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Revision of the West Indian Emydid Turtles (Testudines)

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ABSTRACT

The systematics of emydid turtles, genus *Trachemys*, in the West Indies is analyzed using external morphology, osteology, and biochemical data. Results indicate the presence of seven recognizable taxa: *T. terrapen* in Jamaica and the northern Bahamas, *T. decorata* on Hispaniola, *T. stejnegeri stejnegeri* in Puerto Rico, *T. s. vicina* on Hispaniola, *T. s. malonei* on Great Inagua (southern Bahamas), *T. decussata decussata* in Cuba, and *T. d. angusta* in Cuba and the Cayman Islands. Three previously described taxa—*T. felis* (Barbour), *T.*

granti (Barbour and Carr), T. d. plana (Barbour and Carr)—are placed in the synonymies of T. terrapen, T. d. angusta, and T. d. decussata, respectively. The description of each valid taxon includes a complete synonymy, new diagnostic characters, distribution, and ecological notes. Also included are a taxonomic key and discussion of possible evolutionary origins. Phylogenetic evidence suggests that the West Indian segment of Trachemys is paraphyletic and therefore does not constitute a natural taxonomic complex.

RESUMEN

La taxonomía de las tortugas emydid del género Trachemys de Las Indias Occidentales está analyzada usando morfología externa, osteología, y datos bioquímicos. Se reporta la indicación de la presencia de siete taxa reconocible: T. terrapen en Jamaica y en el norte de las Bahamas, T. decorata in Espaniola, T. stejnegeri stejnegeri en Puerto Rico, T. s. vicina en Espaniola, T. s. malonei en Gran Inagua (al sur de las Bahamas), T. decussata decussata en Cuba, y T. d. angusta en Cuba y las Islas de Gran Cayman. Tres taxa descritas antes—T. felis (Barbour), T. granti (Barbour y Carr), y T.

d. plana (Barbour y Carr)—están puestas en sinonimías de T. terrapen, T. d. angusta y T. d. decussata, respectivamente. La descripcion de cada taxon valido incluye un sinonimía completo, nuevo genio diagnostico, distribución, y notas ecológicas. También incluído, hay una taxonomía por clave y discusión de posible origens evolucionarios. La evidencia sugire que la seccion de Trachemys de Las Indias Occidentales tiene dos evoluciones (paraphyletic) y por lo tanto no constituye una taxonomía compleja natural.

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INTRODUCTION

Freshwater or semiaguatic turtles that inhabit the West Indies belong to the slider genus Trachemys (Seidel and Smith, 1986). family Emydidae. Their behavior is typical of the widely distributed continental species, T. scripta. They are opportunistic aquatic omnivores with well-developed basking habits; they utilize diverse aquatic habitats but become terrestrial during dry periods. Although their congeneric relationship to T. scripta is evident from similarities in cranial and carapace morphology (McDowell, 1964; Seidel and Smith, 1986), specific identities and distributions have remained poorly understood. Pregill (1981a) stated that turtles are perhaps the least-studied vertebrates in the West Indies. Collectively, the West Indian Trachemys forms a geographically discrete but taxonomically confused assemblage. The present study was undertaken to define more clearly the systematics and distribution of these species.

Boulenger (1889) considered all West Indian emydids conspecific with T. scripta. Barbour and Carr's (1940) treatise, recognizing nine forms and six species in the Greater Antilles and Bahamas, has remained the only comprehensive taxonomic analysis of these freshwater turtles. In 1941 these authors described an additional species from the Cayman Islands. Although their analysis was thorough, Barbour and Carr (1940, 1941) were limited by the small number of available specimens. They stated "It would be foolish to say that the last word concerning the systematic status of the various West Indian terrapins is said in this paper We lack material from too many areas to do more than sketch an outline" (Barbour and Carr, 1940: 381). Grant (1948) emphasized the inadequate sample sizes employed by Barbour and Carr (1940, 1941) and indicated that reliable partitioning of the West Indian emydids would require examination of many more specimens. In the absence of any other broad systematic analysis of West Indian emydids, it is not surprising that the taxonomy of this group has remained unstable. Subsequent authors have recognized as many as five species (Henderson and Schwartz, 1984; Schwartz and Henderson, 1985; Schwartz and Thomas, 1975) or as few as one (Wermuth and Mertens, 1961, 1977; Rivero, 1978; and Obst, 1983). Taxonomic recognition of the Bahamian populations has remained especially controversial (Wermuth and Mertens, 1961; Williams, 1956). Schwartz (1978) suggested that all Antillean emydids are conspecific except for a second distinct species (Trachemys decorata) on Hispaniola. Contributing to the confusion has been frequent use of labile taxonomic characters, including coloration and markings, which in some cases were described from nonliving specimens. Problems of identification are compounded by a widespread tendency for West Indian Trachemys to lose their markings as they reach maturity and to develop pronounced melanism in adult males. Although the extent of species divergence and geographic distribution has remained uncertain, it appears that all taxa are allopatric (Seidel and Inchaustegui Miranda, 1984).

Bickham and Baker (1976a, 1976b) examined G- and C-band karyotypes and found no variation in the subfamily Emydinae, including several species of West Indian Trachemys. Recently, Seidel and Adkins (1987) described biochemical divergence among the West Indian Trachemys. The present systematic review, based on morphological analysis of over 500 specimens (living and preserved), reevaluates species relationships among these turtles, and provides new taxonomic characters for diagnoses. Nomenclature, descriptions, geographic distributions, and a proposed phylogeny (based on morphological and biochemical characters) are also presented.

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MATERIALS AND METHODS

For morphometric analysis 12 disjunct populations (A-L) of Trachemys were identified (fig. 1), representing all islands and subregions in the West Indies presumed to support natural populations. In addition to museum specimens, series of live individuals were examined from all localities except Cuba. Fifty mensural characters, including scute, head, and shell dimensions (sensu Seidel and Inchaustegui Miranda, 1984) were measured on 516 adult specimens > 100 mm in carapace length. Specimens of this size usually could be recognized as males by their relatively longer foreclaws and longer tails. Morphological variation, distance, and clustering among the 12 populations were defined by stepwise discriminant analysis (BMDP7M; Dixon, 1977) and principal components analysis (PCA) (SPSS-PAL; Kim, 1975). These multivariate techniques were applied to evaluate overall divergence or homogeneity and test which populations are morphologically distinct. Initially sexes were treated separately and two discriminant analvses (male and female) were conducted to avoid any influence of sexual dimorphism. The linearly related effects of size (age) on character variation were removed by regression analysis which produced 49 residual characters regressed from carapace length. A second discriminant analysis was conducted to determine if populations remained morphologically distinct when sexes were combined. This analysis utilized seven sets of principal components as variables (extracted from the original set of 50 characters) to isolate that portion of each variable correlated to size or sex. The taxonomic utility of each set of principal components to discriminate between or among populations was tested by multivariate analysis of variance (SAS-MANOVA; Barr et al., 1976). These data were further analyzed by cluster analysis to illustrate morphological affinities in the form of hierarchial phenograms. Mahalanobis' distances, calculated from discriminant scores, were used in single, complete, and average linkage cluster analyses (BMDP1M; Dixon, 1977).

Thirty-three mensural characters were measured on 46 skulls of turtles from Puerto Rico (3), Hispaniola (9), Cuba (18), Jamaica (4), Cayman Islands (4), Great Inagua (6), and Cat Island (2). Most of these measurements are defined in Seidel (1981). The taxonomic value of cranial and external measurements was evaluated by constructing ratios and testing mean differences by analysis of variance. Qualitative characters were also recorded from more than 500 living and preserved specimens. These included all previously published diagnostic features such as contour, shape, color, and markings of the carapace plastron, and head (Barbour and Carr, 1940).

Cladistic relationships among all morphologically distinct populations (Operational Taxonomic Units) of West Indian *Trachemys* were analyzed by phylogenetic analysis

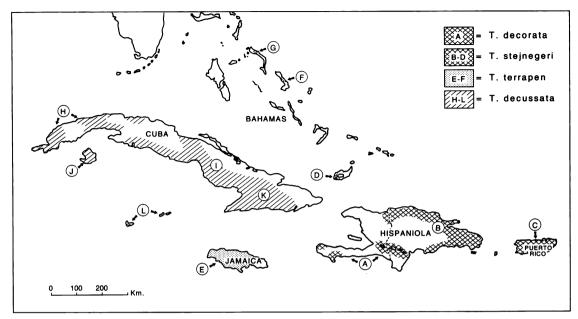


Fig. 1. Distribution of *Trachemys* in the West Indies. Populations analyzed by discriminant analysis are identified by the following letters (sample sizes in parentheses): A (36) Cul de Sac-Valle de Neiba Plain and Tiburon Peninsula, Hispaniola; B (80) coastal regions of north-central and western Hispaniola; C (80) Puerto Rico; D (35) Great Inagua, Bahamas; E (38) Jamaica; F (29) Cat Island, Bahamas; G (15) Eleuthera, Bahamas; H (40) Pinar del Rio Province, western Cuba; I (42) Habana, Matanzas, and Las Villas provinces, central Cuba; J (11) Isla de Pinos, Cuba; K (22) Camaguey and Oriente provinces, eastern Cuba; L (88) Cayman Islands.

using parsimony (PAUP; unpublished algorithm written by D. L. Swofford, Illinois Natural History Survey). This analysis was based on 32 characters that show taxonomic variation within Trachemys, including external morphology (Legler, 1960; Legler and Webb, 1970; Seidel and Inchaustegui Miranda, 1984; present study), cranial osteology (Seidel, 1981; present study), and protein electrophoresis (Seidel and Adkins, 1987). The wide-ranging polytypic species Trachemys scripta was treated as two Operational Taxonomic Units: (1) T. s. scripta and T. s. elegans in the United States and (2) subspecies of T. scripta from Mexico to South America (following Moll and Legler, 1971; Williams, 1956). Character states were scored as present (1) or absent (0) and polarities were based on outgroup comparisons and trees rooted with Pseudemys. Character states were examined in all five species of Pseudemys, a genus that includes cooters (P. concinna and P. floridana) and redbelly turtles (P. alabamensis, P. nelsoni, and P. rubriventris) and is probably the closest extant outgroup to sliders. Until recently (Seidel and Smith, 1986), species of *Trachemys* and *Pseudemys* were generally considered congeners. Polarities for some characters were also determined by a composite outgroup of *Chrysemys*, *Graptemys*, *Malaclemys*, and *Pseudemys*.

All specimens examined are identified by catalog numbers in the Specimens Examined list. Museum abbreviations follow Leviton et al. (1985) except for MES (reference collection of M. E. Seidel, Marshall University), JBI (collection of John B. Iverson, Earlham College), SJI (special collection in The Museo Nacional de Historia Natural, República Dominicana), and TTM (Texas Tech Museum, Lubbock).

STATISTICAL RESULTS

Discriminant analysis of 263 adult female turtles (using 49 residuals from 50 external morphological characters) produced three distinct clusters for the 12 populations pro-

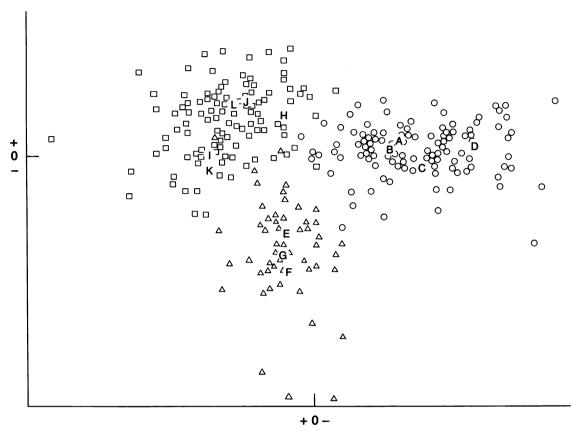


Fig. 2. Plot of the first two canonical variates, derived from 49 morphometric characters ("size-free" residuals from linear regression) of female *Trachemys*. Coefficients are listed in table 1. Letters indicating location of population means are identified in fig. 1. Individual turtles are represented by open circles (populations A–D), triangles (E–G), and squares (H–L).

jected on the first and second canonical axes (fig. 2). Cuba and Cayman Island turtles (H-L) separate from Hispaniola, Puerto Rico, and Great Inagua turtles (A-D) on the first canonical axis and these two groups separate from Jamaica, Cat Island, and Eleuthera turtles (E-G) on the second canonical axis. Results for 254 adult males were very similar but more overlap was observed between Cuban populations (H-K) and the others. The first two axes collectively accounted for 61 percent of the total dispersion in females and 59 percent in males. Of the 49 characters analyzed, 26 did not pass a tolerance test in both male and female analyses collectively, and therefore did not significantly contribute to group separation. Coefficients for variables which did contribute are listed in table 1. Although some character differences were apparent between males and females, sexual dimorphism was not pronounced. Because discriminant analysis indicated no significant difference (P > 0.01) in either sex comparing turtles from Isla de Pinos, Cuba (J) to Pinar del Rio, western Cuba (H), these turtles were combined (under population H) for further analysis. Combining males and females for PCA, I produced seven principal components from the original 50 external morphological characters. The first factor extracted (PC I) was determined to be a general size variable based on criteria described by Wiley (1981: 352). This component was omitted to remove some of the effect of age-related size variation in the samples. Discriminant analysis based on PC II-VII indicated no significant difference (P > 0.01) comparing Eleuthera turtles (G) to Cat Island (F) and Jamaica (E) populations, and comparing the eastern Cuba (including Rio Jobabo) population (K)

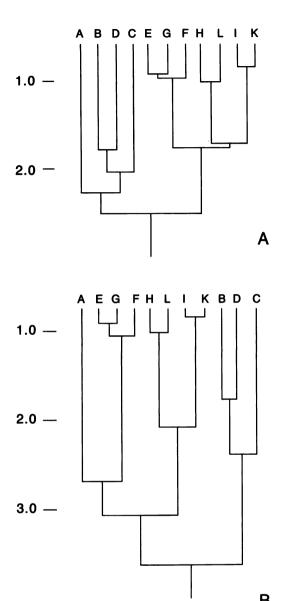


Fig. 3. BMDP1 cluster analysis (A single linkage, B average and complete linkage) using Mahalanobis' distances calculated from discriminant scores of principal components II–IV (extracted from 50 morphometric characters). Letters indicating populations of West Indian *Trachemys* (males and females combined) are identified in fig. 1 and population J is combined under H.

to turtles from central Cuba (I). Cluster analysis of 11 populations based on Mahalanobis' distances calculated from discriminant scores (PC II–VII) produced three major population

clusters (BCD, EFG, and HIKL; fig. 3). The only important difference between single and complete or average linkage is that the former (fig. 3A) indicates an affinity between population A and cluster BCD whereas the latter (fig. 3B) suggests that population A is more similar to EFG.

Homogeneity within each of the three population clusters was further tested by multivariate analysis of variance using PC II-VII followed by pairwise comparison between means. Very little difference (separation by less than two components) was observed comparing Jamaica turtles (E) to Cat Island (F) and Eleuthera (G) populations, and Cayman turtles (L) to the western Cuba population (H). In summary, based on the 50 mensural characters analyzed, no substantial morphological difference was apparent among populations E, F, G, among H, J, L, or between I and K. Although F, L, and K have been described as distinct taxa (T. felis, T. granti, and T. decussata plana, respectively; Barbour and Carr, 1940, 1941) no diagnostic morphometric character reliably distinguishes them from populations on Eleuthera (G) and Jamaica (E), western Cuba (H) and Isla de Pinos (J), and central Cuba (I), respectively. Therefore, EFG, HJL, and IK were each considered single taxa for phylogenetic analysis.

CLADISTIC ANALYSIS

Binary-coded character states and polarities used for cladistic analysis are presented in table 2. The PAUP algorithm produced three resolved trees which varied only in the nodes joining populations B, C, and D. This unresolved trichotomy forms a monophyletic sister-group to population A (fig. 4), consistent with their morphological similarities (figs. 2 and 3a). Also similar to phenetic results, populations HJL appear as the sistergroup to IK. The consistency index for this cladogram is 0.593 and the length is 54.0. In analyzing phylogenetic relationships at low taxonomic levels (such as species and subspecies of Trachemys), available characters tend to be simple, making homoplasy hard to detect and reversal more possible (Arnold, 1981). Furthermore, if a global or composite outgroup is used, the number of characters

TABLE 1

Coefficients for Variables of External Morphology in Female and Male Discriminant Analyses

Characters are described in Seidel and Inchaustegui Miranda (1984).

	Fei	male	M	Male	
Variable	Axis 1	Axis 2	Axis 1	Axis 2	
Carapace width—1	_	_	-0.10	-0.07	
Carapace width-2	_	-0.01	_	0.04	
Shell height—1	-0.07	_	0.03	-0.09	
Shell height—3	0.17	_	_		
Cervical scute length	-0.24	-0.06	_	_	
Anterior vertebral scute I width	-0.03	-0.05	-0.12	-0.05	
Posterior vertebral scute I width	_	_	0.14	-0.11	
Vertebral scute I length	-0.03	0.10	0.12	0.20	
Lateral gular scute length	-0.04	-0.45	_	_	
Pectoral scute length	0.13	0.19	0.31	0.15	
Femoral scute length	_	_	-0.09	0.02	
Plastron width - 1 (gular)	-0.20	_	-0.22	0.19	
Plastron width-2	-0.05	0.15	_	_	
Plastron width-5	0.10	_	-0.05	-0.15	
Axillary-marginal scute V contact	_	-0.05	_	_	
Bridge length	_	_	0.07	-0.03	
Submarginal scute VII-VIII length	0.15	-0.06	_	_	
Cervical scute underlap	0.14	0.11	_	_	
Gular scute overlap	_	_	-0.29	-0.44	
Head width-2	_	_	-0.35	0.29	
Interorbital width	0.13	-0.37	_		
Upper jaw length	-0.37	0.15	_	_	
Snout depth	0.36	0.07	0.73	-0.24	

for which polarity can be determined may be reduced. When the phylogeny of West Indian Trachemys was examined based on a composite outgroup of Chrysemys, Graptemys, Malaclemys, and Pseudemys, polarities could be determined for 22 of the 32 characters (see asterisks, table 2). When only those 22 characters were used for phylogenetic analysis, the sister-group relationships between populations A and BCD and between HJL and IK did not change.

TAXONOMIC CONCLUSIONS

Although results from cladistic analysis (fig. 4) suggest that *T. scripta* is not a monophyletic taxon, resolution of the problem awaits a comprehensive survey of this wide-ranging species. Because populations of West Indian *Trachemys* are mostly or entirely allopatric (fig. 1), the possibility of interbreeding in nature cannot be examined. Therefore, taxonomic assignments to species and subspecies must be based on morphological and biochemical similarity and monophyly. Cladis-

tic and phenetic results provide evidence for three or four higher-level evolutionary lines of species divergence (figs. 2-4). Population A from central and western Hispaniola is retained as the monotypic species, T. decorata (Barbour and Carr). Populations B, C, and D from eastern Hispaniola, Puerto Rico, and southern Bahamas (Great Inagua) are assigned to T. stejnegeri (Schmidt). Populations E, F, and G from Jamaica and the northern Bahamas (Eleuthera and Cat Island) are assigned to the monotypic species, T. terrapen (Lacépède). Populations H, I, J, K, and L from Cuba and the Cayman Islands are assigned to T. decussata (Gray). This arrangement conserves Barbour and Carr's (1940) species allocations for the Greater Antillean emydids.

Barbour and Carr (1940) judiciously recognized a close relationship among turtles on Puerto Rico (*T. stejnegeri stejnegeri*), Hispaniola (*T. s. vicina* and *T. decorata*), and Great Inagua (*T. malonei*) by placing them in a "stejnegeri" subgroup. Present results

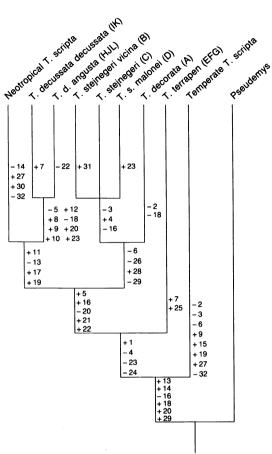


Fig. 4. Cladistic relationships among populations of West Indian *Trachemys* and *T. scripta* expressed by the PAUP algorithm based on binary coding of 32 characters (table 2). The tree is rooted with *Pseudemys* as the outgroup. Letters indicating populations are identified in fig. 1. Character states defining each stem or branch leading to a terminal taxon are numbered as in table 2 and identified as loss of the character (–) or addition of the character (+).

support that interpretation and indicate that these taxa (populations A–D) form a monophyletic complex (fig. 4). Biochemical data also indicate close relationships within this group (Seidel and Adkins, 1987). Using morphological similarities, I follow Barbour and Carr (1940) in assigning turtles on Puerto Rico (population C) to the nominate race, T. s. stejnegeri, and turtles on eastern and northern Hispaniola (population B) to T. s. vicina. This conspecific relationship is not surprising considering the many examples of faunal affinity and exchange between Hispaniola and

Puerto Rico (Gill, 1978; Pregill, 1981a) and the theory that a portion of eastern Hispaniola was at one time joined to western Puerto Rico (Guyer and Savage, 1986). Population D on Great Inagua was originally described as Pseudemys malonei by Barbour and Carr (1938), who (1941) noted its relationship to turtles on Hispaniola. Specific rank of this southern Bahamian population has generally been accepted (Schwartz and Thomas, 1975; Pritchard, 1979; Groombridge, 1982), although Williams (1956) suggested that malonei is neither native nor taxonomically recognizable. Principal components and discriminant analyses show that population D is morphologically distinct (P < 0.01), but more similar to T. s. vicina (B) than to the nominate race (C) (fig. 3). Moreover, Trachemys on Great Inagua (D) forms an unresolved trichotomy with populations B and C (fig. 4). Therefore, malonei is relegated to a subspecies of T. stejnegeri. Geological evidence indicates that the southern Bahamas are an older group of isolated islands that never have been interconnected as have the northern Bahamas (Schwartz, 1968). It is likely that T. s. malonei represents a "natural" population founded by dispersal from nearby Hispaniola or Puerto Rico.

The taxonomic status of T. decorata (population A, from the Cul de Sac-Valle de Neiba Plain of Hispaniola) has been the most controversial of the "stejnegeri" group. Pritchard (1979) proposed that all turtles on Hispaniola belong to the monotypic, but polymorphic, species T. decorata. However, Seidel and Inchaustegui Miranda (1984) confirmed the presence of two distinct allopatric morphotypes on Hispaniola and suggested a subspecific relationship between T. s. vicina and decorata. Present results using outgroup comparisons further emphasize divergence between Hispaniola Trachemys. T. decorata (population A) falls outside the trichotomous clade (fig. 4) and outside the clusters (fig. 3) formed by subspecies of T. stejnegeri (populations B, C, and D). Divergence of population A is especially apparent from complete- or average-linkage cluster analysis (fig. 3B). Therefore T. decorata is retained as a monotypic species related to T. stejnegeri.

Trachemys from Jamaica have consistently been assigned to the species T. terrapen

(Barbour and Carr, 1940; Wermuth and Mertens, 1961; Schwartz and Thomas, 1975). Present results clearly indicate that Jamaican turtles (population E) are specifically divergent from other Antillean populations (figs. 2-4), but not morphologically distinct from turtles in the northern Bahamas on Eleuthera (G) and Cat Island (F). Trachemys was first discovered on Cat Island in 1933 by L. A. Hodsdon (Hodsdon and Pearson, 1943) and later described by Barbour (1935) as a new species, Pseudemys felis. In 1961 and 1963 Albert Schwartz collected series of turtles (almost identical to the Cat Island population) near Hatchet Bay, Eleuthera, and assigned them to T. (Chrysemys) felis (Schwartz and Thomas, 1975). Taxonomic recognition of T. felis has been questioned by Williams (1956) and Wermuth and Mertens (1961). Pritchard (1979) and Pritchard and Trebbau (1984) stated that T. felis may represent a population of turtles introduced from Jamaica, and Seidel and Adkins (1987) found no biochemical difference between Cat Island and Jamaica Trachemys. Evidence that other Jamaican reptiles (i.e., Sphaerodactylus argus argus) have been transported by man to the Bahamas is cited in Schwartz (1968). The distance between Jamaica and the northern Bahamas (fig. 1), their relatively short geological history, and barriers to natural dispersal (Barbour and Carr, 1941; Schwartz, 1968) strongly suggest human introduction of Trachemys on Cat Island and Eleuthera, perhaps within very recent times. The ephemeral nature of their aquatic habitats threatens the survival of these populations (Groombridge, 1982) and might indicate a relatively short history of habitation. To the contrary, Barbour and Shreve (1935) suggested that the presence of Trachemys in small temporary ponds on Cat Island indicates unique terrestrial adaptations acquired over a long residence. However, there is no direct evidence that Bahamian populations have any specialized behavioral or physiological tolerance to drought conditions. Moreover, populations of Trachemys on Jamaica, Grand Cayman, and Puerto Rico can also apparently survive terrestrial dormancy during dry periods (Grant, 1940; personal field observ.). Barbour and Carr (1940) reported that T. felis is closely allied to T. terrapen, but distinguished

from the Jamaican form by having a shorter, higher, more circular carapace with a distinct keel and relatively few, but deep, rugosities on the costal scutes. However, present comparisons by regression analysis of shell height/ carapace length showed no significant differences (P > 0.05) among Cat Island (F), Eleuthera (G), and Jamaican (E) turtles. Furthermore no consistent differences in keel prominence or rugosities were noted. In light of overall morphological (figs. 2 and 3) and biochemical (Seidel and Adkins, 1987) homogeneity among these populations, and absence of taxonomic characters to separate them, T. felis is placed in the synonymy of T. terrapen.

Trachemys turtles on Cuba (populations H, I, J, and K) share a similar morphology (fig. 3) and appear to be monophyletic (fig. 4). Therefore, they are retained as T. decussata (sensu Barbour and Carr, 1940). However, previous subspecific allocations of Cuban Trachemys are not supported by present results. Turtles from the Rio Jobabo system of Oriente Province (K) were originally described as T. d. plana (Barbour and Carr, 1940) based on their broader and flatter carapace compared to the nominate race, T. d. decussata (I). Many of the specimens examined from central Cuban provinces (I) in the present study also have shallow, broad shells, and no significant difference (P > 0.05) between populations I and K was detected by discriminant analysis. Therefore, T. d. plana is placed in the synonymy of T. d. decussata. This supports Grant's (1948) opinion (followed by Williams, 1956) that T. d. plana is not distinguishable from T. d. decussata. Trachemys specimens from Isla de Pinos (J) and Pinar del Rio Province (H) are morphologically similar to, but distinct from, the nominate race (figs. 2 and 3); and (combined with population L) appear to form the sistergroup to IK (fig. 4). These turtles (HJ) are assigned to the subspecies T. d. angusta (Barbour and Carr).

Trachemys turtles on the Cayman Islands (L), 300 km south of Cuba, were first reported by Garman (1888) and much later described as a new species, T. granti, by Barbour and Carr (1941). These authors, as well as Grant (1940), indicated that Cayman turtles are most similar to T. felis and T. terrapen and

TABLE 2

Matrix for Cladistic Analysis of 32 Binary-coded Morphological and Biochemical Characters (columns) of

Trachemyne and Pseudemyne Turtles

below and states are indicated present (1) or absent (0). The primitive (plesiomorphic) condition is considered to be the state present in Pseudemys and the opposite condition is the derived (apomorphic) state. For those characters with an asterisk, it Letters in parentheses indicating populations of West Indian species are identified in fig. 1. Characters 1-32 are identified was possible to determine polarities by examining a composite outgroup which included Chrysemys, Graptemys, and Malaclemys, in addition to Pseudemys. Because electrophoretic data were not available for T. d. decussata, biochemical character states (25-33) for that subspecies were assumed to be the same as T. d. angusta.

*1. Markings on lateral scutes of carapace distinctly ocellate (Moll and Legler, 1971).

Juvenile and sometimes adult plastron with a continuous, or partially interrupted, wavy symmetrical figure (Seidel and Inchaustegui Miranda, 1984).

Supratemporal (postorbital) stripe never deep red (Moll and Legler, 1971; Seidel and Inchaustegui Miranda, 1984).

Foreclaws of mature males usually very elongated (Moll and Legler, 1971; Seidel and Inchaustegui Miranda, 1984).

5. Snout elongated in mature males (Moll and Legler, 1971).

. Vermiculate type melanism or no melanism in old males. Plastral pattern very faded or lost in adults.

*8. Interorbital width of cranium less than 15.0% of the condylobasal length.

Postorbital length (arch) of cranium less than 15.3% of the condylobasal length.

*10. Premaxillary height of cranium less than 7.5% of the condylobasal length.

Cranium shallow, depth at the anterior apex of the basisphenoid less than 31.5% of the condylobasal length. Tomial edge of the maxilla flared laterally, not tapered inward.

13. Squamosal blunt, not tapered posterodorsally.

Squainosai oium, not apered post
 Cutting edge of dentary smooth.

Continued TABLE 2

*15. Anterior midline of the alveolar surface continuous with the ventral median portion of the dentary, not set apart as a ledge or shelf. Old adult females frequently larger than 300 mm carapace length.

*17. Old adult males frequently larger than 200 mm carapace length.

*18. Carapace flared posteriorly, width at marginal seam VII-VIII usually greater than 75% of the carapace length.

*19. Inguinal scute projected laterally to a point (angle).

Gular scutes broad, plastron width at gular-humeral seam greater than 23% of the carapace length.

Nuchal (cervical) scute short, dorsal length less than 7.3% of the carapace length. Gular scutes short, median length less than 15% of the carapace length.

First vertebral scute narrow, anterior width less than 15% of the carapace length. Pygal bone long, extended beyond marginal-vertebral seam (Hay, 1908),

A concentrated skeletal muscle protein with an isoelectric point 6.2. A concentrated liver protein with an isoelectric point 6.2.

A concentrated liver and muscle protein with an isoelectric point 5.5. A concentrated cardiac muscle protein with an isoelectric point 6.0.

A concentrated cardiac muscle protein with an isoelectric point 6.4. *30. A concentrated cardiac muscle protein with an isoelectric point 6.9.

*31. A concentrated kidney protein with an isoelectric point 6.6.

A fast anodal electromorph for glycerol-3-phosphate dehydrogenase (Seidel and Adkins, 1987).

21. 22. *24.

23.

*25. *26. *27.

*28.

originated by dispersal from Jamaica. Williams (1964) indicated that Cayman turtles are more closely allied to turtles on Cuba than to Jamaican turtles but later reversed that decision (Williams, 1969). Barbour (1914) stated that turtles occurring on Grand Cavman probably represent an importation from Cuba. It is also interesting that Barbour and Carr (1941) noted the local name for the Cayman turtle "hig-a-tee" or "hicatee" is likely a corruption of the Cuban name "jicotea," suggesting the possibility of introduction from Cuba. Nevertheless, their specific diagnosis of T. granti was based on an assumed affinity to T. terrapen from Jamaica. Barbour and Carr's (1941) only character comparison to T. decussata was the brown or grayish color observed on the head and limbs of three captive Cayman turtles which presumably distinguished them from Cuban turtles (which typically have greenish soft parts). Among more than 100 living Trachemys examined on Grand Cayman (personal field observ.) most, especially young adults, had yellowishgreen soft parts similar to Cuban turtles described by Barbour and Carr (1940, 1941). Another similarity is the large size of males on Grand Cayman (maximum recorded carapace length = 264 mm). Based on present multivariate analysis of mensural characters and qualitative morphology, it is evident that Trachemys from the Cayman Islands (L) belong to T. decussata and are nearly indistinguishable from population H. Therefore, T. granti is placed in the synonymy of T. d. angusta. Whether the Cayman population is the result of human introduction or recent natural dispersal from Isla de Pinos or Pinar del Rio, Cuba, remains uncertain. Williams (1964) noted that 70 percent of the total Cayman herpetofauna is Cuban in origin, presumably by rafting across water.

In conclusion, the present taxonomic arrangement of West Indian emydids is similar to that of Barbour and Carr (1940), but does not recognize T. felis or T. d. plana as valid taxa and relegates T. malonei to a subspecies of T. stejnegeri. Species allocations by other authors are not defensible based on monophyly or overall morphological similarities. Williams' (1956) arrangement (followed by Schwartz and Thomas, 1975), which considered Puerto Rican (C) and Hispaniolan (B) Trachemys conspecific with Cuban and Cay-

man races of T. decussata, is contradicted by cluster and cladistic analyses, as well as biochemical comparisons (Seidel and Adkins, 1987). Figure 3 shows greater morphological similarity between T. decussata (H, L, I, K) and T. terrapen (E, G, F) than between T. decussata and T. steinegeri (B. C. D), and figure 4 indicates that T. decussata sensu lato (including B, C, D, HL, IK) is a paraphyletic taxon (note position of neotropical T. scripta). Wermuth and Mertens' (1961) allocation of all West Indian Trachemys to subspecies of T. terrapen is also unacceptable because it creates a paraphyletic species with regard to the phylogenetic position of neotropical T. scripta (fig. 4).

CHARACTER ANALYSIS

Comparisons of external morphology (50 mensural characters) among *T. decussata*, *T. terrapen*, and the *T. stejnegeri* series (including *T. decorata*) revealed significant difference in nine character ratios (six of which are illustrated in fig. 5).

T. terrapen, populations EFG, has wider (P < 0.01) gular scutes (mean plastron width at gular-humeral seam/carapace length 0.239 ± 0.012 SD) compared to T. decussata $(0.222 \pm 0.014 \text{ SD})$ and T. steinegeri series $(0.208 \pm 0.015 \text{ SD})$; longer nuchals (mean dorsal length of cervical scute/carapace length = 0.077 ± 0.007 SD) than T. decussata and T. stejnegeri (0.070 \pm 0.008 and 0.064 ± 0.007 SD, respectively); wider nuchal underlap (mean cervical scute width at posterior margin of ventral underlap/carapace length = 0.050 ± 0.006 SD) than T. decussata and T. stejnegeri (0.037 \pm 0.007 and 0.035 ± 0.007 SD, respectively); and a posteriorly flared carapace (mean carapace width at marginal seam VII-VIII/carapace length = 0.780 ± 0.032 SD) compared to T. decussata and T. stejnegeri (0.717 \pm 0.033 and 0.756 ± 0.031 SD, respectively).

T. decussata, populations HIJKL, has inguinal scutes that project laterally (mean seam length for submarginals VII–VIII/carapace length = 0.070 ± 0.014 SD) compared to T. stejnegeri and T. terrapen (0.096 ± 0.018 and 0.098 ± 0.017 , respectively); shorter gular scutes (mean gular scute length/carapace length = 0.128 ± 0.011 SD) than T. stejnegeri and T. terrapen (0.139 ± 0.010 and 0.155 ± 0.010

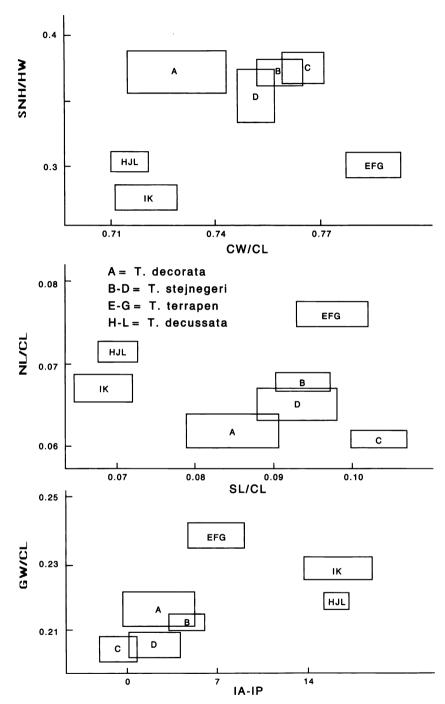


Fig. 5. Graphic representation of diagnostic characters for species of West Indian *Trachemys*. Above: Graph of percent carapace width/carapace length (CW/CL) versus percent snout depth/head width (SNH/HW). Center: Graph of percent submarginal seam length (scutes VII–VIII)/carapace length (SL/CL) versus percent cervical (=nuchal) scute length/carapace length (NL/CL). Below: Graph of the difference between inguinal-marginal VIII seam contact and inguinal-marginal VI contact (IP-IA) versus percent gular scute width/carapace length (GW/CL). Letters represent populations (males and females combined) identified in fig. 1. Rectangles are formed by lines 2 standard errors above and 2 standard errors below means.

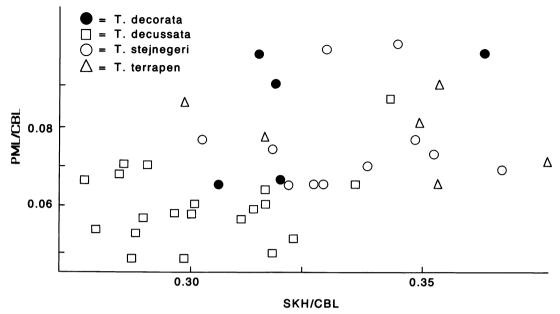


Fig. 6. Plot of individual *Trachemys* skulls according to their percent skull height/condylobasal length (SKH/CBL) versus percent premaxillary height/condylobasal length (PML/CBL).

0.012 SD, respectively); and a more posteriorly aligned inguinal scute (mean difference between inguinal-marginal VIII seam contact in mm and inguinal-marginal VI contact = 15.9 ± 10.5 SD) compared to T. stejnegeri (2.2 ± 7.7 SD) and T. terrapen (7.2 ± 9.2 SD).

The T. stejnegeri series, populations ABCD, has a greater snout-premaxillary depth (mean distance from symphysis of upper jaw to roof of the skull/head width = 0.370 ± 0.047 SD) compared to T. terrapen and T. decussata (0.305 \pm 0.029 and 0.295 \pm 0.038 SD, respectively); and a deeper median notch between posterior marginals (intermarginal XII seam length/carapace length = 0.072 ± 0.010 SD) than T. terrapen and T. decussata (0.081 \pm 0.010 and 0.084 \pm 0.012 SD, respectively).

Analysis of 33 skull measurements revealed three character ratios in which T. decussata differs from the other species. T. decussata has a shorter (P < 0.01) premaxillary height (mean depth of premaxilla/condylobasal length = 0.061 ± 0.009 SD) than the T. stejnegeri series (0.078 ± 0.013 SD) and T. terrapen (0.079 ± 0.009 SD); more shallow cranium (mean height of skull at anterior apex of the basisphenoid/condylobasal

length = 0.304 ± 0.018 SD) than T. stejnegeri (0.332 \pm 0.019 SD) and T. terrapen $(0.342 \pm 0.028 \text{ SD})$ (fig. 6), and a shorter distance between orbits (mean interorbital width/condylobasal length = 0.148 ± 0.020 SD) compared to T. stejnegeri and T. terrapen $(0.169 \pm 0.017 \text{ and } 0.176 \pm 0.012 \text{ SD, re}$ spectively). Qualitatively, in T. decussata the tomial edge of the maxilla flares laterally and is not tapered inward or constricted below the anterior margin of the orbit, as in T. stejnegeri and the squamosal tapers posterodorsally, in contrast to T. stejnegeri, with a more blunt posterior border when viewed laterally (fig. 7). The cranium of T. terrapen is somewhat intermediate for these characters, but appears more similar to that of the T. stejnegeri group than T. decussata (fig. 8). No difference was observed between T. decorata and T. stejnegeri skulls.

Six character ratios of external morphology were found to be useful in diagnosing T. decorata and subspecies of T. stejnegeri (fig. 9). Width of vertebral scute I in population D, T. s. malonei (mean anterior vertebral width/carapace length for males = 0.120 ± 0.010 SD, and for females = 0.127 ± 0.014 SD), is narrower (P < 0.01) than in populations A-C (mean ratio range for males = 0.154-

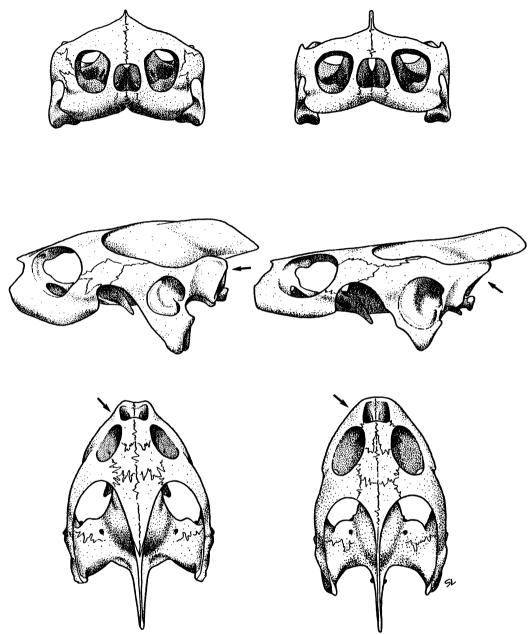


Fig. 7. Anterior, lateral, and dorsal illustrations of the cranium in *T. stejnegeri* (left) and *T. decussata* (right). Arrows indicate diagnostic characters described in text.

 0.169 ± 0.019 –0.027 SD and for females = 0.160– 0.188 ± 0.023 –0.029 SD), and shell height (at seam between vertebrals II–III) is greater (mean shell height/carapace length for males = 0.389 ± 0.012 SD and for females = 0.426 ± 0.021 SD) compared to populations A–C (mean range for males =

0.371– 0.377 ± 0.015 –0.019 SD and for females = 0.387– 0.405 ± 0.018 –0.023 SD).

Femoral scute length (mean ratio of femoral length/carapace length = 0.121 ± 0.015 SD) and axillary scute length (mean axillary length/carapace length = 0.150 ± 0.016 SD) of population A, T. decorata, are greater than

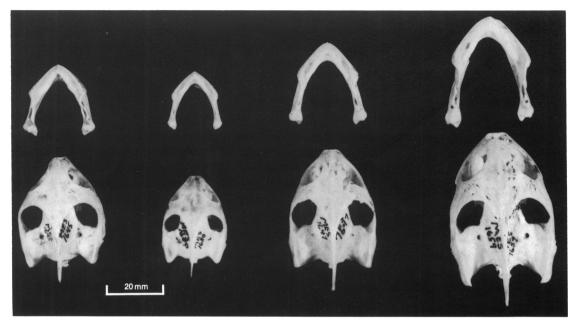


Fig. 8. Dorsal views of skulls of West Indian Trachemys. From left to right: T. decorata (MES 1645), T. terrapen (MES 1680), T. stejnegeri (MES 1647), T. decussata (MES 1659).

in populations B–D (mean femoral range = 0.090– 0.103 ± 0.008 –0.013 SD and axillary range = 0.126– 0.136 ± 0.011 –0.013 SD). Vertebral scutes (mean vertebral I length/carapace length = 0.166 ± 0.011 SD) and pectoral scutes (mean pectoral length/carapace length = 0.141 ± 0.017 SD) are shorter in population C, *T. s. stejnegeri*, than in populations A, B, and D (mean vertebral range = 0.171– 0.175 ± 0.007 –0.011 SD, and pectoral range = 0.168– 0.176 ± 0.012 –0.021 SD).

Mensural characters in Cuban turtles may be more influenced by sexual dimorphism than in other species (Sampedro Marin et al., 1983). Three sexually dimorphic ratios were found useful in diagnosing subspecies of T. decussata (fig. 10). Anterior width of the carapace is narrower in population HL, T. d. angusta (mean width at marginal seam III–IV/carapace length for males = 0.546 ± 0.028 SD and for females = 0.580 ± 0.025 SD), compared to that in population IK, T. d. decussata (mean width of anterior carapace for males = 0.599 ± 0.025 SD, and for females = 0.603 ± 0.033 SD); shell height of HL (at seam between vertebrals II–III) is great-

er (mean shell height/carapace length for males = 0.372 ± 0.018 SD, and for females = 0.391 ± 0.019 SD) than in population IK (mean shell height of males = 0.344 ± 0.021 SD, and for females = 0.366 ± 0.021 SD); upper jaw length of HL (from midline of premaxillary notch to symphysis of upper and lower jaw) is longer (mean jaw length/head width at tympanum in males = 0.649 ± 0.034 SD and for females = 0.628 ± 0.028 SD) than in populations IK (mean jaw length/head width in males = 0.620 ± 0.033 SD, and females = 0.596 ± 0.033 SD).

Most qualitative observations of shell and scute shape, coloration, and markings revealed individual and age-specific variation equal to or greater than differences between populations. The following qualitative characters (employed by Barbour and Carr, 1940, 1941) were found to have little diagnostic value: prominence and position of rugosities (wrinkles) on carapace, carapace shape (rounded or straight-sided) in dorsal view, prominence of arch or keel on vertebral scutes, flaring of posterior marginal scutes, extension of plastral figure to gular (dorsal) overlap,

notching of the upper jaw, ground color of soft parts or carapace, and striping on the limbs or tail. Nevertheless, Moll and Legler (1971) noted that color and markings are important in the taxonomy of emydid turtles, especially *Trachemys*.

In all West Indian Trachemys, markings on the head, limbs, carapace, and plastron are evident in juveniles but fade or disappear with age. Plastral patterns of T. terrapen and T. decussata are generally continuous or partially interrupted symmetrical figures which become obscured and frequently disappear entirely with age (figs. 11 and 12). No plastral pattern was evident in 42 and 64 percent of the adults examined in populations E and FG, respectively, and 64–80 percent in populations H-L. In T. stejnegeri, the plastral pattern often persists (at least anteriorly) with age and consists of a wavy, ocellated, symmetrical figure which is mostly continuous (figs. 13–15). The plastron of T. decorata has distinct unconnected ocellated circles or ovals (fig. 16). Plastral pattern was entirely absent in only 2, 8, 14, and 25 percent of the adults in populations A, B, D, and C, respectively. In all West Indian populations of *Trachemys*, the plastron of old adult females is typically unmarked or shows evidence of weak melanism (Seidel and Inchaustegui Miranda, 1984). This condition also appears in large females of some neotropical populations of T. scripta (e.g., Pritchard and Trebbau, 1984: pl. 38).

The carapace markings of hatchling or small juvenile T. terrapen, T. decussata, T. decorata, and T. stejnegeri are quite similar. These species have a small dark oval or blotch encircled by a yellow or orange ring on each vertebral, pleural, and marginal scute. This pattern frequently contacts the posterior border of the scute or overlaps the seam, especially on marginals, but no consistent variation among populations or species was obvious. Configuration and pigmentation of head-striping, particularly the supratemporal, does appear to have taxonomic value. Again, all very young specimens have distinct markings on the head and neck, but in some populations of T. terrapen these fade or become lost entirely in subadults. The supra-

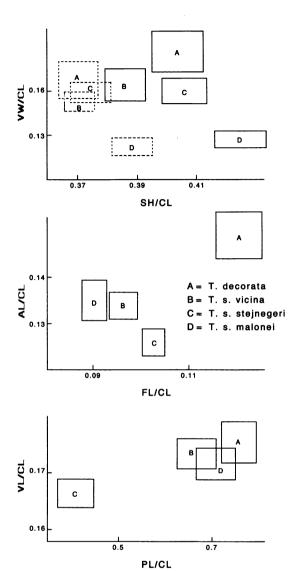


Fig. 9. Graphic representation of diagnostic characters for *T. decorata* and subspecies of *T. stejnegeri*. Above: Graph of percent shell height/carapace length (SH/CL) versus percent vertebral scute width/carapace length (VW/CL). Broken lines = male, solid lines = female. Center: Graph of percent femoral scute length/carapace length (FL/CL) versus axillary scute length/carapace length (AL/CL). Males and females combined. Below: Graph of percent pectoral scute length/carapace length (PL/CL) versus vertebral scute length/carapace length (VL/CL). Male and females combined. Letters indicate the location of means, and rectangles are formed by lines 2 standard errors above and 2 standard errors below means.

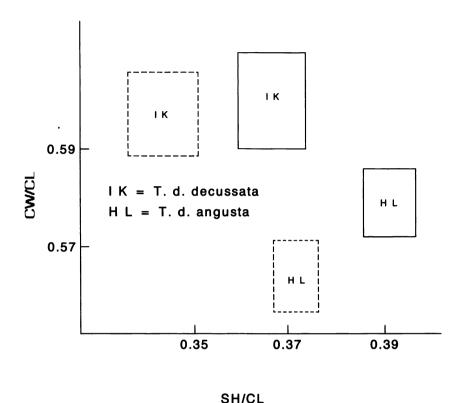


Fig. 10. Graphic representation of diagnostic characters for the subspecies of *T. decussata*: percent shell height/carapace length (SH/CL) versus carapace width/carapace length (CW/CL). Rectangles are formed by lines 2 standard errors above and 2 standard errors below means. Broken lines = males, solid lines = females. Turtles from Isla de Pinos (J, fig. 1), Cuba, are included under *T. d. angusta* (HL).

temporal stripe was absent in 49 and 62 percent of the adults in populations E and FG, respectively; 5-22 percent in populations H-L; and 0–17 percent in populations A–D. The color of this stripe varies among (and sometimes within) populations from gray or pale vellow to orange or red. At least some red or orange pigmentation occurs in all species, but dark red is most prominent in T. stejnegeri (83-95% of the individuals had deep-red supratemporals). The only other head markings of diagnostic value are the orbitocervical and mandibular stripes. In 83 percent of the adult T. decorata these stripes were joined below the tympanum; and in 0, 4, and 12 percent of T. stejnegeri populations D, C, and B, respectively, they were joined (Seidel and Inchaustegui Miranda, 1984). This character is much more variable (and therefore of little diagnostic value) in T. decussata and T. terrapen (populations E-L).

Melanism in adult male West Indian Trachemys is common and was formerly believed to characterize a distinct species, T. rugosa (Danforth, 1925). At least partial melanism was observed for all populations but the specific pattern of pigment change varies among species (fig. 17). In T. stejnegeri, this condition appears quite similar to melanism in the continental form, T. scripta elegans (McCoy, 1968). Head stripes are lost and replaced by a mottled pattern of dark-brown or black, and pale yellow; the diagnostic plastral pattern is lost and a broad zone of dark pigmentation develops along the plastral seams. Pigmentation disappears on the anterior surface of the carapace (which assumes a light tan or "bone" color) while the middle and posterior surfaces become nearly solid black. Melanism appears to be nearly absent in T. decorata (Seidel and Inchaustegui Miranda, 1984). The pattern of melanism in male

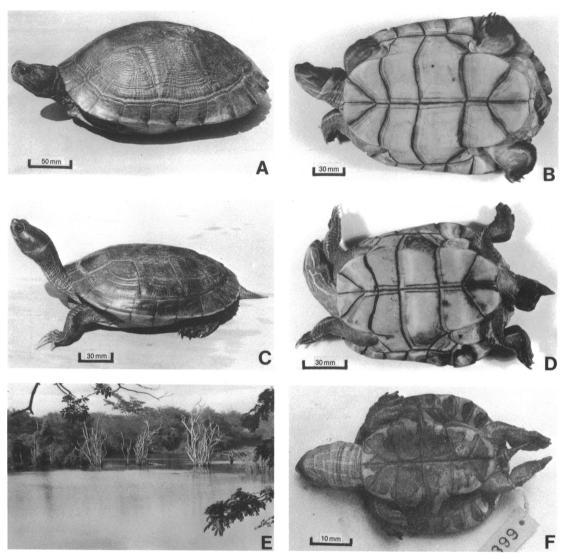


Fig. 11. T. terrapen. A. Dorsolateral view of adult female (MES 1279). B. Ventral view of adult female (MES 1862). C. Dorsolateral view of adult male (MES 1283). D. Ventral view of adult male (MES 1860). E. Pond habitat near Rosewell, Clarendon Parish, Jamaica. F. Ventral view of hatchling (MCZ 52399).

T. decussata is somewhat different from that of T. stejnegeri (fig. 17). As the head and neck become mottled, the area originally occupied by a supratemporal stripe loses pigment (especially in T. d. angusta) and the entire surface of the carapace assumes a vermiculate or speckled pattern of dark-brown to black on unpigmented patches. The plastron of T. d. decussata also frequently assumes a vermiculate pattern similar to that of the cara-

pace, but the plastral pattern of old male T. d. angusta consists of narrow areas of black pigmentation following the seams. Male melanism in T. terrapen is usually less pronounced than in other species (except T. decorata). Brown pigment, rather than black, develops in vermiculate markings and patches on the plastron, and along the plastral seams (fig. 17). In one relatively small male T. terrapen (AMNH 60733, 158 mm carapace

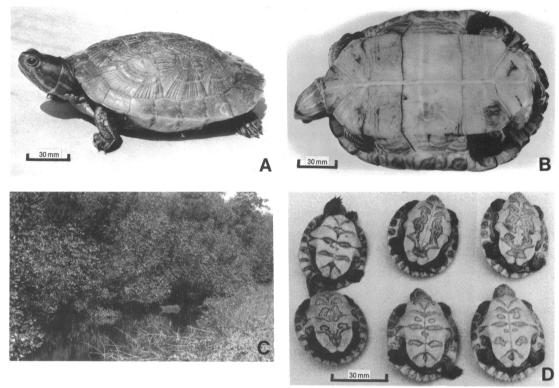


Fig. 12. T. d. angusta. A. Dorsolateral view of young female (MES 1678). B. Ventral view of adult female (MES 1864). C. Mangrove swamp habitat near South Sound, Grand Cayman. D. Ventral view of hatchlings from a single clutch of eggs (MES 1684–87 and two uncataloged).

length) this condition is very prominent. A mottled head pattern develops similar to that of *T. decussata*, but markings are not as dark.

Variations in plastral shape are also apparent among species of West Indian Trachemys. The epiplastron of T. stejnegeri and T. decorata was rounded anteriorly, turned upward, and constricted at the gular-humeral seam in 62, 77, 79, and 86 percent of populations B, C, D, and A, respectively. In T. terrapen, this condition occurred in 15 and 25 percent (populations E and FG, respectively) of the individuals and in T. decussata 11, 13, 45, and 45 percent (populations IK, J, H, and L, respectively). In general, the anterior epiplastral border of T. terrapen and T. d. decussata is truncate in ventral view, not turned upward nor emarginate at the gular-humeral seam. The contour of the ventral plastral surface is also variable among taxa. In the T. stejnegeri series the plastron is frequently convex (44-77% of the individuals in populations A-D) whereas most *T. decussata* individuals have a flat or slightly concave plastron (only 0-13% of the individuals in populations H-L were convex). The plastral surface of *T. terrapen* is somewhat intermediate or more variable (21% of population E and 52% of FG were convex). This character appears to be correlated to the presence of an angle or curvature of the pectoroabdominal seam. A convex plastron produces a rounded or curved seam at the base of the bridge (*T. decorata* and *T. stejnegeri*) whereas a flat or concave plastron results in an obtuse seam below the bridge (*T. decussata*) (compare fig. 12B with figs. 13-16B).

Maximum size, expressed as carapace length, also varies among West Indian *Trachemys*. In all species, females are larger than males. *T. decussata* appears to be the largest species, reaching a maximum male size of 268 mm (FMNH 34665, Cuba) and female size of 388 mm (MCZ 33948; Barbour and

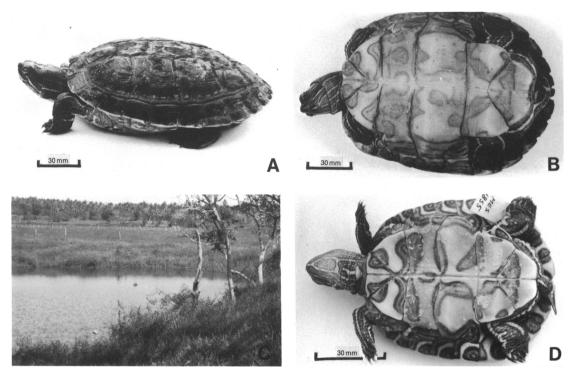


Fig. 13. T. s. stejnegeri. A, B. Lateral and ventral views of young female (MES 1863). C. Pond habitat near Isabela, Puerto Rico. D. Ventral view of juvenile (MES 1855).

Carr, 1940, Cuba). Some individuals of T. decorata approach these sizes as evidenced by a male 219 mm (MCZ 36862, Haiti) and female 341 mm (Inchaustegui Miranda, 1976, República Dominicana). The largest T. terrapen specimens measured were only 198 mm (male, MCZ 38997, Cat Island) and 271 mm (female, FMNH 29198, Cat Island). However, Lynn and Grant (1940) commented that adult Trachemys on Jamaica regularly attain a carapace length of 300 mm or more. T. stejnegeri appears to be moderate-size, with a maximum recorded male size of 210 mm (MES 1648, Puerto Rico) and maximum female size of 273 mm (AMNH 6335, República Dominicana). Grant (1931) reported a specimen of T. stejnegeri from Puerto Rico (presumably female) which was 300 mm long, but apparently the measurement was taken along the curve of the carapace. This might also explain the large size of T. terrapen reported by Lynn and Grant (1940). The most striking difference in size is the frequency of large male T. decussata specimens (27% of 100 adults measured were larger than 200

mm). The only other males which measured over 200 mm carapace length were two specimens of *T. decorata* (MCZ 36862–63) and one *T. stejnegeri* (MES 1648). Minimum size (hatchlings) of *T. stejnegeri* may also be small compared to *T. decussata*. The carapace lengths of four Puerto Rican turtles hatched in captivity were 37.6, 38.1, 39.0, and 40.1 mm while six captive hatchlings from Grand Cayman measured 38.1, 40.0, 40.3, 40.4, 40.7, and 40.9 mm.

The length of the front claws is another sexually dimorphic character in *Trachemys*. Although all adult West Indian *Trachemys* males have longer foreclaws than females, there appears to be interspecific variation in the degree of dimorphism. Elongated foreclaws are clearly an adaptation in *T. scripta elegans* for male titillation of females during courtship (Jackson and Davis, 1972). Seidel and Inchaustegui Miranda (1984) reported that the foreclaws of male *T. s. vicina* are relatively longer than those of *T. decorata*. However, these authors also noted that no difference in courtship behavior was ob-

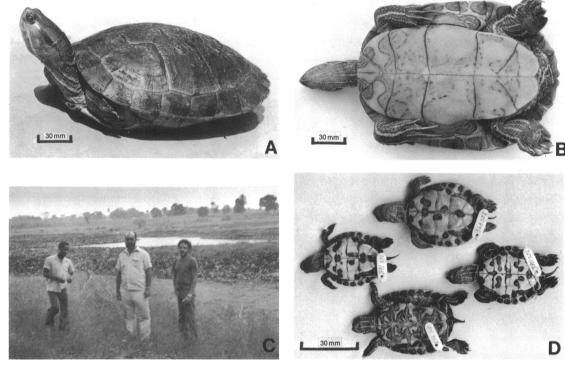


Fig. 14. T. s. vicina. A. Dorsolateral view of young female (MES 1275). B. Ventral view of adult male (MES 1668). C. Pond habitat near Guerra, Distrito Nacional, República Dominicana (S. J. Inchaustegui Miranda, center, with field assistants). D. Above, ventral view of hatchling T. decorata (SJI 368); central left and right, hybrid T. s. vicina × T. decorata hatched in captivity (SJI 390-91); below, hatchling T. s. vicina (SJI 255); scale is an approximation.

served between the two species (both employ titillation). Present observations indicate that the foreclaws of T. s. steinegeri and T. s. malonei are consistently long, similar to T. s. vicina, but many T. terrapen and T. decussata adult males have relatively short foreclaws similar to those of T. decorata. There may be a direct relationship between the degree of melanism and average length of the foreclaws in populations. Foreclaw length in T. decorata, T. terrapen, and T. decussata males appears to be more variable than the consistently elongate foreclaws of T. steinegeri. I have observed courtship involving titillation in all species of West Indian Trachemys, including T. decussata from the Cayman Islands and T. terrapen from Jamaica. At least some, if not all, of the Mexican and Central American populations of T. scripta completely lack elongation of male claws (Davis and Jackson, 1973; Moll and Legler, 1971). This

condition is apparently accompanied by a rudimentary type of courtship in which titillation does not occur and the male aggressively chases and bites the female. Although foreclaw elongation is not pronounced in all West Indian populations, they all seem to have elaborate courtship similar to northern races of *T. scripta*.

Seidel and Adkins (1987) identified variation in biochemical characters among West Indian Trachemys. Isoelectric focusing revealed interspecific polymorphism in seven highly resolved and concentrated protein bands (table 3). No protein difference was found between Jamaican (E) and Cat Island (F) populations of T. terrapen which share a unique liver electromorph (pI = 6.2) not found in other Trachemys or Pseudemys examined. Subspecies of T. stejnegeri are biochemically very similar to each other except for a unique kidney electromorph found in T. s. vicina

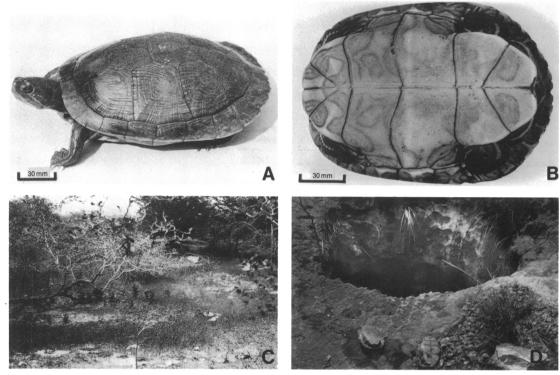


Fig. 15. T. s. malonei. A, B. Dorsolateral and ventral views of young female (MES 1858). C. Dried habitat on Great Inagua (Horse Pond; May 1983). D. Limestone sink-hole which functions as a natural "pit-fall" trap for turtles moving over land on Great Inagua.

(pI = 6.6). T. s. stejnegeri (C), T. s. vicina (B), T. s. malonei (D), and T. decorata (A) share a heart muscle protein (pI = 6.0) not found in other turtles. From analysis of 10 protein systems by starch-gel electrophoresis, Seidel and Adkins (1987) found relatively little polymorphism among Trachemys. Glycerol-3-phosphate dehydrogenase was the only enzyme which revealed interspecific variation. All populations of West Indian Trachemys and Pseudemys showed a fast and slow anodal band for this protein, whereas neotropical and temperate T. scripta showed a medium and/or slow band. On starch gel no unique allozyme appeared within an insular species or group of species.

SYSTEMATIC ACCOUNTS

A chronological list of all synonyms and orthographic variations thereof is presented for each valid taxon. Each combination or onymorph appears with reference to its first use, including author, date, and pagination. Some citations are parenthetically noted and localities are included for type specimens. Distribution of each taxon is defined and, in some cases, supplemented with ecological and taxonomic notations.

Trachemys terrapen (Lacépède) Jamaican Slider

Testudo terrapen Lacépède, 1788: 129 (type locality "Jamaica"; no holotype designated).

Testudo palustris Gmelin, 1789: 1041 (type locality "Jamaica"; no holotype designated).

Testudo fasciata: Suckow, 1798: 40 (type locality "... Amboina and Virginia," here revised to Jamaica; no holotype designated).

Testudo rugosa Shaw, 1802: 28 (type locality unknown; no holotype designated; specific identity remains uncertain, see Mittleman, 1947).

Emys rugosa livida: Gray, 1831: 30. Emys decussata: Gosse, 1851: 187.

Emys rugosa: Gosse, 1851: 189.

Chrysemys scripta rugosa: Boulenger, 1889: 79. Trachemys palustris: Baur, 1893: 776.

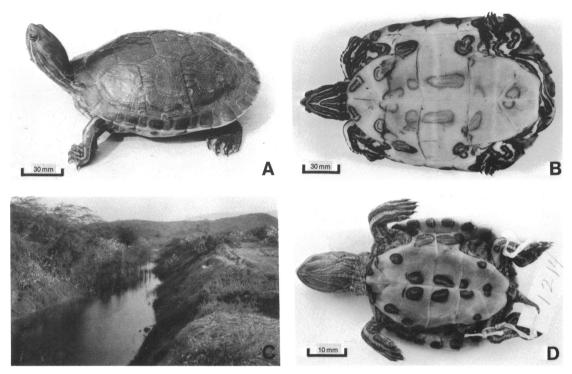


Fig. 16. *T. decorata*. A. Dorsolateral view of young female (MES 1861). B. Ventral view of young female (MES 1861). C. Aquatic habitat near Cabral, Barahona Province, República Dominicana. D. Ventral view of hatchling (MES 1214).

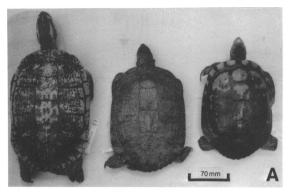
Chrysemys scripta palustris: Siebenrock, 1909: 464. Pseudemys palustris: Stejneger, 1904: 710. Pseudemys felis Barbour, 1935: 205 (type locality "Tea Bay, Cat Island, Bahamas"; holotype, MCZ 38385, adult female, collected by W. G. Albury and C. S. Dooley, 1935, examined by author). Pseudemys palustris felis: Mertens, 1939: 39. Pseudemys terrapen: Barbour and Carr, 1940: 391. Pseudemys terrapen terrapen: Mertens and Wermuth, 1955: 366.

Pseudemys terrapen felis: Parsons, 1960: 118. Chrysemys terrapen: McDowell, 1964: 274. Chrysemys felis: Schwartz, 1968: 259. Chrysemys decussata felis: Schwartz, 1968: 259. Chrysemys terrapen terrapen: Obst, 1983: 23. Chrysemys terrapen felis: Obst, 1983: 23. Trachemys terrapen: Seidel and Inchaustegui Miranda, 1984: 468 (first use of combination). Trachemys terrapen terrapen: Iverson, 1985: 5. Trachemys terrapen felis: Iverson, 1985: 5. Trachemys felis: Seidel and Adkins, 1987: 485.

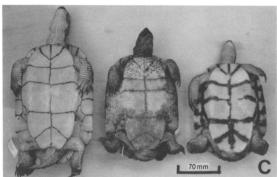
CONTENT: *Trachemys terrapen* is a monotypic species.

DESCRIPTION AND DIAGNOIS: A moderatesize *Trachemys*, males 100–200 mm in car-

apace length and females 110-270 mm. The adult carapace is uniform brown or olive, weakly keeled with longitudinal ridges or rugosities at the base of each pleural scute, and posterior marginals are serrate (fig. 11). In juveniles and some young adults, the pleural scutes have a dark spot encircled by a vellow or orange ring and a similar ocellate figure overlapping the seam between each pair of marginals. The plastron of adults is usually yellow or light tan and unmarked, but in juveniles there may be evidence of an interrupted figure, especially on the gular scutes. The undersides of marginal scutes in the bridge area have a faded ocellate figure overlapping the seams. The skin is gray or grayish brown with relatively few markings in adults other than four pale yellow stripes along the underside of the neck and chin, and two weakly defined light bands on the forelegs. In juveniles, additional yellow stripes along the lateral portions of the head and hindlimbs may be present, including a supratemporal stripe which is occasionally orange. All mark-







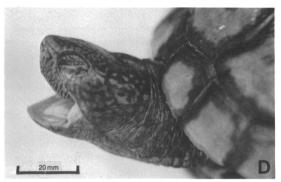


Fig. 17. Pattern variation among melanistic male *Trachemys*. A, C. Dorsal and ventral views of *T. decussata* (MES 1630) left, *T. terrapen* (ASFS 14427) center, *T. stejnegeri* (MES 1656) right. B. Anterior dorsolateral view of *T. decussata* (MES 1630). D. Anterior dorsolateral view of *T. stejnegeri* (MES 1656).

ings fade or disappear with age, sometimes within the second or third year (except for

populations in western Jamaica). The tomium (of the jaws) is smooth or slightly serrate

TABLE 3
Frequency of Variable Isoelectromorphs Identified in *Trachemys* (modified from Seidel and Adkins, 1987)

Neotropical T. scripta includes samples from Mexico (San Luis Potosi and Yucatan) and South America (captive reared). Temperate T. scripta includes samples of T. s. scripta and T. s. elegans. Sample sizes are in parentheses following each taxon and letters identify populations designated in figure 1. Proteins (electromorphs) are identified by their isoelectric points (pI), tissue sources, and character numbers from table 2.

	pI = 6.2 (liver) 25	pI = 6.2 (muscle) 26	pI = 5.5 (liver) (muscle) 27	pI = 6.0 (heart) 28	pI = 6.4 (heart) 29	pI = 6.9 (heart) 30	pI = 6.6 (kidney) 31
T. stejnegeri stejnegeri (10) C	_	_	_	0.30	_	_	_
T. stejnegeri vicina (6) B	_	_	_	0.50	_	_	0.33
T. stejnegeri malonei (2) D	_	_	_	0.50	_	-	_
T. decorata (8) A	_	_	_	0.38	_	_	_
T. terrapen (10) EF	1.00	1.00	_	_	0.50	_	_
T. decussata (6) L	_	0.50	_	-	0.50	_	_
Neotropical T. scripta (5)	_	0.80	0.60	_	0.60	0.60	
Temperate T. scripta (4)	_	0.50	0.75	_	0.75	_	_
Pseudemys nelsoni (4)	_	0.50	_	_	_	_	_

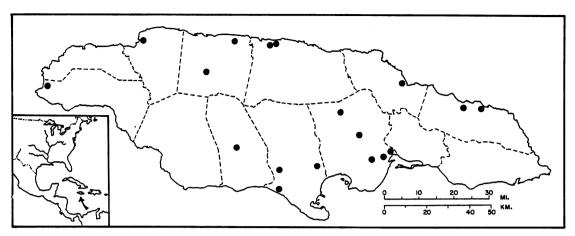


Fig. 18. Distribution of T. terrapen in Jamaica. Dots indicate known localities.

and the median ridge of the alveolar surface is weakly developed. The snout of mature males is relatively short, and melanism is not pronounced in older individuals.

T. terrapen is distinguished from all other species of Trachemys by the following characteristics: carapace flared posteriorly, width at marginal VII–VIII seam usually greater than 76 percent of carapace length; dorsal length of cervical scute usually more than 7 percent of carapace length; ventral underlap of cervical scute typically broad, greater than 4 percent of carapace length; anterior width of the plastron (at gular–humoral seam) more than 23 percent of carapace length; plastral scutes with concentrations of black pigment along the borders of seams.

DISTRIBUTION AND REMARKS: Trachemys terrapen is widely distributed on Jamaica (fig. 18), but also occurs in the northern Bahamas in small, temporary limestone sinks on Cat Island and Eleuthera. Bahamian populations, formerly identified as T. felis (Schwartz and Thomas, 1975), are presumably the result of human introduction (see Taxonomic Conclusions). In Jamaica, T. terrapen inhabits more permanent bodies of fresh water at low elevations, including rivers, streams, ponds, and swamps. Populations on western Jamaica (Hanover, Westmoreland, Saint James, and Trelawny parishes) retain their head and plastral markings as young adults whereas eastern populations (Clarendon, Saint Ann, Saint Catherine, and Saint Andrew parishes) become more uniformly olive-brown with

age. Bahamian T. terrapen individuals lose their markings with age and therefore appear more similar to turtles in eastern Jamaica. especially populations near Kingston. T. terrapen (P. felis) has also been reported from Andros Island in the northern Bahamas (Schwartz and Thomas, 1975). Only three specimens of Trachemys have been taken from Andros. Two of these (a partially melanistic adult male, MES 1274, which resembles T. steinegeri, and an adult female, MES 1268, resembling T. terrapen) were obtained by the author, June 1982, from an artificial pond on North Andros Island. It was later learned that these specimens were transported from Paradise Island (Hog Cay, New Providence) by a local resident, Mrs. J. Porter. Further inquiries made to natives suggest that freshwater turtles do not naturally occur on North Andros. The third specimen (an adult female, ASFS V27474) was collected on South Andros (crossing a road about 1 km north of Congo Town) by Albert Schwartz, May 1972). This location is near a freshwater marsh which, according to local residents, contained turtles (Albert Schwartz, personal commun.). Although the specimen has characteristics typical of T. terrapen, the presence and identity of an established Trachemys population on South Andros remains uncertain pending additional field observation. A "hybrid" population of Trachemys in artificial ponds on Hog Cay (Paradise Island), New Providence, has been recognized as a composite of human introductions from other

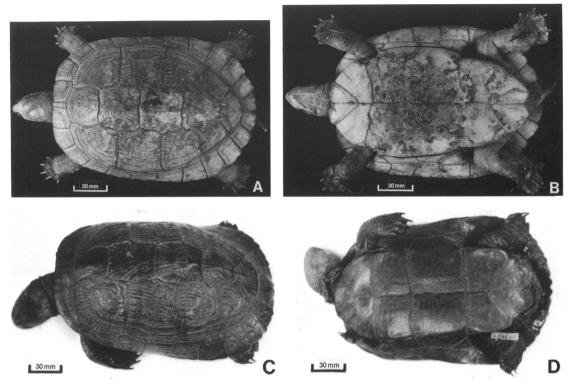


Fig. 19. A, B. Dorsal and ventral views of the holotype (BMNH 1947.3.4.79) of *T. d. decussata* (Gray). C, D. Dorsal and ventral views of the holotype (MCZ 34340) of *T. d. angusta* (Barbour and Carr).

West Indian islands and perhaps the United States (Campbell, 1978; Groombridge, 1982). Biochemical evidence supports the theory that these turtles are a T. stejnegeri × terrapen hybrid swarm, probably due to importations from Great Inagua and Cat Island (Seidel and Adkins, 1987). Recently a late Pleistocene fossil emydine (appendicular and plastral elements) was discovered on San Salvador, 70 km SE of Cat Island (Gregory Pregill, personal commun.). This may substantiate the presence of Trachemys in the northern Bahamas prior to the arrival of man. One final and very questionable locality for Trachemys (terrapen?) in the northern Bahamas is Craton's (1968) reference to freshwater turtles on Long Island. This is probably a mistaken reference intended for Cat Island. Based on his extensive fieldwork in the Bahamas, Albert Schwartz (personal commun.) is relatively certain that Trachemys does not occur on Long Island.

Trachemys decussata (Gray) North Antillean Sliders

Emys decussata Gray, 1831: 28 (type locality, "America Boreali"; holotype, BMNH 1947.-3.4.79, cataloged as a male, but reidentified from photograph as an adult female by MES, collected [origin] by J. E. Gray, not examined by author, fig. 19A, B).

Emys rugosa: Cocteau and Bibron, 1843: 17. Emys vermiculata Gray, 1844: 25 (type locality, "West Indies"; holotype formerly in BMNH, now lost).

Ptychemys decussata: Agassiz, 1857: 434.

Trachemys rugosa: Agassiz, 1857: 436.

Emys jamao: Duméril, 1861: 435 (nomen nudum).

Clemmys decussata: Strauch, 1862: 127.

Emys gnatho Vilaró in Poey, 1867: 204 (type locality, "Cuba"; no holotype designated). Pseudemys decussata: Gray, 1870: 47. Chrysemys scripta rugosa: Boulenger, 1889: 79. Pseudemys palustris: Stejneger, 1904: 710. Chrysemys scripta palustris: Siebenrock, 1909: 464.

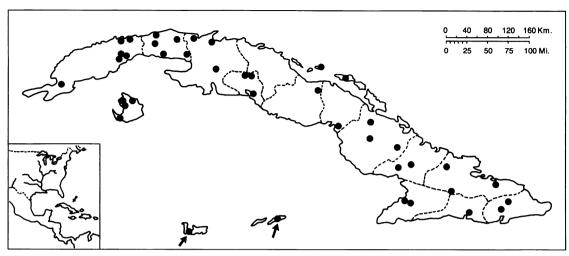


Fig. 20. Distribution of T. decussata in Cuba and the Cayman Islands. Dots indicate known localities.

Pseudemys rugosa: De Sola and Greenhall, 1932: 129.

Pseudemys terrapen: Mertens and Wermuth, 1955:

Chrysemys decussata: McDowell, 1964: 274.

Chrysemys terrapen: Obst, 1983: 23.

Trachemys decussata: Seidel and Inchaustegui Miranda, 1984: 468 (first use of combination).

Content: Two subspecies are recognized: *Trachemys decussata decussata* and *T. d. angusta*.

DESCRIPTION AND DIAGNOSIS: A relatively large Trachemys, males 115-270 mm in carapace length and females 120-390 mm. The adult carapace is brown or olive, weakly keeled, and sometimes has small ridges radiating from the center of pleural scutes (fig. 12). In juveniles and some young adults the pleural scutes may have a dark spot encircled by a yellow or orange ring and a similarly ocellate figure on the dorsal and ventral marginal seams. The plastron of adults is usually yellow and unmarked. In juveniles the plastron has a continuous or interrupted wavy symmetrical figure, which may also occur on the bridge. The skin is grayish brown or green with yellow stripes on the neck and limbs. These markings are much less pronounced in adults. The supratemporal stripe of juveniles may be orange or pink. The tomium (of the jaws) is smooth or slightly serrate and the median ridge of the alveolar surface is weakly developed. The foreclaws of mature males are often elongate, melanism is pronounced in older individuals, and the snout is relatively short.

T. decussata is distinguished from all other species of Trachemys by the following combination of characteristics: plastral surfaces of adults either flat or slightly concave; epiplastron truncate anteriorly; inguinal scutes posteriorly aligned (often barely or not in contact with marginal VI) and projected laterally to form an angle; gular scute short, usually less than 13 percent of carapace length; cranium shallow (less than 32% of its length) with the maxilla flared laterally and the squamosal tapered posterodorsally.

DISTRIBUTION: T. decussata occurs on mainland Cuba as well as Isla de Pinos, Cayo Coco and Cayo Santa Maria (Garrido and Juame, 1984), and the Cayman Islands (fig. 20). A thorough understanding of the range and extent of morphological variation of Trachemys in Cuba awaits further study.

Trachemys decussata decussata (Gray) Common Cuban Slider

Emys decussata Gray, 1831: 28 (see species synonymy).

Pseudemys decussata decussata: Barbour and Carr, 1940: 396.

Pseudemys decussata plana Barbour and Carr, 1940: 405 (type locality, "Rio Jobabo, Western Oriente, Cuba"; holotype, MCZ 34134, adult male, collected by T. Barbour, 1932, examined by author).

Pseudemys rugosa rugosa: Mittleman, 1947: 176.

Pseudemys rugosa decussata: Mittleman, 1947:

Pseudemys terrapen decussata: Mertens and Wermuth, 1955: 366.

Pseudemys terrapen plana: Parsons, 1960: 118. Pseudemys terrapen rugosa: Wermuth and Mertens. 1961: 158.

Chrysemys decussata decussata: Schwartz and Thomas, 1975: 47.

Chrysemys terrapen decussata: Obst, 1983: 23. Chrysemys terrapen plana: Obst, 1983: 23.

Trachemys decussata decussata: Iverson, 1985: 4 (first use of this combination).

Trachemys decussata plana: Iverson, 1985: 4.

DIAGNOSIS: A race with a relatively shallow carapace, broader anteriorly than posteriorly. Most adults have no or only very faded markings on the head and limbs.

DISTRIBUTION AND REMARKS: T. d. decussata occurs in a diversity of freshwater habitats throughout lower elevations of central and eastern Cuba, including La Habana, Matanzas, Las Villas, Camaguey, and Oriente provinces. Populations in the Rio Jobabo system (Oriente Province), originally described by Barbour and Carr (1940) as T. (P.) d. plana, are referable to T. d. decussata (see Taxonomic Conclusions).

Trachemys decussata angusta (Barbour and Carr) Taco River Slider

Emys decussata: Garman, 1888: 103. Chrysemys palustris: English, 1912: 599. Pseudemys rugosa: Grant, 1940: 52.

Pseudemys decussata angusta Barbour and Carr, 1940: 402 (type locality, "Taco River, Pinar del Rio, Cuba"; holotype, MCZ 34340, adult female, collected by G. S. Villalba and F. E. Convillon, 1932, examined by author, fig. 19C, D). Pseudemys decussata decussata: Barbour and Carr.

Pseudemys decussata decussata: Barbour and Carr, 1940: 402 (in part, specimens from Isla de Pinos).

Pseudemys granti Barbour and Carr, 1941: 59 (type locality, "... Grand Cayman ..."; holotype, MCZ 46045, adult female collected by Rodriguez Benitez, 1941, examined by author).

Pseudemys rugosa angusta: Mittleman, 1947: 176. Pseudemys terrapen granti: Mertens and Wermuth, 1955: 367.

Pseudemys decussata granti: Williams, 1956: 157. Pseudemys terrapen angusta: Parsons, 1960: 118. Chrysemys terrapen granti: Williams, 1969: 369. Chrysemys decussata granti: Schwartz and Thomas, 1975: 47.

Chrysemys terrapen angusta: Obst, 1983: 23.
Trachemys decussata angusta: Iverson, 1985: 4
(first use of this combination).

Trachemys decussata granti: Iverson, 1985: 4.

DIAGNOSIS: A race very similar to the nominotypical form but distinguished by a carapace which is deeper and narrower anteriorly. Markings on the head, neck, and limbs are often prominent, even in adults, and the upper jaw is slightly elongate.

DISTRIBUTION AND REMARKS: T. d. angusta occurs in freshwater habitats of western Cuba (Pinar del Rio Province), Isla de Pinos (La Habana Province), and the Cayman Islands. Barbour and Carr (1940) defined a range for T. d. angusta which included only western Pinar del Rio Province, Cuba. However, present results indicate that populations on Isla de Pinos and Grand Cayman are also referable to T. d. angusta (see Statistical Results and Taxonomic Conclusions). Barbour and Carr (1940) included Isla de Pinos (50 km S of Cuba) in the distribution of T. d. decussata based on examination of only two specimens (MCZ 10985 and 11735). Reexamination of those turtles and nine additional specimens from Isla de Pinos indicates their distinct affinity to T. d. angusta.

T. d. angusta in the Cayman Islands (formerly assigned to T. granti, see Taxonomic Conclusions) appears to be well-established on Grand Cayman, inhabiting freshwater ponds and mangrove swamps. Their relatively large population size and ability to inhabit brackish water (Dunson and Seidel, 1986) might indicate a long, perhaps prehistoric period of habitation on Grand Cayman. However, the possibility of human introduction from Cuba cannot be discounted. During the 19th century extensive travel and trade occurred between Grand Cayman and Isla de Pinos in particular (John Davies, personal commun.). Also, among a diversity of fossilized reptile bones which have recently been recovered from "Cow Wells" on Grand Cayman, remains of Trachemys are conspicuously absent (Gary Morgan and Richard Franz, personal commun.). Trachemys has also been reported from Cayman Brac, 150 km NE of Grand Cayman. According to Garman (1888) and Grant (1940), the occurrence there in a small series of ponds is the result of turtles transported from Grand Cayman

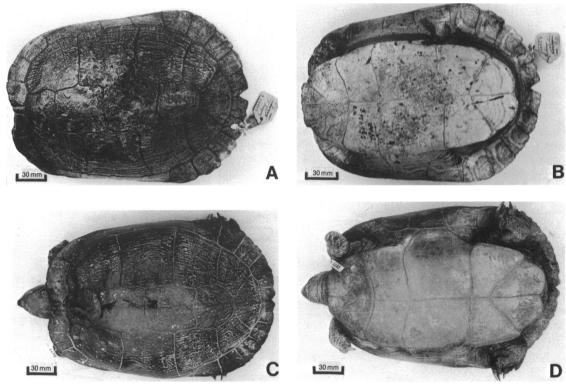


Fig. 21. A, B. Dorsal and ventral views of the holotype (USNM 25642) of T. s. stejnegeri (Schmidt). C, D. Dorsal and ventral views of the holotype (FMNH 5977) of T. s. vicina (Barbour and Carr).

and released by Stephen Foster in 1875. A fluid-preserved subadult (MCZ 44854 paratype, collected by Chapman Grant, 1939), an adult skull (UF 21745, collected by T. Patton and W. F. Greenhood in 1965), and a nearly complete adult skeleton (MES 1801, collected by the author in 1986) from Cayman Brac are indistinguishable from Grand Cayman specimens. There are no reports of *Trachemys* on the third Cayman island, Little Cayman.

Trachemys stejnegeri (Schmidt) Central Antillean Sliders

Emys decussata (nec Gray): Duméril and Bibron (nec Gray), 1835: 279.

Emys rugosa: Gundlach, 1881: 307.

Clemmys decussata: Strauch, 1862: 127.

Chrysemys scripta rugosa: Boulenger, 1889: 79.

Pseudemys palustris: Stejneger, 1904: 710.

Chrysemys scripta palustris: Siebenrock, 1909: 464.

Pseudemys stejnegeri: Schmidt, 1928: 147 (type locality, "San Juan, Porto Rico..."; holotype,

USNM 25642, adult female collected on the U.S. Fish Comm. Sci. Survey, 1899, examined by author, fig. 21A, B).

Pseudemys decussata: Grant and De Sola, 1934: 75.

Pseudemys terrapen: Mertens and Wermuth, 1955: 367.

Chrysemys decussata: McDowell, 1964: 274. Chrysemys stejnegeri: Bickham and Baker, 1976a: 703.

Chrysemys terrapen: Obst, 1983: 23. Trachemys stejnegeri: Seidel and Inchaustegui Miranda, 1984: 468 (first use of combination).

CONTENT: Three subspecies are recognized: Trachemys stejnegeri stejnegeri, T. s. vicina, and T. s. malonei.

DESCRIPTION AND DIAGNOSIS: A moderatesize *Trachemys*, males 105–210 mm in carapace length and females 110–280 mm. The adult carapace is light brown to chestnut, relatively smooth but weakly keeled, and serrate along the posterior marginals. In adults, the carapace is usually unmarked except for light bands or faded ocelli on the marginals. In

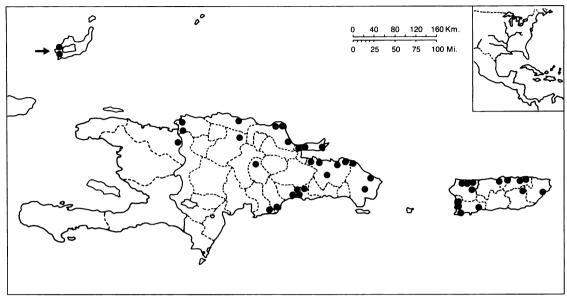


Fig. 22. Distribution for *T. stejnegeri* in Hispaniola, Puerto Rico, and Great Inagua. Dots indicate known localities

juveniles the pleural scutes have a dark spot encircled by a yellow or orange ring. The yellow to orange plastron, in all but very old individuals, has a symmetrical, wavy figure. The skin is grayish brown or grayish green with pale black-bordered yellow stripes on the head, neck, and limbs. The tomium (of the jaws) is smooth or slightly serrate and the median ridge of the alveolar surface is weakly developed. The foreclaws of mature males are distinctly elongate, the snout is relatively long, and melanism is pronounced in old individuals.

T. stejnegeri is distinguished from all other species of Trachemys by the following combination of characteristics: supratemporal stripe deep or dark red; symmetrical figure of connecting lines on adult plastron; ventral surface of plastron frequently convex; epiplastron rounded anteriorly, turned upward, and usually constricted at the gular-humeral seams; deep notch at intermarginal XII seam; snout depth more than 35 percent of head width; femoral scutes relatively short, less than 11 percent of carapace length; axillary scutes short, usually less than 14 percent of carapace length.

DISTRIBUTION: T. stejnegeri occurs on Puerto Rico, northern and eastern Hispan-

iola, Great Inagua (Bahamas), and Marie-Galante (Lesser Antilles) (fig. 22).

Trachemys stejnegeri stejnegeri (Schmidt)
Puerto Rican Slider

Pseudemys stejnegeri Schmidt, 1928: 147 (see species synonymy).

Pseudemys palustris stejnegeri: Mertens, 1939: 39. Pseudemys stejnegeri stejnegeri: Barbour and Carr, 1940: 406.

Pseudemys terrapen stejnegeri: Mertens and Wermuth, 1955: 367.

Pseudemys decussata stejnegeri: Williams, 1956: 157.

Chrysemys decussata stejnegeri: Schwartz and Thomas. 1975: 47.

Chrysemys terrapen stejnegeri: Obst, 1983: 23. Trachemys stejnegeri stejnegeri: Iverson, 1985: 5 (first use of combination).

DIAGNOSIS: A race with relatively short vertebral and pectoral scutes, and axillary scutes rarely contacting the fifth marginal. The supratemporal stripe is distinctly red and the plastron is yellow with a dark symmetrical pattern (fig. 13).

DISTRIBUTION AND REMARKS: T. s. stejnegeri occurs in rivers, lakes and ponds throughout low elevations of Puerto Rico. Although natural populations of T. s. stejnegeri appear to be restricted to Puerto Rico. Schwartz and Thomas (1975) cited introductions of T. s. stejnegeri and T. s. vicina on Marie-Galante (a small island 25 km SE of Guadeloupe, Lesser Antilles). Reports of both forms on this small island have apparently resulted from difficulty in distinguishing the two subspecies using traditional key characters (markings defined by Barbour and Carr, 1940) rather than evidence of multiple introduction and sympatry. Marie-Galante presently supports a population of T. steinegeri in small, but seemingly "permanent" freshwater ponds in the region of Pirogue and Saint Marc (personal field observ., March 1984). Considering the distance between this location and the Greater Antilles, and absence of Trachemys from intervening islands, a "natural" origin for this population is very unlikely.

Analysis of scute morphometry of five specimens examined (ASFS X6016, MES 1704–1707) and protein polymorphism (Seidel and Adkins, 1987) indicate that turtles on Marie-Galante are referable to T. s. stejnegeri, and therefore represent a probable introduction from Puerto Rico. T. s. stejnegeri has also been reported on two small islands east of Puerto Rico. Grant (1932) indicated that Trachemys occurs on Vieques, a small island 15 km E of Puerto Rico. This was based on a captive turtle he observed in a cistern and reports he received from local residents.

More recently, Robert S. Adamcik (U.S. Fish and Wildl. Serv.) provided photographs (MES 1703) of an adult female Trachemys. collected by Bruce Hall at Pilon, Vieques (May 1982). However, recent field surveys on Viegues (R. S. Adamcik, personal commun. and personal observ., 1983) have produced no additional sightings of *Trachemys*. There is no permanent "natural" freshwater habitat on the island which might support a native population and it is likely that the occasional T. s. stejnegeri found on Vieques are transported from Puerto Rico and released by local residents. Recently, Richard Thomas (personal commun.) reported to the author that Trachemys occurs in a pond on Culebra Island, 30 km E of Puerto Rico. Determining the status of this population will require further field observation.

Trachemys stejnegeri vicina (Barbour and Carr) Dominican Slider

Pseudemys palustris: Schmidt, 1921: 20. Pseudemys palustris palustris: Mertens, 1939: 37. Pseudemys stejnegeri vicina Barbour and Carr, 1940: 408 (type locality, "Sanchez, San Domingo"; holotype, FMNH 5977, adult female, collected by Emil Kaempfer, 1924, examined by author, fig. 21C, D).

Pseudemys terrapen vicina: Mertens and Wermuth, 1955: 367.

Pseudemys decussata vicina: Williams, 1956: 157. Chrysemys decussata vicina: Schwartz and Thomas, 1975: 48.

Chrysemys stejnegeri vicina: Bickham and Baker, 1976a: 703.

Pseudemys decorata: Pritchard, 1979: 125. Chrysemys terrapen vicina: Obst. 1983: 23.

Trachemys stejnegeri vicina: Seidel and Inchaustegui Miranda, 1984: 468 (first use of combination).

DIAGNOSIS: A race with a relatively long first vertebral scute, and axillary scutes usually contacting the fifth marginal. The supratemporal stripe is distinctly red and the plastron is yellow or sometimes pale orange anteriorly, with a dark symmetrical pattern (fig. 14).

DISTRIBUTION AND REMARKS: T. s. vicina occurs in rivers, ponds, and marshes throughout the coastal lowlands of República Dominicana from Peravia Province in the south to the Rio Massacre system of Haiti in the north. Details of the distribution and geographic variation are discussed in Cochran (1941) and Seidel and Inchaustegui Miranda (1984).

Trachemys stejnegeri malonei (Barbour and Carr) Inagua Island Slider

Pseudemys malonei Barbour and Carr, 1938: 76 (type locality, "... Ponds near Northwest Point, Great Inagua Islands, B.W.I."; holotype, MCZ 44338, adult female, collected by Malone, McLean and Shreve, 1938, examined by author, fig. 23A, B).

Pseudemys palustris malonei: Mertens, 1939: 39. Pseudemys terrapen malonei: Mertens and Wermuth, 1955: 367.

Chrysemys malonei: Schwartz, 1968: 260. Chrysemys terrapen malonei: Obst, 1983: 23.

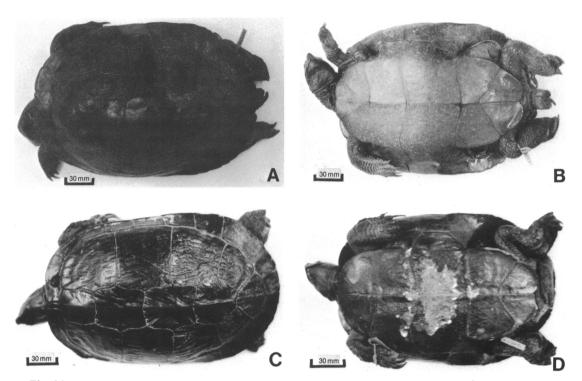


Fig. 23. A, B. Dorsal and ventral views of the holotype (MCZ 44338) of T. s. malonei (Barbour and Carr). C, D. Dorsal and ventral views of the holotype (MCZ 36862) of T. decorata (Barbour and Carr).

Trachemys stejnegeri malonei: Iverson, 1985: 5 (first use of this combination).

Trachemys malonei: Seidel and Adkins, 1987: 485.

DIAGNOSIS: A race with a relatively deep carapace and a first vertebral scute which narrows anteriorly. The supratemporal stripe is dark red or maroon and the plastron is pale yellow with a dark, symmetrical pattern (fig. 15).

DISTRIBUTION AND REMARKS: T. s. malonei occurs only in the southern Bahamas on the island of Great Inagua. This race has previously been considered a monotypic species by most authors (see Taxonomic Conclusions). T. s. malonei is restricted to small, mostly temporary, freshwater ponds on eastern Great Inagua (fig. 15). Similar to T. terrapen on Cat Island, survival of this population is threatened by the unstable nature of its aquatic habitats (personal field observ., fig. 15C, D; Groombridge, 1982; K. Bjorndal, personal commun.). Noteworthy is a specimen of T. s. malonei (UF 49423) collected on neighboring Pine Cay (Caicos Islands) by

W. Auffenberg in 1975. This turtle almost certainly was transported from Great Inagua, and extensive field observations in the Caicos Islands have produced no additional evidence of *Trachemys* (J. B. Iverson, personal commun.).

Trachemys decorata (Barbour and Carr) Hispaniolan Slider

Clemmys decussata: Strauch, 1862: 127.

Pseudemys palustris: Stejneger, 1904: 710.

Pseudemys palustris palustris: Mertens, 1939: 37.

Pseudemys decorata Barbour and Carr, 1940: 409

(type locality, "Fond Parisien, Haiti"; holotype,

MCZ 36862, adult male, collected by M. Audain, 1933, examined by author, fig. 23C, D).

Pseudemys terrapen decorata: Mertens and Wermuth, 1955: 366.

Chrysemys decorata: McDowell, 1964: 274. Chrysemys terrapen decorata: Obst, 1983: 27. Trachemys decorata: Seidel and Inchaustegui Miranda, 1984: 468 (first use of combination). Trachemys steinegeri decorata: Iverson, 1985: 5.

CONTENT: Trachemys decorata is a monotypic species.

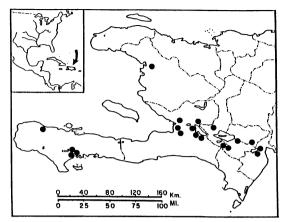


Fig. 24. Distribution of *T. decorata* on Hispaniola. Dots indicate known localities.

DESCRIPTION AND DIAGNOSIS: A moderate to large-size Trachemys, males 110-220 mm in carapace length and females 115-340 mm. The adult carapace is light brown to chestnut, relatively smooth, but weakly keeled and serrate along the posterior marginals. In juveniles, and often young adults, the pleural and marginal scutes have a dark spot encircled by a yellow or orange ring. The plastron and bridge are yellow with scattered, dark, ocellated circles or ovals, mostly unconnected (fig. 16). The skin is grayish brown with conspicuous black-bordered yellow stripes on the head, neck, limbs, and tail. The tomium (of the jaw) is smooth or slightly serrate and the median ridge of the alveolar surface is weakly developed. The foreclaws of mature males are distinctly elongate, the snout is relatively long, and melanism is not pronounced in old individuals.

T. decorata is distinguished from all other species of Trachemys by the following combination of characteristics: plastral figure of circles or unconnected ovals; supratemporal stripe yellow or pale green; orbitocervical and mandibular stripes usually joined below tympanum; femoral scutes relatively long, more than 11 percent of carapace length; axillary scutes long, usually more than 14 percent of carapace length.

DISTRIBUTION AND REMARKS: T. decorata occurs in freshwater lakes and ponds in the Cul de Sac-Valle de Neiba plain and Tiburon Peninsula of Hispaniola (fig. 24). It is likely that disjunct populations also occur north

along the coastal region of the Golfe de la Gonave. There is a single specimen (SMF 26315, apparently typical *T. decorata*) from Gonaives, Haiti in the Senckenberg Museum, Frankfurt, Germany (Uwe Fritz, personal commun.). Other details of distribution, as well as geographic variation, are discussed in Bickham (1980) and Seidel and Inchaustegui Miranda (1984).

BIOGEOGRAPHY AND EVOLUTION

In spite of the exhaustive number of studies on West Indian zoogeography, theories on faunal origins remain very controversial. Rosen (1975) has proposed that virtually the entire Caribbean biota was fragmented by plate tectonics (vicariance) from an ancestral continental biota. Hedges (1982), Mac-Fadden (1981), and especially Pregill (1981b) have questioned the totality of vicariance and advocate dispersal in explaining at least some of the faunal distributions in the Caribbean. Over-sea dispersal of Trachemys would certainly be possible. These turtles can survive in seawater for more than a week (Dunson and Seidel, 1986) and have been seen swimming in open sound (Fred Burton, personal commun.) or emerging from the sea to nest on beaches (Pritchard and Trebbau, 1984). Geological evidence indicates that during the Mesozoic the Greater Antilles (Hispaniola, Puerto Rico, Jamaica, and part of Cuba) originated as a tectonic plate (proto-Antilles) between North and South America (Malfait and Dinkelman, 1972; Rosen, 1975) which decoupled and moved eastward no later than Eocene time (Perfit and Heezen, 1978). This relative plate movement presumably resulted in the eastward migration of the proto-Greater Antilles away from Nuclear Central America to their present-day position (see Hedges, 1982, for a review of geological evidence). It is likely that relatively large areas of that plate have remained above sea level since movement began (Khudoley and Myerhoff, 1971; MacFadden, 1980), although Pregill (1981b) argues that the Greater Antilles were not continuously emergent until late Oligocene or early Miocene.

Usually only one extant species of *Trachemys*, *T. scripta*, is recognized on continental North and South America (Seidel and Smith,

1986) but Dixon (1987) recently recognized T. s. gaigeae as a distinct species. Fossil species of Trachemys have been reported from the Pliocene of Idaho and Florida, T. idahoensis (Seidel and Jackson, 1989; Weaver and Robertson, 1967; Zug, 1969), Upper Miocene of Oklahoma and Kansas, T. hillii (Adler, 1968), and Miocene of Florida, T. inflata (Weaver and Robertson, 1967). A late Pleistocene fossil of T. stejnegeri from Puerto Rico was described by Pregill (1981a), but Tertiary fossils of terrestrial vertebrates are virtually absent from the West Indies. Whether this implies that inhabitation did not occur until the Quaternary period (Pregill, 1981b) or simply reflects lack of conditions suitable for fossilization is subject to controversy (Poinar and Cannatella, 1987). In addition to this major void, hypotheses on the zoogeographic origin(s) of West Indian Trachemys are limited by an incomplete knowledge of the taxonomy and character-state distribution of T. scripta, especially throughout the neotropics (Moll and Legler, 1971; Pritchard and Trebbau, 1984; Williams, 1956). There appear to be at least two major evolutionary lines of this polytypic species, T. s. scripta and T. s. elegans in temperate North America and a neotropical lineage of T. scripta which ranges into South America (Moll and Legler, 1971; Williams, 1956). Trachemys in the West Indies is primarily distributed throughout the Greater Antilles, and its presence outside that region is presumably the result of recent dispersals or human introduction (see Taxonomic Conclusions). An introduced population of T. scripta has apparently become well established on Guadeloupe, Lesser Antilles (Schwartz and Thomas, 1975).

Vicariance alone (sensu Rosen, 1975) does not adequately explain the present distribution of *Trachemys* in the West Indies. Pregill (1981b) pointed out that if the Caribbean plate was separated from the continent by late Eocene, currently shared mainland and West Indian genera (i.e., *Trachemys*) must have evolved in parallel throughout the Cenozoic. Recognizing this to be unlikely, he suggested a mid-Tertiary appearance (dispersal) of modern vertebrate genera in the West Indies, as indicated by the fossil record from North and South America. Nevertheless, if an ancestral form of *Trachemys* occurred on the

proto-Antillean plate during the early Cenozoic, separation of that plate may have resulted in divergence of North American (T. scripta) and West Indian progenitors. Subsequent (late Tertiary?) intra-Caribbean vicariance may have led to isolation (speciation) of Trachemys on Cuba, Jamaica, North and South paleoislands of Hispaniola (Seidel and Inchaustegui Miranda, 1984), and Puerto Rico: followed by dispersals to Great Inagua and perhaps the Cayman Islands. The sistergroup formed by neotropical T. scripta and T. decussata (fig. 4) suggests that these species share an exclusive common ancestor which is difficult to understand using a vicariance model. It is interesting to note that Barbour and Carr (1940) also found Cuban turtles (T. decussata) most similar to Central American T. scripta (ornata). This presumably monophyletic relationship might be explained by dispersal of Trachemys from Cuba back to Nuclear Central America. Reinvasion of Trachemys into this region may have produced a lineage which successfully invaded the tropics and maintained at least partial isolation from northern Trachemys (T. s. scripta-elegans). Moll and Legler (1971) concluded that the arrival of Trachemys in the neotropics was fairly recent based on their analysis of reproductive habits.

Alternative and perhaps more reasonable theories on the origin of West Indian Trachemys involve multiple invasions from continental America. If evolutionary rates were relatively constant, Jamaican Trachemys (T. terrapen) might be the product of early dispersal and Cuban Trachemys might represent more recent dispersal. This would explain a common ancestry for T. decussata and modern neotropical T. scripta (fig. 4). Hedges (1982) suggested that there may have been a land connection between Cuba and Hispaniola as recently as late Pliocene and that Jamaica has remained separated from the other Antilles for a much longer period. This would offer another explanation for the outgroup position of T. terrapen.

The only viewpoint which seems to be shared by most recent investigators of the Caribbean region is that the biogeography of the Greater Antillean biota is exceedingly complex and is probably the result of both dispersal and vicariance (either of the Rosen

model, or intra-Caribbean). Although several zoogeographic theories could explain the origin(s) of emydid turtles in this region it appears that West Indian Trachemys are not monophyletic (fig. 4). Furthermore, their phylogeny suggests that T. scripta is at least a diphyletic species comprising a northern group (T. s. scripta and T. s. elegans) in the United States and a southern complex in the neotropics of middle America. Variations of such partitioning have been suggested by Moll and Legler (1971), Pritchard and Trebbau (1984), Ward (1984), Weaver and Rose (1967), and Williams (1956). Definite conclusions on the taxonomic status of T. scripta await a geographically broad and comprehensive analysis of neotropical populations (Legler, 1987).

KEY TO ADULT TRACHEMYS OF THE WEST INDIES

- 1A. Little or no evidence of markings on head, limbs, and plastron; carapace broad and flared posteriorly; broad cervical scute underlap (5.0% of carapace length); broad gular scutes (24% of carapace length)
- 1B. Markings present or absent on head, limbs, and plastron; carapace narrow or moderately wide, not prominently flared posteriorly; narrow cervical scute underlap (3.5-3.7% of carapace length); narrow gular scutes (21-22% of carapace length) ... 2

- 3A. Plastral pattern of unconnected ocellated circles or ovals; supratemporal stripe pale yellow or yellowish-green; orbitocervical and mandibular stripes usually joined below tympanum; interfemoral scute seam long (12% of carapace length) T. decorata
- 3B. Plastral pattern of continuous or partially in-

- 4A. First vertebral scute short (16% of carapace length); interpectoral scute seam short (14% of carapace length); axillary scute usually not in contact with fifth submarginal

 T. s. stejnegeri
- 4B. First vertebral scute long (17-18% of carapace length); interpectoral scute seam long (17-18% of carapace length); axillary scute usually contacting fifth submarginal ... 5
- 5B. Carapace relatively shallow (37% of length in males, 39% in females); first vertebral scute broad anteriorly (15% of carapace length in males and 16% in females)
- 6A. Carapace narrow anteriorly (width at marginal seam III-IV 56-58% of carapace length) and relatively deep (37% of carapace length in males, 39% in females); upper jaw elongate (65% of head width in males and 63% in females) ... T. d. angusta

SPECIMENS EXAMINED

- Trachemys terrapen Jamaica: AMNH 60733. ASFS (CM) 14363-67, 14427-30. MCZ 7377, 26787, 39700-04, 52399. MES 1271, 1279, 1281-82, 1285, 1635, 1679-81, 1862. TTM R-7402, R-7395-96. UMMZ 82026-27, 85932-33. USNM 10351, 10353, 29193, 83747-48, 83788, 108242-43. UU 6645-55. Cat Island: AMNH 89779-80. ASFS V2249-51. FMNH 29198. MCZ 38385-86, 38995-97, 3900-05, R163133-35, field numbers 163146, 163149. MES 1269, 1273, 1276, 1283, 1860. UMMZ 78494-95. USNM 102447, 121119-20. Eleuthera: ASFS 17413, 17417-22, 17610-17. South Andros Island: ASFS V27474. New Providence (putative hybrids): MES 1268, 1274.
- Trachemys decussata decussata Cuba (La Habana, Matanzas, Las Villas, and Camaguey provinces): AMNH 44872-73, 44875-80,

59680-81, 78585, 78588-89, 78591-93, 82917, 92838-41. FMNH 34662-66. MCZ 1917, 29277, 34140, 34143, 34145, 36867-70. UMMZ 70984-91, 79523-28, 115706-07, 120498-502. USNM 7873, 9675-76, 9750-51, 10173-78, 27638, 49596-98, 86821-25, 90330, 94451, 102448, 115524. Cuba (Oriente Province): MCZ 34128, 34130-36, 34138, 34357-63, 36871. UMMZ 106311, 120503-06.

Trachemys decussata angusta — Cuba (Pinar del Rio Province): AMNH 78392, 82928-34. MCZ 34334-45, 34347-52. USNM 27639, 55691-92. Cuba (Isla de Pinos): AMNH 82918-27. CM 3030a, 3030b, 3057a, 3057b. MCZ 10985, 46246. Cayman Islands: ASFS 16150-51, 16212-22. MCZ 46045-46, 44854-55. MES 1266, 1272, 1277, 1286, 1627-30, 1636-37, 1639, 1659, 1671-72, 1675, 1678, 1684-87, 1864. MES field numbers 1-29, 43-53, 55-61, 65-67, 70, 72, 74-77, 79, 80, 95 (+2 uncataloged). UF 21745.

Trachemys decorata — Hispaniola (Cul de Sac-Valle de Neiba plain): AMNH 24191–92, 45088, 49723. FMNH 51970–72. MCZ 1891–92, 36852–57, 36859–66, R152055–74, 164842–43, 165201. MES 1214, 1619, 1645–46, 1660–61, 1861 (1 uncataloged). SJI 344, 346, 367–72 (+2 uncataloged). TTM R-7393–94, R-7408. UF 20250–51, 33567–68, 49420, 49429–30, 51486. USNM 59093–96, 62565, 63096, 81091, 123793, 123804. Haiti (Tiburon Peninsula): CM 90043–44. USNM 51994, 80932–33, 82565.

Trachemys stejnegeri stejnegeri — Puerto Rico: AMNH 15186. FMNH 12483-87, 12489. MCZ 5833-34, 36872-73, 37295-96, 44345, 68861-62, R136039. MES 1267, 1270, 1280, 1284, 1612-18, 1620, 1647-49, 1855, 1863 (+5 uncataloged). MES field numbers 5-7, 9-16, 22-23. UMMZ 37297, 74418-23, 116907-08. USNM 25642-44, 25653. UU 6625-28, 6630-31, 6633-35, 6637-40, 6642-43 (UPR 1872). Marie-Galante: ASFS X6016. MES 1704-07.

Trachemys stejnegeri vicina — Hispaniola: AMNH 6332–35, 6337, 39850. CM 90045–56. FMNH 5977–78. MCZ 43651–54. MES 1275, 1278, 1622, 1650–58, 1667–70 (+1 uncataloged). SJI 255, 390–391, 453–57, 464–65, 467–71, 474–76, 478–86 (+1 uncataloged). TTM R-7379–80, R-7392, R-7406–07. UF 49427–28, 49431, 49440, 54726–30. USNM 198298–303. UU 13102, 13106, 13108.

Trachemys stejnegeri malonei — Great Inagua: AMNH 70619, 70901–06, 72460, 89771–78. ASFS 10376. FMNH 29175, 30867. MCZ 44338–43, 44346–47. MES 1682, 1858. UF 34815, 42550. UMMZ 107600, 121121–27. Caicos Islands: UF 49423.

Trachemys scripta scripta and Trachemys scripta

elegans — United States: MES 136, 862, 1436, 1710, 1717 (+5 uncataloged). USNM 51358-60, 83173-79, 83184-86, 91308.

Trachemys scripta ssp. — Mexico: AMNH 70722, 94558, 103784–87. JBI field series 85–115, 85–116, 85–189, 85–196. MES 107–08, 129. USNM 30746, 46281, 51068, 66198. Guatemala: AMNH 71614, 72606. USNM 51876, 71429. Honduras: AMNH 70567. USNM 129587–88. Nicaragua: AMNH 12413–14, 66148, 115654–55. Panama: USNM 54085, 54088. South America: MES 1711 (+1 uncataloged).

Pseudemys alabamensis — AMNH 10767. MCZ 1659-61, 1663, 1898. MCZ 1659-61, 1663, 1898.

Pseudemys nelsoni — AMNH 75640. MCZ 54131, 54684. MES 1689–90, 1709. UMMZ 127059–60

Pseudemys rubriventris — AMNH 71276, 71280, 71282, 71293, 76175, 79132, 71934, 80218, 81869, 90641—42, 90644. CM 34409, 37272, 39672, 45188. FMNH 22137. MCZ 1666, 1671, 1674, 1677, 12877, 76679, 157828. MES 132, 1712.

Pseudemys floridana — AMNH 50985, 64156, 69899, 75641, 110189. MCZ 1635, 1651, 19179, 46221–22. FMNH 8222, 22074. UMMZ 12937, 44976, 130081.

Pseudemys texana — AMNH 111960. MCZ 46483. MES 75, 1702. UMMZ 133836, 154982. USNM 26424, 26438, 78518.

Pseudemys concinna — AMNH 69901–02, 69905–06, 69908, 75649, 80233. CM 60560. CM (field series) 38068–69, 38071–72, 38077, 38107, 38132, 38134, 38155. MCZ 1636–39, 1642, 1648–50, 1652, 1664, 12764, 29080–81, 42372, 43030, 54675, 54679–80. FMNH 22138, 22473. MES 489, 526, 528–29, 863, 865, 870, 1694, 1713–14. UMMZ 88488, 101754, 127058, 128176, 129385. USNM 8920, 9659, 15990, 60895, 79449, 86728, 102679, 104397. WVBS 3155, 3965, 4093.

REFERENCES

Adler, K. K.

1968. Synonymy of the Pliocene turtles *Pseudemys hillii* Cope and *Chrysemys limnodytes* Galbreath. J. Herpetol. 1: 32–38.

Agassiz, L.

1857. Contributions to the natural history of the United States of America, first monograph. Vol. 1, part 2, North American Testudinata. Boston: Little, Brown, 643 pp.

Arnold, E. N.

1981. Estimating phylogenies at low taxo-

nomic levels. Z. Zool. Syst. Evolutionsforsch. 19: 1-35.

Barbour, T.

1914. A contribution to the zoogeography of the West Indies, with special reference to amphibians and reptiles. Mem. Mus. Comp. Zool. 44: 209-259.

1935. A new Pseudemys from Cat Island, Bahamas. Occas. Pap. Boston Soc. Nat. Hist. 8: 205-206.

Barbour, T., and A. F. Carr

1938. Another Bahamian freshwater tortoise. Proc. N. Engl. Zool. Club 17: 75-76.

1940. Antillean terrapins. Mem. Mus. Comp. Zool. 54: 381-415.

 Terrapin from Grand Cayman. Proc. N. Engl. Zool. Club 18: 57-60.

Barbour, T., and B. Shreve

1935. Concerning some Bahamian reptiles, with notes on the fauna. Proc. Boston Soc. Nat. Hist. 40(5): 347-366.

Barr, A. J., J. H. Goodnight, J. P. Sall, and J. T. Helwig

1976. SAS user's guide. Raleigh: SAS Institute Inc.

Baur, G.

1893. Two new species of North American Testudinata. Am. Nat. 27: 675-676.

Bickham, J.

1980. Chrysemys decorata. Cat. Am. Amphib. Reptiles 235: 1–2.

Bickham, J., and R. J. Baker

1976a. Karyotypes of some neotropical turtles. Copeia 1976(4): 703–708.

1976b. Chromosome homology and evolution of emydid turtles. Chromosoma 54: 201-219.

Boulenger, G. A.

1889. Catalogue of the chelonians, rhynchocephalians and crocodiles in the British Museum (Natural History). London: Taylor and Francis.

Campbell, D. G.

1978. The ephemeral islands, a natural history of the Bahamas. New York: Macmillan.

Cochran, D. M.

1941. The herpetology of Hispaniola. U.S. Natl. Mus. Bull. 177: 1-398.

Cocteau, J. T., and G. Bibron

1843. Reptilia. *In* Ramon de la Sagra's Histoire physique, politique et naturelle de l'ile de Cuba. Paris.

Craton, M.

A history of the Bahamas. London: Collins Press.

Danforth, S. T.

1925. Porto Rican herpetological notes. Copeia 147: p. 79.

Davis, J. D., and C. G. Jackson

1973. Notes on the courtship of a captive male *Chrysemys scripta taylori*. Herpetologica 29(1): 62-64.

DeSola, R., and A. M. Greenhall

1932. Two species of terrapin in Cuba: the Antillean terrapin, *Pseudemys rugosa*, and the Cuban terrapin, *Pseudemys decussata*. Copeia 1932(3): 129-133.

Dixon, J. R.

1987. Amphibians and reptiles of Texas. College Station: Texas A&M Univ. Press.

Dixon, W. J.

1977. BMD biomedical computer programs. Berkeley: Univ. California Press.

Duméril, A. H. A.

1861. Catalogue des poissons, reptiles de la collection du Museum d'Histoire Naturelle de Paris. Arch. Mus. Natl. Hist. Nat.. Paris 10: 435-445.

Duméril, A. H. A., and G. Bibron

1835. Erpétologie générale ou histoire naturelle complète des reptiles, vol. 2, 680 pp.

Dunson, W. A., and M. E. Seidel

1986. Salinity tolerance of estuarine and insular emydid turtles (*Pseudemys nelsoni* and *Trachemys decussata*). J. Herpetol. 20(2): 237-245.

English, T. M. S.

1912. Some notes on the natural history of Grand Cayman. Handbook of Jamaica for 1912, pp. 598-600.

Garman, S.

1888. Reptiles and batrachians from the Caymans and the Bahamas. Bull. Essex Inst. 20: 101-113.

Garrido, O. H., and M. L. Juame

1984. Catalogo descriptivo de los anfibios y reptiles de Cuba. Donana, Acta Vertebrata 11(2): 5-128.

Gill, F. B.

1978. Zoogeography in the Caribbean. Acad. Nat. Sci. Philadelphia, Spec. Publ. 13: 128 pp.

Gmelin, J. F.

1788-89. Caroli a Linné, Systema naturae per regna tria natural, secondum classes, ordines, genera, species cum characteribus differentiis, synonymis, locis. 1(3): 1038-1516.

Gosse, P. H.

1851. A naturalist's sojourn in Jamaica. London: Longman.

Grant, C.

1931. Notes on *Pseudemys stejnegeri* Schmidt. Copeia 1931(3): 142.

- 1932. The herpetology of Vieques Island. J. Dep. Agric. Puerto Rico 16: 37-39.
- 1940. The herpetology of the Cayman Islands. Bull. Inst. Jamaica Sci. Ser. 2: 65 pp.
- 1948. Pseudemys in the West Indies. J. Entomol. Zool. 40: 26-28.
- Grant, C., and C. R. DeSola
 - 1934. Antillean tortoises and terrapins: distribution, status and habits of *Testudo* and *Pseudemys*. Copeia 1934(2): 73–79.
- Gray, J. E.
 - 1831. Synopsis reptilium. London: Treuttel, Wurz Co.
 - 1844. Catalogue of the tortoises, crocodiles and amphisbaenians in the collection of the British Museum, London.
 - 1870. Supplement to the catalogue of shield reptiles in the collection of the British Museum. Part I, Testudinata (tortoises). London: Taylor and Francis.
- Groombridge, B.
 - 1982. The IUCN Amphibia-Reptilia red data book Part I, Gland. Switzerland: IUCN.
- Gundlach, J.
 - 1881. Apuntas para la fauna Puerto-riquena. Anal. Soc. Esp. Hist. Nat. 10: 305-317.
- Guyer, C., and J. M. Savage
 - 1986. Cladistic relationships among anoles (Sauria: Iguanidae). Syst. Zool. 35: 509–531.
- Hay, O. P.
 - 1908. The fossil turtles of North America. Carnegie Inst. Washington Publ. 75.
- Hedges, S. B.
 - 1982. Caribbean biogeography: implications of recent plate tectonic studies. Syst. Zool. 31(4): 518-522.
- Henderson, R. W., and A. Schwartz
- 1984. A guide to the identification of the amphibians and reptiles of Hispaniola.

 Milwaukee Public Mus. Spec. Publ. Biol.

 Geol. 4: 1-70.
- Hodsdon, L. A., and J. F. W. Pearson
 - 1943. Notes on the discovery and biology of two Bahamian freshwater turtles of the genus *Pseudemys*. Proc. Florida Acad. Sci. 6(2): 17-23.
- Inchaustegui Miranda, S. J.
 - 1976. Las tortugas Dominicanas de agua dulce Chrysemys decussata vicina y Chrysemys decorata (Testudinata, Emydidae). Anu. Acad. Cien. República Dominicana.
- Iverson, J. B.
 - 1985. Checklist of the turtles of the world with English common names. Soc. Study Amphib. Reptiles Herpetol. Circ. 14: 1–14.

- Jackson, C. G., and J. D. Davis
 - 1972. A quantitative study of the courtship display of the red-eared turtle, *Chrysemys scripta elegans* (Wied.). Herpetologica 28: 58-64.
- Khudoley, K. M., and A. A. Meyerhoff
 - 1971. Paleogeography and geological history of Greater Antilles. Geol. Soc. Am. Mem. 129: 1-199.
- Kim, J. O.
 - 1975. Factor analysis. In N. H. Nie et al. (ed.), SPSS statistical package for the social sciences, pp. 468-514. New York: McGraw-Hill.
- Lacépède, B. G. E.
 - 1788. Histoire naturelle des quadrupedes ovipares et des serpens. Synopsis Methodica 2: 443-462.
- Legler, J. M.
 - 1960. A new subspecies of slider turtle (*Pseudemys scripta*) from Coahuila, Mexico. Univ. Kansas Publ. Mus. Nat. Hist. 13: 73–84.
 - 1987. The genus *Pseudemys* in Mexico. Abstract, Joint Annual Meeting Soc. Study Amphib. Reptiles Herpetol. League, p. 106.
- Legler, J. M., and R. G. Webb
 - 1970. A new slider turtle (*Pseudemys scripta*) from Sonora, Mexico. Herpetologica 26: 157–168.
- Leviton, A. E., R. H. Gibbs, E. Heal, and C. E. Dawson
 - 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3): 802–832.
- Lynn, W. G., and C. Grant
- 1940. The herpetology of Jamaica. Bull. Inst. Jamaica 2: 1–48.
- MacFadden, B. J.
 - 1980. Rafting mammals or drifting islands?: biogeography of the Greater Antillean insectivores *Nesophontes* and *Solenodon*. J. Biogeogr. 7: 11-22.
 - 1981. Comments on Pregill's appraisal of historical biogeography of Caribbean vertebrates: vicariance, dispersal, or both? Syst. Zool. 30(3): 370–372.
- Malfait, B. T., and M. G. Dinkelman
 - 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean plate. Bull. Geol. Soc. Am. 83: 251–272.
- McCoy, C. J.
 - 1968. The development of melanism in an Oklahoma population of *Chrysemys*

scripta elegans (Reptilia-Testudinidae). Proc. Oklahoma Acad. Sci. 47: 84-87.

McDowell, S. B.

1964. Partition of the genus Clemmys and related problems in the taxonomy of aquatic Testudinidae. Proc. Zool. Soc. London 143: 239-279.

Mertens, R.

 1939. Herpetologische Ergebnisse einer Reise nach der Insel Hispaniola, Westindien. Abh. Senckenberg. Naturforsch. Ges. 449: 1–84.

Mertens, R., and H. Wermuth

1955. Die rezenten Schildkröten, Krokodile und Brückenechsen. Zool. Jahrb. Abt. Syst. 83: 323–440.

Mittleman, M. B.

1947. The allocation of *Testudo rugosa* Shaw. Herpetologica 3: 173–176.

Moll, E. O., and J. M. Legler

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

Obst, F. J.

1983. Schmuckschildkröten, die gattung *Chrysemys*. Wittenberg Lutherstadt, Germany: A. Ziemsen Verlag.

Parsons, T. S.

1960. The structure of the choanae of the Emydidae (Testudines, Testudinidae). Bull. Mus. Comp. Zool. 123: 113-127.

Perfit, M. R., and B. C. Heezen

1978. The geology and evolution of the Cayman Trench. Bull. Geol. Soc. Am. 89: 1155–1174.

Poey, F.

1865-68. Repertorio fisico-natural de la Isla de Cuba 2(9): p. 204.

Poinar, G. O., Jr., and D. C. Cannatella

1987. An Upper Eocene frog from the Dominican Republic and its implication for Caribbean biogeography. Science 237: 1215-1216.

Pregill, G.

1981a. Late Pleistocene herpetofaunas from Puerto Rico. Misc. Publ. Univ. Kansas Mus. Nat. Hist. 71: 1–72.

1981b. An appraisal of the vicariance hypothesis of Caribbean biogeography and its application to West Indian terrestrial vertebrates. Syst. Zool. 30: 147-155.

Pritchard, P. C. H.

1979. Encyclopedia of turtles. Neptune, N.J.: T. F. H. Publish., Inc.

Pritchard, P. C. H., and P. Trebbau

1984. The turtles of Venezuela. Soc. Study Amphib. Reptiles Contrib. Herpetol. 2: 1-403.

Rivero, J. A.

1978. Los anfibios y reptiles de Puerto Rico.
Universidad de Puerto Rico Editorial
Universitaria, Puerto Rico.

Rosen, D. E.

1975. A vicariance model of Caribbean biogeography. Syst. Zool. 24: 431–464.

Sampedro Marin, A., V. Berovides Alvarez, A. Perera Puga, and P. Lorente Diaz

1983. Datos morfométricos y ecológicos de *Pseudemys decussata* (Reptilia: Chelonia) en la Ciénaga de Zapata, Cuba. Reporte de investigacion del instituto de Zoologia. Academia de Ciencias de Cuba 8: 1-15.

Schmidt, K. P.

1921. Notes on the herpetology of Santo Domingo. Bull. Am. Mus. Nat. Hist. 44(2): 7-20.

1928. Amphibians and land reptiles of Porto Rico with a list of those reported from the Virgin Islands. New York Acad. Sci. Scient. Survey P.R. and V.I. 10: 1–160.

Schwartz, A.

1968. The geckos (*Sphaerodactylus*) of the southern Bahama Islands. Ann. Carnegie Mus. 39: 227-271.

1978. Some aspects of the herpetogeography of the West Indies. *In F. B. Gill (ed.)*, Zoogeography in the Caribbean, the 1975 Leidy Medal Symposium. Acad. Natur. Sci. Philadelphia Spec. Publ. 13: 31-51.

Schwartz, A., and R. W. Henderson

1985. A guide to the identification of the amphibians and reptiles of the West Indies exclusive of Hispaniola. Milwaukee Public Museum.

Schwartz, A., and R. Thomas

1975. A checklist of West Indian amphibians and reptiles. Carnegie Mus. Nat. Hist. Spec. Publ. 1: 1-216.

Seidel, M. E.

1981. A taxonomic analysis of pseudemyd turtles (Testudines: Emydidae) from the New River and phenetic relationships in the subgenus *Pseudemys*. Brimleyana 6: 25–44.

Seidel, M. E., and M. D. Adkins

1987. Biochemical comparisons among West Indian *Trachemys* (Emydidae: Testudines). Copeia 1987(2): 485–489.

Seidel, M. E., and S. J. Inchaustegui Miranda

1984. Status of the trachemyd turtles (Testudines: Emydidae) on Hispaniola. J. Herpetol. 18(4): 468-479.

Seidel, M. E., and D. R. Jackson

1989. Evolution and fossil relationships of slider turtles. *In J. W. Gibbons (ed.)*,

The life history and ecology of the slider turtle. Smithsonian Publications, in press.

Seidel, M. E., and H. M. Smith

1986. Chrysemys, Pseudemys, Trachemys (Testudines: Emydidae): did Agassiz have it right? Herpetologica 42(2): 242– 248.

Siebenrock, F.

1909. Synopsis der rezenten Schildkröten. Zool. Jahrb. Suppl. 10(3): 429-618.

Shaw, G.

1802. General zoology, or systematic natural history. London: G. Kearsley.

Stejneger, L.

1904. The herpetology of Porto Rico. Rep. U.S. Natl. Mus. 1902: 553-724.

Strauch, A.

1862. Chelonologische Studien, mit besonderer Beziehung auf die Schildkrötensammlung der kaiserlichen Akademie der Wissenschaften zu St. Petersburg. Mem. Acad. Imp. Sci. St. Petersburg ser. 7, 5(7): 1–196.

Suckow, F. W. L.

1798. Anfangsgrunde einer naturgeschichte der Thiere, vol. 3, p. 40.

Ward, J. P.

1984. Relationships of chrysemyd turtles of North America (Testudines: Emydidae). Spec. Publ. Texas Tech Mus. 21: 1-50.

Weaver, W. G., Jr., and J. S. Robertson 1967. A re-evaluation of fossil turtles of the Chrysemys scripta group. Tulane Stud. Geol. 5(2): 53–66.

Weaver, W. G., Jr., and F. L. Rose

1967. Systematics and fossil history of the genus *Chrysemys*. Tulane Stud. Zool. 14: 63–73.

Wermuth, H., and R. Mertens

1961. Schildkröten, Krokodile, Brückenechsen. Jena, Germany: VEB Gustav Fischer Verlag.

1977. Liste der rezenten Amphibien and Reptilien: Testudines, Crocodylia, Rhynchocephalia. Berlin: Das Tierreich.

Wiley, E. O.

1981. Phylogenetics, the theory and practice of phylogenetic systematics. New York: Wiley.

Williams, E. E.

1956. Pseudemys scripta callirostris from Venezuela with a general survey of the scripta series. Bull. Mus. Comp. Zool. 115: 145–160.

1964. Remarks on the relationships of the reptiles and amphibians of the Cayman Islands. Occas. Pap. Mollusks Mus. Comp. Zool. 2(31): 383–384.

1969. The ecology of colonization as seen in the zoogeography of anoline lizards in small islands. Q. Rev. Biol. 44(4): 345–389.

Zug, G. R.

1969. Fossil chelonians, *Chrysemys* and *Clemmys*, from the Upper Pliocene of Idaho. Great Basin Nat. 29(2): 82–87.

