > H > F > G > P	—	Legler (1965)
Sternotherus carinatus	F > H > An	Based on mean of scute measurements	Tinkle (1958)
Sternotherus depressus	H > F > An	Based on mean of scute measurements	Tinkle (1958)
Sternotherus minor minor	H > F > An	Based on mean of scute measurements	Tinkle (1958)
Sternotherus minor peltifer	H > F > An	Based on mean of scute measurements	Tinkle (1958)
Pelomedusidae			
Peltocephalus dumerilianus	F > (P = Ab = An)	—	Pritchard and Trebbau (1984)
Podocnemis erythrocephala	Ab > (P > < F)	—	Pritchard and Trebbau (1984)
	Ab > (P, F) > IG > G	—	Mittermeier and Wilson (1974)
Podocnemis expansa	Ab > IG > G : Ab > P > F	—	Pritchard and Trebbau (1984)
Podocnemis unifilis	IG > G : Ab > (P, F)	—	Pritchard and Trebbau (1984)
Podocnemis vogli	IG > G : Ab > (P = F)	—	Pritchard and Trebbau (1984)
Platysternidae			
Platysternon megacephalum shiui	An > H > F > P > Ab > G	—	Ernst & McCord (1987)
Testudinidae			
Chersina angulata	Ab > G > (H > < An) > F ≥ P	Adults	Loveridge and Williams (1957)
	Ab > H > G > An > P > F	Juveniles	Loveridge and Williams (1957)
Geochelone carbonaria	Ab > (F = H, G, P, An)	—	Pritchard and Trebbau (1984)
Geochelone denticulata	Ab > H > F > (P, An, G)	—	Pritchard and Trebbau (1984)
Geochelone pardalis babcocki	Ab > H ≥ (G > < F) ≥ P or < An	—	Loveridge and Williams (1957)
Geochelone pardalis pardalis	Ab > H ≥ (G > < F) ≥ P > < An	—	Loveridge and Williams (1957)
Geochelone sulcata	Ab > H > F > G ≥ P > An	—	Loveridge and Williams (1957)
Gopherus agassizi	Ab > H > G > F > An > P	Based on mean of scute measurements	Auffenberg (1976)
Gopherus berlandieri	Ab > H > G > F > An > P	Male: based on mean of scute measurements	Auffenberg (1976)
	Ab > H > G > F > P > An	Female: based on mean of scute measurements	Auffenberg (1976)
Gopherus flavomarginatus	Ab > G > H > F > An > P	Male: based on mean of scute measurements	Auffenberg (1976)
	Ab > G > F = H > P > An	Female: based on mean of scute measurements	Auffenberg (1976)

TABLE 1. CONTINUED.

Family/species	Formula	Comments	Reference
Gopherus polyphemus	Ab > H > F > G > P > An	Based on mean of scute measurements	Auffenberg (1976)
Homopus areolatus	Ab > H > An > (G, P, F subequal)	"Usually"	Loveridge and Williams (1957)
Homopus boulengeri	Ab > H > (G, P, F, An variable)	—	Loveridge and Williams (1957)
Homopus femoralis	Ab > H > (An > < F) ≥ G ≥ P	P typically shortest	Loveridge and Williams (1957)
Homopus signatus	Ab > H > An > (G, I, P, F, variable subequal)	"I" appears to be a typographical error	Loveridge and Williams (1957)
Kinixys belliana belliana	Ab > H > (G, P, F, An, all extremely variable)	—	Loveridge and Williams (1957)
Kinixys belliana nogueyi	Ab > H > (G ≥ < F) > (P > < An)	—	Loveridge and Williams (1957)
Kinixys erosa	Ab > H > (G, P, F, An, all extremely variable)	—	Loveridge and Williams (1957)
Kinixys homeana	Ab > H > (G, P, F, An, very variable) F or An shortest	—	Loveridge and Williams (1957)
Malacochersus tornieri	Ab > H > (P > < F) ≥ G ≥ An	—	Loveridge and Williams (1957)
Psammobates geometricus	Ab > G or < H ≥ F ≥ An ≥ P; F usually > An	—	Loveridge and Williams (1957)
Psammobates oculifera	Ab > H > (G, F, An) > P; G usually > An, sometimes ≤	—	Loveridge and Williams (1957)
Psammobates tentorius tentorius	Ab > H > < G > < An > < F > P	—	Loveridge and Williams (1957)
Psammobates tentorius trimeni	Ab > H ≥ (P, An) ≥ G	—	Loveridge and Williams (1957)
Psammobates tentorius verroxii	Ab > H > (An > < G) ≥ (F > < P); An typically > G or F, P usually shortest	—	Loveridge and Williams (1957)
Testudo graeca graeca	Ab > (G, H, P, F, An, very variable)	—	Loveridge and Williams (1957)
Testudo kleinmanni	Ab > (G, H, P, An, subequal) > F	—	Loveridge and Williams (1957)

TABLE 2. MEASURES OF VARIATION IN PF AMONG DIFFERENT TURTLES AND CATEGORIES. TS = total sample, M = males, F = females, J = juveniles.

Diversity measure	Species/category											
	Chinemys reevesii				*Graptemys pulchra*				*Platemys platycephala*			
	TS	M	F	J	TS	M	F	J	TS	M	F	J
Number of PF	27	20	18	11	18	8	9	11	35	21	23	15
MPV	0.11	0.17	0.16	0.44	0.14	0.18	0.17	0.33	0.30	0.75	0.58	0.31
H′	0.906	0.867	0.818	0.874	0.769	0.436	0.699	0.883	1.409	1.289	1.023	1.056
H'_{max}	1.431	1.301	1.255	1.041	1.255	0.903	0.954	1.041	1.544	1.322	1.362	1.176
J′	0.633	0.666	0.652	0.840	0.613	0.483	0.733	0.848	0.913	0.975	0.751	0.898

lated 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 number of PF, and f_i is the number of observations per PF. H′ increases with the number of PF observed in a sample, and also with more even distributions of PF within the sample. Relative diversity within samples was calculated using

$$J' = \frac{H'}{H'_{max}}$$

where J′ is a measure of homogeneity or evenness (Pielou, 1966) which expresses observed diversity as a proportion of maximum possible diversity and

$$H'_{max} = \log k$$

where H'_{max} is the value obtained if all PF in a sample were represented equally. The difference between diversity indices (H′) was tested using procedures outlined in Zar (1984). The Shannon-Weiner index has been criticized as inappropriate when data are sampled nonrandomly (Brillouin, 1962), but alternative formulations do not always provide an acceptable measure of heterogeneity between samples (Peet, 1974).

Cumulative frequency distributions were plotted to determine the effect of sample size on number of PF observed. These curves were then smoothed using the rarefaction technique of Sanders (1968) which generated an expected number of PF based on random sampling from various hypothetical sub-samples. These rarefaction curves are useful for comparing species with different sample sizes since they are based on the shape of each cumulative frequency distribution and not sample size. Although Sanders' method overestimates diversity in samples exhibiting maximum evenness (J′), samples such as ours displaying low evenness are not adversely affected (Hurlbert, 1971).

Hypotheses involving categorical data were tested using the G-test of independence (Zar, 1984). ANOVA procedures were executed using the ABSTAT statistical package (Anderson-Bell, 1984). Males and females were analyzed separately in those species with pronounced sexual size dimorphism (*G. pulchra*—Lovich, 1985; *C. reevesii*—Lovich et al., 1985).

TABLE 3. PL STATISTICS FOR PF OBSERVED IN *Chinemys reevesii.*

		Plastron length (mm)					
		Males		Females		Juveniles	
Plastral formula	n	n	Range	n	Range	n	Range
Ab > P > F > G > An > H	99	43	35.5–144.0	50	49.4–223.0	6	29.7–62.4
Ab > F > P > G > An > H	50	24	54.2–113.8	18	54.9–160.6	8	25.0–65.9
P > Ab > F > G > An > H	32	22	59.0–161.0	10	53.0–165.0	—	—
Ab > P > G > F > An > H	16	4	63.7–121.3	12	60.0–223.0	—	—
Ab > P = F > G > An > H	7	2	72.0–90.5	3	59.3–107.2	2	31.6–63.9
P > F > Ab > G > An > H	5	3	57.2–126.8	2	48.6–75.2	—	—
Ab > F > P > G > H > An	5	3	60.1–99.7	1	67.0	1	31.1
F > Ab > P > G > An > H	4	2	56.8–56.9	1	87.9	1	70.9
Ab > P > F > G > H > An	4	1	83.1	2	68.0–105.2	1	55.7
P > Ab > G > F > An > H	4	1	122.2	3	131.8–173.1	—	—
F > P > Ab > G > An > H	4	2	58.2–70.2	—	—	2	46.7–48.1
Ab > F > G > P > An > H	4	2	88.7–197.0	1	79.3	1	56.8
F = Ab > P > G > An > H	2	1	64.8	—	—	1	31.8
Ab > G > F > P > An > H	2	1	58.0	1	62.7	—	—
P > Ab = F > G > An > H	2	1	72.0	—	—	1	25.0
Ab > F > P > An > G > H	1	—	—	1	55.0	—	—
Ab > F > P > H > G > An	1	—	—	—	—	1	28.7
Ab > P > F > An > G > H	1	—	—	1	84.1	—	—
An > F > Ab > P > H > G	1	—	—	1	63.2	—	—
P > F > G > Ab > An > H	1	1	67.3	—	—	—	—
F > P = Ab > G > An > H	1	1	68.4	—	—	—	—
P = F > Ab > G > An > H	1	—	—	1	112.3	—	—
P = F > G > Ab > An > H	1	1	73.4	—	—	—	—
Ab > P = An > G > F > H	1	1	96.3	—	—	—	—
P > F > Ab > An > G > H	1	1	88.4	—	—	—	—
Ab > P > G = F > An > H	1	—	—	1	105.4	—	—
P > Ab > G = F > An > H	1	—	—	1	103.1	—	—

RESULTS

All species exhibited extensive variation among PF. Juveniles had higher diversity indices (H′) than mature males and females except in *P. platycephala* (Table 2). *Platemys platycephala* had more PF and thus higher diversity; presumably because seven scutes were ranked instead of six. *Chinemys reevesii* had a significantly higher diversity index than *G. pulchra* (one-tailed t-test, t = 2.22, 281 df, $0.01 < P < 0.025$). Specific details for each species are given below.

Chinemys reevesii.—A total of 27 PF were observed in the sample of *C. reevesii* (Table 3). Four of these formulae were represented in over 78% (n = 197) of the specimens examined. All others were relatively rare. The modal formulae of males and females were the same but differed for juveniles. Variation in the richness and evenness of PF as measured by various techniques is given in Table 2.

A condensed 2 × 4 contingency table was constructed using each of the first three PF in Table 3 and the sum of all others to compare their relative frequencies among males and females under the null hypothesis that sex and PF are independent. There is insufficient evidence to conclude that PF and sex are not independent based on this analysis (G = 6.1; $P > 0.10$). The mean PL of males in each PF with at least two observations were not significantly different (ANOVA; F = 1.71; 9,97 df; $P = 0.10$). However, significant differences were observed among the PL of females under the same criterion (ANOVA; F = 2.27; 7,92 df; $P = 0.04$).

Midseam scute lengths ranked in relatively specific orders (Table 4). For example, G and H scute lengths were never the greatest. In contrast, the Ab scute was the largest of the six in approx. 76% (n = 192) of the specimens examined. P and F scutes were more variable than the others in regard to relative rank position. Equalities (ties) between scute lengths were un-

TABLE 4. PLASTRON SCUTE RANK MATRIX FOR *Chinemys reevsii* SHOWING THE PERCENTAGE OF SPECIMENS OBSERVED WITH SCUTE MEASUREMENTS FALLING INTO EACH RELATIVE RANK POSITION. Numerals in parentheses indicate sample size. TS = total sample (including juveniles), M = males, F = females. Vertical sum of each category may not total to 100% because of rounding error.

		Scute					
Rank	Category	G	H	P	Ab	F	An
Largest seam 1	TS	0	0	18.3 (46)	76.2 (192)	3.6 (9)	0.4 (1)
	M	0	0	24.8 (29)	69.2 (81)	4.3 (5)	0
	F	0	0	14.6 (16)	82.7 (91)	0.9 (1)	0.9 (1)
2	TS	0.8 (2)	0	49.6 (125)	16.3 (41)	27.4 (60)	0
	M	0.9 (1)	0	42.7 (50)	21.4 (25)	29.1 (34)	0
	F	0.9 (1)	0	60.0 (66)	13.6 (15)	21.8 (24)	0
3	TS	10.3 (26)	0	25.0 (63)	4.8 (12)	54.8 (138)	0
	M	7.7 (9)	0	25.6 (30)	5.1 (6)	57.3 (67)	0
	F	14.5 (16)	0	19.1 (21)	3.6 (4)	58.2 (64)	0
4	TS	86.1 (217)	0.4 (1)	2.8 (7)	0.8 (2)	7.9 (20)	1.2 (3)
	M	90.6 (106)	0	2.6 (3)	1.7 (2)	4.3 (5)	0.9 (1)
	F	80.0 (88)	0	2.7 (3)	0	13.6 (15)	1.8 (2)
5	TS	1.6 (4)	4.0 (10)	0	0	0.4 (1)	94.1 (237)
	M	0.9 (1)	3.4 (4)	0	0	0.9 (1)	95.7 (112)
	F	1.8 (2)	3.6 (4)	0	0	0	94.5 (104)
Smallest seam 6	TS	0.4 (1)	95.6 (241)	0	0	0	4.0 (10)
	M	0	96.6 (113)	0	0	0	2.6 (3)
	F	0.9 (1)	96.4 (106)	0	0	0	2.7 (3)
Ties	TS	0.8 (2)	0	4.4 (11)	2.0 (5)	6.0 (15)	0.4 (1)
	M	0	0	4.3 (5)	2.6 (3)	4.3 (5)	0.9 (1)
	F	1.8 (2)	0	3.6 (4)	0	5.5 (6)	0

common, appearing in 14% (n = 34) of the *C. reevesii* examined.

Graptemys pulchra.—Eighteen PF were observed in our sample of *G. pulchra* (Table 5). Over 84% (n = 111) of the specimens examined exhibited one of four different formulae. Males, females and juveniles shared the same modal formulae. PF diversity values varied extensively among sexes (Table 2).

A condensed 3 × 2 contingency table was analyzed using each of the first two PF in Table 5 and the sum of all others to compare their relative frequencies among males and females. The results suggest that PF and sex are not independent (G = 14.9; $P < 0.001$). The mean PL of males in each PF with a least two observations were significantly different (ANOVA; F = 22.67; 1,37 df; $P < 0.0001$). However, differences were not significant among females (ANOVA; F = 1.05; 3,45 df; $P = 0.38$).

The G, H and P scutes were never the largest (Table 6), and the Ab scute was almost always the largest. P and F scutes exhibited the greatest variability in rank position.

Platemys platycephala.—This species exhibited the greatest diversity (n = 35) of PF (Table 7). No combination of PF constituted a clearly defined majority among specimens. The modal formulae of males, females and juveniles were all different. The diversities (H′) and relative diversities (J′) observed in our samples were high (Table 2). This variation produced data that were too sparse for meaningful interpretation of differences in the relative frequency of PF among sexes, or for comparisons of the mean PL of each sex among PF.

In spite of considerable variation in the PF of specimens examined, certain midseam scute lengths again ranked in a somewhat consistent fashion (Table 8). G, H and P scutes were never the largest.

DISCUSSION

The relationships between scute proportions and seam contacts have been of great interest to turtle taxonomists since turtles exhibit few meristically variable features. Previously, the most thorough analysis of plastral scute varia-

TABLE 5. PL STATISTICS FOR PF OBSERVED IN *Graptemys pulchra*.

		Plastron length (mm)					
		Males		Females		Juveniles	
Plastral formula	n	n	Range	n	Range	n	Range
Ab > An > F > P > G > H	62	33	70.2–113.6	19	77.0–225.0	10	42.6–60.8
Ab > An > P > F > G > H	28	6	68.0–88.0	15	61.7–230.0	7	40.3–63.2
Ab > An > F > G > P > H	13	1	82.4	11	61.7–235.0	1	56.2
Ab > An > P > G > F > H	8	1	63.5	4	132.7–166.0	3	41.7–62.3
An > Ab > F > P > G > H	4	0	—	0	—	4	47.5–56.4
An > Ab > P > F > G > H	3	1	71.8	0	—	2	40.3–42.2
Ab > An > F > G = P > H	2	1	92.9	0	—	1	35.0
Ab > An = P > F > G > H	2	0	—	0	—	2	59.1–64.2
Ab > An > G = F > P > H	1	0	—	1	213.0	0	—
Ab > An > F > P > H > G	1	0	—	1	208.0	0	—
Ab > An > F > H > P > G	1	0	—	1	202.0	0	—
An > Ab > P > G > F > H	1	0	—	0	—	1	43.7
Ab = An > F > P > G > H	1	1	86.2	0	—	0	—
F > Ab > An > P > G > H	1	0	—	0	—	1	63.8
Ab = An > P > F > G > H	1	1	98.0	0	—	0	—
Ab > An > P > G = F > H	1	0	—	0	—	1	51.4
Ab > F = An > P > G > H	1	0	—	1	222.0	0	—
Ab > P > An > F > G > H	1	0	—	1	210.0	0	—

TABLE 6. PLASTRON SCUTE RANK MATRIX FOR *Graptemys pulchra* SHOWING THE PERCENTAGE OF SPECIMENS OBSERVED WITH SCUTE MEASUREMENTS FALLING INTO EACH RELATIVE RANK POSITION. Numerals in parentheses indicate sample size. TS = total sample (including juveniles), M = males, F = females. Vertical sum of each category may not total to 100% because of rounding error.

		Scute					
Rank	Category	G	H	P	Ab	F	An
Largest seam 1	TS	0	0	0	91.7 (121)	0.7 (1)	6.1 (8)
	M	0	0	0	93.3 (42)	0	2.2 (1)
	F	0	0	0	100.0 (54)	0	96.3 (52)
2	TS	0	0	0.7 (1)	6.8 (9)	0	88.6 (117)
	M	0	0	0	2.2 (1)	0	93.3 (42)
	F	0	0	1.9 (1)	0	0	1.9 (1)
3	TS	0	0	31.8 (42)	0	63.6 (84)	1.5 (2)
	M	0	0	20.0 (9)	0	80.0 (36)	0
	F	0	0	35.2 (19)	0	59.3 (32)	0
4	TS	16.7 (22)	0.7 (1)	53.0 (70)	0	26.5 (35)	0
	M	4.5 (2)	0	75.6 (34)	0	17.8 (8)	0
	F	27.8 (15)	1.9 (1)	38.9 (21)	0	29.6 (16)	0
5	TS	78.8 (104)	0.8 (1)	11.4 (15)	0	6.8 (9)	0
	M	93.3 (42)	0	2.2 (1)	0	2.2 (1)	0
	F	66.7 (36)	1.9 (1)	24.1 (13)	0	7.4 (4)	0
Smallest seam 6	TS	1.5 (2)	98.5 (130)	0	0	0	0
	M	0	100.0 (45)	0	0	0	0
	F	3.7 (2)	96.3 (52)	0	0	0	0
Ties	TS	3.0 (4)	0	3.0 (4)	1.5 (2)	2.3 (3)	3.8 (5)
	M	2.2 (1)	0	2.2 (1)	4.5 (2)	0	4.5 (2)
	F	1.9 (1)	0	0	0	3.7 (2)	1.9 (1)

TABLE 7. PL STATISTICS FOR PF OBSERVED IN *Platemys platycephala.*

		Plastron length (mm)					
		Males		Females		Juveniles	
Plastral formulae	n	n	Range	n	Range	n	Range
IG > F > Ab > An > G > P > H	11	2	114.6–130.0	4	108.5–116.6	5	47.9–90.0
IG > Ab > F > An > G > P > H	11	1	143.1	1	104.4	9	55.6–88.3
IG > Ab > F > G > An > P > H	9	1	125.0	—	—	8	38.3–60.8
IG > Ab > An > F > G > H > P	8	1	120.7	2	134.7–147.9	5	45.8–89.4
F > Ab > IG > An > H > G > P	8	1	140.2	7	133.3–157.1	—	—
IG > Ab > F > An > G > H > P	6	1	121.6	1	113.8	4	53.5–91.3
IG > F > Ab > An > G > H > P	5	—	—	1	141.0	4	50.5–87.5
Ab > F > IG > An > P > G > H	5	1	152.7	4	134.0–144.5	—	—
IG > Ab > F > An > G > H > P	4	—	—	1	111.4	3	74.4–79.5
IG > Ab > F > An > P > G > H	4	1	131.8	1	121.1	2	53.9–88.3
IG > Ab > F > An > H > G > P	4	2	138.2–141.4	2	143.6–154.7	—	—
F > IG > Ab > An > P > G > H	4	1	133.4	3	133.1–135.1	—	—
IG > Ab > F > G > An > H > P	3	—	—	—	—	3	60.8–88.9
F > Ab > IG > H > An > P > G	3	2	123.5–135.8	1	133.0	—	—
F > Ab > IG > An > P > G > H	3	1	131.5	2	128.8–134.6	—	—
Ab > F > IG > An > P > H > G	3	3	135.0–149.3	—	—	—	—
IG > Ab > An > F > P > G > H	2	1	111.1	—	—	1	73.8
F > IG > AB > An > H > G > P	2	1	140.7	1	133.3	—	—
Ab > IG > F > An > G > P > H	2	2	138.1–141.4	—	—	—	—
Ab > IG > F > An > P > G > H	2	1	122.7	1	136.4	—	—
Ab > IG > F > An > P > H > G	2	1	145.4	1	118.1	—	—
Ab > F > IG > An > G > H > P	2	1	145.1	1	122.7	—	—
Ab > IG > F > An > H > G > P	2	2	133.7–139.1	—	—	—	—
IG > F > An > G > Ab > P > H	1	—	—	1	118.5	—	—
IG > Ab > H > F > G > An > P	1	—	—	1	129.9	—	—
IG > F > Ab > An > H > G > P	1	—	—	—	—	1	94.9
IG > Ab > G > F > An > P > H	1	—	—	—	—	1	67.6
F > Ab > IG > G > P > An > H	1	—	—	1	126.2	—	—
F > Ab > An > IG > H > G > P	1	1	119.0	—	—	—	—
F > IG > Ab > An > G > H > P	1	—	—	1	114.5	—	—
F > Ab > An > IG > P > G > H	1	—	—	1	135.6	—	—
F > Ab > IG > An = P > G > H	1	—	—	1	123.0	—	—
IG > Ab > F > An = G > H > P	1	—	—	—	—	1	57.7
IG > Ab > An = G > F > H > P	1	—	—	—	—	1	55.4
An > IG > F > Ab > P = G > H	1	—	—	—	—	1	59.5

tion in turtles was presented by Mosimann (1956) for *Kinosternon integrum.* He observed that the length of all plastral scute midseam contact lengths were significantly correlated with PL, but that the largest scutes exhibited the highest correlations. High correlations were also reported between these variables by Ernst and Lovich (1986) for *P. platycephala.* Variation in abnormal plastral scutellation was detailed by Zangerl (1969), who observed that repetitive variants were often taxa specific. Others have examined carapacial scute variation and associated carapacial formulae as a method for quantifying inter- and intra-specific differences in turtles (Tinkle, 1958, 1962). Berry (1978) used plastron scute proportions to identify the remains of several species of turtles found at an archaeological site. Nutaphand (1979) differentiated two species of tortoises in Thailand partly on the basis of plastron scute morphology. In *Geochelone nutapundi,* the pectoral scutes meet at the midline forming a typical midseam contact zone. In contrast, the pectoral scutes of *G. emys* are widely separated, resulting in only five midseam contact zones on the plastron. This unusual condition invites further investigation, and the taxonomic validity of these species requires confirmation (McKeown et al., 1982).

TABLE 8. PLASTRON SCUTE RANK MATRIX FOR *Platemys platycephala* SHOWING THE PERCENTAGE OF SPECIMENS OBSERVED WITH SCUTE MEASUREMENTS FALLING INTO EACH RELATIVE RANK POSITION. Numerals in parentheses indicate sample size. TS = total sample (including juveniles), M = males, F = females. Vertical sum of each category may not total to 100% because of rounding error.

Rank	Category	Scute						
		IG	G	H	P	Ab	F	An
Largest seam 1	TS	62.4 (73)	0	0	0	15.4 (18)	21.4 (25)	0.9 (1)
	M	35.7 (10)	0	0	0	39.3 (11)	25.0 (7)	0
	F	37.5 (15)	0	0	0	17.5 (7)	45.0 (18)	0
2	TS	13.7 (16)	0	0	0	62.4 (73)	23.9 (28)	0
	M	28.6 (8)	0	0	0	46.4 (13)	25.0 (7)	0
	F	17.5 (7)	0	0	0	55.0 (22)	27.5 (11)	0
3	TS	22.2 (26)	0.9 (1)	0.8 (1)	0	20.5 (24)	43.6 (51)	11.1 (13)
	M	32.1 (9)	0	0	0	14.3 (4)	42.8 (12)	10.7 (3)
	F	42.5 (17)	0	2.5 (1)	0	25.0 (10)	20.0 (8)	10.0 (4)
4	TS	1.7 (2)	11.9 (14)	2.6 (3)	0	0.8 (1)	10.3 (12)	70.1 (82)
	M	3.6 (1)	3.6 (1)	7.1 (2)	0	0	7.1 (2)	78.6 (22)
	F	2.4 (1)	5.0 (2)	2.5 (1)	0	0	7.5 (3)	80.0 (32)
5	TS	0	43.6 (51)	15.4 (18)	23.9 (28)	0.8 (1)	0.8 (1)	13.7 (16)
	M	0	28.6 (8)	25.0 (7)	35.7 (10)	0	0	10.7 (3)
	F	0	32.5 (13)	25.0 (10)	37.5 (15)	2.5 (1)	0	2.5 (1)
6	TS	0	34.2 (40)	30.8 (36)	32.5 (38)	0	0	1.7 (2)
	M	0	46.4 (13)	25.0 (7)	28.6 (8)	0	0	0
	F	0	57.5 (23)	20.0 (8)	17.5 (7)	0	0	5.0 (2)
Smallest seam 7	TS	0	6.8 (8)	50.4 (59)	41.9 (49)	0	0	0
	M	0	21.4 (6)	42.8 (12)	35.7 (10)	0	0	0
	F	0	5.0 (2)	50.0 (20)	45.0 (18)	0	0	0
Ties	TS	0	2.6 (3)	0	1.7 (2)	0	0	2.6 (3)
	M	0	0	0	0	0	0	0
	F	0	0	0	0	0	0	2.5 (1)

Taylor (1970) suggested that the two conditions occur as normal variants in *G. emys*. Plastral scute proportions have also been suggested as important characters for distinguishing *Geochelone travancorica* and *G. forsteni* from *G. elongata* (Pritchard, 1979).

Our results indicate that PF are more variable than was previously thought. The large number of formulae observed within a species, coupled with the fact that formulae and their relative diversities may differ between sexes or size classes invites caution in the use of a single formula to characterize a given species. In spite of this variation, the actual number of PF observed within a species is small compared to the total number of permutations that would be possible assuming random arrangement. For example, there are six factorial or 720 permutations of six scutes when order is not important and ties are not included. Considering this, the total number of PF observed in the sample of *C. reevesii* and *Graptemys pulchra* is only 2.5 and 1.5% (respectively) of the total variation possible under the previous assumption. In the case of *P. platycephala* where seven measurements were ranked, there are 5040 permutations (not including ties). Yet, only 0.6% of this hypothetical variation was actually seen in our sample. Clearly, the relative size of plastral scutes is not random. Mosimann (1956) and Tinkle (1962) both suggested that genetic regulation may be important in controlling the amount of variation observed among scute proportions, but empirical data are not available to test this hypothesis.

The amount of variation actually observed in PF may be due to nonbiological factors. Important considerations include sample size and sampling technique (random vs nonrandom) (Fig. 1). Our data for *P. platycephala* suggest that most PF are represented in a sample as small as 50. In contrast, over 125 specimens of *C. reevesii*

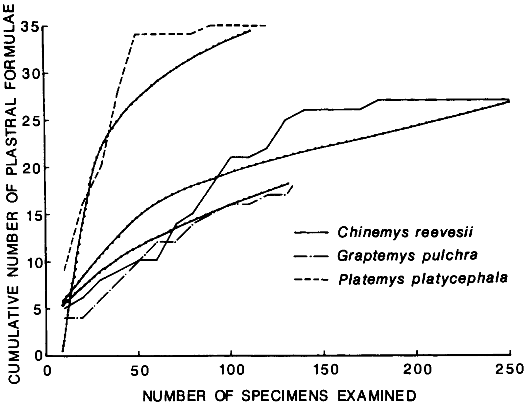

Fig. 1. Relationship between the cumulative number of PF observed and sample size. The number of PF were counted for every 10 specimens in the order in which they were examined. Smoothed curves were generated using the rarefaction technique of Sanders (1968), and are also based on sample size intervals of 10. Refer to text for details.

were examined before an overwhelming majority of PF were categorized. The data for *G. pulchra* imply that the full potential variation in PF is not yet evident after examination of 132 specimens. Although the number of PF within a species is small compared to the number of random permutations that are possible, these observations suggest that fairly large samples may be required for full interpretation of potential variation. Nonrandom sampling biased toward one sex or certain size classes may also result in an incomplete portrayal of variation.

Our data also suggest the possibility of an ontogenetic component. The mean PL of female *C. reevesii* were significantly different among certain PF. Similar differences were also observed for male *G. pulchra*. It is conceivable that PF may change as a turtle grows. If this were true, we would expect the greatest number of changes to occur in rapidly growing immature specimens. Indeed, the highest variation in *G. pulchra* and *C. reevesii* as measured by our MPV is seen in juveniles. The data for *P. platycephala* are contradictory; however, Ernst and Lovich (1986) observed that PF based on mean scute length measurements were different between various size classes of *P. platycephala*.

Previous investigators have also suggested an ontogenetic component in the variation of scute proportions. Mosimann (1956) observed that the Ab scute increased in proportion with PL in *K. integrum* while H scute length decreased. He also found negative correlations between adjacent scutes after adjustment for body size, suggesting that as one scute increases, the other decreases, leading to increasing ratio variability. However, he concluded that plastron scute midlines show little demonstrable change relative to body size. Slight changes in the ratio between Ab and An scute lengths relative to PL were reported by Tinkle (1958) for *Sternotherus minor*, which he attributed to differential growth. Differential growth patterns of plastron scutes were also observed by Liu and Hu (1939–40) for *C. reevesii*. Shealy (1976) noted changes in plastral scutellation with age in *G. pulchra*. These included a decrease in P length and an increase in H length. In addition, the plastron scutes of large females often exhibited poorly defined or "wandering" midlines resulting in the formation of abnormal scutes. Moll and Legler (1971) observed laminal fusion of plastral scutes in *T. scripta*, particularly large females, and suggested that the phenomenon was due to cessation of growth. Ontogenetic fusion of plastral scutes was discussed in detail by Moll (1980) for *Batagur baska*.

Unfortunately, data such as these (including ours), which are usually based on preserved specimens, can only include a single observation per individual. Further analysis on the possible dynamic aspects of PF will be required with repeated observations over time to confirm the existence of this phenomenon.

PF may also vary between sexes, as shown in this study for *G. pulchra*. This may be a partial function of size because of the extreme sexual size dimorphism observed in this species. Coker (1910) observed that female *Malaclemys terrapin*, another sexually dimorphic species, display a greater proportion of scute abnormalities than males. In contrast, Little (1973) reported no sexual differences in the plastral and bridge seam contacts for *G. pulchra*, but provided no evidence to substantiate his claim. Sexual differences may also be important in species such as tortoises where males exhibit pronounced gular extensions (Weaver, 1970; Pritchard, 1979; McRae et al., 1981; McKeown et al., 1982; Rose and Judd, 1982).

It is also possible that environmental factors may influence the proportions observed among plastral scutes. Previous researches have suggested the possible influence of forest fires (Knoll, 1935) and embryonic hydric regimes (Lynn and Ullrich, 1950) on scute variation in turtles. Mosimann (1956) speculated that conditions favoring or not favoring rapid growth would ultimately affect the ratios observed among age classes, and Tinkle (1958, 1962) and Little (1973) suggested the potential for geographic variation among populations.

Taxonomic utility of PF.—Although previous investigators have often used PF as a species-specific trait (Table 1), the results of this study suggest a limited utility because of high individual variation. Similar conclusions were reached by Mosimann (1956) and Tinkle (1962). Broad phylogenetic comparisons may be possible after examining variation within a large group. Inspection of Table 1 reveals that in a large proportion of PF reported for tortoises, the H scute ranks in second place, a condition rarely reported for emydids. Careful interpretation is required since sexual differences in tortoises are important, as mentioned above. In general, however, individual PF are not consistent in indicating a particular taxonomic relationship or strengthening those based on other techniques, a situation also reported for carapacial seam contacts (Tinkle, 1962).

In spite of these shortcomings, PF can be of use taxonomically if the within species variability is considered and is properly interpreted. For example, although each species may be represented by numerous PF, none or few may be shared with other species. In our study, the two comparable cryptodiran taxa (*C. reevesii* and *G. pulchra*) exhibited no overlap. Differences in the relative ranking of G and An scutes are responsible for much of the variation observed between these species (Tables 4 and 6). Wood and Moody (1976) reported no shared PF between *Hydromedusa maximilliani* and *H. tectifera*. However, their results were based on a sample of only 19 specimens. Thus, a given species may be represented by a unique suite of PF. This is not the case in several species of closely related *Graptemys* which share large proportions of their PF, even when based on small sample sizes (Lovich, unpubl.).

Further studies will be required to determine the exact nature of variation in PF within and among various turtle species, genera, and families. Until then, PF will remain an important taxonomic measure only when large sample sizes are employed to identify the range of individual variation. Very large samples may be required to reveal rare PF. Comparisons between species should be tempered with an understanding of potential sampling, ontogenetic, sexual and environmental effects.

Material Examined

List of museum specimens of *G. pulchra* examined. Locality data can be obtained from the senior author on request.

CM: 62162-63, 67438-44, 67454-62, 67473-82, 94883, 94903-06, 94909, 94916-20, 94935-36, 94938-41, 94946, 94948-49, 94966-67, 94970-73, 94976-81, 94983, 94994, 94997-98, 95007, 95010-11, 95015, 95050, 95055-59, 95272-73, 95302, 95361-62, 95553, 95559, 95561, 95563, 95570-73, 95577, 95616-18, 95632, 95634, 95645-47, 95650, 95663-65, 95674, 95688, 95709-10, 95739-43, 95781-84, 95792-800, 95852-56, 95875, 95879, 95999

USNM: 8808 (2 specimens [TYPES])

Acknowledgments

Special thanks are extended to all the people who helped make this study possible. S. Gotte helped with data entry and D. Gantz assisted with data manipulation. J. Novak provided useful criticisms regarding statistical techniques. C. J. McCoy and E. Censky provided us with generous access to collections at Carnegie Museum. S. Lovich and M. Fulmer patiently proofed earlier versions of the manuscript typed by M. Reneau. Manuscript preparation was supported by the Department of Energy grant DE-AC09-76SR00819 to the University of Georgia, Savannah River Ecology Laboratory.

Literature Cited

Anderson-Bell. 1984. ABSTAT Users manual. Anderson-Bell, Canon City, Colorado.

Auffenberg, W. 1976. The genus *Gopherus* (Testudinidae): Pt. I. Osteology and relationships of extant species. Bull. Florida St. Mus. Biol. Sci. 20:47–110.

Berry, J. F. 1978. Identification of the inscribed turtle shells of Shang, Appendix 1. *In:* Sources of Shang history. D. N. Keightley (ed.). University of California Press, Berkeley, California.

———, and J. M. Legler. 1980. A new turtle (genus *Kinosternon*) from northwestern Mexico. Contrib. Sci., Nat. Hist. Mus. Los Angeles County (325):1–12.

Boulenger, G. A. 1889. Catalogue of the chelonians, rhynocephalians, and crocodiles in the British Museum (Natural History). Taylor & Francis, London, England.

Brillouin, L. 1962. Science and information theory. Academic Press, New York, New York.

Busack, S. D., and C. H. Ernst. 1980. Variation in

Mediterranean populations of *Mauremys* Gray 1869 (Reptilia, Testudines, Emydidae). Ann. Carnegie Mus. Nat. Hist. 49:251–264.

COKER, R. E. 1910. Diversity in the scutes of Chelonia. J. Morphol. 21(1):1–75.

DE ROOIJ, N. 1915. The reptiles of the Indo-Australian Archipelago. Vol. I. Lacertilia, Chelonia, Emydosauria. E. J. Brill, Leiden, The Netherlands.

DOBIE, J. L. 1981. The taxonomic relationship between *Malaclemys* Gray, 1844 and *Graptemys* Agassiz, 1857 (Testudines: Emydidae). Tulane Stud. Zool. Bot. 23:85–102.

ERNST, C. H. 1978a. *Rhinoclemmys annulata*. Cat. Amer. Amph. Rept. 250.1–250.2.

———. 1978b. *Rhinoclemmys areolata*. *Ibid.* 251.1–251.2.

———. 1978c. *Rhinoclemmys funerea*. *Ibid.* 263.1–263.2.

———. 1978d. *Rhinoclemmys nasuta*. *Ibid.* 264.1.

———. 1978e. *Rhinoclemmys pulcherrima*. *Ibid.* 275.1–275.2.

———. 1978f. *Rhinoclemmys punctularia*. *Ibid.* 276.1–276.2.

———. 1978g. *Rhinoclemmys rubida*. *Ibid.* 277.1–277.2.

———. 1983. Geographic variation in the neotropical turtle, *Platemys platycephala*. J. Herpetol. 17: 345–355.

———. 1988. Redescriptions of two Chinese *Cuora* (Reptilia:Testudines:Emydidae). Proc. Biol. Soc. Wash. 101:155–161.

———, AND R. W. BARBOUR. 1989. Turtles of the world. Smithsonian Institution Press, Washington, D.C. In Press.

———, AND J. E. LOVICH. 1986. Morphometry in the chelid turtle, *Platemys platycephala*. Herpetological J. 1:66–70.

———, AND W. P. MCCORD. 1987. Two new turtles from Southeast Asia. Proc. Biol. Soc. Wash. 100: 624–628.

HURLBERT, S. H. 1971. The nonconcept of species diversity: a critique of alternative parameters. Ecology 52:577–586.

KNOLL, C. M. 1935. Shield variation, reduction, and age in a box terrapin, *Terrapene carolina*. Copeia 1935:100.

LEGLER, J. M. 1960. A new subspecies of slider turtle (*Pseudemys scripta*) from Coahuila, Mexico. Univ. Kansas Publ. Mus. Nat. Hist. 13:73–84.

———. 1965. A new species of turtle, genus *Kinosternon*, from Central America. Univ. Kansas Publ. Mus. Nat. Hist. 15:615–625.

———, AND J. CANN. 1980. A new genus and species of chelid turtle from Queensland, Australia. Contrib. Sci. Natur. Hist. Mus. Los Angeles County 324:1–18.

———, AND R. G. WEBB. 1970. A new slider turtle (*Pseudemys scripta*) from Sonora, Mexico. Herpetologica 26:157–168.

LEVITON, A. E., R. H. GIBBS, JR., E. HEAL AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

LITTLE, R. B. 1973. Variation in the plastral scutellation of *Graptemys pulchra* (Reptilia, Chelonia, Emydidae). Assoc. SE Biol. Bull. 20:65–66.

LIU, C., AND S. HU. 1939–40. Notes on growth of *Geoclemys grangeri*. Peking Nat. Hist. Bull. 14:253–266.

LOVERIDGE, A., AND E. E. WILLIAMS. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. Bull. Mus. Comp. Zool. Harvard 115: 161–557.

LOVICH, J. E. 1985. *Graptemys pulchra*. Cat. Amer. Amphib. Rept. 360.1–360.2

———, C. H. ERNST AND S. W. GOTTE. 1985. Geographic variation in the Asiatic turtle *Chinemys reevesii* (Gray) and the status of *Geoclemys grangeri* Schmidt. J. Herpetol. 19:238–245.

LYNN, W. G., AND M. C. ULLRICH. 1950. Experimental production of shell abnormalities in turtles. Copeia 1950:253–262.

LYONS, D. D. 1969. Keys to shell-bones of Bornean emydid turtles. Sarawak Museum Journal 17:89–95.

MAO, S. H. 1971. Turtles of Taiwan. Commercial Press, Ltd., Taipei, Republic of China.

MCDOWELL, S. B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London 143: 239–279.

MCKEOWN, S., J. O. JUVIK AND D. E. MEIER. 1982. Observations on reproductive biology of the land tortoises *Geochelone emys* and *Geochelone yniphora* in the Honolulu Zoo. Zoo Biology 1:223–235.

MCRAE, W. A., J. L. LANDERS AND G. D. CLEVELAND. 1981. Sexual dimorphism in the gopher tortoise (*Gopherus polyphemus*). Herpetologica 37:46–52.

MITTERMEIER, R. A., AND R. A. WILSON. 1974. Redescription of *Podocnemis erythrocephala* (Spix, 1824), an Amazonian pelomedusid turtle. Papéis Avulsos Zool., São Paulo 28:147–162.

MOLL, E. O. 1980. Natural history of the river terrapin, *Batagur baska* (Gray) in Malaysia (Testudines: Emydidae). Malaysian J. Sci. 6(A):23–62.

———. 1986. Survey of the freshwater turtles of India. Part I: the genus *Kachuga*. J. Bombay Nat. Hist. Soc. 83:538–552.

———, B. GROOMBRIDGE AND J. VIJAYA. 1986. Redescription of the cane turtle with notes on its natural history and classification. J. Bombay Nat. Hist. Soc. (Supplement) 83:112–126.

———, AND J. M. LEGLER. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. Bull. Los Angeles County Mus. Nat. Hist. (11):1–102.

MOSIMANN, J. E. 1956. Variation and relative growth in the plastral scutes of the turtle *Kinosternon inte-*

grum Leconte. Misc. Publ. Mus. Zool., Univ. Michigan (97):1–43.

NUTAPHAND, W. 1979. The turtles of Thailand. Siam Farm Zoological Garden, Bangkok, Thailand.

PAOLILLO O., A. 1985. Description of a new subspecies of the turtle *Rhinoclemmys punctularia* (Daudin) (Testudines: Emydidae) from southern Venezuela. Amphibia—Reptilia 6:293–305.

PEET, R. K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 5:285–307.

PIELOU, E. C. 1966. The measurement of diversity in different types of biological collections. J. Theoret. Biol. 13:131–144.

POPE, C. H. 1935. Natural history of Central Asia. Vol. 10. The reptiles of China. American Museum of Natural History, New York, New York.

PRITCHARD, P. C. H. 1979. Encyclopedia of turtles. TFH Publ., Inc. Neptune, New Jersey.

———, AND P. TREBBAU. 1984. The turtles of Venezuela. Contrib. Herpetol. no. 2. Soc. Stud. Amph. Rept.

RHODIN, A. G. J., AND R. A. MITTERMEIER. 1983. Description of *Phrynops williamsi*, a new species of chelid turtle of the South American *P. geoffroanus* complex, pp. 58–73. *In:* Advances in herpetology and evolutionary biology. Essays in honor of Ernest E. Williams. A. G. J. Rhodin and K. Miyata (eds.). Museum of Comparative Zoology, Cambridge, Massachusetts.

———, ——— AND J. R. MCMORRIS. 1984. *Platemys macrocephala,* a new species of chelid turtle from central Bolivia and the Pantanal Region of Brazil. Herpetologica 40:38–46.

ROSE, F. L., AND F. W. JUDD. 1982. Biology and status of Berlandier's tortoise (*Gopherus berlandieri*), pp. 57–70. *In:* North American tortoises: conservation and ecology. R. B. Bury (ed.). U.S. Fish and Wildl. Serv. Wildl. Res. Rep. 12.

SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. Amer. Natur. 102:243–282.

SHEALY, R. M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur, in Alabama. Bull. Florida St. Mus. Biol. Sci. 21:47–111.

SMITH, H. M., AND R. B. SMITH. 1980("1979"). Synopsis of the herpetofauna of Mexico. Vol. 6. Guide to Mexican turtles. John Johnson, North Bennington, Vermont.

TAYLOR, E. H. 1970. The turtles and crocodiles of Thailand and adjacent waters. Univ. Kansas Sci. Bull. 49:87–179.

TINKLE, D. W. 1958. The systematics and ecology of the *Sternothaerus carinatus* complex (Testudinata, Chelydridae). Tulane Stud. Zool. 6:3–56.

———. 1962. Variation in shell morphology of North American turtles. I. The carapacial seam arrangements. *Ibid.* 9:331–349.

WALBAUM, J. J. 1785. Beschreibung der spenglerischen Schildkröte, pp. 122–131. PL III: Schrif. Berlin. Gesell. Naturf. Freunde, VI (Not seen by authors; as cited in Pope, 1935).

WARD, J. P. 1984. Relationships of chrysemyd turtles of North America (Testudines: Emydidae). Spec. Publ. Mus. Texas Tech Univ. (21):3–50.

WEAVER, W. G. 1970. Courtship and combat behavior in *Gopherus berlandieri.* Bull. Florida St. Mus. Biol. Sci. 15:1–43.

WOOD, R. C., AND R. T. J. MOODY. 1976. Unique arrangement of carapace bones in the South American chelid turtle *Hydromedusa maximilliani* (Mikan). Zool. J. Linn. Soc. 59:69–78.

ZANGERL, R. 1969. The turtle shell, pp. 311–339. *In:* Biology of the Reptilia, Vol. 1. Morphology A. C. Gans, A. d'A. Bellairs and T. S. Parsons (eds.). Academic Press, New York, New York.

———, AND R. G. JOHNSON. 1957. The nature of shield abnormalities in the turtle shell. Fieldiana, Geology 10:341–362.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs, New Jersey.

(JEL) SAVANNAH RIVER ECOLOGY LABORATORY, DRAWER E, AIKEN, SOUTH CAROLINA 29801 AND (CHE) GEORGE MASON UNIVERSITY, DEPARTMENT OF BIOLOGY, FAIRFAX, VIRGINIA 22030. Accepted 10 Aug. 1988.