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Morphometric Analysis and Taxonomy of Cooter and Red-Bellied Turtles in the North American Genus *Pseudemys* (Emydidae)

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ABSTRACT. – Examination of 30 mensural and 15 qualitative external characters in *Pseudemys* (cooter and red-bellied turtles) indicated extensive morphological overlap among recognized subspecies and species. Because variation in *P. concinna* appears to be clinal, occurring throughout most of its range, recognition of the subspecies *P. c. hieroglyphica*, *P. c. metteri*, and *P. c. mobilensis* cannot be justified. Two cooters in Florida, *P. c. suwanniensis* and *P. floridana peninsularis*, are morphologically distinct and may be recognized as species. Similarly, two southwestern species, *P. gorzugi* and *P. texana*, are recognizable. The Florida cooter, *P. f. floridana*, and river cooter, *P. c. concinna*, could not be distinguished morphometrically, but may be separated by their markings in some parts of their range. Interactions of these two forms are complex and it is recommended that *floridana* be considered a variant (subspecies) of *P. concinna*. Electrophoretic analysis indicated no protein polymorphism among cooters. However, two proteins, presumably homologous, separate the red-bellied turtles (*P. alabamensis*, *P. nelsoni*, *P. rubriventris*) from the cooters (*P. concinna*, *P. gorzugi*, *P. peninsularis*, *P. suwanniensis*, *P. texana*).

The genus *Pseudemys* Gray comprises the cooter and red-bellied turtles which inhabit the eastern, central, and southwestern United States. They are relatively large (up to 420 mm carapace length), basking species with striped head markings, and primarily herbivorous feeding habits.

Taxonomic relationships in *Pseudemys* have been problematic as indicated by their extensive history of species/subspecies revisions (see Smith and Smith, 1980, for a review). Frequently in areas of sympatry, evidence of sporadic hybridization (or limited introgression) has been reported (Seidel and Palmer, 1991). Some populations with intermediate (hybrid?) characters are widely distributed, which suggests subspecific relationships. These interactions have been examined in Florida (Crenshaw, 1955) and Louisiana (Fahey, 1980). Part of the problem has arisen from the absence of clearly defined, quantifiable characters that separate the species of *Pseudemys*. Another problem has been the relatively small number of specimens examined, especially from northern populations. One of the broader analyses of *Pseudemys* relied heavily on cranial musculature and osteology (Ward, 1984). Unfortunately, those characters are of little use in field identification or in evaluation of fluid-preserved museum material. Seidel (1981), and more recently Iverson and Graham (1990) and Seidel and Palmer (1991), have characterized the morphology of *P. rubriventris*, *P. concinna*, and *P. floridana* in the eastern United States. They examined relatively large series of specimens using large numbers of external morphometric characters. However, throughout much of the range of *Pseudemys*, the taxonomic status of species and subspecies remains poorly defined, especially for *P. concinna* and *P. floridana*. The red-bellied turtles (*P. rubriventris*, *P. nelsoni*, and *P. alabamensis*) have been treated as a single species by some authors (Wermuth and Mertens, 1977; Obst, 1985), and the species status of *P. texana* (Etchberger and Iverson, 1990) and *P. gorzugi* (Ernst, 1990) have been questioned (Dixon, 1987; Iverson, 1992).

To date, there has been no comprehensive analysis of morphological variation in *Pseudemys*. The following taxa are currently recognized (but not uniformly accepted) by recent authors: *P. alabamensis*, *P. rubriventris*, *P. nelsoni*, *P. concinna concinna*, *P. c. hieroglyphica*, *P. c. metteri*, *P. c. mobilensis*, *P. c. suwanniensis*, *P. gorzugi*, *P. texana*, *P. floridana floridana*, and *P. f. peninsularis* (Ernst, 1990; Ernst and Barbour, 1989; Iverson, 1992). Placement of *P. f. hoyi* in the synonymy of *P. concinna* (Ward, 1984) has become generally accepted. Based mostly on cranial features, Ward partitioned the genus *Pseudemys* into two subgenera: *Pseudemys* (including *P. floridana* and *P. concinna*) and *Ptychemys* (including *P. alabamensis*, *P. nelsoni*, *P. rubriventris*, and *P. texana*). Iverson (1992) followed this arrangement but noted that the closest relative of *P. texana* may be *P. concinna*. The present study is directed at testing and identifying additional characters which may be used in separating taxa of *Pseudemys*. It evaluates geographic variation throughout the range of the genus. The morphological identity (validity) of taxa was analyzed, but the intention was to minimize taxonomic revision. Efforts to determine the primitive or derived state (polarity) for some morphometric characters were not conclusive. Nevertheless, an estimate of phylogenetic relationships in *Pseudemys* is presented based on a limited number of characters for which polarity could be determined.

MATERIALS AND METHODS

For morphometric analysis, 761 adult fluid-preserved *Pseudemys*, from 199 localities throughout most of the range of the genus (Fig. 1), were analyzed. Specimens included freshly collected individuals with typical coloration as well as museum material (see Specimens Examined). All turtles were tentatively identified *a priori* using traditional qualita-

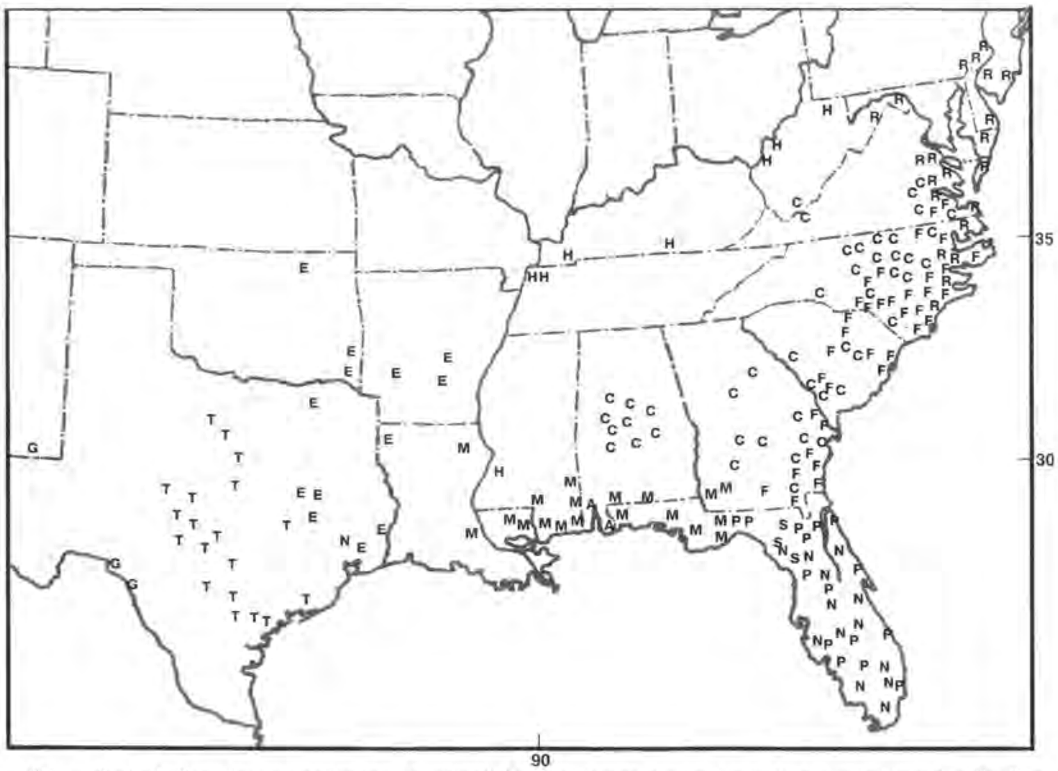

Figure 1. Localities of adult *Pseudemys* specimens examined by morphometric analysis. Letters represent collection sites for *P. alabamensis* (A), *P. c. concinna* (C), *P. c. metteri* (E), *P. f. floridana* (F), *P. gorzugi* (G), *P. c. hieroglyphica* (H), *P. c. mobilensis* (M), *P. nelsoni* (N), *P. f. peninsularis* (P), *P. rubriventris* (R), *P. c. suwanniensis* (S), and *P. texana* (T).

tive characters that have been applied to distinguish species and subspecies of *Pseudemys* (Ernst and Barbour, 1972, 1989; Conant and Collins, 1991). If assignment was questionable, that was noted. The identifications often agreed with specific assignments in museum collections, although many specimens are catalogued in collections as "*Pseudemys* sp.?" or only tentatively assigned to species. Species assignments to *P. concinna* and *P. floridana* were especially difficult for many specimens from coastal plain areas. This problem is so acute along the northern Gulf of Mexico (Mount, 1975; Fahey, 1980; Dundee and Rossman, 1989) that all *Pseudemys* in that area were tentatively assigned to *P. c. mobilensis*.

Character states for 15 qualitative characters were recorded for each turtle. Twenty-six shell characters (scute and skeletal form) were measured on each specimen with calipers (Helios) or an angle goniometer (Jamar). Two head-neck stripes, head width, and maxillary cusp length were also measured. These 30 measurements included most of the quantifiable external characters that have been used to diagnose species and subspecies of *Pseudemys*, as well as additional characters suspected to have taxonomic value: carapace length along midline (CL), carapace width at sulcus between marginals V-VI (CW), carapace width at sulcus between marginals VII-VIII (SW), plastron length along midline (PL), shell height at sulcus between vertebrals II-III (CH), shell height at sulcus between vertebrals III-IV (SH), cervical scute dorsal length (CS), cervical scute dorsal posterior width (CD), cervical scute ventral length (CU), cervical scute ventral posterior width (CV), marginal XII length (MH), marginal XII anterior dorsal width (MA), marginal XII posterior (ventral) width (MP), lateral angle of carapace formed by dorsal and ventral surfaces of marginal VI (SA), posterior angle of carapace formed by midline slope of vertebral V and midline sulcus of anal scutes (PG), anal notch depth (AN), length of interfemoral sulcus (IL), shortest distance between inguinal scute and pectoral-abdominal sulcus (IE), anterior plastral lobe width (PW), posterior plastral lobe width (XW), taper of anal scutes measured as the angle formed by posterior extension of lines along the lateral edge of the anal scutes (AA), epiplastron thickness at mid-humeral scute (ET), depth of epiplastral lip measured as the distance between the anterior tip of the intergular sulcus and a line formed by resting a straightedge across the dorsal epiplastral lip (EP), cervical scute recession measured from anterior tip of cervical scute to a straight line along the anterior tip of first pair of marginals (NR), ventral extension of posterior carapace measured from posterior tip of interanal sulcus to posterior edge of vertebral V (AV) and to posterior tip of intermarginal XII sulcus (AP), head width at anterior margin of tympanum (HW), length of cusps on upper tomium (LC), greatest width of supratemporal stripe (SS), and width of post-symphyseal (ventral) stripe at level of tympanum (GS). All of these characters are illustrated in Seidel and Palmer (1991).

For multivariate analysis, only turtles with a midline carapace length >120 mm were included, and males and females were analyzed separately. This reduced the effects of ontogenetic and sexually dimorphic character variation, which may be pronounced in *Pseudemys* (Gibbons and

Lovich, 1990). Principal components analysis (PCA-SAS; Barr et al., 1982) was applied, thus avoiding assignment of individuals to groups (species and subspecies). Morphological similarity or divergence was examined by observing clustering of individuals on bivariate plots of their principal component scores. That provided a test to determine if *a priori* identifications based on qualitative characters could be corroborated by mensural characters. It also provided a more objective means to determine morphological overlap between species and possible cases of hybridization or intergradation. In a small number of cases, if *a priori* assignment of a specimen was noted as questionable (based on qualitative characters) and its PCA plot was clearly outside its species cluster but within the range of another species, it was reidentified. Otherwise, taxonomic reassignment was avoided.

Multivariate analysis of variance (MANOVA-SAS) followed by Fisher's least significant difference (*t*-tests) were used to test for utilitarian taxonomic characters that might provide a more objective (quantitative) means for identifying species of *Pseudemys*. Thirty-one character ratios were constructed from 27 of the original 30 characters. These included character ratios that have been reported to be useful in discriminating between forms of *Pseudemys*. Despite theoretical problems with using ratios in statistical analyses, their effectiveness in taxonomic studies of turtles has been clearly demonstrated (Iverson and Graham, 1990). The numbers of character ratios distinguishing each taxon (average between male and female) were represented by cluster analysis (BMDP1M.2; Dixon, 1981) as morphological distances. This method employed complete and average linkage methods, and provided alternative comparisons using "unweighted" characters.

Large series of hatchling *Pseudemys* were also examined. However, very young individuals were difficult to distinguish from each other. Morphological characters, including markings, that were found to be diagnostic in adults of these species were often impossible to resolve in young turtles or extremely variable, even within a single brood of hatchlings.

For further analysis of variation in *Pseudemys*, tissue proteins from 63 turtles representing all taxa, except *P. c. suwanniensis* and *P. c. mobilensis*, were analyzed by electrophoresis following the procedures of Seidel and Adkins (1987, 1989). General banding patterns (profiles) of proteins were examined by isoelectric focusing of kidney, liver, and muscle extracts and compared to samples from *Trachemys*, *Graptemys*, and *Chrysemys*. Homogenates were applied to ultrathin (0.1 mm) polyacrylamide gels (Crescent-Serva, 1992/93 catalog) pH 7-8 and 6-9. Gels were placed in a cooling cell (2°C) and focused for 3-5 hrs at constant power (2.0 watts, maximum 1700 volts) using an LKB 2103 power supply and Biorad electrodes. Immediately after focusing, gels were fixed in trichloroacetic acid and stained with a triphenylmethane dye. Gels were scored for presence or absence of bands which were compared to a standard containing proteins with known isoelectric points (pI).

A phylogeny for species of *Pseudemys* was estimated based on one electrophoretic and 14 morphometric characters. Cladistic relationships were defined by phylogenetic analysis using parsimony (PAUP version 2.4, unpublished algorithm by D.L. Swofford, Illinois Natural History Survey). Polarities of character states were based on outgroup comparisons and trees rooted with *Trachemys* and *Graptemys*.

RESULTS

Statistical Analysis.— Initially individuals of all taxa of *Pseudemys* were collectively analyzed by principal components analysis. The first factor (PC I) extracted from the 30 morphometric characters measured was size-related, as expected (Wiley, 1981). It accounted for more than 50% of the total variance in male and female turtles and all loading coefficients (eigenvectors) were high and positive (except angle of anal scute, AA). PC II accounted for 25% of the remaining variance in males and 23% in females. PC III accounted for 15% of the remaining variance (after PC I and II) in males and 17% in females. When individuals of all taxa were plotted according to their PC II and PC III scores, extensive morphological variation and overlap was indicated. *Pseudemys rubriventris* (R), *P. nelsoni* (N), and *P. alabamensis* (A) formed a relatively distinct morphological cluster, as did *P. f. peninsularis* (P). However, little separa-

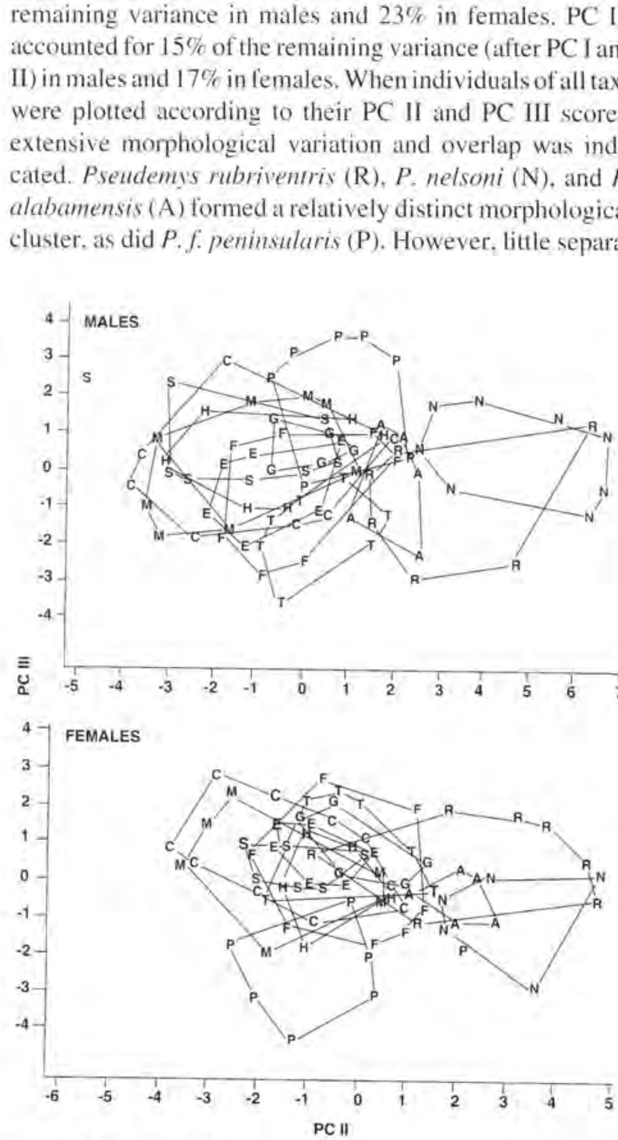

Figure 2. Plot of adult *Pseudemys* based on principal components two and three. Letters represent taxa identified in Fig. 1 and lines connect the most dispersed individuals, except for one outlying male *P. c. suwanniensis* (S).

Table 1. Factor loadings (eigenvectors) for the most influential morphometric characters from principal components analysis.

		PC II		PC III	
		Male	Female	Male	Female
Cervical scute ventral length	(CU)	0.31	0.32	---	---
Cervical scute ventral width	(CV)	---	---	0.34	-0.53
Cervical scute dorsal width	(CD)	---	---	0.52	---
Marginal scute XII length	(MH)	-0.16	---	---	---
Anal notch depth	(AN)	---	-0.21	-0.22	0.15
Epiplastral lip depth	(EP)	---	---	-0.32	---
Cervical scute recession	(NR)	-0.25	---	-0.20	0.62
Supratemporal stripe width	(SS)	-0.30	-0.41	---	0.23
Post-symphyseal stripe width	(GS)	---	-0.35	0.38	-0.27
Length of tomial cusps	(LC)	0.36	0.43	-0.34	0.20
Cervical scute dorsal length	(CS)	---	0.14	-0.18	---
Epiplastron thickness	(ET)	0.22	---	---	---
Distance between inguinal scute and pectoral-abdominal sulcus	(IE)	---	---	0.14	---
Length of interfemoral sulcus	(IL)	-0.24	-0.16	---	---
Taper (angle) of anal scutes	(AA)	0.40	0.44	---	---
Posterior slope (angle) of carapace	(PG)	0.31	---	---	---
Lateral angle of carapace	(SA)	0.29	0.20	0.15	-0.22

tion was seen among subspecies of *P. concinna*, *P. f. floridana*, *P. gorzugi*, and *P. texana* (C,E,F,G,H,M,S,T: Fig. 2). The most influential mensural character loadings on PC II and PC III are identified in Table 1. Ratios formed from these characters were found to be useful in defining taxa. Three additional sets (male and female) of principal components II and III were analyzed by treating *P. concinna* and *P. floridana*; *P. c. metteri*, *P. gorzugi* and *P. texana*; and *P. alabamensis*, *P. nelsoni* and *P. rubriventris* as separate groups based on geographic proximity and/or previously applied classification. Comparing plots for *P. concinna* and *P. floridana* it is evident that *P. f. peninsularis* is the most morphologically distinct taxon (Fig. 3). No overlap was seen between *P. f. peninsularis* and *P. c. suwanniensis*, with which it is broadly sympatric in Florida. In contrast, plots for *P. f. floridana* (F) broadly overlap with those of *P. concinna* subspecies (C,E,H,M,S) which overlap extensively with each other (Fig. 3). *Pseudemys gorzugi*, *P. texana*, and *P. c. metteri*, all of which occur allopatrically in Texas, appear relatively distinct (especially males), when plotted separately on PC II and PC III (Fig. 4). When the three red-bellied turtles (all allopatric) were plotted, *P. nelsoni* showed only slight morphological overlap with the other species, whereas more extensive overlap was observed between *P. rubriventris* and *P. alabamensis* (Fig. 5). A single extralimital specimen of *P. nelsoni* from Liberty Co., Texas, plotted near the middle of the *P. nelsoni* cluster.

Results from cluster analysis based on character ratios (Table 2) are congruent with patterns shown by principal components analysis (Fig. 6). Most obvious is the separation of *P. f. peninsularis* (P) from all other clusters. Red-bellied turtles (A,N,R) form a group distinct from *P. concinna*, *P. f. floridana*, *P. gorzugi*, and *P. texana* (C,E,F,G,H,M,S,T). *Pseudemys texana* and *P. gorzugi* (G) cluster separately from subspecies of *P. concinna* (C,E,H,M,S) and *P. f. floridana* (F). *Pseudemys c. suwanniensis* appears outside the cluster formed by the other subspecies of *P. concinna* and *P. f. floridana*.

Electrophoretic Analysis. — Results from isoelectric focusing revealed extremely little protein variation among populations and taxa of *Pseudemys*. Although large numbers of protein bands were revealed in muscle, heart, and kidney homogenates, only a single banding pattern in liver was polymorphic in *Pseudemys*. A well-defined band at pI 8.2

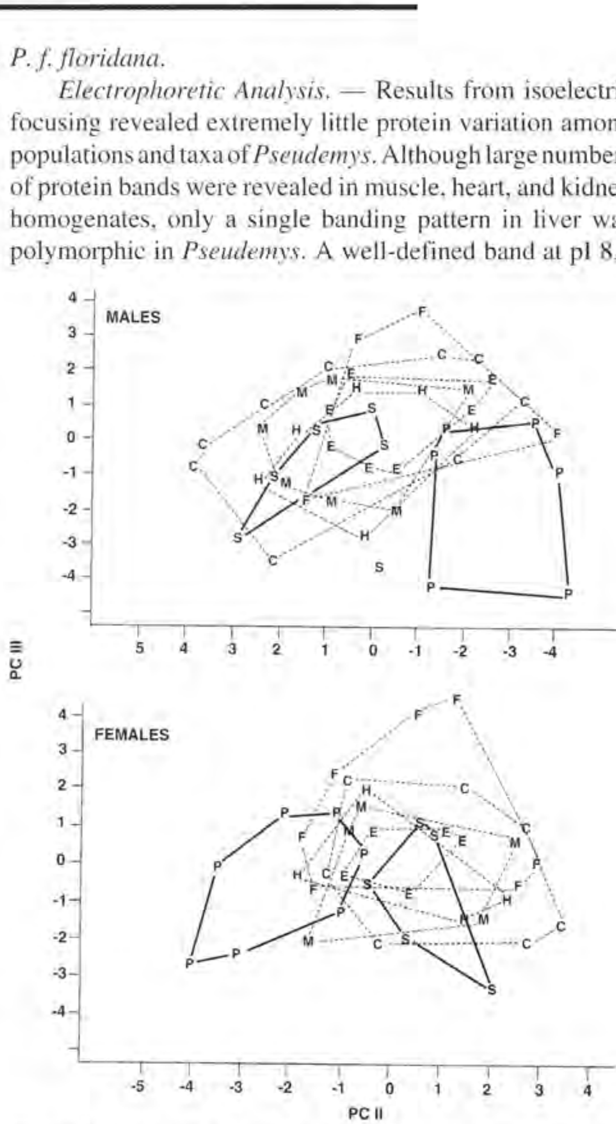

Figure 3. Plot of adult cooters based on principal components two and three. Letters represent taxa identified in Fig. 1 and lines connect the most dispersed individuals, except for one outlying male *P. c. suwanniensis* (S).

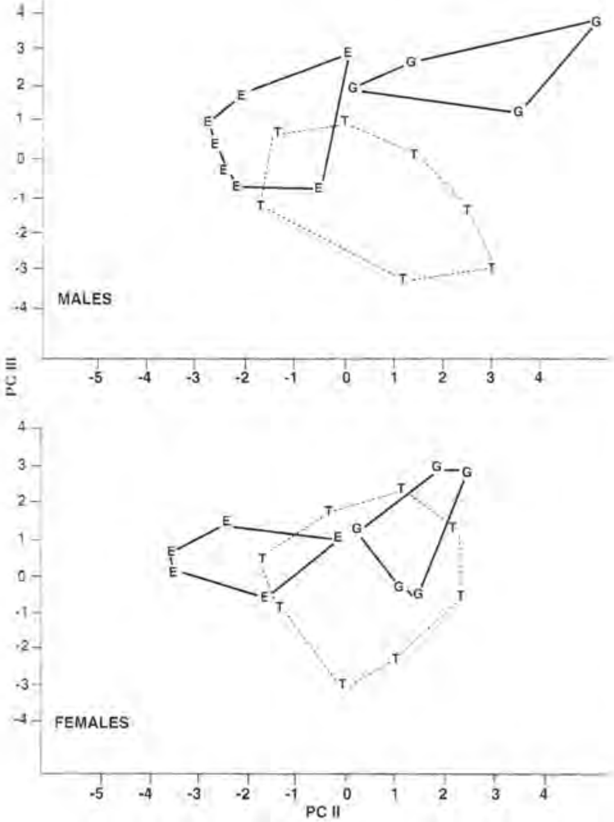

Figure 4. Plot of adult *P. c. metteri* (E), *P. gorzugi* (G) and *P. texana* (T) based on principal components two and three. Lines connect the most dispersed individuals.

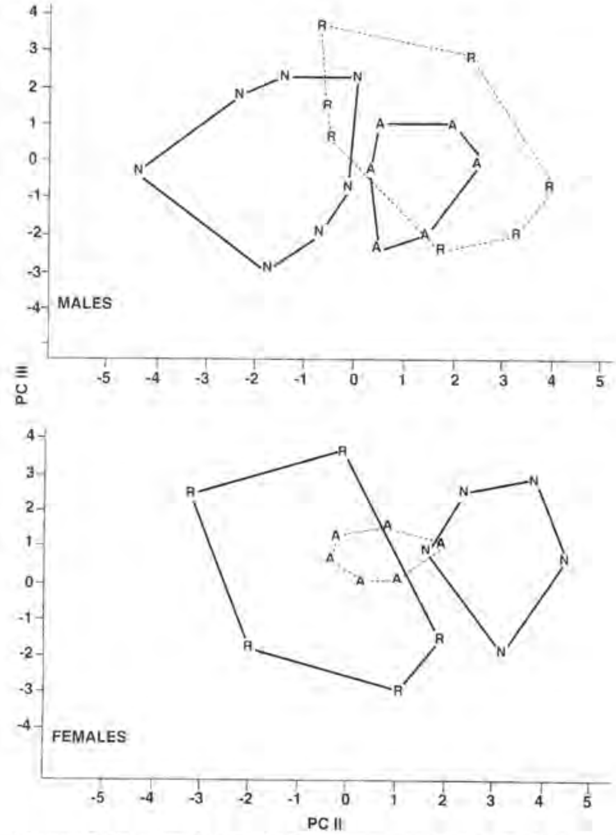

Figure 5. Plot of adult *P. alabamensis* (A), *P. nelsoni* (N), and *P. rubriventris* (R) based on principal components two and three. Lines connect the most dispersed individuals.

appeared in liver of all red-bellied turtles examined (18 *P. rubriventris*, 4 *P. nelsoni*, and 2 *P. alabamensis* (Fig. 7). This protein band appeared in only two other individuals: *P. concinna* NCSM 28688 (Gates Co., North Carolina) and *P. concinna* MES 529 (Summers Co., West Virginia). Considering their geographic origin, this could represent introgression from *P. rubriventris*. Another band (pI 8.4), presumably representing a homologous protein, appeared in nearly all of the other *Pseudemys* (including 8 *P. texana* and 5 *P. gorzugi*) as well as *Trachemys scripta*, but was absent from all red-bellied turtles. The electromorph (pI 8.2) found in red-bellied turtles was not found in specimens of *Trachemys*, *Graptemys*, and *Chrysemys* examined, so this protein was considered derived (apomorphic).

Table 2. Matrix (for cluster analysis) indicating the number of morphometric characters (ratios) for which mean differences ($P<0.01$) were found between taxa. Letters, indicating taxa, are identified in Fig. 1.

		FEMALE												
		A	R	N	P	F	M	S	C	H	E	G	T	
	A	0	7	8	12	10	14	20	17	13	11	11	15	
	R	6	0	13	27	15	15	23	22	15	14	9	22	
	N	13	15	0	17	19	21	23	20	21	16	16	19	
	P	17	25	23	0	21	15	22	19	22	21	21	23	F
M	F	8	16	23	20	0	5	16	11	7	9	10	18	E
A	M	17	14	22	17	11	0	13	8	2	2	6	9	M
L	S	15	21	25	18	14	12	0	16	13	13	8	18	A
E	C	17	18	24	22	13	8	8	0	5	5	9	11	L
	H	14	18	20	21	8	8	10	6	0	0	6	9	E
	E	11	17	25	18	9	8	18	8	11	0	6	5	
	G	14	17	20	24	14	11	12	14	10	15	0	5	
	T	17	22	28	27	24	18	21	20	16	17	15	0	
						MALE								

Cladistic Analysis. — Coded character states and polarities are presented in Table 3. The PAUP algorithm produced six trees from which a strict consensus tree (Rohlf, 1982) was computed. Unresolved trichotomies appear at two locations: the node joining species of red-bellied turtles and the node linking *P. c. suwanniensis*, *P. concinna–P. f. floridana*, and *P. texana–P. gorzugi* (Fig. 8). These results are very similar to those produced by cluster analysis (Fig. 6), except for the position of *P. f. peninsularis*.

Character Analysis and Taxonomic Descriptions

Many of the character states in *Pseudemys* are based upon continuous variables with considerable overlap. Nevertheless, collectively they are useful in separating taxa and analysis of variance indicated mean differences ($P<0.01$) for the mensural characters cited below and listed in Tables 4 and 5.

The red-bellied turtles (*P. alabamensis*, *P. nelsoni*, *P. rubriventris*) are distinguished from most of the cooters by the following characters: upper tomium with prominent notch bordered on each side by toothlike cusps, length of cusp 3-7% of head width LC/HW (character state shared with *P. texana* and *P. gorzugi*); supratemporal stripe narrow,

Table 3. Matrix for cladistic analysis (PAUP) of *Pseudemys*. Characters 1-15 are identified below and states are indicated present (1 or 2) absent (0). The primitive (plesiomorphic) conditions (0) are considered to be the states present in *Trachemys* and/or *Graptemys* and the derived (apomorphic) states (1 or 2) are: 1. liver protein with an isoelectric point 8.2, 2. epiplastral lip of females prominently curved (1), 3. angle of xiphiplastron in females broad, 4. epiplastron of females thick, 5. supratemporal stripe broad, 6. post-symphyseal stripe broad, 7. prominent cusps on upper tomium, 8. interfemoral sulcus of males short, 9. inguinal scutes extend forward, 10. ventral surface of cervical scute moderate length (1) or short (2), 11. dorsal surface of cervical scute very wide (1) or narrow (2), 12. nuchal bone projected forward, 13. deep anal notch in males, 14. lateral angle (slope) of carapace steep, 15. posterior carapace very steeply sloped (1) or weakly sloped (2) (see Tables 4 and 5). Because electrophoretic data were not available for *P. c. mobilensis* and *P. c. suwanniensis*, their biochemical character state (character #1) was assumed to be the same as the other designated subspecies of *P. concinna*.

Character Number	Prot. pI8.2 1	EP/PL 2	AA 3	ET/PL 4	SS/HW 5	GS/HW 6	LC/HW 7	IL/PL 8	IE/CL 9	CU/CS 10	CD/CL 11	NR/CD 12	AN/PL 13	SA 14	PG 15
P. rubriventris	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0
P. nelsoni	1	0	1	1	0	1	1	1	0	0	0	0	0	1	1
P. alabamensis	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0
P. f. peninsularis	0	0	0	0	0	1	0	0	0	1	1	1	0	1	0
P. f. floridana	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
P. c. mobilensis	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
P. c. suwanniensis	0	1	0	0	1	1	0	0	0	2	0	0	0	0	0
P. c. concinna	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
P. c. hieroglyphica	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
P. c. metteri	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
P. texana	0	1	0	0	1	1	1	0	1	1	2	0	1	0	2
P. gorzugi	0	0	0	0	2	1	1	1	1	1	0	0	0	0	2

5-9% of head width SS/HW (shared with *P. f. peninsularis*); ventral side of cervical scute long, greater than 50% of the dorsal length CU/CS; angle formed by lateral edges of xiphiplastron-anal scutes (AA) broad in females, 70-80°; and plastral ground color in living specimens pink, coral, or deep orange, except in some adult *P. nelsoni* which are yellow. *Pseudemys nelsoni* is distinct from *P. alabamensis* and *P. rubriventris* by having the following character states: steeper slope (angle) of the posterior carapace (PG), 55-65° in males and 65-75° in females; interfemoral sulcus in males short, less than 10% of plastron length (IL/PL); and wider post-symphyseal stripe, greater than 9% of head width (GS/HW). The relatively short interfemoral scutes of *P. nelsoni* was also noted by Ward (1984). *Pseudemys alabamensis* has a slightly broader stripe (8%) than *P. rubriventris* (6-7%); and *P. alabamensis*, especially females, has a slightly thicker epiplastron, 2.7% of plastron length (EP/PL). For further descriptions of the species of red-bellied turtles see Graham (1991), Jackson (1978a), and McCoy and Vogt (1985).

Pseudemys f. peninsularis is distinguished from all other cooters by the following combination of characters: nuchal bone projected forward, recession of cervical scute less than 1% of carapace length (NR/CL), and in males recession is less than 20% of the cervical scute width (NR/CD) (Figs. 9 and 10B,C); dorsal surface of the cervical scute wide posteriorly, greater than 4.5% of carapace length (CD/

Table 4. Morphometric characters useful in distinguishing taxa of female *Pseudemys*. Standard errors are in parentheses below means. Sample sizes (N) follow taxa names. Symbols for characters (ratios) are defined in text.

FEMALE	(N)	SS/HW	GS/HW	LC/HW	ET/PL	IE/CL	NR/CL	CU/CS	CD/CL	EP/PL	AA	SA	PG
P. rubriventris	67	0.062	0.059	0.040	0.024	0.099	0.015	0.547	0.033	0.024	72.2	113.3	55.5
		(.003)	(.002)	(.002)	(.001)	(.003)	(.001)	(.011)	(.001)	(.001)	(1.3)	(1.4)	(1.1)
P. nelsoni	8	0.079	0.102	0.043	0.033	0.129	0.007	0.667	0.026	0.021	80.5	120.3	69.0
		(.013)	(.010)	(.003)	(.002)	(.011)	(.001)	(.035)	(.003)	(.002)	(2.6)	(2.3)	(2.5)
P. alabamensis	9	0.068	0.081	0.046	0.031	0.092	0.012	0.572	0.038	0.029	74.0	109.4	62.8
		(.007)	(.003)	(.004)	(.002)	(.010)	(.002)	(.024)	(.001)	(.003)	(1.8)	(3.8)	(1.6)
P. f. peninsularis	33	0.082	0.123	0.000	0.027	0.114	0.006	0.474	0.053	0.029	55.3	114.2	56.5
		(.004)	(.004)	0.000	(.001)	(.004)	(.001)	(.019)	(.003)	(.002)	(1.1)	(1.3)	(0.9)
P. f. floridana	72	0.112	0.093	0.002	0.025	0.108	0.015	0.492	0.034	0.031	63.1	106.6	58.0
		(.004)	(.003)	(.001)	(.001)	(.003)	(.001)	(.017)	(.001)	(.001)	(0.9)	(1.1)	(0.9)
P. c. mobilensis	27	0.134	0.112	0.001	0.024	0.109	0.014	0.403	0.037	0.027	56.7	95.7	54.5
		(.006)	(.004)	(.001)	(.001)	(.004)	(.001)	(.034)	(.003)	(.002)	(1.7)	(2.3)	(1.1)
P. c. suwanniensis	20	0.163	0.121	0.000	0.028	0.107	0.021	0.324	0.038	0.034	55.1	88.1	47.0
		(.005)	(.003)	0.000	(.001)	(.004)	(.001)	(.012)	(.001)	(.002)	(2.1)	(1.4)	(0.7)
P. c. concinna	58	0.141	0.118	0.006	0.023	0.104	0.019	0.386	0.035	0.027	59.6	96.8	52.6
		(.004)	(.003)	(.002)	(.001)	(.003)	(.001)	(.012)	(.001)	(.001)	(1.3)	(1.8)	(0.9)
P. c. hieroglyphica	21	0.114	0.096	0.005	0.021	0.103	0.015	0.427	0.037	0.030	61.2	97.2	51.4
		(.007)	(.005)	(.002)	(.001)	(.004)	(.001)	(.029)	(.002)	(.001)	(1.5)	(2.2)	(1.7)
P. c. metteri	13	0.111	0.082	0.006	0.020	0.111	0.016	0.450	0.030	0.030	55.7	102.1	53.6
		(.006)	(.006)	(.003)	(.001)	(.009)	(.001)	(.028)	(.002)	(.002)	(2.0)	(1.9)	(1.7)
P. texana	28	0.103	0.106	0.047	0.021	0.071	0.014	0.408	0.029	0.038	55.5	93.6	54.0
		(.009)	(.012)	(.009)	(.001)	(.003)	(.001)	(.050)	(.001)	(.001)	(1.6)	(2.2)	(1.5)
P. gorzugi	6	0.149	0.119	0.045	0.020	0.060	0.018	0.408	0.034	0.028	67.3	92.0	49.3
		(.006)	(.002)	(.005)	(.001)	(.003)	(.004)	(.030)	(.004)	(.001)	(4.8)	(6.2)	(2.6)

Table 5. Morphometric characters useful in distinguishing taxa of male *Pseudemys*. Standard errors are in parentheses below means. Sample sizes (N) follow taxa names. Symbols for characters (ratios) are defined in text.

MALE	(N)	SS/HW	GS/HW	LC/HW	IL/PL	IE/CL	NR/CL	CU/CS	CD/CL	NR/CD	AN/PL	SA	PG
P. rubriventris	23	0.074	0.070	0.044	0.124	0.096	0.016	0.562	0.034	0.494	0.033	107.1	45.4
		(.004)	(.003)	(.003)	(.005)	(.006)	(.002)	(.019)	(.002)	(.052)	(.002)	(2.9)	(1.9)
P. nelsoni	26	0.079	0.109	0.045	0.094	0.032	0.009	0.670	0.034	0.259	0.037	111.4	56.1
		(.005)	(.004)	(.003)	(.004)	(.001)	(.001)	(.019)	(.001)	(.027)	(.002)	(1.5)	(0.9)
P. alabamensis	8	0.088	0.082	0.043	0.124	0.091	0.012	0.651	0.034	0.380	0.045	98.4	49.2
		(.007)	(.004)	(.004)	(.006)	(.009)	(.002)	(.097)	(.002)	(.071)	(.003)	(2.3)	(0.9)
P. f. peninsularis	29	0.088	0.127	0.000	0.143	0.099	0.006	0.504	0.053	0.166	0.046	109.5	45.8
		(.005)	(.005)	0.000	(.003)	(.003)	(.001)	(.033)	(.002)	(.015)	(.002)	(1.2)	(0.9)
P. f. floridana	50	0.137	0.099	0.001	0.144	0.100	0.015	0.499	0.035	0.485	0.045	92.7	47.1
		(.006)	(.004)	(.001)	(.003)	(.003)	(.001)	(.025)	(.001)	(.033)	(.001)	(1.3)	(0.8)
P. c. mobilensis	46	0.145	0.112	0.000	0.144	0.111	0.016	0.342	0.033	0.503	0.046	86.3	43.6
		(.005)	(.003)	0.000	(.003)	(.003)	(.001)	(.009)	(.001)	(.032)	(.002)	(1.1)	(0.7)
P. c. suwanniensis	21	0.159	0.121	0.000	0.149	0.110	0.020	0.295	0.042	0.500	0.041	83.1	41.9
		(.005)	(.004)	0.000	(.004)	(.005)	(.001)	(.011)	(.002)	(.036)	(.002)	(1.3)	(0.7)
P. c. concinna	90	0.163	0.127	0.001	0.139	0.100	0.018	0.382	0.034	0.549	0.040	88.0	42.6
		(.005)	(.003)	(.001)	(.002)	(.002)	(.001)	(.014)	(.001)	(.024)	(.001)	(1.1)	(0.5)
P. c. hieroglyphica	24	0.141	0.115	0.002	0.144	0.098	0.013	0.381	0.039	0.368	0.041	87.5	44.4
		(.006)	(.004)	(.002)	(.004)	(.004)	(.001)	(.018)	(.002)	(.048)	(.002)	(1.8)	(1.0)
P. c. metteri	23	0.114	0.088	0.001	0.165	0.098	0.019	0.432	0.031	0.657	0.048	93.4	45.0
		(.006)	(.005)	(.001)	(.005)	(.007)	(.001)	(.016)	(.001)	(.044)	(.002)	(1.6)	(0.9)
P. texana	48	0.112	0.099	0.042	0.128	0.058	0.013	0.346	0.029	0.477	0.055	83.2	41.3
		(.004)	(.003)	(.002)	(.003)	(.003)	(.001)	(.009)	(.001)	(.038)	(.002)	(1.4)	(0.8)
P. gorzugi	11	0.224	0.129	0.037	0.096	0.042	0.012	0.414	0.036	0.335	0.036	88.1	40.0
		(.016)	(.003)	(.005)	(.004)	(.004)	(.002)	(.017)	(.002)	(.040)	(.002)	(2.3)	(0.8)

CL); sides of shell steep, lateral angle of carapace (SA) greater than 100° in males (Fig. 9) and 110° in females; supratemporal stripe narrow, 7-10% of head width (SS/HW); supratemporal and para-median head stripes confluent behind the eye or continuing anteriorly as one line ("hairpin" marking), upper tomium entirely rounded, no evidence of notch or cusps; inframarginal spots solid (without light center) and not present posterior to the bridge.

Pseudemys texana and *P. gorzugi* are distinguished from other cooters by the following: cusps on upper jaw prominent, 3-6% of head width (LC/HW); inguinal scute extends forward and lateral edge of the pectoral scute extends posteriorly, distance between inguinal scute and pectoral abdominal sulcus less than 8% of carapace length IE/CL (Figs. 10D,E and 11). Ward (1984) noted the presence of large inguinal scutes in the original description of *gorzugi*. *Pseudemys gorzugi* is distinct from *P. texana* by having the following character states: short interfemoral seam, especially in males, less than 10% of plastron length (IL/PL); anal notch of males shallow, less than 4% of plastron length (AN/PL); anterior plastron less curved in females, depth of epiplastral lip less than 3% of plastron length (EP/PL); and supratemporal stripe broad, especially in males, greater than 15% of head width SS/HW (Fig. 12). For further descriptions of *P. texana* and *P. gorzugi* see Etchberger and Iverson (1990) and Ernst (1990).

Few characters separate the recognized forms of river cooters, *P. concinna*. However, *P. c. suwanniensis* may be distinguished from other subspecies by having short underlap of the cervical scute, cervical scute ventral length less than 35% of dorsal length (CU/CS); nuchal bone generally not projected forward, recession of cervical scute greater than 2% of carapace length (NR/CL); epiplastral lip curved, especially in females; and ground color of carapace, legs, and head sooty black with five light green/yellow stripes between the eyes.

Pseudemys f. floridana may generally be distinguished from eastern *P. concinna* by the following character states: posterior shell depth (at vertebral III-IV sulcus) 36-38% of carapace length in females, 32-33% in males; vertical or curved lines on second pleural scute (no "c" mark or swirl pattern); markings absent from plastron; and fewer than 11 head stripes at posterior edge of tympanum (Fig. 10A).

DISCUSSION

Natural hybridization (probably very limited) has been reported between red-bellied turtles and cooters (Crenshaw, 1955, 1965; Carr and Crenshaw, 1957; Seidel and Palmer, 1991). Nevertheless, present results reveal that red-bellied turtles (*P. alabamensis*, *P. nelsoni*, and *P. rubriventris*) collectively are morphometrically and biochemically distinct from cooters (Figs. 6, 7, and 8). Presence of a shared, derived liver protein (pI 8.2) supports the thesis that red-bellied turtles form a monophyletic group (subgenus *Ptychemys*; Iverson, 1992). Because this protein and the broadly angled xiphiplastron of red-bellied turtles do not appear in *P. texana*, Ward's (1984) inclusion of *P. texana* in *Ptychemys* can be rejected (Table 3 and Fig. 8). Furthermore, some of the character states which Ward used to diagnose *Ptychemys* are not present in *P. texana* (i.e., "carapace strongly rugose...posterior marginals without notch"). The similarities in cranial morphology of these turtles (which Ward emphasized), including cusps on the upper jaw, may have arisen as homoplasies resulting from convergent trophic habits (Jackson, 1978b). Some morphological overlap occurs among the three red-bellied turtles, especially *P. alabamensis* and *P. rubriventris*. However, they appear

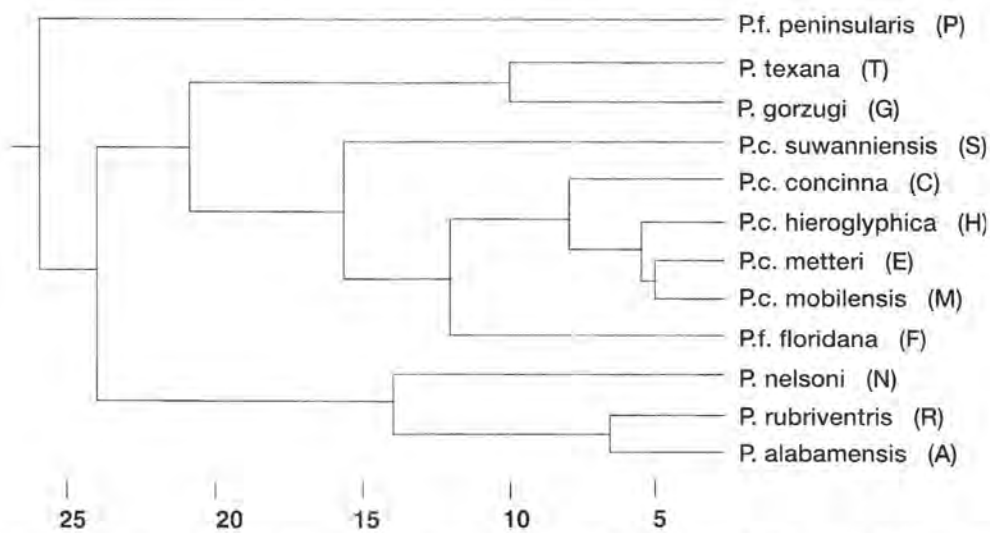

Figure 6. Dendrogram illustrating the results of complete linkage cluster analysis. Distances on the horizontal axis represent the numbers of morphometric characters (averages between male and female listed in Table 2) that separate taxa. Results from average linkage cluster analysis produced the same topology except that the positions of *P. c. suwanniensis* and the cluster of *P. texana* and *P. gorzugi* are reversed.

distinct enough to be recognized as separate species. Species status for *P. alabamensis*, *P. nelsoni*, and *P. rubriventris* is further supported by their broadly disjunct geographic ranges (Iverson, 1992). The single isolated specimen of *P. nelsoni* from Liberty Co., Texas, likely represents an introduction.

Morphometric analysis revealed very little distinction among some of the recognized subspecies of river cooters, *Pseudemys concinna*. The subspecies *P. c. metteri*, *P. c. hieroglyphica*, *P. c. concinna*, and *P. c. mobilensis* have been described primarily on color pattern and markings. However, geographic variation of these characters throughout most of the Mississippi and other Gulf of Mexico drainage systems occurs so gradually that it suggests clinal rather than subspecific variation. In many parts of this region, assignment to subspecies is arbitrary. Mount (1975) found that he could not separate the three subspecies that reportedly occur in Alabama (*concinna*, *hieroglyphica*, and *mobilensis*) and recommended that they, along with *P. c. suwanniensis*, be placed in the synonymy of *P. c. concinna*. Ward (1984) dealt with the problem by placing *P. c. mobilensis* in the synonymy of *P. c. hieroglyphica* and defining a broad region from Texas and Missouri to Georgia and Florida as a zone of intergradation for *metteri*, *hieroglyphica*, and *concinna*. As pointed out by Frost and Hillis (1990), this area of reported intergradation is larger than the defined ranges of each subspecies and therefore taxonomic recognition is unwarranted. Although the appearance of river cooters from opposite ends of their range (i.e., Texas and Virginia) is quite different, delineation of range limits for the variants is essentially impossible. Therefore, based on extensive morphometric overlap and biochemical similarity it is recommended that *P. c. metteri*, *P. c. hieroglyphica*, as well as *P. c. mobilensis*, be placed in the synonymy of *P. c. concinna*.

River cooters in northern peninsular Florida, currently recognized as *P. c. suwanniensis*, appear distinct. Although morphometric analysis (PCA) did not separate this taxon from other populations of *P. concinna*, there are characters by which it can be distinguished. Cluster analysis (Fig. 6) separated *suwanniensis* from all forms of *P. concinna* and *P. f. floridana*. Because *P. c. suwanniensis* appears to be allopatric to other *P. concinna* (Conant and Collins, 1991), the recommendation that it be considered a separate species

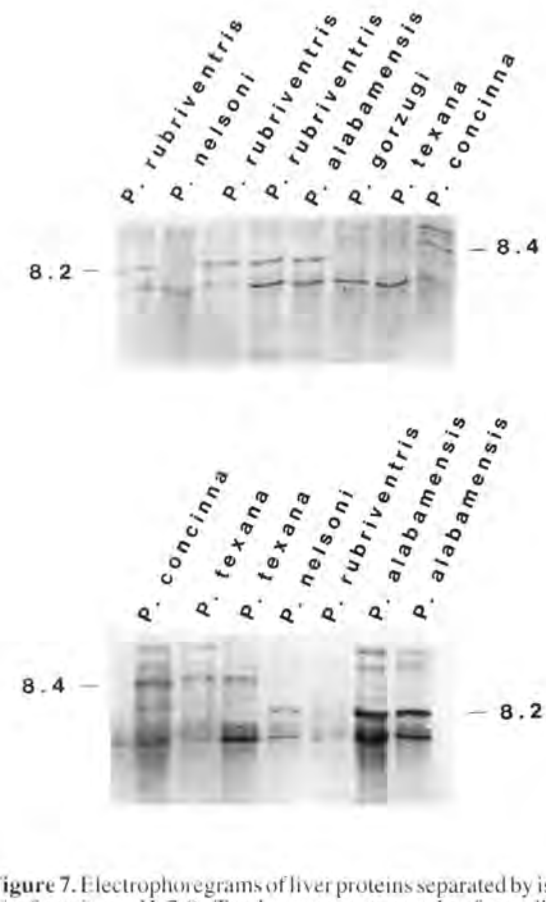

Figure 7. Electrophoregrams of liver proteins separated by isoelectric focusing, pH 7-8. Tracks represent samples from different individual turtles and variable electromorphs are identified by their isoelectric points (pI) 8.2 or 8.4.

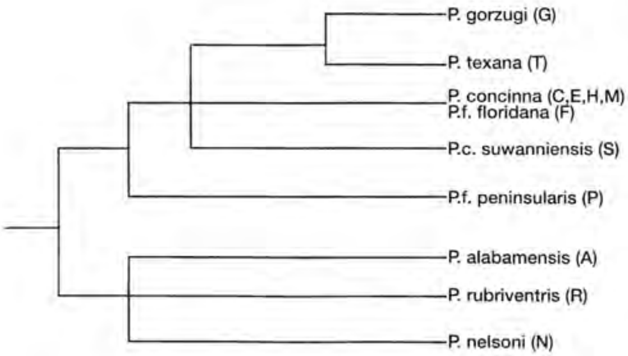

Figure 8. Strict consensus tree (derived from the PAUP algorithm) expressing phylogenetic relationships among species of *Pseudemys* based on one electrophoretic and 14 morphometric characters listed in Table 3. The consistency index is 0.70 and length is 27. The tree is rooted with an outgroup of *Trachemys* and *Graptemys*. *Pseudemys c. concinna*, *P. c. metteri*, *P. f. floridana*, *P. c. hieroglyphica*, and *P. c. mobilensis* (C, E, F, H, M) are treated as a composite because no difference in polarized character states was found among these subspecies.

(Frost and Hillis, 1990) can be accepted. Its range is limited to the Gulf drainages of northern peninsular Florida from the Santa Fe River and lower Suwannee system south to rivers north of Tampa Bay (Iverson and Etchberger, 1989; and Fig. 13). Pritchard (1979) suggested that movement patterns of this turtle may be unique among *Pseudemys*: limited terrestrial activity, cryptic nesting, and "migration" from rivers to open sea water.

The range of the Suwannee cooter, *P. suwanniensis*, is completely within the range of the peninsular cooter, *P. f. peninsularis*, and they appear to be morphologically distinct (Fig. 3). These two taxa occur together, along with *P. nelsoni*, in the lower Suwannee River system, Rainbow River, and Withlacoochee River of Florida (Marchand, 1940; Iverson and Etchberger, 1989). *Pseudemys f. peninsularis* also occurs sympatrically with *P. concinna* in the Ochlockonee River system in the Florida panhandle (CM 95927-28, 17054-55). Phylogenetic and cluster analysis (Figs. 6 and 8) indicated that *P. f. peninsularis* has a number of characters which separate it from all other *Pseudemys*. Unfortunately, *P. f. peninsularis* is poorly represented in the fossil record, known only from Pleistocene deposits in Florida (Jackson, 1988). Carr (1938a) described *peninsularis* as a subspecies of *P. floridana* and reported that it intergrades with *P. f. floridana* in northern Florida. However, the present morphometric analysis (PCA) does not support this. Individuals from northern Florida (presumed intergrades) did not generally plot in the zones of overlap on PC II and III (Fig. 3). Based on these observations, it is proposed that the peninsular cooter be elevated to full species status, *P. peninsularis*. Its range includes most of peninsular Florida and west in the panhandle to the Ochlockonee River (Fig. 13). Turtles from the Homosassa and Rainbow rivers (Citrus and Levy Counties, Florida), considered by Giovanetto and Morris (1992) to be intergrades with *P. f. floridana*, are

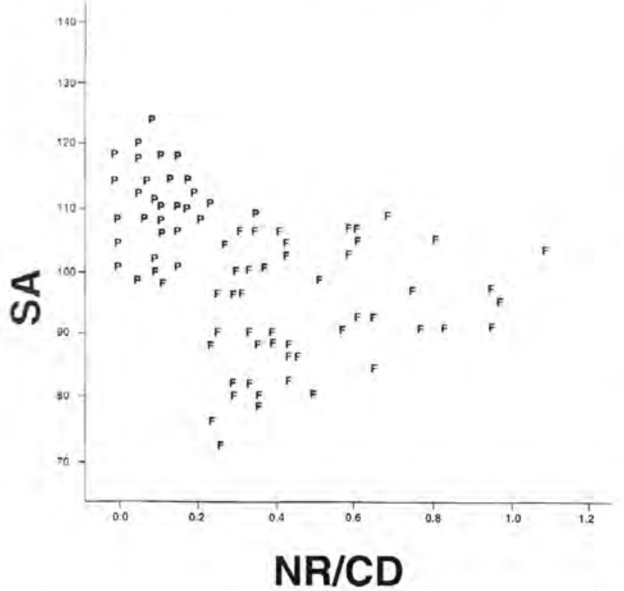

Figure 9. Bivariate plot of cervical scute recession/cervical scute width (NR/CD) versus lateral angle of carapace (SA) for male *P. f. floridana* (F) and *P. f. peninsularis* (P).

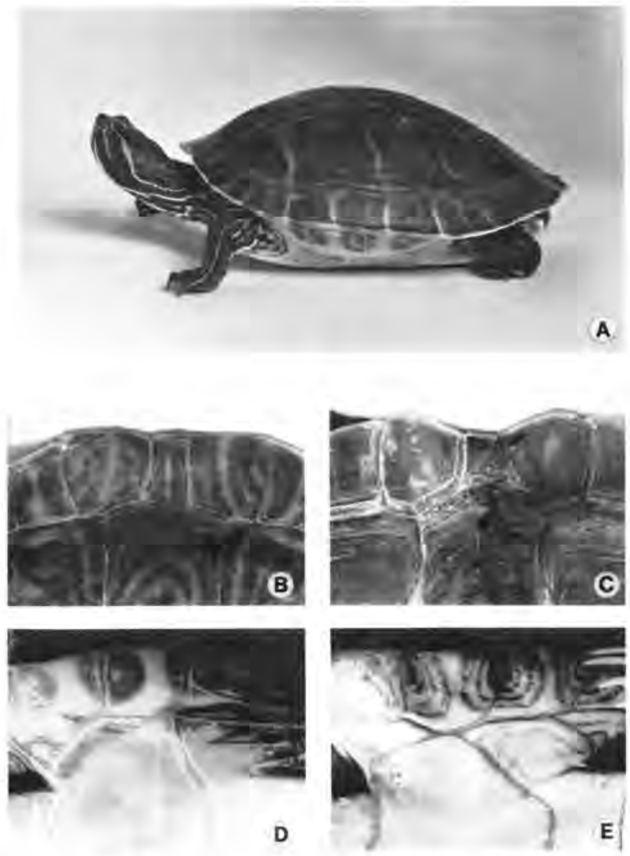

Figure 10. Lateral view (A) of a young female *Pseudemys f. floridana* from Onslow County, North Carolina (photo provided by The North Carolina Wildlife Resources Commission); (B) anterior dorsal view of the carapace of *P. f. peninsularis* illustrating the nuchal bone projected forward; (C) anterior dorsal view of the carapace of *P. concinna* illustrating recession of the cervical scute (nuchal not projected); (D) plastral view of the right bridge in *P. concinna* illustrating a relatively short inguinal scute; (E) plastral view of the right bridge in *P. texana* illustrating forward extension of the inguinal scute and posterior lateral extension of the pectoral scute.

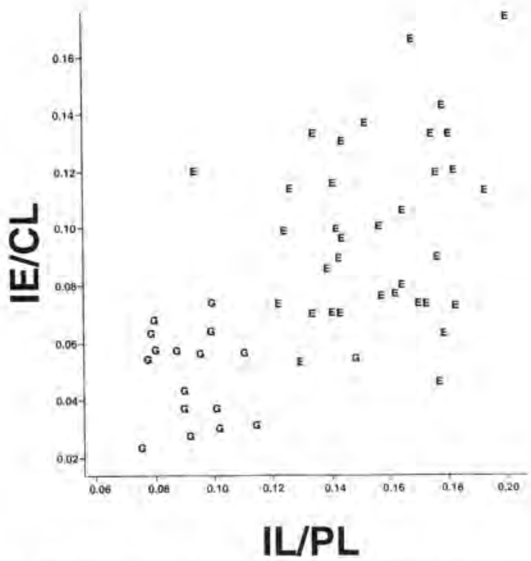

Figure 11. Bivariate plot of interfemoral sulcus length/plastron length (IL/PL) versus distance between inguinal scute and pectoral-abdominal sulcus/carapace length (IE/CL) for *P. c. metteri* (E) and *P. gorzugi* (G).

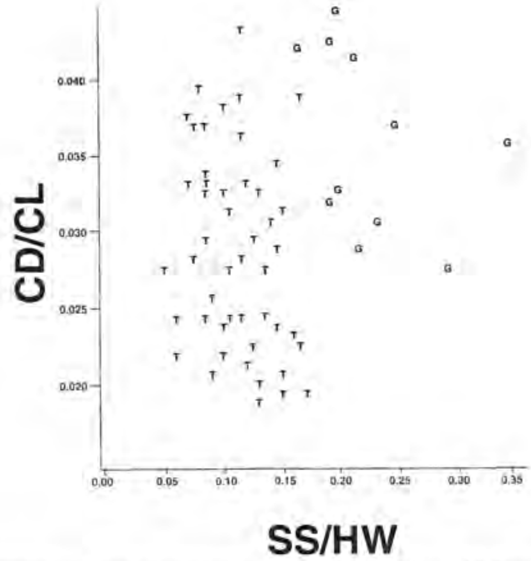

Figure 12. Bivariate plot of supratemporal stripe width/head width (SS/HW) versus cervical scute width/carapace length (CD/CL) for male *P. gorzugi* (G), and *P. texana* (T).

presumably typical variants of *P. peninsularis* based on intergradation coefficients the authors present and geographic location. It is possible that some of the variation they observed is the result of introduction in these highly tourist-oriented areas. Unfortunately the investigators did not preserve voucher specimens (L.A. Giovanetto, *pers. comm.*).

Distinction between the Florida cooter *P. f. floridana* and river cooter *P. concinna* has remained one of the most perplexing problems in turtle taxonomy. Recently, Seidel and Palmer (1991) were unable to separate these taxa in the central Atlantic drainages using morphometric characters, and indicated they might be conspecific. The present analysis, which examined many additional turtles from more southern and western portions of the range, still did not clearly distinguish these species. Specific assignment of some individuals was impossible using all of the reported key characteristics. Local populations are sometimes polymorphic, demonstrating nearly a full range of character states. Along the Atlantic slope drainages, there is a *P. c. concinna* morphotype (shallow carapace with swirl markings, plastron with dark central figure and head with more than 11 head stripes) which inhabits Piedmont sections of rivers. It is easily distinguished by color patterns/markings from a *P. f. floridana* morphotype (deep carapace with wavy light bars on costal scutes and no markings on plastron) which occurs on the coastal plain (Seidel and Palmer, 1991). However, these turtles are not morphometrically distinct, and based on their markings, they appear to intergrade along some regions of the Fall Line in North Carolina, South Carolina, and Georgia. In other regions near the Fall Line and upper coastal plain of these states, turtles with distinct *P. concinna* features inhabit portions of rivers (e.g., Savannah River) in close proximity to lentic waters inhabited by turtles with very typical *P. floridana* markings (e.g., Carolina bays near Aiken, South Carolina). Nevertheless, the two distinct forms (color pattern morphotypes) do not seem to occur in the same body of water (microsympatry). Perhaps different habitat preferences are sufficient to maintain reproductive isolation in some regions, but not in others (where they intergrade). Thus, gene flow may be intermittent. Similar situations may occur along the coastal plain and Fall Line of the Gulf drainages. Although the present study did not examine especially large numbers of turtles from these areas, accounts of interactions between *concinna* and a "*floridana*" type turtle in Alabama (Mount, 1975) and Louisiana (Fahey, 1980; Dundee and Rossman, 1989) are similar to those for the Atlantic states. Clearly, the relationships of these *Pseudemys* are complex and do not conform to traditional species paradigms, especially the "biological species". Hedges (1990) noted that "speciation is a dynamic process and we should expect borderline cases." If *P. f. floridana* and *P. c. concinna* in the Atlantic states are considered taxonomically distinct, they are best treated as subspecies (following in part, Carr, 1935, 1952). Because Agassiz (1857), who selected *concinna* over *floridana*, was apparently the first reviser to treat these turtles conspecifically (Smith and Smith, 1980; Bour, in press; H.M. Smith, *pers. comm.*), *floridana* and *concinna* are recognized as subspecies of *P. concinna* (rather than *P. floridana sensu* Carr, 1952) following Article 24 of the International Code of Zoological Nomenclature (ICZN, 1985). Obviously, the range limits of these two subspecies are difficult to define. Nevertheless, *Pseudemys c. concinna* is here considered to be broadly distributed in lotic habitats from eastern Texas, Oklahoma and Kansas, throughout the Mississippi and other northern Gulf drainages, northeast to Virginia along the Atlantic Piedmont, and extending to the coastal plain in some of the larger rivers (Fig. 13). *Pseudemys c. floridana* occurs along the southern Atlantic coastal plain (in generally lentic waters) from Virginia south to the Florida panhandle.

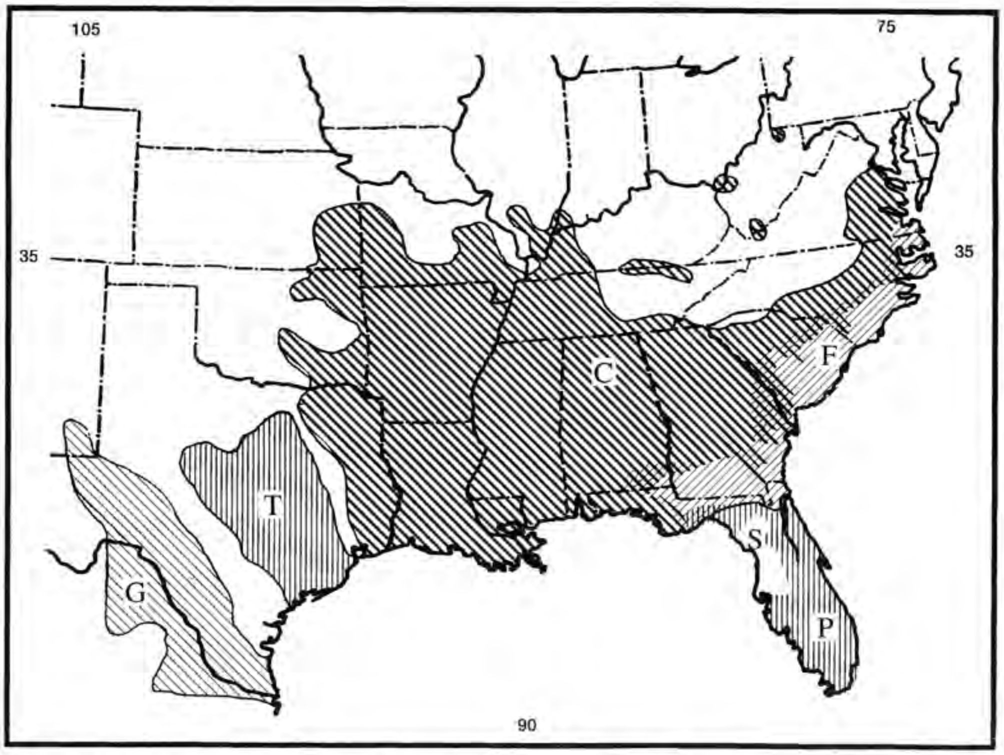

Figure 13. Distribution of cooters (*P. c. concinna*, C; *P. c. floridana*, F; *P. gorzugi*, G; *P. peninsularis*, P; *P. suwanniensis*, S; and *P. texana*, T) in the United States and Mexico. Not indicated, the range of *P. peninsularis* (P) also occurs throughout the distribution of *P. suwanniensis* (S).

In areas near the Fall Line it forms zones of intergradation, parapatry or macrosympatry with *P. c. concinna*.

A problem with the type location for *P. c. floridana* persists, whether it is recognized at the species or subspecies level. Carr (1935), Ward (1984) and Bour (in press) have all pointed out that LeConte's (1829) type locality "St. John's river of East Florida", without designated type specimens, was in a region of intergradation. Now this location may be viewed as a region of parapatry or sympatry for *P. c. floridana* and *P. peninsularis*. Bour (in press) has recently located the shell (MNHN 9170) of a turtle he believes was part of LeConte's type series, but its specific identification remains uncertain. Clearly this problem needs to be addressed if *floridana* continues to be recognized as a taxon distinct from *P. c. concinna*. Characterization of the western limits of *P. c. floridana* remains tentative. Analysis of more specimens from the lower Mississippi drainage and along the western Gulf coastal plain (western Florida to Texas) might reveal populations referable to *P. c. floridana*. However, further examination may also cast more doubt on the utility of taxonomically recognizing *floridana*. Finally, it is noteworthy that juvenile *P. c. floridana* and *P. c. concinna* often cannot be distinguished, and sometimes hatchlings from a single clutch of eggs show a full range of subspecific character states. Development of diagnostic markings may be ontogenetic, but the possibility that these taxonomic differences are only phenotypic, induced by environmental conditions (e.g., lentic or lotic habitats or nest site conditions), should not be entirely discounted. Recently, Etchberger

concentration and temperature of incubating slider turtle eggs (*Trachemys scripta*) can influence the presence of plastral markings. However, similar tests on incubating eggs of *Pseudemys concinna* were not as conclusive (M.A. Ewert, *pers. comm.*).

In the southwestern extreme of the range, two additional *Pseudemys* are recognizable: *P. texana*, endemic to the Brazos, Colorado, and San Antonio river systems of central Texas; and *P. gorzugi*, endemic to the lower Rio Grande and Pecos river systems of Mexico (Coahuila, Nuevo Leon, and Tamaulipas), Texas, and New Mexico (Fig. 13). Ward's (1984) elevation of *P. c. texana* to a species has been generally accepted (Dixon, 1987; King and Burke, 1989; Conant and Collins, 1991; Iverson, 1992) and is supported by morphometric results. However, his placement of *gorzugi* as a subspecies of *P. concinna* remained controversial. Ernst's (1990) elevation of *P. c. gorzugi* to species status was questioned by Iverson (1992) because it was done without analysis. The present study using principal components (Fig. 4), cluster analysis (Fig. 6), and cladistics (Fig. 8), indicates that *P. texana* and *P. gorzugi* are distinct from each other and from other species of *Pseudemys*. They are apparently allopatric and species level recognition is acceptable. A more detailed examination of *P. texana* and *P. gorzugi* (in progress, author with J.R. Dixon) should clarify the taxonomy and distribution of these turtles in Texas.

In conclusion, there continues to be ample evidence that relationships in the genus *Pseudemys* are complex. Nevertheless, based on review of previous work and results from

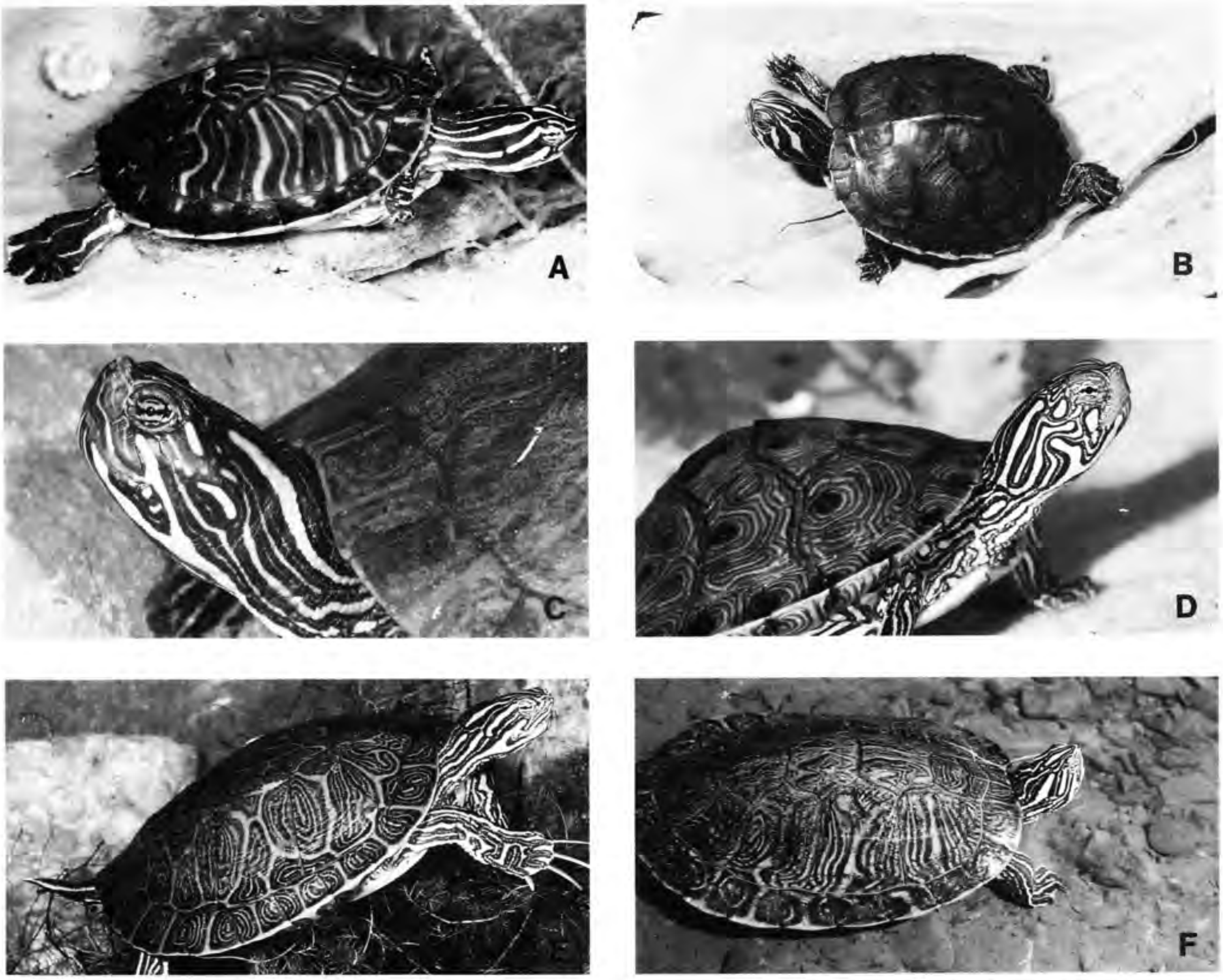

Figure 14. Dorsolateral views of the species of cooters recognized in this paper: (A) young *Pseudemys peninsularis*, Florida; (B) juvenile *P. suwanniensis*, Marion Co., Florida; (C) female *P. gorzugi*, Maverick Co., Texas; (D) juvenile *P. texana*, Palo Pinto Co., Texas; (E) male *P. concinna*, Warren Co., North Carolina; (F) female *P. concinna*, Summers Co., West Virginia. Photographs A-E by R. Wayne Van Devender.

Pseudemys is recommended:

Subgenus *Ptychemys* Agassiz, 1857
- *Pseudemys alabamensis* Baur, 1893
- *Pseudemys nelsoni* Carr, 1938b
- *Pseudemys rubriventris* (LeConte, 1829)

Subgenus *Pseudemys* Gray, 1855
- *Pseudemys concinna concinna* (LeConte, 1829)
- *Pseudemys concinna floridana* (LeConte, 1829)
- *Pseudemys gorzugi* Ward, 1984
- *Pseudemys peninsularis* Carr, 1938a
- *Pseudemys suwanniensis* Carr, 1937
- *Pseudemys texana* Baur, 1893

Species of cooters (subgenus *Pseudemys*) are illustrated in Fig. 14.

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Specimens Examined

Abbreviations for museums follow Leviton et al. (1985) with the following additions: MES = private collection of the author; SREL = Savannah River Ecology Laboratory collection.

Pseudemys alabamensis – Alabama: AMNH 107675-76; CM 67347, 95935-95940, 95964, 95966-69, 95972, 95992-93

Pseudemys nelsoni – Florida: AMNH 5935, 64257, 73625; CM 4751, 12995, 62087, 95192; MES 1789, 1894, 1897-98; UF 4154, 4171-72, 4174, 7165, 7274-75, 7279, 7289, 24677, 30064, 30073, 30116, 48191, 56337-38, 56340-42, 65127-28, 65897. Texas: H.M. Carty (uncat.)

Pseudemys rubriventris – Delaware: AMNH 72745. Maryland: AMNH 71284, 76176. New Jersey: AMNH 71279, 71283, 71285-86, 76177, 125100; MES 132,1751. North Carolina: MES 1896; NCSM 9360, 16669-70, 16672, 17910, 20116, 20166, 22818, 25080, 28658-59, 28704, 28752-53, 28871, 28897, 28899, 29275-76, 29278, 30034; AMNH 72746, 80218-19, 81869, 90640-44; CM 53026. Pennsylvania: AMNH 76175; CM 27420, 28969, 29400, 29457, 29502, 31244, 32651. Virginia: AMNH 71276-77, 79134, 82138, 129302, 129312; CM 13262, 23136, 125188, 125195, 125198, 125216; USNM (Field Series) 114462, 140441-47, 140759, 157085-88, 157853, 158685, 158881, 159372, 159366, 159568-69, 159572-73; MES 1888-90. West Virginia: CM 26630; MES 1902

Pseudemys concinna concinna – Alabama: AMNH 114546; CM 62076, 94995, 95001, 95012, 95020, 95275, 95289-91, 95292-300, 95365, 95368, 95383, 95586-87, 95596-99, 95612, 95614, 95698-99, 95705, 95712, 95714-18, 95730-31, 95735-38, 95744-45, 95774-75, 95777, 95801-05, 95808-09, 95811, 95829, 95971. Georgia: CHM 2481; SSM 6875, 8161, 9885, 9964, 10362, 11294; UGAMNH 4251-52, 15921, 15996, 16015-16, 19504; UF 2318, 2327, 6716, 13602, 13656-2, 13689(2). North Carolina: CHM 2479-80; NCSM 6184, 8518, 11364, 11373, 13759, 13810, 13966, 15030, 15135, 17045, 17276, 17339, 17938, 19169, 19356, 19432, 20128, 20236, 20240, 20253, 22966, 24030, 24182, 25044, 25181, 25205-06, 25234, 25265, 26061, 26225, 26525-7, 28688, 29279, 29595, 29968-69, 30038, 30280-81, 30431-34; USNM (Field Series) 158447. South Carolina: CHM 2235, 2239, 2248, 2457, 2459, 2487; MES 1790, 1875; SREL 2137, 2229; UGAMNH 4246, 4249. Virginia: USNM (Field Series) 141102, 141105, 141364, 158811; MES 489. West Virginia: MES 863

Pseudemys concinna (*P. c. metteri*) – Arkansas: AMNH 90084; CM 25417, 61675-78, 64089, 94831, 94880, 95179-82, 95186-89; MES 1884. Louisiana: CM S-4276. Oklahoma: CM 60389, 61666-74, 88635, Texas: TCWC 55088, 57934, 67317, 69819-20; TNHC 23051

Pseudemys concinna (*P. c. hieroglyphica*) – Kentucky: MES 1883, 1895. Mississippi: CM 94892, 94898, 94911-13, 94924, 94929, 94944-45, 95014, 95047-48, 95638-39, 95642. Tennessee: CM 95444-48, 95450-54, 95483, 95485, 95499, 95533, 96061, 96114-15, 96118, 96149-51; MES 1741, 1886. West Virginia: MES 870, 1887, 1901; WVBS 3155, 3965

Pseudemys concinna (*P. c. mobilensis*) – Alabama: CM 95897-98, 95906, 95913-14, 95916, 95932-34, 95941-55, 95957-63, 95973, 95986. Florida: CM 95927; UF 6580, 7878.4-78.5, 8825, 13622, 13690, 13691.2-91.3, 48189, 65580, 65582. Georgia: UF 2321, 2323-24, 2330, 13601, 13603, 13655, 13656.1, 13657, 13659. Louisiana: CM 35287, 62080, 62086; UF 7362, 12032. Mississippi: AMNH 46775; CM 94947, 94965, 95346, 95568-69, 95673, 95683, 95686-87, 95889; UGAMNH 4206-07

Pseudemys concinna floridana – Georgia: CHM 2482; SSM 4094, 4151, 4161, 4473-74, 7601, 8506, 10389, 10880, 11293, 11688; UF 13667-1, 22117; UGAMNH 417, 4100, 4116, 4118, 4250, 16011-12, 16017-19, 19519. North Carolina: NCSM 5881, 5883-85, 5927-30, 10330, 11365, 13812-16, 14783, 16476, 17046, 17302, 17581-82, 19353-54, 20190, 20678, 20928, 21001-02, 21603, 23405, 24334, 25737, 25739, 25833, 26344, 26528, 28657, 28705, 28740, 28898, 29301, 29617, 30001, 30291-92, 30423-30, 30701, 31026, 31028, 31073; USNM (Field Series) 158448; USNM 144148. South Carolina: AMNH 50985; CHM 759, 811, 2233-34, 2456, 2458, 2460, 2462-68, 2477(2)-78, 2483-86, 2488, 2504-10, 2512-13; SREL 117; UGAMNH 4247-48. Virginia: CM 24447; MES 1900; USNM (Field Series) 159365

Pseudemys suwanniensis (*P. c. suwanniensis*) – Florida: UF 13587, 13604, 13606, 13612.1-12.2, 13615.2-15.4, 13630, 13642.1-42.4, 13645, 13649.1-49.3, 13663, 13665.1-65.2, 13666, 13673.2-73.3, 13677, 13680.1, 13684, 13686.1-86.4, 13691.1, 30079, 30120, 30122, 54814-15, 65578-79, 65581; UGAMNH 4145-46

Pseudemys peninsularis (*P. f. peninsularis*) – Florida: AMNH 8081-82, 82139, 117736, 128962; CM S-4750, 9867, S-9875, S-9877, 17052-55, 33990, 95928; MES 1885, 1916; UF 13581.1-81.2, 13584-85, 13586.2, 13588, 13593, 13594, 13594.2, 13594.7, 13595.3, 13599.1, 13613, 13618.2-18.3, 13640, 13640.3, 13646, 13652.2-52.3, 13671.3, 13674.1, 13675, 13679.1-79.2, 13679.4-79.5, 13681.1-81.2, 13685.1-85.2, 30096, 45852, 45856, 65891-92(2)-93(2), 65893-96; UGAMNH 4101-02, 16013

Pseudemys texana – Texas: CM 3053R, 3089R, 61658-60, 61662-65, 61868, 61870-75, 61902, 61907-08; MES 1870, 1911-12; TCWC 42345, 65308, 66066-68, 66070, 66097, 66157, 66949(2)-55, 68481-82, 68488, 68492, 68494, 68527, 68529-30, 68588, 68603-04, 68620, 68622, 68705, 68708-10, 69818, 69824, 69860, 69862, 69874; TNHC 21985, 28602-04, 28627, 28629, 28647, 30780, 32281, 50357-60, 50893-95

Pseudemys gorzugi – New Mexico: MES 1893-94; MSB 51861, 51863-67, 51869, 51871. Texas: TCWC 64567, 68711; TNHC 32663; UMMZ 85086-87; USNM 20848, 26423

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