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The Genus *Pseudemys* in Mesoamerica: Taxonomy, Distribution, and Origins

Abstract

Pseudemys is the most diverse and wide-ranging genus in an emydine group that includes *Graptemys*, *Chrysemys*, and *Malaclemys*. *Pseudemys scripta* (Schoepff) 1792 is treated as a polytypic species with 17 or 18 subspecies and a latitudinal range of 77 degrees. At least 12 subspecies occur in Mesoamerica. This study is based on 2,308 specimens; 29 variables were analyzed. Brief accounts of taxonomy and distribution are given for each subspecies. Populations in the Río Nazas of northern Mexico and the Lago de Nicaraqua are described as new. All matters pertaining to distribution are considered by natural drainage systems and their recent histories. The distribution of *P. scripta* in Mesoamerica is explained as a series of dispersal events ranging from simple dispersal along coastal plains to headwater dispersal across continental divides. Distributions appear to be largely natural, but humans could have caused or influenced almost any of the events hypothesized.

Pseudemys scripta has crossed the Mesoamerican landmass five times, as follows: from the Atlantic to the Pacific via the Rio Grande and the interior basins of northern Mexico, via the Isthmus of Tehauntepec, via the Río San Juan and Lake Nicaragua, and via the Isthmus of Panama; and from the Pacific to the Atlantic, from the Río Tuira of Panama to the Río Atrato of Colombia. Relatively recent colonization and differentiation of *P. scripta* in Mesoamerica is proposed (Pleistocene or later). The following three groups of *scripta*-like taxa are proposed: the three subspecies in the United States; Mesoamerican populations; and Antillean populations. In the U.S. subspecies, males are much smaller than females and have greatly elongated foreclaws, which are used in a complex Liebespiel. Mesoamerican populations lack these sexually dimorphic characters and the Liebespiel. The dimorphic characters and the courtship behavior exhibited by U.S. subspecies are considered to be precopulatory isolating mechanisms in a zone where more than one species of *Pseudemys* (plus other striped emydines) are sympatric. *Pseudemys scripta* is the only striped emydine south and west of the Rio Grande.

Introduction

The Northern Hemisphere emydine genera *Graptemys*, *Malaclemys*, *Pseudemys*, and *Chrysemys* seem to be closely related (the *Chrysemys* complex of McDowell, 1964). I refer to this assemblage hereinafter as the *Chrysemys* group; the group excludes *Deirochelys*, and I consider *Chrysemys* to be monotypic (*Chrysemys picta*). These genera share most of the following characters: pale stripes on the soft skin; a pattern of pale ocelli, whorls, or vertical bars on the lateral scutes; a dusky, usually concentric plastral figure; distinct and extreme patterns of sexual dimorphism (adult size, foreclaws, head size, melanism); mating behavior often complex; regular thermoregulatory basking (Moll and Legler, 1971; Ernst and Barbour, 1972; pers. obs.). *Pseudemys* is the most diverse and widely distributed of these genera. One of its species, *Pseudemys scripta*, is remarkable in ranging over 77 degrees of latitude and nearly encompassing the latitudinal range of all other New World emydines (*Emydoidea* and parts of *Clemmys* and *Chrysemys* being the exceptions).

The objective of this study was a stable, natural classification of *Pseudemys scripta*. My emphasis was on taxonomic research and zoogeography rather than on nomenclatural change. This account is prepared as general information, not as a scientific monograph. My approach to this problem has been deliberate in the interest of thoroughness; this has made the work of compilers difficult. We must all be grateful to Hobart and Rosella Smith (1979) for the arduous job of compiling keys, synonymies, and references to the turtles of Mexico. I have concentrated on relationships and zoogeography.

In my early days as a student I heard dark mutterings and witnessed a lot of hand waving about "difficult" taxonomic groups and about not having enough "material." A "difficult group" seemed to have the following characteristics: (1) no one knew much about it, (2) one couldn't learn much about it by looking in specimen jars, (3) finding and studying the animals required a lot of work. In the case of turtles, systematic research often involves starting almost de novo by gathering the necessary collections. I did so for Mesoamerican *Pseudemys*.

In 1958 Wendell L. Minckley and I visited the basin of Cuatro Ciénegas, Coahuila, in search of an aquatic box turtle (*Terrapene coahuila*) and found that most of the aquatic organisms in the basin were endemic (Minckley, 1969). Among these was *Pseudemys scripta taylori*. This taxon was obviously part of the "*scripta* series" we knew in the United States, but relating the new taxon to the rest of the group was an ordeal because *Pseudemys scripta* had not been adequately studied. It was soon evident that *P. scripta* extended far into Mesoamerica. I date the present study from that time (Legler, 1960b).

The "problems" of generic nomenclature are not addressed here. Seidel and Smith (1986) provide the most

recent review of the subject. This study deals with the group I recognize as a single polytypic species, *Pseudemys scripta* (Schoepff) 1792, as outlined in Moll and Legler (1971).

Materials and Methods

The study is based on 2,308 specimens for which complete data were available (Table 7.1). The 29 variables analyzed were carapace length (as a raw datum), 3 stripe character states, and 25 measurements expressed as percentages of carapace length. Early hypotheses were formed with the aid of simple descriptive statistics before the advent of computers. Multidiscriminant analysis was used in the final stages; in nearly all cases the early hypotheses were congruent with the final analyses. Computer analysis saved time but produced no surprises.

DATA STORAGE

All data used in this study have been stored (raw and transformed) in ASCII files at the University of Utah.

Table 7.1. Summary of specimens examined

Population	Male	Female	Immature	Total
Pseudemys scripta				
scripta	12	14	19	45
troosti	5	5	5	15
elegans	106	73	279	458
elegans/taylori	6	6	7	19
taylori	51	62	15	128
gaigeae	16	23	11	50
hartwegi	7	13	14	34
hiltoni	30	14	10	54
nebulosa	7	5	7	19
yaquia	15	5	5	25
ornata	17	21	11	49
grayi	13	22	22	57
elegans/cataspila	2	2	0	4
cataspila	44	17	15	76
venusta	224	238	108	570
emolli	31	36	39	106
GDULCE	5	25	24	54
CAPAC	46	48	32	126
Río Atrato	0	1	1	2
callirostris	1	2	22	25
dorbigni	0	2	4	6
P. felis	6	4	10	20
P. malonei	6	12	0	18
P. granti	7	6	8	21
P. terrapen	18	12	20	50
P. vicina/decorata	3	5	2	10
P. decorata	6	4	14	24
P. vicina	16	8	14	38
P. decussata				
angusta	10	6	0	16
decussata	66	87	38	191
plana	4	2	2	8
P. concinna	5	6	12	23
P. floridana	6	3	5	14
P. nelsoni	3	3	4	10
Total	794	792	779	2,365

These files and the collections of specimens will be available to other workers when the study is completed. The data used in this study can be tested or reinterpreted with a minimum of effort. Specimens and data now at UU will eventually be transferred to one or more public museums.

MEASUREMENTS

Terminology for scutes and bones follows Moll and Legler (1971). Measurements were designed to express what I could detect with ordinary human senses and to be repeatable. Measurement techniques are shown in Figure 7.1. Basic measurements express the size of the smallest rectilinear box into which the shell would fit. A videotape describing turtle measurements is available from the author (Legler, 1982). Data were rejected for any structure that was broken or anomalous.

The following is a list of measurements, other data, and their abbreviations: LC, length of carapace; WC, width of carapace; LP, length of plastron, maximal; WPHP, width

a.

b.   c.

FIGURE 7.1. a–c, lateral, dorsal, and ventral views of a *Pseudemys scripta* shell, showing method of measurement. Note that a single measurement expressed the mean length of right and left plastral scutes. Width of central scutes was measured from points common to three scutes. Central lengths were measured along the midline. Carapace and plastron lengths were maximal and measured in a plane usually tangential to the true frontal plane. *AB*, length of abdominal scute; *BR*, length of bridge; *HT*, height of shell, maximal; *LC*, length of carapace; *LC1*, length of C1 (first central scute); *LC3*, length of C3; *LP*, length of plastron; *WC1A*, width of C1, anterior; *WC1P*, width of C1, posterior; *WC4*, width of C4; *WPHP*, width of plastron, humeropectoral seam; *WPMF*, width of plastron, midfemoral scute.

of plastron, humeropectoral seam; WPMF, width of plastron, midfemoral scute; HT, height of shell, maximal; GUL, length of gular scute; HUM, length of humeral scute; PEC, length of pectoral scute; AB, length of abdominal scute; FEM, length of femoral scute; AN, length of anal scute; LC1, length of C1 (first central scute); LC2, length of C2; LC3, length of C3; LC4, length of C4; LC5, length of C5; WC1A, width of C1, anterior; WC1P, width of C1, posterior; WC2, width of C2; WC3, width of C3; WC4, width of C4; WC5, width of C5; WH, width of head, maximal, at tympanum; FING, length of ungual phalanx, third digit, manus; BR, length of bridge (mean of right and left); POSEYE, postorbital stripe connected to eye? (+ or −); POSNCK, postorbital stripe connected to neck stripe? (+ or −); MANDNCK, mandibular stripe connected to neck stripe? (+ or −).

STATISTICAL ANALYSIS

Final analysis was done with various BMDP statistical software programs (Version 1982) on a mainframe computer (see Dixon, 1983). The programs most used were BMDP7M, stepwise discriminant analysis; BMDP3D, comparison of two groups with t tests; and BMDP7D, description of groups with histograms and analysis of variance. BMDP7M will not tolerate incomplete data sets. Missing data points resulted mainly from the rejection of measurements from broken or deformed parts. Missing data were estimated with BMDPMD. Spot checks of estimated data corresponded almost exactly to my own interpolative method of estimation with specimens ranked by population, sex, and carapace length. My own tolerance of estimated data was inversely proportional to the need for specimens in the sample. Percentages of estimated values higher than 10% were tolerated only to avoid eliminating a population from the analysis. The alternative was to reject the character; this accounted for the removal of several characters from the original data base. Thus it was possible to use the same combination of characters for all populations of *Pseudemys* considered.

Analyses of adults were done separately by sex; the analysis was repeated for all adults if the results were not significantly different between sexes (this was common). Statistical comparisons of immature specimens have been avoided in recent turtle studies (Berry, 1978; Iverson, 1981). I used juveniles in some analyses because (1) some former studies of *Pseudemys scripta* (Müller, 1940; Williams, 1956) were based substantially on young turtles and (2) at least some juveniles are available from nearly all geographic regions, whereas there are many gaps in the availability of adults. Carapace length and finger length were excluded from the analysis of juveniles.

Data on stripes were "yes or no" character states: connection of postorbital stripe to the eye or to a neck stripe (expressing degree of isolation of postorbital mark), and
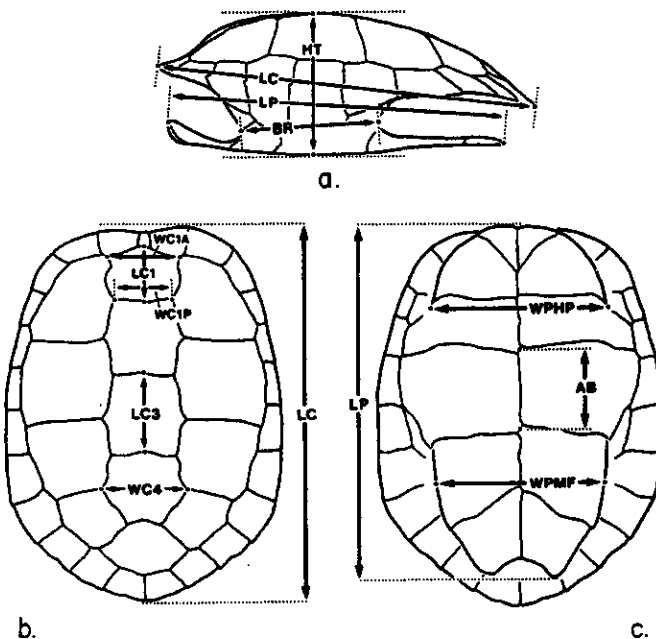
connection of mandibular stripe to a neck stripe. These character states were recorded for each of the pertinent stripes on each side but were ultimately expressed in a manner that indicated a connection was present on one or both sides. These stripe character states, although qualitatively different from body measurements, were included in the multidiscriminant analyses because (1) they are important in my own visual discrimination of the populations and (2) they are probably used by the turtles in the same way (see Conclusions, below).

Measurements were also made of isolated stripes or expansions of the postorbital stripe whether isolated or not. These were not used in the main analysis because they were not available for some populations. However, they were useful in diagnosing some subspecies.

On all BMDP7M plots there are outliers that distort the cluster and the mean. Outliers were removed if they resulted from anomaly or error, but most outliers were normally exceptional individuals (e.g., the largest *P. s. venusta*, the smallest male *P. s. cataspila*, etc.). Such specimens were left in the data base.

a.   b.

FIGURE 7.2.   Head striping in *Pseudemys:* a, lateral and ventral views of derived conditions; b, lateral and ventral views of hypothesized ancestral condition of continuous stripes. All stripe patterns in *Pseudemys* can be derived by interruptions, obliterations, and fusions of the stripes shown here. Stripes mentioned in the text are identified: *M*, mandibular; *PO*, postorbital; *POC*, primary orbitocervical; *S*, symphyseal.

LOCALITIES

Specific localities (although they exist) are avoided in this chapter; distributions are couched in the context of drainage systems and known place names on easily available maps. Latitudes (N) and longitudes (W) are abbreviated for easy reference. In a few cases, actual coordinates are given (e.g., lat. 11-4, long. 68-15), but more often a single meridian or parallel is given to signify where that line intersects the coastline or stream in question. The easiest way to actually locate localities is on World Aeronautical Charts (WAC) or Operational Navigational Charts (ONC), both of which are 1:1,000,000. Most of the Mexican localities are listed in Smith and Smith (1979).

Mesoamerica, for purposes of this study, begins just south of the U.S.-Mexican border and extends approximately to the Río Atrato of northern Colombia. The northern political boundaries are congruent with a major faunal transition.

COLOR AND PATTERN

STRIPES.   Pale stripes on the soft skin range from yellow to cream. They are most regular and evident on the head and neck. The stripes appear in all members of the *Chrysemys* group and seem to be homologous within that group. Similar stripes in other emydids may have evolved independently (e.g., *Ocadia*).

Stripes vary in distinctness by virtue of width, degree of contrast with ground color, and the extent to which they are outlined in black. Between the main or primary stripes there are lesser numbers of secondary and tertiary stripes.
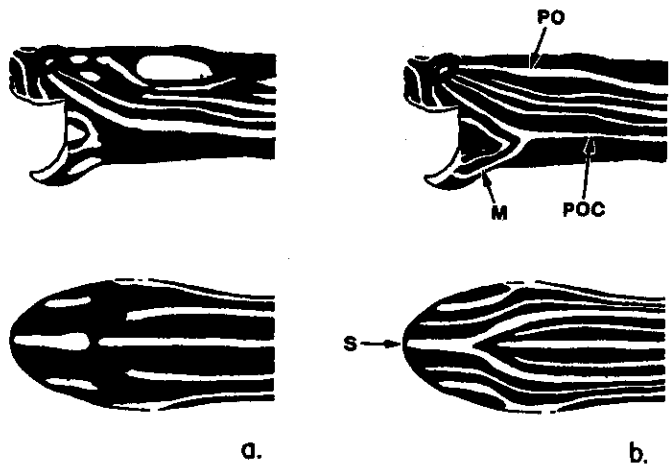
The basic and presumably ancestral pattern is that of unbroken, parallel stripes, extending from the face, snout, and mouth to the base of the neck (Fig. 7.2). Substantial modification of this plan occurs when stripes fuse with other stripes or are fragmented, when isolated parts assume various shapes, and when stripes or derived fragments acquire a color other than some shade of yellow (usually red or orange). The degree of pattern fragmentation is low in *P. s. scripta*, *P. s. elegans*, and *P. s. ornata* and very high in *P. s. callirostris*. A survey of stripe patterns appears in Table 7.2.

Isolated, brightly colored, or otherwise distinctive marks in the temporal region seem always to be modifications of the postorbital stripe. In some populations (e.g., *P. s. venusta*) the widened primary orbitocervical becomes the dominant mark on the side of the head. The pale stripes and the dark background can undergo vast ontogenetic changes, becoming completely obliterated or obscured through melanism or fading. Fading reaches its extremes in the Antillean populations but is important also (especially on the throat) in *nebulosa* and other Mesoamerican populations. Extremes of melanism and fading are characteristic of U.S. and Antillean populations but are rare in Mesoamerica. Despite the potential for ontogenetic change, the connections of the stripes do not change with age, and if visible at any stage, they are easily quantifiable and useful.

Stripes may have evolved initially as disruptive markings. Modifications in the basic patterns later evolved as species-specific combinations that may serve as premating isolating mechanisms in zones of sympatry (see Con-

Table 7.2. Stripe patterns in 18 populations of *Pseudemys scripta*

Taxon	Color of POM	N	Eye	Neck	Mand.	Sym.	PI
elegans USA	Red	97	98.6	35.7	84.1	97.1	.789
elegans Rio Grande	Red	154	58.9	6.3	56.8	100.0	.555
taylori	Red	101	27.1	10.4	0.0	86.9	.311
gaigeae	Br. orange	50	0.0	0.0	54.5	100.0	.386
hartwegi	Dk. or. yellow	34	0.0	35.5	0.0	33.3	.172
hiltoni	P. dusky or.	54	17.8	15.6	46.3	50.0	.324
nebulosa	P. dusky or.	18	0.0	0.0	66.7	33.3	.250
yaquia	P. or. yellow	25	76.0	100.0	16.0	68.0	.650
ornata	P. or. yellow	5	40.0	60.0	20.0	80.0	.500
grayi	P. yellow	58	96.9	97.0	9.1	70.0	.683
cataspila	P. or., dk. or. yellow	74	44.3	74.3	24.3	64.9	.520
venusta	P. or. yellow	570	90.9	96.5	15.7	41.8	.615
emolli	P. or. yellow	106	27.4	83.3	17.9	90.5	.548
GDULCE	P. or. yellow	54	100.0	96.2	3.8	38.5	.596
CAPAC	P. or. yellow	126	98.2	97.3	49.6	32.4	.694
Río Atrato	Brick red (1)	2	100.0	100.0	100.0	0.0	.750
callirostris	Reddish or.	25	0.0	47.8	0.0	0.0	.120
dorbigni	Or. yellow (2)	5	80.0	100.0	40.0	100.0	.800

Note: Color of postorbital mark (POM) or expansion and stripe connections is as follows: eye and neck--frequency with which postorbital stripe enters the orbit or joins a neck stripe; "mand." and "sym." indicate whether mandibular stripe and symphyseal stripes join neck stripes. Frequencies apply to joined condition on one or both sides. Ergo data for *hartwegi* show that postorbital mark is always isolated from eye on one or both sides and that symphyseal stripe joins a neck stripe on one or both sides in 33% of specimens examined. PI = pattern integrity, a general expression of disruption of the ancestral pattern of continuous stripes ([sum of four frequencies]/400). Most stripes are broken in *callirostris* (.120), and relatively few are broken in *venusta* (.615). (Personal observation except (1) = Medem, 1962, and (2) = Freiberg, 1967b.) Abbreviations: p., pale; dk., dark; br., bright; or., orange.

clusions, below). However, the distinctive stripe patterns in Mesoamerican populations of *P. scripta* are probably nonadaptive.

SHELL PATTERN. Although shell patterns can be used to characterize populations, they are not easy to quantify and were not used in the statistical analysis.

Carapace. The basic carapace pattern consists of ocelli on the lateral and marginal scutes and a variable pattern on the central scutes. The pale marks of the carapace range from yellow through pinkish orange to dark orange. The lateral ocelli vary in shape but are usually vertical ellipses. Ocelli consist of two to four concentric rings that vary in their distinctness; there may be one or more side branches in various directions from the peripheral ring. The outermost ring normally becomes the most prominent ring. The ocellar center often becomes a dark bull's-eyelike figure.

There are four lateral ocelli on each side. Each is centered over an intercostal osseous suture, placing it usually on the posterior half of a lateral scute. There are eight costal bones. If we count the nuchal-costal suture as the first intercostal suture (IC1), then the ocelli are centered on even-numbered intercostal sutures. This seems to be constant. The centers of the ocelli vary in their juxtaposition to interlaminal seams because the seams vary in their juxtaposition to the sutures.

Two extremes of carapace pattern are the unmodified ocellar pattern of many Mesoamerican *scripta* and the ver-

tically barred pattern of U.S. *P. scripta. Pseudemys s. elegans* usually has four vertical bars, each of which occurs near the center of a lateral scute and is oriented over the approximate center of an underlying costal bone (i.e., C1, C3, C5, C7). The vertical bars are modifications of the ocellar pattern. In fact, ocelli *and* bars can be observed in many *elegans*. It is clear that the vertical bars are derived from the anterior parts of the ancestral ocelli.

The marginal ocelli are in two series: supramarginal and inframarginal. They are clearly centered on the intermarginal seams. Those on the superior surfaces show a variation and modification similar to the principal lateral ocelli; those below are less complex and more like the plastral pattern. Marginal ocelli seem to be only slightly modified in derived carapace patterns, such as in *P. s. elegans*.

The most common feature of the central scute pattern is a pair of parenthetical marks, one on either side of the middorsal line. These marks may connect in two longitudinal series or form a completely separate pair of marks on each scute. In populations with complex patterns, there is commonly an intricate pattern of triangles, rhomboids, or irregular polygons between the parenthetical marks. A series of straight marks on and parallel to the middorsal line may be emphasized to form a middorsal stripe. Anywhere on the carapace, as on the soft skin, the pattern can be altered and complicated by the intercalation of other pale lines. Some shells have a confusing reticular appearance.
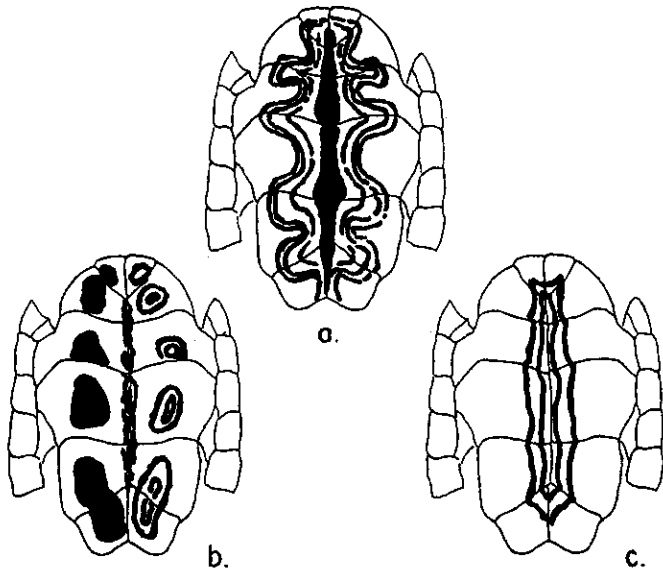
FIGURE 7.3. Plastral pattern in *Pseudemys scripta*. *a*, full "*Chrysemys*" pattern. *b* and *c*, two derived conditions: *b*, composite figure showing isolated whorls on one side and isolated whorls overlaid by solid blotches on the other side; *c*, reduced plastral pattern (e.g., *hartwegi*). Whorls and blotches in *b* occur in *elegans, hiltoni,* and *nebulosa;* the whorls are present at hatching, and the blotches develop later.

Plastron. The basic plastral pattern in *P. scripta* is a dusky, concentric figure, usually lacking sharply defined edges, that is greater than half the plastral area (Fig. 7.3). Whorls or fingerlike projections extend laterally along the interlaminal seams. This basic pattern is most easily seen in juveniles. Some modifications of this pattern are isolation of some or all of the seam-following whorls (e.g., *P. s. elegans, P. decorata*), loss of lateral whorls and narrowing (e.g., some *P. s. venusta*), and extreme fading (e.g., *P. s. scripta, P. terrapen*). The concentric pattern remains visible throughout life in *Chrysemys picta* and *P. s. venusta* with only minor change. Secondary deposition of melanin causes striking changes in some populations, but these changes occur over the concentric pattern. In *P. s. elegans* (rarely in *P. s. scripta*) the isolated whorls are overlaid by solid blotches of melanin, some of which can be seen in a shed scute. The dusky whorls remain clearly visible in the soft tissue beneath the scute, but only if the scute can be removed. This explains the solid black fingerprintlike smudges seen in the subspecies *elegans, hiltoni, nebulosa,* and sometimes *scripta*. A full concentric pattern is here regarded as ancestral; it occurs in all genera of the *Chrysemys* group, all other plastral patterns can logically be derived from it, and it appears in the young of nearly all species of *Pseudemys*.

The ancestral *P. scripta* had a pattern of unbroken yellow stripes on the head and neck, an ocellar carapace pattern, and a dusky, concentric plastral pattern. This pattern is more common in Mesoamerica than elsewhere in the broad range of *P. scripta*.

Results and Discussion

Pseudemys scripta is aquatic. All matters pertaining to geographical distribution are considered by natural drainage systems and their recent histories. Analysis began with the assumption that each drainage system could contain a distinctive population. Progressive amalgamation of smaller populations, assisted by multidiscriminant analysis, formed the assemblages here defined as subspecies.

ACCOUNTS OF SUBSPECIES

There are 17 or 18 subspecies of *Pseudemys scripta;* 17 are considered below. Two are described as new herein. Populations on the Pacific Coast of Central America (CAPAC) may be named when their status is resolved. Mexico has the greatest diversity, with 11 subspecies. My personal knowledge of the three South American subspecies is slight, based on a total of 31 specimens; by comparison, my knowledge is substantial for all populations north and west of the Río Atrato in Colombia. Mesoamerican populations are considered in four geographic groups: the Northern Isolates; the Gulf Coast–Caribbean series; the Pacific Coast series; and the Lake Nicaragua–Pacific series, from Lake Nicaragua and the Pacific Coast of Central America southward to the Isthmus of Panama. South American populations are included simply for completeness.

The following brief accounts of subspecies give current subspecific epithet, literature reference to type description, type locality, a brief statement of geographic distribution, and any qualifying or supporting information necessary to the account. Note that the designation and description of *P. s. hartwegi* is formalized. Figure 7.4 shows the geographic ranges of the subspecies discussed; the map is diagrammatic and does not show individual localities. Smith and Smith (1979) had access to all of the material in my data base. Their localities are accurate to 30 minutes of longitude or latitude (± about 50 km at the Tropic of Cancer).

UNITED STATES POPULATIONS. These three subspecies form a natural group that has differentiated within the United States (excluding *P. s. gaigeae;* see USASCRIP in Conclusions, below). They are not considered in any detail here except to compare them with Mesoamerican populations. Satisfactory summaries of knowledge appear in Pritchard (1979), Ernst and Barbour (1972), and Carr (1952).

P. s. scripta (Schoepff), 1792:16.

Type locality: Restricted to Charleston, South Carolina (Schmidt, 1953).
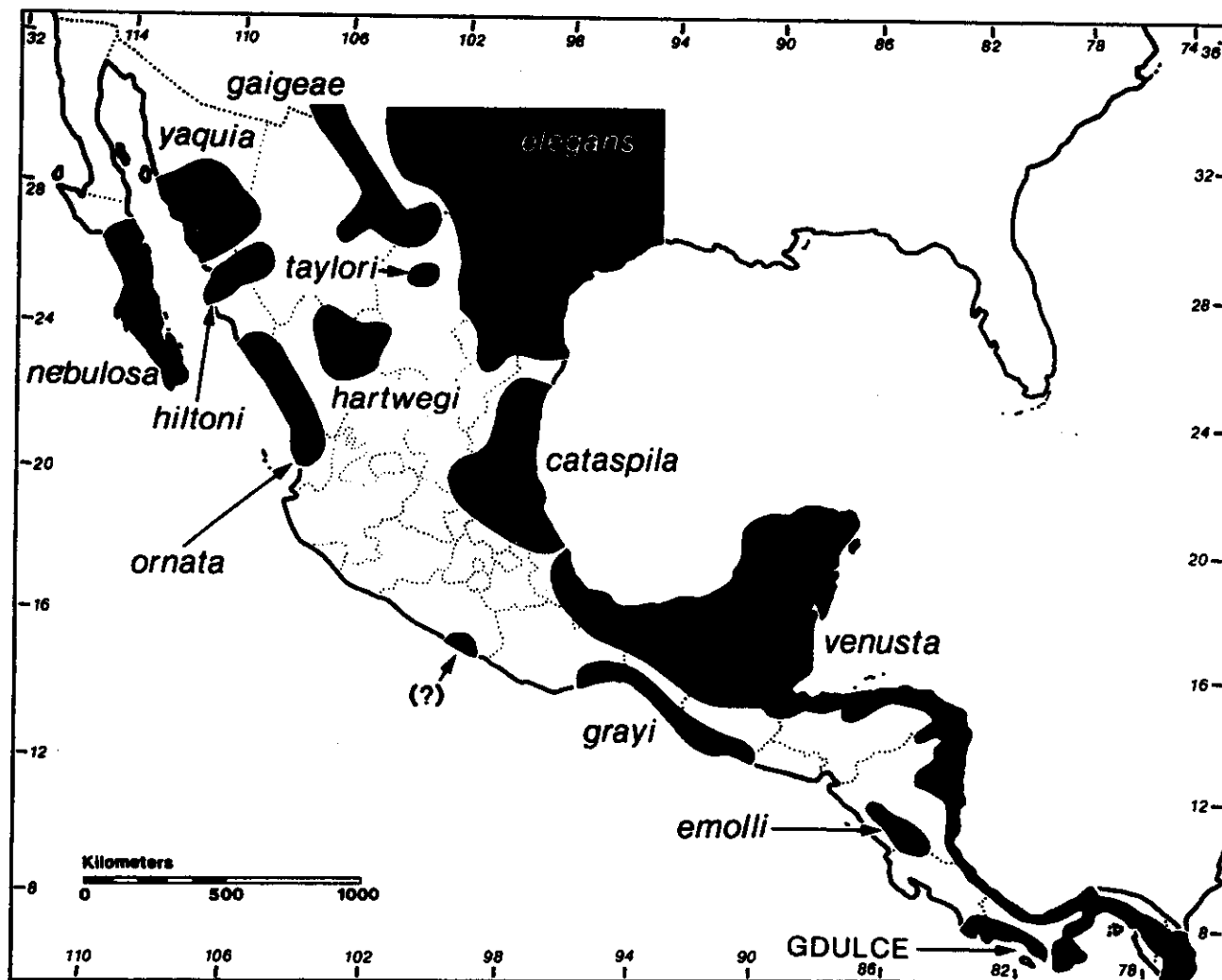
FIGURE 7.4. Distribution of the subspecies of *Pseudemys scripta* in Mesoamerica. The ranges shown are diagrammatic and approximate. No attempt is made to show the U.S. distribution of *elegans*, *scripta*, and *troosti*.

Distribution: Eastern coastal plain, Virginia to northern Florida.

P. s. troosti (Holbrook), 1836:55.

Type locality: Cumberland River, Tennessee.

Distribution: Upper parts of Cumberland and Tennessee rivers from extreme southwestern Virginia to extreme northeastern Alabama.

P. s. elegans (Wied), 1839:213.

Type locality: Fox River, New Harmony, Indiana.

Distribution: In Mexico, the lower Rio Grande and its tributaries. Elsewhere, the Mississippi drainage from southern Michigan to the Gulf of Mexico (eastward to Ohio, Kentucky, Tennessee, and Alabama; westward to Nebraska, Kansas, Oklahoma, and Texas); Gulf drainages between New Orleans and Brownsville; the Pecos drainage.

NORTHERN ISOLATES.

P. s. taylori Legler, 1960b:73–84.

Type locality: 16 km south of Cuatro Ciénegas, Coahuila, Mexico.

Distribution: Basin of Cuatro Ciénegas, Coahuila.

P. s. gaigeae Hartweg, 1939:1.

Type locality: Boquillas, Rio Grande, Brewster County, Texas.

Distribution: Upper Rio Grande above the Big Bend region and Río Conchos drainages of Texas, New Mexico, Chihuahua, and Coahuila.

P. s. hartwegi (see below).

Distribution: Río Nazas drainage of Durango and Coahuila.

GULF COAST–CARIBBEAN SERIES.

P. s. cataspila (Günther), 1885:4.

Type locality: Restricted to Tampico, Tamaulipas, Mexico (Smith and Smith, 1979).

Distribution: Río San Fernando drainage of Tamaulipas (mouth at lat. 24-45) southward to Punta del Morro (lat. 19-55).

Remarks: Little suitable habitat for *Pseudemys* exists between the Río San Fernando and Brownsville. Four juveniles from La Laca (lat. 25-6, long. 98-7) show a great range of variation that includes characters of both *elegans* and *cataspila*.

P. s. venusta (Gray), 1855:24.

Type locality: Honduras or British Honduras (see Smith and Smith, 1979:495).

Distribution: From the beginning of the coastal plain just south of Punta del Morro southward through the lowlands of Veracruz, Oaxaca, and Tabasco to the base of the Yucatán Peninsula; thence across and around the Yucatán Peninsula through northern Guatemala, Quintana Roo, and British Honduras; thence eastward along the Caribbean coast of Guatemala, Honduras, Nicaragua, Costa Rica, and Panama. The population in the Río Chagres drainage (studied by Moll and Legler, 1971) is here included in *venusta*. Populations on the Pacific side of Panama are still under investigation.

Remarks: It is possible that *venusta* has colonized the Pacific coast of Panama and Costa Rica northward to the Golfo Dulce. The population in the Río Atrato of Colombia is placed in *venusta*.

PACIFIC COAST SERIES.

P. s. hiltoni Carr, 1942:1.

Type locality: Guirocoba, Sonora, Mexico, 453 m.

Distribution: Río Fuerte drainage of Sonora and Sinaloa.

P. s. nebulosa (Van Denburgh), 1895:84.

Type locality: Los Dolores, Baja California Sur, Mexico.

Distribution: Baja California Sur southward from San Ignacio.

P. s. yaquia Legler and Webb, 1970:157–168.

Type locality: Río Mayo, Conicarit, Sonora, Mexico.

Distribution: Sonora, Yaqui, and Mayo drainages in Sonora.

P. s. ornata (Gray), 1831:30.

Type locality: Mazatlán, Sinaloa, Mexico.

Distribution: From Culiacán, Sinaloa, southward to the region of Cabo Corrientes.

Remarks: A population near Acapulco may be *ornata* but is not considered in this work. The range of *ornata* may extend northward into the Río Sinaloa drainage.

P. s. grayi (Bocourt), 1868:121.

Type locality: Río Nagualate, Guatemala.

Distribution: From the region of Salina Cruz, Oaxaca, southeastward the coastal lagoons of Oaxaca and Chiapas, along the Pacific coast of Guatemala to just east of Acajutla, El Salvador.

Remarks: *P. s. grayi* seems to flourish in coastal lagoons.

LAKE NICARAGUA–PACIFIC SERIES.

P. s. emolli (see below).

Distribution: Drainage of Lago de Nicaragua and Lago de Managua in Nicaragua and adjacent Costa Rica; an indeterminate distance down the San Juan River.

Remarks: Populations at the source of the San Juan just north of San Carlos are clearly *emolli;* populations near the mouth are clearly *venusta*.

GDULCE (abbreviation for "Golfo Dulce").

Distribution: From the region of Puerto Cortés and Palmar Sur, Costa Rica, definitely to Horconcitos, Panama, on the Golfo de Chiriquí; most closely related to *venusta*.

Remarks: The taxonomic position of this population is still under study.

CAPAC (abbreviation for "Central America Pacific").

Distribution: Pacific side of Panama from the Azuero Peninsula at least to the Isthmian region.

Remarks: This population is under study.

SOUTH AMERICAN POPULATIONS.

P. s. callirostris (Gray), 1855:25.

Type locality: Río Magdalena, Colombia (restricted; see Müller, 1940).

Distribution: Río Magdalena, Río Cauca, and their combined deltas in Colombia eastward to eastern Falcón Province, Venezuela (near Puerto Cabello).

P. s. chichiriviche Pritchard and Trebbau, 1984:37–38.

Type locality: Lago de Tacarigua, Falcón, Venezuela (lat. 11-4, long. 68-15).

Distribution: Small coastal river systems between the Río Tocuyo in Falcón and Morón, Carabobo, Venezuela.

Remarks: No specimens of *P. s. chichiriviche* have been examined.

P. s. dorbigni (Duméril and Bibron), 1835:272.

Type locality: Buenos Aires.

Remarks: I am provisionally placing all remaining populations of South American *P. scripta* in the synonymy of *P. s. dorbigni*.

NEW TAXA.

Pseudemys scripta hartwegi new subspecies
(Fig. 7.5, Tables 7.2–7.6)

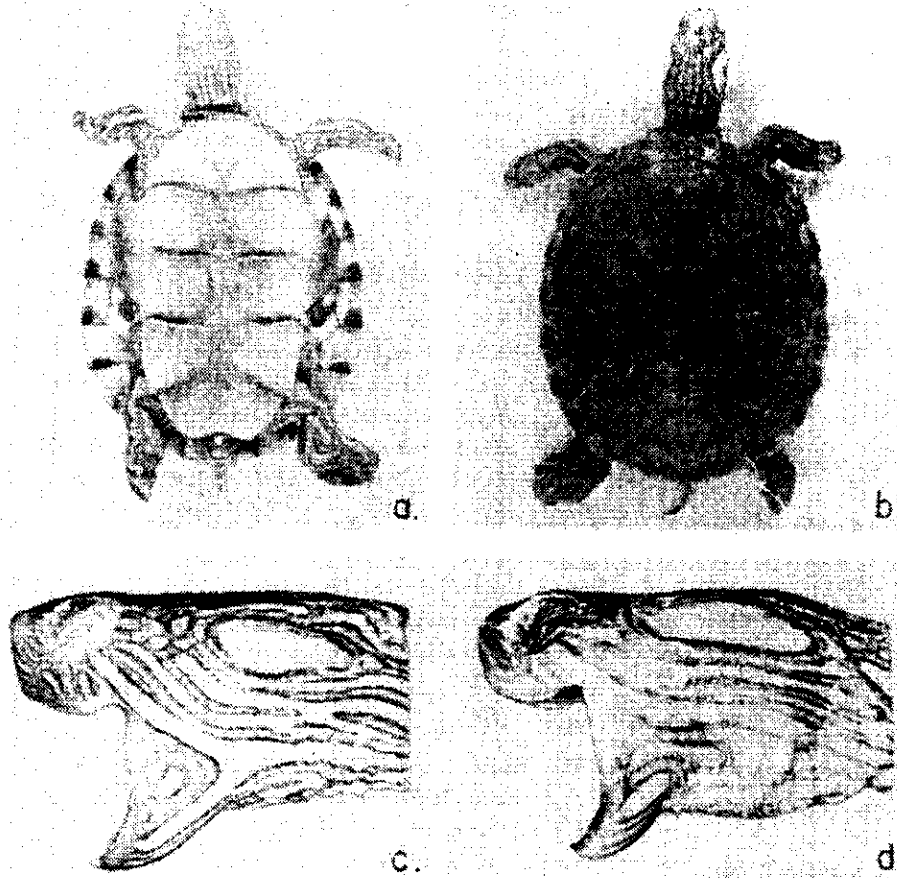*P. s. gaigeae;* Hartweg, 1939 (part).

FIGURE 7.5.   *a* and *b*, ventral and dorsal views of holotype of *Pseudemys scripta hartwegi* new subspecies, UU 3802, carapace length 95 mm; *c*, *P. s. gaigeae*, immature female, KU 51205, Río Conchos, 1.6 km northwest of Ojinaga, Chihuahua; *d*, *P. s. hartwegi*, male paratype, MSU 1140. Both heads are slightly larger than life.

P. s. hartwegi Legler nomen nudum; Smith and Smith, 1979:469.

I first became aware of this taxon in 1959; a description was prepared but was consistently delayed as studies of *Pseudemys* progressed. Hobart Smith and I agreed to the inclusion of this taxon in the work on Mexican turtles (Smith and Smith, 1979:469). It was included as *Pseudemys scripta hartwegi* Legler nomen nudum, in a manner that

would ensure the name was available for my use at a later date.

Holotype: UU 3802, immature; carapace length 95 mm; Río Nazas, 1.2 km east of Presa Lázaro Cardenas, Durango, Mexico. Collected by Roger Conant, 2 October 1961. Whole specimen in alcohol.

Paratypes: Total of 29 specimens, all from Río Nazas drainage. Coahuila: MCZ 4550 female (shell only), 4551 three juveniles, San Pedro [de las Colonias]; USNM

Table 7.3. Relative proportions of head stripes for two new taxa, *Pseudemys scripta emolli* and *Pseudemys scripta hartwegi*, compared with those of their nearest geographic neighbors

Taxon	LPO/LC	WPO/LC	LMS/LC	WPO/LPO	LMS/LPO
elegans	0.13 ± 0.022	0.04 ± 0.007	0.11 ± 0.019	0.31 ± 0.073	0.78 ± 0.163
taylori	0.12 ± 0.015	0.03 ± 0.009	0.10 ± 0.012	0.27 ± 0.054	0.83 ± 0.085
gaigeae	0.08 ± 0.013	0.04 ± 0.008	0.10 ± 0.020	0.49 ± 0.085	1.42 ± 0.378
hartwegi	0.12 ± 0.014	0.05 ± 0.012	0.05 ± 0.012	0.44 ± 0.089	0.47 ± 0.093
hiltoni	0.07 ± 0.008	0.03 ± 0.008	0.09 ± 0.016	0.43 ± 0.084	1.33 ± 0.259
nebulosa	0.06 ± 0.007	0.03 ± 0.013	0.10 ± 0.024	0.45 ± 0.170	1.60 ± 0.378
venusta	0.11 ± 0.018	0.03 ± 0.007	0.09 ± 0.017	0.25 ± 0.037	0.82 ± 0.185
emolli	0.06 ± 0.027	0.03 ± 0.009	0.09 ± 0.016	0.56 ± 0.129	1.61 ± 0.394
GDULCE	0.11 ± 0.018	0.04 ± 0.009	0.09 ± 0.015	0.30 ± 0.044	0.86 ± 0.081
CAPAC	0.11 ± 0.012	0.03 ± 0.007	0.09 ± 0.017	0.27 ± 0.051	0.89 ± 0.173

Note: Mean and one standard deviation are given. Abbreviations: LC, carapace length; LPO, length of postorbital mark; WPO, width of postorbital mark; LMS, length of mandibular stripe.

Table 7.4. Comparison of *Pseudemys scripta hartwegi* new subspecies with *P. s. gaigeae* Hartweg

Pseudemys scripta gaigeae	Pseudemys scripta hartwegi
1. Gular and pectoral scutes shorter, 12% and 16% of carapace length, respectively (see Table 7.5).	Gular and pectoral scutes relatively longer, 14% and 19% of carapace length, respectively.
2. Abdominal scute the longest scute of plastron, anal scute second longest in 95% of specimens.	Anal scute longest or anal and abdominal scutes subequal in length.
3. Plastral pattern more or less continuous from gular scute to anal scute, consisting of two or more concentric lines (distinct at least in young) and distributed about equally on anterior and posterior halves of plastron.	Plastral pattern concentrated chiefly on posterior half of plastron (behind pectoro-abdominal seam); small markings on pectorals, humerals, and gulars, if present, usually isolated from rest of pattern; pattern lacks distinct concentric arrangement (except in juveniles).
4. Middorsal keels obtuse or wanting, occasionally distinct in young.	Middorsal keels ordinarily distinct and black on posterior halves of first four central scutes (all ages).
5. Radial corrugations on central scutes indistinct or wanting in adults.	Radial corrugations on central scutes usually distinct in adults.
6. A dark spot on each of first three lateral scutes (and usually on the fourth) slightly less distinct in adults than in young.	Dark spots on lateral scutes obscure or wanting.
7. Dark spots on upper and lower surfaces of marginals obscure, tending to be pale-centered; those of upper surfaces much less distinct than spots on laterals.	Dark spots on upper and lower surfaces of marginals bold, solid, and frequently pale-bordered, contrasting sharply with ground color.
8. Postorbital mark (an isolated, black-bordered portion of postorbital stripe) relatively small, often pointed behind, in shape of teardrop.	Postorbital spot relatively large, usually not pointed behind, more nearly in shape of perfect oval.
9. Symphyseal stripe forked behind, one or both rami continuous with a ventral longitudinal neck stripe.	Symphyseal stripe not forked behind but separated by a black border and usually a hiatus from other ventral, longitudinal neck stripes; posterior end flanked by a pair of spots in some specimens.
10. Mandibular stripe forming a Y with a stripe from lower orbital border to neck or continuous with a separate neck stripe in 55% of specimens; mandibular stripe longer than postorbital mark in 97% of specimens.	Mandibular stripe short, ovoid, not linear, never continuous with any other stripe; half or less than half the length of postorbital mark in all specimens.

Note: Descriptions are based on all specimens examined.

105265, 105267–68 males, 105266, 105269 females, 21 km west of San Pedro [de las Colonias]; KU 29357 juvenile, 8 km south of San Pedro de las Colonias. Durango: USNM 103760 female, Río Nazas; UU 17583, 4700–4701 females, 3848–49, 4702 juveniles, from the type locality; USNM 60921 juvenile, Lerdo; AMNH 67494 juvenile,

24 km southwest of Lerdo; UU 4703–5 females, 4706–7 males, 16 km north-northwest Rodeo; MSU 1137–40 females, 1141 male, 2.4 km northwest of Nazas.

Diagnosis: A subspecies of *Pseudemys scripta* closely related to *P. s. gaigeae* and distinguished by the following combination of characters: anal lamina usually longer than abdominal; plastral pattern brown, relatively narrow, concentrated posterior to pectoro-abdominal seam; carapace pattern chiefly indistinct except for bold, circumferential series of dark-centered ocelli, one on each marginal scute; and isolated stripe on mandibular ramus half or less than half as long as isolated postorbital mark. *Pseudemys s. hartwegi* has the shortest mandibular stripe of any subspecies of *P. scripta* other than *callirostris*. See Table 7.4 for a detailed comparison with *P. s. gaigeae*.

Distribution: Río Nazas drainage of Durango and Coahuila.

Remarks: The type locality is in the tail water below and within sight of the dam itself. This section of the river has a gallery forest of mature Mexican cypress (*Taxodium mucronatum;* Conant, 1963). The subspecies may be nearing extinction in the vicinity of San Pedro de las Colonias. A large female (274 mm, UU 17583) obtained 26 May 1976 at the type locality contained 48 enlarged ovarian follicles in three sets (no corpora lutea).

Etymology: Named in honor of Norman E. Hartweg (1904–64), who made the first efforts in modern taxonomic studies of Mesoamerican chelonians.

Pseudemys scripta emolli new subspecies
(Fig. 7.6, Tables 7.2, 7.3, 7.6, 7.7)

Holotype: UU 6728 immature female, original number FVN 370; carapace length 194 mm; Río Tepetate, 2.5 km northeast of Granada, Granada Province, Nicaragua. Collected by E. O. Moll and F. V. Nabrotzky, 16–18 May 1964. Whole specimen in alcohol.

Allotype: UU 6765 male, original number FVN 369; carapace length 179 mm; same data as holotype.

Paratopotypes: UU 6731, 6733 immature females; same data as holotype.

Paratypes: Total of 103 specimens (38 females, 30 males, 35 immature of all stages), all from Lago de Nicaragua–Río San Juan drainage (Nicaraguan specimens 11 April–1 July 1964), as follows: UU 6712–27, 6729–30, 6732, 6734–64, 6766–73, 13026, several localities near Los Cocos, Granada Province (including Río Tipitapa, Río Moguana, and the lakeshore); UU 6791–6800, El Morillo, Río San Juan Province (15 km north of origin of Río San Juan); UU 6774–76, 6778–85, 6788–90, Río El Limón, 2.4 km southeast of La Virgen, Rivas Province (abreast of Isla Omotepe); UU 6695–6711, Rancho El Paraíso, 16 km east of Managua, Managua Province (short unnamed stream draining to Lago de Managua); UU 6777, 6786–87, Río Sapoá, Peñas Blancas, Guanacaste Province, Costa Rica, 22 August 1961.

Table 7.5. Comparison of *Pseudemys scripta hartwegi* with nearest geographic neighbors for various scute lengths and widths

Taxon	GUL	PEC	AB	AN	WC1A	WC1P
elegans	.16 ± .014	.13 ± .018	.24 ± .018	.20 ± .019	.15 ± .028	.15 ± .014
taylori	.12 ± .010	.14 ± .014	.23 ± .016	.20 ± .016	.20 ± .023	.15 ± .014
gaigeae	.12 ± .010	.16 ± .016	.23 ± .015	.20 ± .013	.20 ± .023	.16 ± .013
hartwegi	.14 ± .010	.19 ± .008	.20 ± .016	.20 ± .013	.21 ± .013	.13 ± .007
hiltoni	.12 ± .012	.14 ± .017	.23 ± .013	.15 ± .020	.14 ± .021	.14 ± .009
nebulosa	.12 ± .010	.15 ± .019	.22 ± .015	.16 ± .020	.15 ± .021	.12 ± .007

Note: Measurements are expressed as percentages of carapace length. Mean and one standard deviation are given. Abbreviations: GUL, PEC, AB, and AN = length of gular, pectoral, abdominal, and anal scutes; WC1A and WC1P = width of first central scute, anterior and posterior.

Table 7.6. Adult size (carapace length, mm) in *Pseudemys scripta*

Taxon	Males					Females				
	N	Max.	Min.	Mean	Med.	N	Max.	Min.	Mean	Med.
elegans	102	214	90	156	126	71	257	107	204	179
taylori	51	179	90	127	124	60	218	93	167	174
gaigeae	16	173	115	140	137	23	220	135	179	183
hartwegi	7	149	124	139	140	14	298	120	177	162
hiltoni	28	320	158	244	253	14	351	207	284	287
nebulosa	7	324	176	227	219	5	285	235	266	273
yaquia	15	268	162	223	230	5	309	241	284	289
ornata	16	359	126	201	193	15	353	153	249	241
grayi	11	278	151	207	198	17	395	209	297	308
cataspila	44	312	125	242	245	16	314	168	273	280
venusta	195	341	110	192	205	213	424	162	232	254
emolli	31	296	162	201	200	36	372	184	286	294
GDULCE	5	187	161	175	178	25	305	218	256	249
CAPAC	43	234	139	182	185	48	320	161	234	233

Note: Number of specimens, maximum (max.), minimum (min.), mean, and median (med.) are given for adults of each sex (specimens examined this study). See text for explanation of GDULCE and CAPAC populations.

Table 7.7. Comparison of *Pseudemys scripta emolli* with nearest geographic neighbors for various scute and shell measurements

Taxon	LP	WPMF	GUL	FEM	LC5	WC5
venusta	.92 ± .027	.43 ± .021	.14 ± .014	.13 ± .017	.17 ± .017	.22 ± .017
emolli	.90 ± .026	.40 ± .016	.13 ± .013	.13 ± .014	.18 ± .015	.24 ± .017
GDULCE	.94 ± .022	.44 ± .016	.14 ± .011	.14 ± .008	.18 ± .017	.23 ± .010
CAPAC	.93 ± .033	.44 ± .020	.15 ± .014	.15 ± .012	.16 ± .015	.22 ± .015

Note: Measurements are expressed as percentages of carapace length. Mean and one standard deviation are given. Abbreviations: LP, length of plastron; WPMF, width of plastron, midfemoral; GUL, length of gular scute; FEM, length of femoral scute; LC5 and WC5, length and width of fifth central scute.
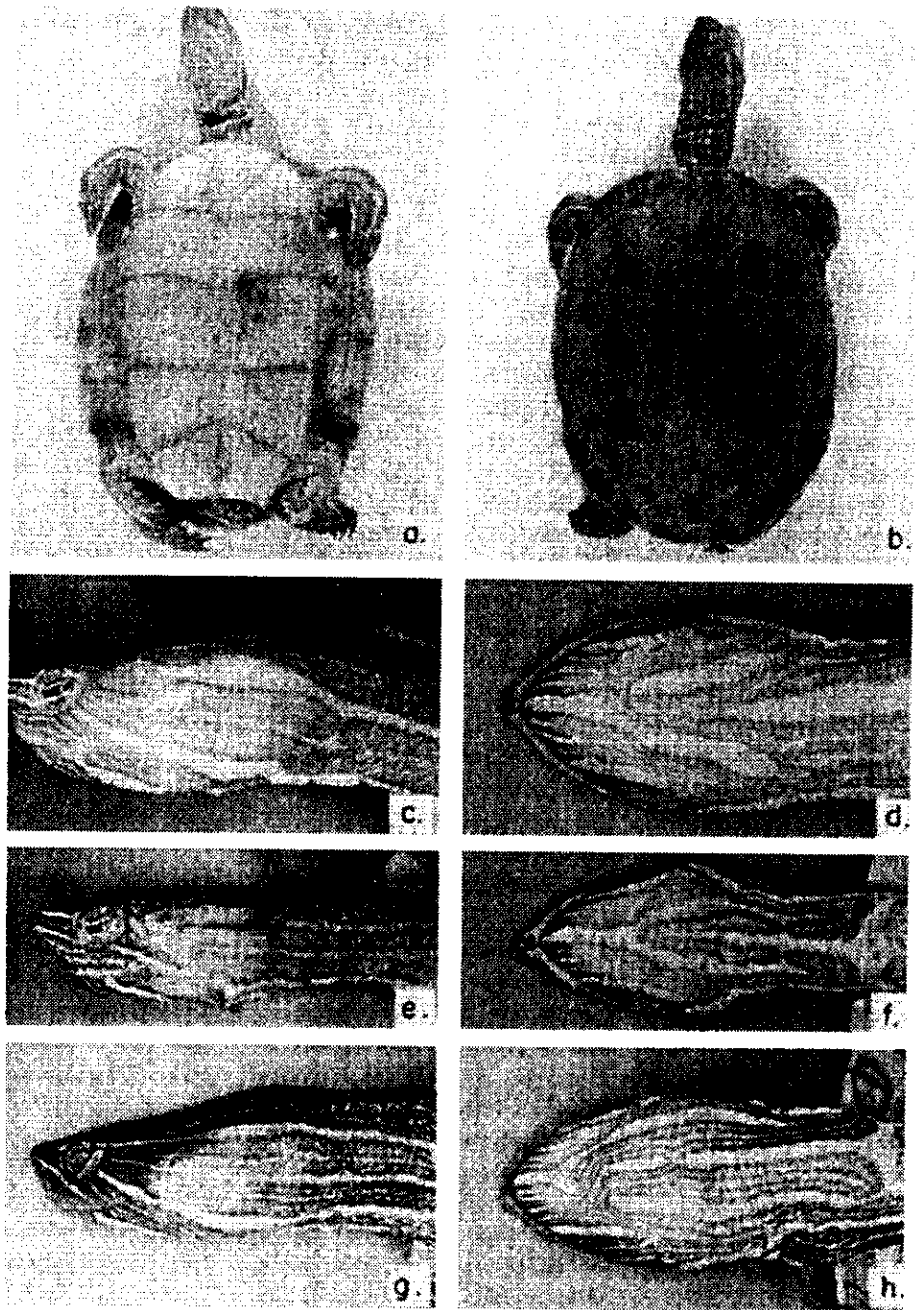
FIGURE 7.6. *a* and *b*, ventral and dorsal views of holotype of *Pseudemys scripta emolli* new subspecies, UU 6728, carapace length 194 mm. *c–h*, lateral and ventral views of heads: *c* and *d*, *P. s. emolli*, female paratype, UU 6697, anterior half of bilobate postorbital mark pale orange, posterior half pale yellow; *e* and *f*, *P. s. emolli*, male paratype, UU 6707; *g* and *h*, *P. s. venusta*, female, UU 6183, 8.8 km northwest of Puerto Cabezas, Zelaya, Nicaragua, thin postorbital stripe uniformly dark orange. Photos are from color transparencies of live turtles. All heads are approximately × 0.75.

Diagnosis: A subspecies of *Pseudemys scripta* closely related to *P. s. venusta* and distinguished from other Central American *P. scripta* by the following combination of characters: a wide postorbital stripe with a constriction at level of tympanum (forming a bilobate figure), or the constriction complete, forming a short isolated postorbital mark approximately half as wide as long; postorbital mark or stripe usually (73%) isolated from eye but connected (83.3%) posteriorly to a neck stripe; mandibular stripe isolated (82.1%) but relatively long, much longer (mean = 1.61 times) than isolated postorbital mark (or part of postorbital anterior to constriction). Symphyseal stripe

usually (90.5%) connected to neck stripes, plastron relatively short (0.90 × LC), posterior plastral lobe relatively narrow (0.40 × LC).

Comparisons: Overall differences in appearance between *Pseudemys scripta emolli* and *P. s. venusta* from the Caribbean coast of Nicaragua (between Puerto Cabezas and Bluefields) are most evident in color and pattern of the head, neck, and shell. In the following brief comparison, the characters stated are for *emolli*, whereas those in brackets are for *venusta:* pattern of carapace dominated by ocelli with large dark brown centers and usually a single pale orange peripheral ring, lacking contrast in gen-

eral [pattern of carapace with more contrast, dark ocellar centers smaller and surrounded usually by more than one pale orange ring]; little or no pattern on central scutes [pattern on central scutes bold, bright, and often complex]; side of head dominated by wide postorbital stripe that is bilobate and often bicolored, the anterior part pale orange and the posterior part pale yellow [postorbital stripe narrow, continuous, and uniformly dark or dull orange]; postorbital stripe chiefly wider than primary orbitocervical [postorbital narrower than primary orbitocervical]; plastral pattern at least slightly reduced in extent and contrast; usually a bowlike figure on the gular scutes, isolated from main plastral pattern or connected to it by a narrow isthmus [plastral pattern extensive and contrasting, continuous from anal to gular regions].

Etymology: The taxon is named for Prof. Edward O. Moll, Eastern Illinois University, my former student, coworker, and companion in Central America and now a prominent chelonian biologist.

Distribution: Lago de Nicaragua, Lago de Managua, lakes and streams connecting the two main lakes, short drainages flowing into the lakes from Nicaragua and extreme northern Costa Rica; an indeterminate distance from Lago de Nicaragua down the Río San Juan. We saw *Pseudemys* in the Laguna Masaya (18 km west northwest of Granada). Populations at the source of the Río San Juan just north of San Carlos are clearly *emolli;* specimens in the San Juan delta near the mouth are clearly *venusta.*

Remarks: The Río Tipitapa flows from Lago de Managua to Lago de Nicaragua and receives many small tributaries in the isthmus between the lakes. Most of the specimens come from this isthmus and the region on the northwest shore of Lago de Nicaragua between Granada and the mouth of the Río Tipitapa. The type locality is a small mud-bottomed creek draining cleared pastureland, reached by driving 1.5 km northwest on the beach from the former Colegio Centro América.

Turtles in the lake were in warm (33° to 35° C) shallow water near the shore, and most were caught by hand. Numerous turtle tracks were visible in the sand between the water and the dense low vegetation on the shore; natives said that turtles came out at night to eat on land (unconfirmed). The turtles may have been seeking relief from the warm receding water. By cutting down the dense vegetation and going through the moist humus at its base, E. O. Moll and F. V. Nabrotzky found 111 *Kinosternon scorpioides* and 7 juvenile *P. s. emolli* buried in an area approximately 4.5 m square; the turtles seemed to be estivating. Some of the larger female *P. s. emolli* from the lakeshore had broad heads and well-developed crushing surfaces on the jaws.

There is a tendency to melanism in the males of this subspecies, but there are no noticeable melanistic tendencies in the females.

SPECIES VERSUS SUBSPECIES

This study regards *Pseudemys scripta* as a polytypic, monophyletic species despite its immense amount of variation and extensive geographic range. Some recent reviews have used this conservative approach (Smith and Smith, 1979), and others have considered one or more of the taxa to be full species (Weaver and Rose, 1967; Ward, 1984). The groups defined by clustering and my own a priori assumptions fit what most biologists would call subspecies. On the other hand, the Northern Isolates are certainly as distinct as many full species, their distinctness being partly due to genetic drift. Similarities of these subspecies to others in the north suggest that gene flow occurred in the past. The potential for gene flow exists nearly everywhere else by virtue of more or less continuous aquatic environments or a nearly continuous coastal plain. In general, all populations of *P. scripta* share enough characters at some stage of ontogeny to suggest that they have common ancestry.

All known stripe and plastral patterns can be derived logically from a hypothetical ancestral pattern. The most radical departures from the ancestral pattern (e.g., the stripes of *P. s. callirostris* and the virtually patternless shell of *P. terrapen*) may have resulted from the founding of populations by a few individuals or one gravid female.

ZOOGEOGRAPHY AND PHYLOGENY

DISPERSAL. The distribution of *Pseudemys* in Mesoamerica requires an understanding of dispersal. Dispersal can be active or passive and can involve movement within or between drainage systems. Dispersal within a system can be upstream or downstream; the latter is ipso facto passive, the former active. Floods are regular and predictable in any true drainage area (excluding spring creeks). Although turtles have ways of staying in place during floods (Moll and Legler, 1971), some are surely displaced downstream and some are displaced to the sea. If this involves displacement over barriers to upstream migration (e.g., falls or rapids), permanent range expansions may result. Being carried to sea in a flood does not necessarily involve swimming in salt water; floods cause considerable dilution in coastal areas, and floods discharge mats of flotsam (usually aquatic vegetation) upon which various animals can be supported. Carr (1952) mentions saltwater tolerance of *P. concinna. Pseudemys s. grayi* occurs at least occasionally in brackish water.

Turtles discharged from a flooded river can come ashore at some distance from the mouth of the river and move along a coastal plain to the mouth of another river. The process is easier and faster if coastal swamps or lagoons exist. This is the simplest mode of dispersal wherever rivers and coastal plains exist. I refer to it as mouth-

to-mouth dispersal, and it is the principal explanation for the coastal distributions considered here.

Dispersal between drainage systems is more difficult to explain when exchanges must occur across a divide. Stream piracy is commonly invoked to explain shared fish faunas in adjacent headwaters. This may involve the actual capture of a tributary in one catchment by headwater erosion of a tributary in another, or the natural damming and actual diversion of part of one drainage to another (e.g., by a lava flow or by an earthquake). Changes in water level during long-term dry cycles cause isolation by creating internal drainage systems.

All these events seem to have occurred in northern Mexico over a period of about 30 million years; some are as recent as Pleistocene. Rarely is there historic evidence of a drainage change in progress or one that is poised to happen (Brand, 1937). Various hypotheses and corroborations have been used to explain the distribution of fishes. These hypotheses do not differ greatly from the basics laid down by Meek (1904). Fish species sharing adjacent headwaters are logically explicable only in this manner; fish cannot survive out of water, and dispersal far upstream from the sea is rare. Minckley et al. (1986) provide the most recent summary of these phenomena in Mexico.

Turtles are pulmonate quadrupeds and can move between streams across terrestrial barriers; they can survive for several days out of water, within certain limits of temperature and humidity. Females predictably nest on land. Also, in a drying stream, movement of turtles from one pool to another is expected. However, turtles do not climb cliffs. None of the foregoing reasons for walking on land can account for the movement of turtles from stream to stream in canyon country (even though the distances are short). Large birds of prey (*Haliaeetus* spp.) could pick up a *Pseudemys* and drop it in another drainage system; eagles of this genus commonly pick up live turtles in northern Australia (pers. obs.) and in Africa (Clayton White, pers. com.). A gravid female on land for the purpose of nesting would be the most likely candidate for this scenario. Introduction by humans is mentioned below.

DRAINAGE HISTORY IN NORTHERN MEXICO. This subject is treated separately because it bears on the origin of several subspecies. The literature has been thoroughly and recently reviewed by Minckley et al. (1986) and Smith and Miller (1986). These authors and others cited by them corroborate most of the remarks that follow. The physiographic features mentioned and the hypothesized dispersal routes are clearly seen on any small-scale topographic map (e.g., U.S. Department of Commerce ONC charts, 1 : 1,000,000).

The present Rio Grande was once two rivers. The two main tributaries of the lower Rio Grande were the Pecos River and another tributary eroding upstream through the Big Bend region southeast of El Paso. The Pecos River also eroded headward and eventually captured parts of other streams (the Canadian River and perhaps other Gulf streams). At some stage the Río Conchos joined the Big Bend tributary; it seems clear that this confluence occurred before the Río Conchos acquired its southern headwaters.

The upper Rio Grande flowed from the San Juan Mountains of southern Colorado southward to interior drainage systems in New Mexico, Texas, and adjacent Mexico; this internal system received contributions also from the east face of the Sierra Madre Occidental. There was a large lake or series of lakes in this region in the Pleistocene. The lower Rio Grande captured the upper Rio Grande and parts of the internal systems in mid-Pleistocene times. Subsequently the entire Rio Grande has flowed to the sea.

There is a large arid area, just south of the U.S.-Mexican border, that contains many dry basins and internal drainage systems. Most of the latter are now dry except in times of heaviest rainfall; a few (e.g., the Río Nazas, Río Aguanaval, and Río Casas Grandes) still flow in places and have fluctuating terminal lakes. All of these basins and drainages contained more water at times in the Pleistocene. The area extends southward approximately to 24 degrees (southern extent of Río Aguanaval), is bounded generally by the Sierra Madre Occidental and the Sierra Madre Oriental, and extends northward to the Rio Grande and at least to the basins (pluvial Lake Palomas) just south of Columbus, New Mexico. This region is termed the central Mexican interior basins by Smith and Miller (1986) and is hereinafter called the interior basins for brevity.

The former confluence of basins and drainages within the northern central region of Mexico—with each other, with the upper Rio Grande and Río Conchos, and with the lower Rio Grande—is generally accepted (although weak in detail). I interpret the evidence as follows. These drainages were all interconnected at some time during the Pleistocene in a manner that permitted exchange of aquatic faunas or gene flow between existing populations. These drainage connections were not all concurrent; they probably occurred in a stepwise fashion as basins overflowed and as low-gradient streams altered their courses or were captured by others.

The ancestral stock of *gaigeae/hartwegi* evolved in this interior basin system. Accounting for the presence of these ancestors in the system is an unsolved zoogeographic problem. Aquatic organisms could have entered this system via the following routes: (1) via drainage exchanges between the upper Rio Grande and the Pecos River, (2) by migration up the Rio Grande, (3) via the Torreón basin. There is evidence that fishes have dispersed via all of these

routes. Route 3 involves the fewest assumptions for turtles.

Just north of Torreón there is a corridor that extends eastward toward Saltillo. This corridor includes the western extent of the range of *hartwegi* (Río Nazas at San Pedro de las Colonias). The corridor is the route of a railroad; just south of Reata the line branches with one track going to Monterrey and another running northward to Monclova. Drainage exchanges could have occurred between the Nazas and the Río San Juan drainage 40 to 50 km northwest of Monterrey or with the Río Salado drainage 95 km northwest of Monterrey. *Pseudemys* could have entered the Río Nazas drainage this way. This may be the route attributed to Arellano (1951) by Conant (1963).

It seems likely that the southernmost Río Conchos tributaries were once confluent with the interior drainages (pers. obs.). Tributaries flowing to the interior basins are narrowly separated from those of the Río Florido approximately 65 km south of Jiménez, Chihuahua. The Mapimían channels are now dry, but they are unquestionably on the general drainage that terminates in lakes near Torreón. The headwaters of the Río Nazas come into close proximity with other Río Florido (Conchos) tributaries approximately 60 km upstream from the Presa El Palmito (= P. Lázaro Cardenas), where tributaries of both systems seem to drain the same small valley.

It is also clear that waters of the interior basins were captured by headwaters of high-gradient Pacific streams in several places. (Whether or not the internal streams were concurrently or directly connected to the Rio Grande is not an issue.) This has resulted in the dispersal of fishes into the Pacific streams, either directly from the interior drainages or in a stepwise fashion southward along the Continental Divide from headwater to headwater. Stream piracy across the Continental Divide is well documented in two places: The Río Papigóchic was formerly a Casas Grandes tributary and now flows to the Río Yaqui; the Río Tunal was formerly a tributary of the Nazas and now flows to the Río Mezquital.

NORTHERN ISOLATES.   Three subspecies occur in northern Mexico, each in a separate drainage that flows to the Rio Grande or has been isolated from that drainage. The Northern Isolates are distinct but probably as closely related to one another as each is to the ancestral stock. The ancestry of these three populations can be traced to the lower Rio Grande. (See Fig. 7.7 for a summary of hypothesized dispersal routes.)

Pseudemys scripta taylori occurs only in the basin of Cuatro Ciénegas. Periodic past isolation of the basin (Minckley, 1969) has produced many endemics in the aquatic biota. The basin presently drains (via the Río Nadadores) to the Río Salado system with its mouth on the lower Rio

Grande at Falcon Reservoir. Typical *P. s. elegans* occurs everywhere else in the Río Salado drainage.

Pseudemys s. taylori is one of four aquatic turtles in the basin: The distinctiveness of *Terrapene coahuila* suggests that its isolation was ancient; *Trionyx ater* is endemic and sometimes hybridizes with *Trionyx spiniferus*, a recent entrant to the basin. *Pseudemys s. taylori* probably evolved in isolation from an ancestral stock during the Pleistocene; the ancestral stock probably gave rise also to *elegans* and *cataspila* during the time that *taylori* was isolated. Although *taylori* is one of the most distinctive subspecies of *P. scripta*, it now intergrades with *P. s. elegans* where the two meet immediately outside the basin (Legler, 1963; pers. obs., 1976).

Pseudemys s. gaigeae and *P. s. hartwegi* were seemingly derived from a common ancestor in the interior basins. The ancestral stock probably entered the interior basins from the Río Salado or the Río San Juan drainage via the corridor east of Torreón and the Río Nazas (Fig. 7.7). This stock may have ranged northward to lat. 27 in wetter times. Increased aridity isolated the stocks that eventually became *gaigeae* and *hartwegi*. Subsequently, *P. s. gaigeae* differentiated in the northern part of the system, which became the headwaters of the Río Conchos (and provided a route to the Rio Grande). *Pseudemys s. hartwegi* differentiated in the south and survived only in the Nazas drainage. The subspecies has become extinct in the Laguna Viesca since 1960 (based on clear photos by John Iverson of specimens at Baylor University). My own explorations indicate that *Pseudemys* did not occur in the Río Aguanaval, Río Carmen, Río Santa María (*Chrysemys picta* occurs there), Río Casas Grandes, or Laguna Bavícora in 1961. Aridity and the increased use of water for irrigation may have placed *hartwegi* populations in danger everywhere except in the immediate region of the Presa El Palmito.

GULF COAST–CARIBBEAN SERIES.   *Pseudemys s. cataspila* ranges from the Río San Fernando (145 km south of Brownsville) to Punta del Morro, Veracruz. Punta del Morro is a well-known headland; it interrupts the coastal plain for about 25 km at lat. 19-55. The distributions of many neotropical species end just south of Punta del Morro, and it is seemingly a barrier of long standing.

Pseudemys s. venusta extends southward from Punta del Morro as a virtually continuous population to Isthmian Panama and the Río Atrato of northern Colombia and is clearly the most wide-ranging subspecies of *P. scripta*. *Pseudemys s. venusta* has an extensive range by virtue of occurring chiefly on a nearly continuous coastal plain. Gene flow is probably unimpeded over most of this range. Within *venusta* there are populations that are distinctive when considered alone but are parts of a cline in the context of the total sample. This is a more conservative treat-
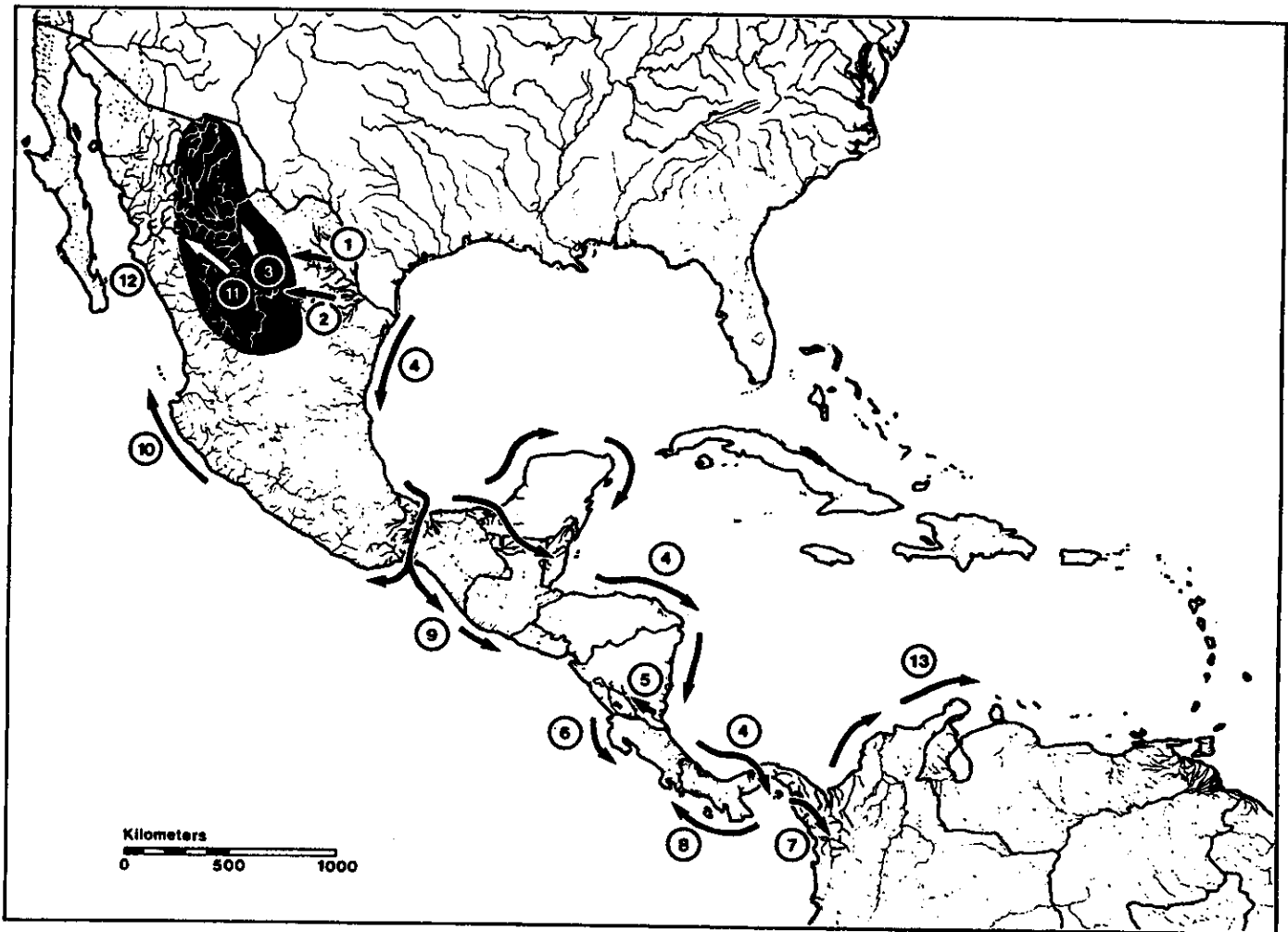
FIGURE 7.7. Hypothesized dispersal events and routes for ancestral stocks of *Pseudemys scripta* in Mesoamerica. The numbered events are neither concurrent nor chronological. The shaded area in northern Mexico shows the approximate extent of the interior basin region discussed in the text. *1*, isolation of *taylori* in basin of Cuatro Ciénegas; *2*, invasion of interior basins by *hartwegi/gaigeae* ancestral stock; *3*, isolation of *gaigeae* in interior drainages later captured by Río Conchos; *4*, coastwise dispersal of *cataspila* and *venusta* through Gulf coastal plain, around and across Yucatán Peninsula, and thence to Isthmian Panama; *5*, isolation of *emolli* in Nicaraguan lakes via Río San Juan; *6*, possible dispersal from Lake Nicaragua to Golfo Dulce region; *7*, colonization of Río Atrato via Río Tuira; *8*, coastwise dispersal of *venusta* to colonize Pacific coast of Central America; *9*, ancestral stock crosses Isthmus of Tehuantepec to found Pacific coast of Mexico and gives rise to *grayi*; *10*, northward dispersal of Pacific stock; *11*, Río Fuerte founded by ancestors in the interior basins; *12*, *hiltoni* crosses Gulf of California; *13*, possible coastwise dispersal of *venusta*-like stock to account for origin of *callirostris*.

ment than that expressed in Moll and Legler (1971).

Isolated aquatic habitats on the Yucatán Peninsula range from cavernous cenotes to small sinkholes, lakes of various sizes, and muddy *aguadas*. *Pseudemys* occurs in most of these, but populations flourish only in the more exposed habitats. Limestone sinks in intermediate stages of senescence are spectacular in their potential for isolation. Near Libre Unión, I observed breeding populations of *P. scripta* in small pondlike habitats (with aquatic vegetation and earthen shoreline) that were surrounded by vertical rock walls at least 12 m high (the crowns of ma-

ture palms were below ground level). Turtles colonize these holes by simply falling in. The chances of overland escape are virtually zero.

Underground water connections in Yucatán could be significant in turtle dispersal. I observed medium-sized tarpon and *P. scripta* in some small cenotes where water was welling up to the surface. These had small surface exposure (less than 15 m²) and were deeper than I could see in crystal-clear water; an underground connection to a larger aquatic system probably existed (and this was the opinion of the natives).

The distribution of *Pseudemys scripta* extends around and across the base of the Yucatán Peninsula. From Quintana Roo to Colón, Panama, the coastal plain is constricted in places (e.g., Omoa and Trujillo, Honduras), and there are some areas from which specimens are unknown (e.g, Coclé del Norte to Colón, Panama), but in no case do these exceptions refute the concept of a single subspecies with a wide range. It may be that *Pseudemys* actually skips some of these drainages.

Pseudemys is common in the Chagres drainage of Panama and occurs across the Isthmus, in suitable habitats, most of which have been altered by humans. Eastward from the Port of Panama, *Pseudemys* occurs in short coastal drainages and the Río Bayano. There are no records for the Tuira-Chucunaque system with its mouth in the Gulf of San Miguel, but I think it is probable that *Pseudemys* occurs in this basin and has colonized the Río Atrato from there (I could establish no evidence for the occurrence of *Pseudemys* on the San Blas coast of Panama, east of Colón). The headwaters of the Tuira interdigitate with those of the Río Atrato; it is possible to portage dugouts between these rivers in the wet season (Colombian natives, pers. com.).

ORIGIN AND RELATIONSHIPS OF *PSEUDEMYS SCRIPTA* EMOLLI. The relationships of *Pseudemys scripta emolli* are shown in Fig. 7.8. There is no reason to doubt its close relationship to *venusta* and its origin from a *venusta*-like stock via migration up the Río San Juan. The Río San Juan drains Lago de Nicaragua, which in turn drains Lago de Managua. The route of the Río San Juan passes through low mountain ranges about midway between the lake and the mouth. The nature of the Río San Juan has changed within historic times. "Rapids" are shown in the area where the river passes through the higher elevations. Parallel to the course of the Río San Juan, but chiefly to the south, there is a clear route from the Atlantic Lowlands to Lago de Nicaragua; Puerto Viejo, Costa Rica, lies in this lowland corridor. The corridor extends narrowly along the south shore of the lake to just north of Rivas (abreast of Isla Zapatera).

The populations to the southeast on the Pacific coast are an unsolved problem. The Golfo Dulce–Golfo de Chiriquí population is more closely related to *venusta* than to either *emolli* or CAPAC (Fig. 7.8). For this reason it is provisionally treated as a disjunct population of *venusta*.

Populations on the Pacific coast of Panama are noticeably paler and less contrasting in all color and pattern than is *venusta* in the Chagres drainage of the Isthmus. Nothing in the computer analysis expresses this pallor, and I therefore regard the matter as unresolved.

We were unable to collect or otherwise establish the presence of *Pseudemys* in the Golfo de Nicoya region in August 1961. *Pseudemys scripta* is common at Palmar Sur (350 km south of Lago de Nicaragua) in lowland country
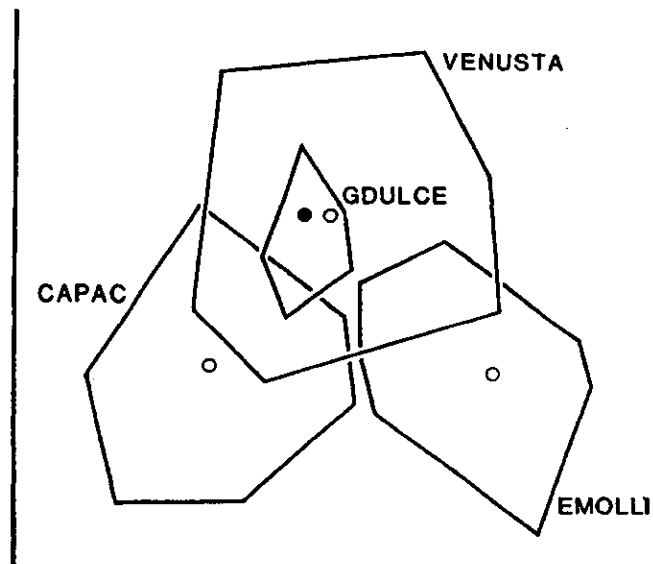

FIGURE 7.8. Plots of adults of *P. s. emolli* ($N = 67$) and their nearest geographic neighbors, *P. s. venusta* ($N = 411$) and two populations on the Pacific side of Costa Rica and Panama, GDULCE ($N = 30$), and CAPAC ($N = 94$). Plots are based on 29 characters (length of carapace, 25 measurements of shell expressed as percentages of carapace length, and 3 stripe characters). Polygons show total dispersion of individuals; dots show population means (the mean for GDULCE is a solid dot). The first (horizontal) and second (vertical) canonical axes account for .457 and .377 of the variation, respectively. This plot tends to corroborate these hypotheses: *emolli* was derived from a *venusta*-like stock; GDULCE is phenetically closer to *venusta* than to either of the other populations (and could be regarded as a disjunct population of *venusta*).

where bananas are grown. The area was formerly laced with streams draining to the Río Térraba near its delta. The turtles are common in oxbows resulting from the realignment of streams for banana growing. The Río Térraba is fast and gravel-bottomed; the only suitable *Pseudemys* habitats in the river itself are man-made (barge harbors, etc.). Presumably the population is more or less continuous along the Golfo de Chiriquí. This population is termed GDULCE in Fig. 7.8.

There are several ways to explain the presence of *venusta* in the Golfo Dulce region: (1) dispersal of a pre-*emolli* stock by coastwise migration from Lago de Nicaragua or by waifs from an overflow of the Nicaraguan lakes; (2) successive waves of colonization from a Panamanian Isthmus stock, with *venusta* crossing the Isthmus of Panama, dispersing up the Pacific coast to the Golfo Dulce, and then differentiating only between the Azuero Peninsula and the Panamanian Isthmus; (3) human introduction by aboriginals or banana growers from the Atlantic side (see Epilogue, below).

The first hypothesis is the most attractive. Overflow of the lakes could easily occur into the Pacific Ocean be-

tween Puerto Somoza and Rivas if the Río San Juan were blocked (there is a history of earthquakes in the region). On the other hand, large gaps in the coastal plain south of San Juan del Sur and the seeming lack of *Pseudemys* near the Golfo de Nicoya argue against coastwise dispersal.

The following turtles occur in sympatry with *P. scripta* near the origin of the Río San Juan at El Morillo: *Kinosternon scorpioides, K. leucostomum, Rhinoclemmys funerea,* and *Chelydra serpentina.* The last three are primarily Atlantic species. *Rhinoclemmys funerea* is unknown from the Pacific side (and I strongly doubt its occurrence there); *Chelydra* and *K. leucostomum* both begin a Pacific distribution south of Lago de Nicaragua. *Chelydra* is known from the Golfo de Nicoya region, Tilarán, and the Palmar Sur region on the Pacific side of Costa Rica (chiefly pers. obs.; also E. H. Taylor and Jaime Villa, pers. com.). *Kinosternon leucostomum* occurs at Palmar Sur (UU 8678–79) but is rare. Except for rare occurrence in the Río Chagres drainage, *K. scorpioides* is completely Pacific in its distribution (and is the common species of *Kinosternon*) northwestward to the latitude of Lago de Nicaragua; thence it occurs commonly on both sides of Central America (UU collection; Iverson, 1986). Ergo, of the five species at El Morillo, three seem to have crossed the Central American landmass via the Río San Juan corridor, and one (*R. funerea*) has reached only as far as the lake.

Because *Pseudemys* shows essentially the same pattern as *Chelydra* and *K. leucostomum,* hypothesis 1 seems to be the most parsimonious explanation of the Golfo Dulce population. However, this does not explain why the population is more closely related to *venusta* than to *emolli.* Perhaps the Golfo Dulce population was founded by *venusta,* from the lakes, before the lake populations differentiated. Hypothesis 2 involves too many assumptions to warrant serious discussion at present.

PACIFIC POPULATIONS OF MEXICO AND GUATEMALA. Distributions on the Pacific side of Mexico and Guatemala are discontinuous and more complex. A *venusta*-like Gulf Coast population in Veracruz probably founded the Pacific coast by crossing the Isthmus of Tehuantepec. Certainly this explains the origin of *grayi.* It is presently the only logical way to account for other Mexican Pacific populations (except *hiltoni*)—by coastwise dispersal, north and west of the Isthmus of Tehuantepec.

Pseudemys s. yaquia occurs in the Río Sonora, Río Yaqui, and Río Mayo. *Pseudemys s. ornata* occurs on the continuous coastal plain from Culiacán, Sinaloa, to the region just north of Cabo Corrientes, Jalisco (lat. 21-0). It may occur from Los Mochis to Culiacán, but no specimens are known. Between Cabo Corrientes and Puerto Angel, the coastal plain is broken; *ornata*-like *scripta* occur near Acapulco, but their status is not considered here. There may be other isolated populations in short pieces of coastal plain (e.g., Manzanillo, Colima, lat. 19-0; Chila, Oa-

xaca, long. 97-0). Duellman (1961) gave no records for *Pseudemys* from the coast of Michoacán or from the Balsas-Tepalcatepec Basin.

Pseudemys s. grayi is known near the mouth of the Río Tehuantepec, but its range may begin to the west at Majada Villalobos. It is most common in the Pacific coastal lagoons beginning just east of Salina Cruz and extending through Chiapas and Guatemala (type locality, long. 91-33) to extreme western coastal El Salvador (long. 89-40), where lava flows from Ilopango and other volcanoes form an impassible headland. There are specimens from Laguna Muchacha, Jutiapa Province, Guatemala (long. 90-10, UU collection).

A small stretch of coastal plain, containing the mouth of the Río Lempa, begins immediately east of La Libertad and extends to a small basin containing the Laguna Olomega (long. 88-04). A headland separates this basin from the principal coastal plain surrounding the Golfo de Fonseca. The Laguna Olomega has satisfactory habitat for *Pseudemys,* but observation and collecting effort convince me that sliders do not occur there. There are no records of *Pseudemys* from the coastal plain of the Golfo de Fonseca. Although this coastal plain is clearly continuous with a lowland corridor extending from La Canoa (lat. 13, long. 87) southeastward to Lago de Managua, *Pseudemys* are known only from the lake. We have been to Chinandega, Nicaragua, and were unable to establish any information to suggest that *Pseudemys* occurred there.

The distribution of *P. s. grayi* therefore stops at Acajutla. All Central American populations of *P. scripta* to the south and east are independent derivatives of *venusta*-like stocks on the Atlantic side (see below).

The relationship of *venusta* to *grayi* deserves special comment. The populations are narrowly separated. They do not occur sympatrically (despite the comment of Bogert, 1961). M. Alvarez del Toro (Smith and Smith, 1979) keeps the two subspecies together in the same zoo ponds in Tuxtla Gutiérrez; the subspecies ignore each other and do not interbreed. These taxa may be incipient species, but it remains to be seen what would happen if they occurred in natural sympatry.

Pseudemys scripta yaquia, P. s. ornata, and *P. s. grayi* comprise a natural series of closely related subspecies. This series is interrupted by the range of *hiltoni* in the Río Fuerte. There is no completely satisfying explanation for the presence of *hiltoni* in this coastal series. The juxtaposition of *yaquia, hiltoni,* and *ornata* may represent the termini of a long chain of subspecies.

The following discussion and hypotheses stipulate the following basic findings of this study (Fig. 7.9): (1) *P. s. hiltoni* and *nebulosa* are more closely related (phenotypically similar) than any other two subspecies of *P. scripta,* and any scenario applicable to one must be applicable to the other; (2) *yaquia, ornata,* and *grayi* are more closely related inter se and to *venusta* than any is to *hiltoni/nebulosa;*
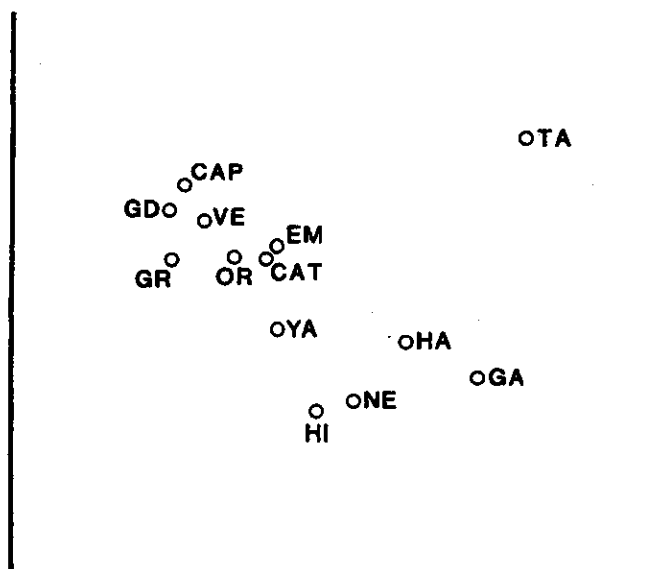
FIGURE 7.9. Plots of adult population means for 13 subspecies of *Pseudemys scripta* in Mesoamerica on the first (horizontal) and second (vertical) canonical axes. Plots are based on the same characters as in Figure 7.8. The first and second canonical axes account for .402 and .211 of the variation, respectively. Abbreviations of subspecies as follows: *CAP*, CAPAC; *CAT, cataspila; EM, emolli; GA, gaigeae; GD*, GDULCE; *GR, grayi; HA, hartwegi; HI, hiltoni; NE, nebulosa; OR, ornata; TA, taylori; VE, venusta; YA, yaquia.*

(3) *hiltoni/nebulosa* is more closely related to *hartwegi/ gaigeae* than to the *yaquia/ornata/grayi* group; (4) the ancestral stock of the *yaquia/ornata/grayi* group reached the Pacific coast via the Isthmus of Tehuantepec. If these taxonomic judgments are incorrect, the hypotheses are necessarily weakened or refuted.

Freshwater fishes in Pacific coast drainages show close relationships to species of the Rio Grande. This can be explained by headwater exchanges with interior basin streams (see Drainage History, above). Many such instances are well substantiated (Meek, 1904; Minckley et al., 1986; Smith and Miller, 1986).

Exchanges between the Río Fuerte and interior basin streams are not mentioned in the literature, and I can see no really good possibilities for this on any map. All of the known drainage exchanges have occurred north (Yaqui-Guzmán) or far south (Nazas-Mezquital) of the Río Fuerte. Headwaters of the Río Fuerte lie close to those of the Río Conchos and the Río Nazas, but in all cases this is in rugged canyon country (e.g., near Creel, Chihuahua). The ancestors of *hiltoni/nebulosa* probably crossed these barriers, but I cannot explain how (see Dispersal, above).

The following hypotheses are presented more or less in the order of their likelihood and parsimony:

1. The ancestors of *hiltoni* reached the Río Fuerte by crossing the divide from the interior basins—from

what is now the Río Nazas or the Río Conchos. The part of this ancestral stock that remained in the interior basins gave rise to *gaigeae* and *hartwegi* (or had already done so). *Pseudemys s. hiltoni* differentiated in the Río Fuerte. If an *ornata*-like population was already present in the Fuerte, it was assimilated by *hiltoni*. Pacific populations in streams flanking the Río Fuerte remained unaffected. If *ornata*-like stocks had not already colonized the Pacific coast, they either bypassed the Fuerte drainage or were assimilated by *hiltoni* if they entered the river.

2. Drainage exchanges between the Río Nazas and the Río Mezquital are well documented. The mouth of the Mezquital (= Río San Pedro) is at Tuxpan, Nayarit, well within the present range of *ornata*. Drainage exchanges between the Yaqui and the Guzmán system (later Rio Grande) are also well documented; exchanges between Yaqui and Conchos headwaters are likely. Although I propose that the ancestors of *hiltoni/nebulosa* were already substantially differentiated from a fully striped *venusta/ ornata*-like ancestor, a fully striped ancestral stock in the interior basins could have independently given rise to *P. s. yaquia* (via the known Papigóchic capture) and to *P. s. ornata* via the Tunal-Mezquital exchange. At some later time, after the differentiation of the *gaigeae/hartwegi* stock, ancestors of *hiltoni/ nebulosa* colonized the Río Fuerte, where they either replaced an existing population or colonized an unoccupied river. No coastal barriers exist between the Río Sonora and the Río San Pedro at Tuxpan.

3. The Río Fuerte is a new drainage system that originated after an *ornata*-like ancestor had colonized the Mexican Pacific coast from the south. This suggestion, although not frivolous, is absolutely without substantiation. But it would solve nearly all the problems.

BAJA CALIFORNIA. *Pseudemys s. hiltoni* and *P. s. nebulosa* are so closely related that it is necessary to invoke a crossing of the Gulf of California to explain their distribution. However, neither the means of crossing nor its direction are clear at this time. The distance from the mainland to the peninsula is about 135 km. If *Pseudemys* could reach the Antilles (200 km, Yucatán to Cuba; 150 km, Key West to Cuba), they could probably traverse the Gulf of California. The Río Fuerte does not seem to be the kind of river that would discharge island-size mats of floating vegetation, but surely there is flotsam of some kind crossing the Gulf of California.

The following authors have alluded to the possibility of human introduction of *P. scripta* into Baja California: Conant (1963); Smith and Smith (1979); R. Murphy (1983, Indians and Jesuit priests mentioned). The idea is

attractive in its simplicity but is difficult to prove. If humans carried *Pseudemys* to Baja California, it seems that they would also have carried *Kinosternon*. That genus is less desirable as food but is edible; it is also used medicinally (pers. obs. in Chihuahua and Durango).

According to R. Murphy (1983), what is now the Cape region of Baja, California, broke away from the Mexican west coast in the Miocene (13 million years B.P.). Several things argue against this history for *Pseudemys*. *Pseudemys s. hiltoni* and *P. s. nebulosa* are too similar to have been isolated that long. If *Pseudemys* was present on a detached piece of the continent, it is probable that *Kinosternon* would also be present. Baja California is one of two Mesoamerican mainland places where *Pseudemys scripta* is not sympatric with a *Kinosternon* (Cuatro Ciénegas is the other). *Kinosternon* is the more likely to survive aridity because it can burrow and utilize seasonal rain pools. On the other hand, by using the Miocene scenario, we could derive *hiltoni* from ancestors in Baja California. However, this would be incongruent with most of what is proposed in this chapter.

ISLAND DISTRIBUTION. *Pseudemys scripta* colonized the Antilles in the same relatively recent period discussed for mainland species. It has prospered in the Antilles and differentiated there. My own work on Antillean *Pseudemys* will be published elsewhere. It seems probable that more than one colonization occurred. It is possible that parts of Central America and South America were also colonized from the Antilles. There are no freshwater turtles of any other kind in the Antilles proper. *Kinosternon leucostomum* occurs with *Pseudemys s. venusta* on Great Corn Island (Nicaragua). *Pseudemys* does not occur on Escudo de Veraguas and other islands off the Panamanian coast near Almirante. Only *Kinosternon leucostomum* occurs on Isla Pinos off the San Blas coast of Panama.

SOUTH AMERICA. The distribution of *Pseudemys* in South America is spotty. I have no scientific experience with this vast area except for northern Colombia. There are three natural ways to explain these spotty distributions: (1) *Pseudemys* occurs in most lowland aquatic habitats and remains chiefly undiscovered; (2) distributions are so recent that populations still exist as small founding colonies; (3) *Pseudemys* has been less successful in South America because aquatic niches there are occupied chiefly by pleurodires. The most recent review of *Pseudemys* in South America is by Pritchard and Trebbau (1984).

SUMMARY OF MAJOR ZOOGEOGRAPHIC EVENTS. *Pseudemys scripta* has crossed the Mesoamerican landmass in five places (Fig. 7.7): (1) from the Gulf of Mexico to the Pacific coast of Mexico via the Rio Grande and interior basins of northern Mexico; (2) from the Gulf of Mexico to the Pacific coast at the Isthmus of Tehuantepec; (3) from the

Caribbean coast to the Pacific coast via the Nicaraguan lakes–Río San Juan corridor; (4) from the Atlantic coast to the Pacific coast at the Isthmus of Panama; and (5) from the Pacific to the Atlantic between the Río Tuira and Río Atrato in northern Colombia. In four of these instances, the dispersal route remains open and is an actual or potential route of gene flow. The Isthmus of Tehuantepec is now a barrier.

OVERALL RELATIONSHIPS

A broad comparison of all *Pseudemys scripta*–like species will serve to place the foregoing remarks in perspective. All of my work suggested that three major groupings existed: the subspecies in the United States, the Antillean taxa, and all Mesoamerican taxa, including those immediately south of the Rio Grande in northern Mexico. To test this idea, 31 definable populations (including all Antilles taxa) were plotted together with BMDP7M: once for all adults (29 characters) and once for all subadults (27 characters, LC and FING omitted). The population clusters were tightly packed and served only to assess relationships between groups of populations (not to scrutinize relationships among taxa). The groupings were as hypothesized above. The populations were then reamalgamated into three large groups designated USASCRIP—*elegans, scripta,* and *troosti;* ANTISCRIP—all Antillean populations; and MESOSCRIP—all mainland populations of *Pseudemys scripta* south (and west) of the lower Rio Grande. Plots for nonadults and adults showed essentially the same results.

The plots for adults are shown in Figure 7.10. Note that MESOSCRIP slightly overlaps both USASCRIP and ANTISCRIP and that the last two groups do not overlap at all. This strongly suggests the following: (1) the relationship of any one group to any other is of approximately equal magnitude; (2) Antillean species are part of the *P. scripta* group, regardless of their taxonomic designation; (3) the differences between MESOSCRIP and USASCRIP are real. The clustering suggests that Antillean populations are more closely related to each other than any is to USASCRIP or to MESOSCRIP (even though Antillean stocks could have been established by separate and distinct invasions from different mainland stocks).

MESOSCRIP constitutes a natural group composed of all the mainland *Pseudemys* south and west of the Pecos–lower Rio Grande, including all South American populations. The difference between USASCRIP and MESOSCRIP is great enough to consider them as different groups of the same polytypic species. The remainder of this report deals with this seeming paradox.

SEXUAL DIMORPHISM AND SYMPATRY

SYMPATRY. *Pseudemys scripta* occurs in microsympatry with *Pseudemys concinna* in the Pecos River and in the tribu-
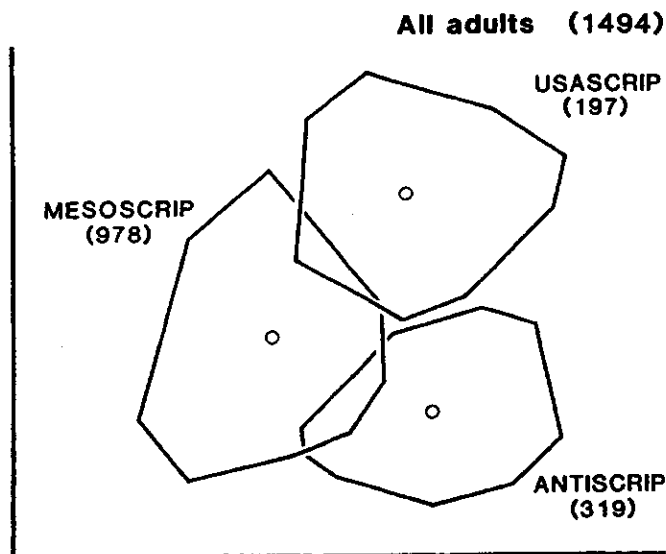
All adults (1494)

FIGURE 7.10. Canonical plots of all adult *Pseudemys scripta* group specimens (*N* = 1,494). All populations in the United States, Mesoamerica (including South America), and the Antilles were first plotted; these formed three basic clusters. Populations in these clusters were then amalgamated into the three groups shown here. The first (horizontal) and second (vertical) canonical axes account for .753 and .247 of the variation, respectively. USASCRIP includes the three subspecies in the United States; ANTISCRIP includes all known Antillean taxa; MESO-SCRIP includes all mainland populations south and west of the Rio Grande. *N* is parenthetical. Plots are based on the same characters as in Figure 7.8.

taries of the lower Rio Grande below Del Rio, Texas. ("Microsympatry" refers to sympatry in which the species occur in close enough proximity to be aware of each other's presence through seeing, smelling, touching, etc.) This is supported by specimens in collections, and I have personally observed the two species within 1 m of one another in clear water at several places in the mentioned drainages (*Chrysemys picta* also occurs in the Upper Pecos, but not necessarily with the two *Pseudemys*). Lower Rio Grande tributaries may extend as far south as lat. 27 (Río Sabinas) in Coahuila and lat. 25-30 in Nuevo León and Tamaulipas.

The Pecos–lower Rio Grande drainage marks the western and southern extremes of intrageneric sympatry for *Pseudemys*. Northward and eastward in the Mississippi drainage, in the Gulf drainages, and along the eastern coastal plain of the United States, *Pseudemys scripta* occurs almost always with at least one other species of *Pseudemys* and sometimes with more than one other species. *Chrysemys picta* and several species of *Graptemys* also occur in this zone of sympatry. It is therefore possible to have at least two species of *Pseudemys* plus at least one other emydine genus occurring in microsympatry. This sympat-

ry reaches its peak in the southeastern United States east of the Mississippi. All of these turtle species have stripes on the head and neck, and all lack mental glands and musk glands (Waagen, 1972; Winokur and Legler, 1975).

South and west of the Pecos–lower Rio Grande there is no emydine sympatry. *Pseudemys scripta* is the only emydine, the only basking turtle, and the only turtle with stripes in all of Mesoamerica and South America. There are a few exceptions. *Chrysemys picta* occurs (naturally) in the Río Santa María of Chihuahua (no *Pseudemys*). In parts of Central America (e.g., the San Juan Delta, the region of Almirante, Panama), *Pseudemys scripta* shares basking logs with *Rhinoclemmys funerea* (pers. obs.); this phenomenon is local and uncommon (*R. funerea* is more characteristic of forest pools and commonly feeds on land at night; *Pseudemys* is chiefly riverine and feeds only in the water). This is the closest sympatric relationship that *Pseudemys* has anywhere in Mesoamerica to the best of my knowledge.

SEXUAL DIMORPHISM AND MATING. Of 38 mensural characters analyzed, 28 were sexually dimorphic (determined with *t* tests at the .05 level). Some of these are easily understandable in terms of adaptive value for reproduction (e.g., height). Others are certainly associated with allometric changes occurring with larger size (e.g., widths of central scutes). But many are not well understood. These statements apply to most kinds of turtles.

This discussion concentrates on sexual dimorphism in adult size, foreclaw length, and shape of snout in profile. Sexual dimorphism in these characters can be demonstrated statistically in all *Pseudemys scripta*. However, this dimorphism is so extreme in some subspecies that statistics are scarcely necessary to express it.

Adult size. Table 7.6 gives carapace length for all specimens of *scripta* I have examined, in terms of extremes, mean, and median for each sex. Obst (1985) gives some adult sizes that exceed any I have seen (almost 500 mm for *venusta*, 600 mm for *grayi*) and should be substantiated in terms of museum numbers (it is possible that the measurements are actually of *Dermatemys*).

There is extreme sexual dimorphism in adult size in the three U.S. subspecies of *P. scripta*. Males mature at a much smaller size than females and never become as large as females; the chances of a mating pair's being the same size are low. By comparison, there is much less size dimorphism in Mesoamerica. Although most females are larger than most males, males often grow as large as females, and the chances of a male's being as large or larger than a female are good (Moll and Legler, 1971). Males of *P. s. elegans* are contrasted to males of all Mesoamerican populations in Figure 7.11.

Foreclaw length. The terminal (ungual) phalanges of the manus are greatly elongated in males of 12 of the
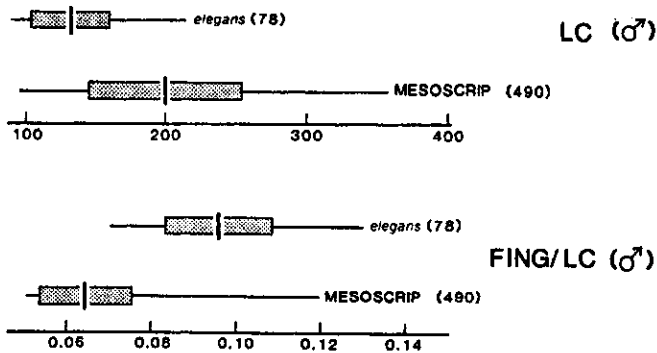
FIGURE 7.11. Sexually dimorphic characters in *Pseudemys scripta*. Males of *P. s. elegans* (representing USASCRIP) are plotted against males of all Mesoamerican populations (MESOSCRIP) for carapace length (LC) and for length of third ungual phalanx of manus (FING), expressed as a percentage of carapace length. Vertical and horizontal lines represent the mean and the extremes, respectively. Rectangles represent one standard deviation of the mean.

17 species in the *Chrysemys* group (not in *Malaclemys*; not in 4 of 9 *Graptemys* species). This character is expressed by length of the ungual phalanx of the third digit in the analysis. This is a male secondary sexual characteristic. Within *Pseudemys scripta* (sensu stricto), long foreclaws occur in the three U.S. subspecies and not in the other subspecies. The phenotype is rarely and irregularly expressed in Mesoamerica. Males of Antillean species have elongated foreclaws.

Shape of snout in profile. Males of all *Pseudemys scripta* have a narrower head and a more pointed snout than females. This is only a statistically demonstrable tendency in U.S. *scripta;* it is extreme in Mesoamerica. Mature males have long, pointed snouts. There is variation, and some subspecies have distinctive profiles. The snout may become bulbous and bosslike with age (e.g., *hiltoni*). Skulls of old large males have a raised, thickened ridge on the upper edge of the narial aperture. Unfortunately, the development and shape of the snout is not expressed by any character recorded in this study. Because a narrowing of the head seems to accompany snout elongation, relative head width is used to characterize snout shape.

Mating. Pseudemys scripta elegans has an elaborate courtship behavior. The male overtakes a female and positions himself in front of her. He then titillates her by rapid vibration of his elongated foreclaws near her face and also by some rapid movements of the head. This complex Liebespiel was first noted by Taylor (1933). Jackson and Davis (1972) gave a thorough description of mating in *P. s. elegans* and suggested that titillation has evolved to replace biting as a means of immobilizing the female and that modifications in the complex Liebespiel could produce distinctive patterns within "the genus or subfamily."

Courtship involving titillation (and probably rapid head movements) occurs in the 12 *Chrysemys* group species that have elongated foreclaws (Carr, 1952; Ernst and Barbour, 1972; Jenkins, 1979; pers. obs.), including the 3 U.S. subspecies of *P. scripta*. It seemingly does not occur in taxa that lack the elongated foreclaws; this includes all Mesoamerican *P. scripta*. Evidence from observed matings is as follows: Davis and Jackson (1973), male *P. s. taylori* with captive females of *P. s. elegans* and *Chrysemys picta*, direct approach with biting; Moll and Legler (1971), *P. s. venusta* in Panama, two natural matings, rear approach and mounting without foreplay; personal observation (with binoculars from a cliff), natural mating, *P. s. hiltoni* male following female and mounting periodically, no face-to-face Liebespiel; personal observation (Taronga Park Zoo, Sydney, Australia), 250 mm male *P. s. dorbigni* courting female *P. s. elegans* (also being courted typically by male *elegans*), no titillation, direct approach with cloacal sniffing and trailing.

The function of elongated foreclaws is seemingly clear, but there is no demonstrable function for the elongated snout. It may permit sexual recognition by head profile in populations where males and females do not differ predictably in size. The snout could also be an erotic prod used in mating.

CONCLUSIONS. The following points summarize my conclusions on sexual dimorphism and sympatry (Fig. 7.12).

1. All USASCRIP (*elegans, scripta, troosti*) share three derived characters:
   a. Males have greatly elongated foreclaws.
   b. There is an elaborate courtship in which the long claws are used.
   c. Males are significantly smaller than females.
2. All MESOSCRIP lack those characters. They have no elongated foreclaws and no elaborate courtship, and the sexes are more or less the same size.
3. Males of MESOSCRIP have a pointed, elongated snout that is not present in USASCRIP.
4. Because the elongated snout of MESOSCRIP is a phenotypic tendency in USASCRIP, and the distinctive phenotypes of USASCRIP show up as occasional variants in MESOSCRIP (pers. obs.), it can be hypothesized that selective factors acting on these phenotypes in the two groups are different.
5. All USASCRIP occur sympatrically with other striped emydines of the *Chrysemys* group in some parts of their ranges. South of lat. 38 this is usually a microsympatric association with another species of *Pseudemys* and at least one other species of striped emydine of the *Chrysemys* group. The elongated foreclaws, the sexual size dimorphism, and the Liebespiel are precopulatory isolating mechanisms that
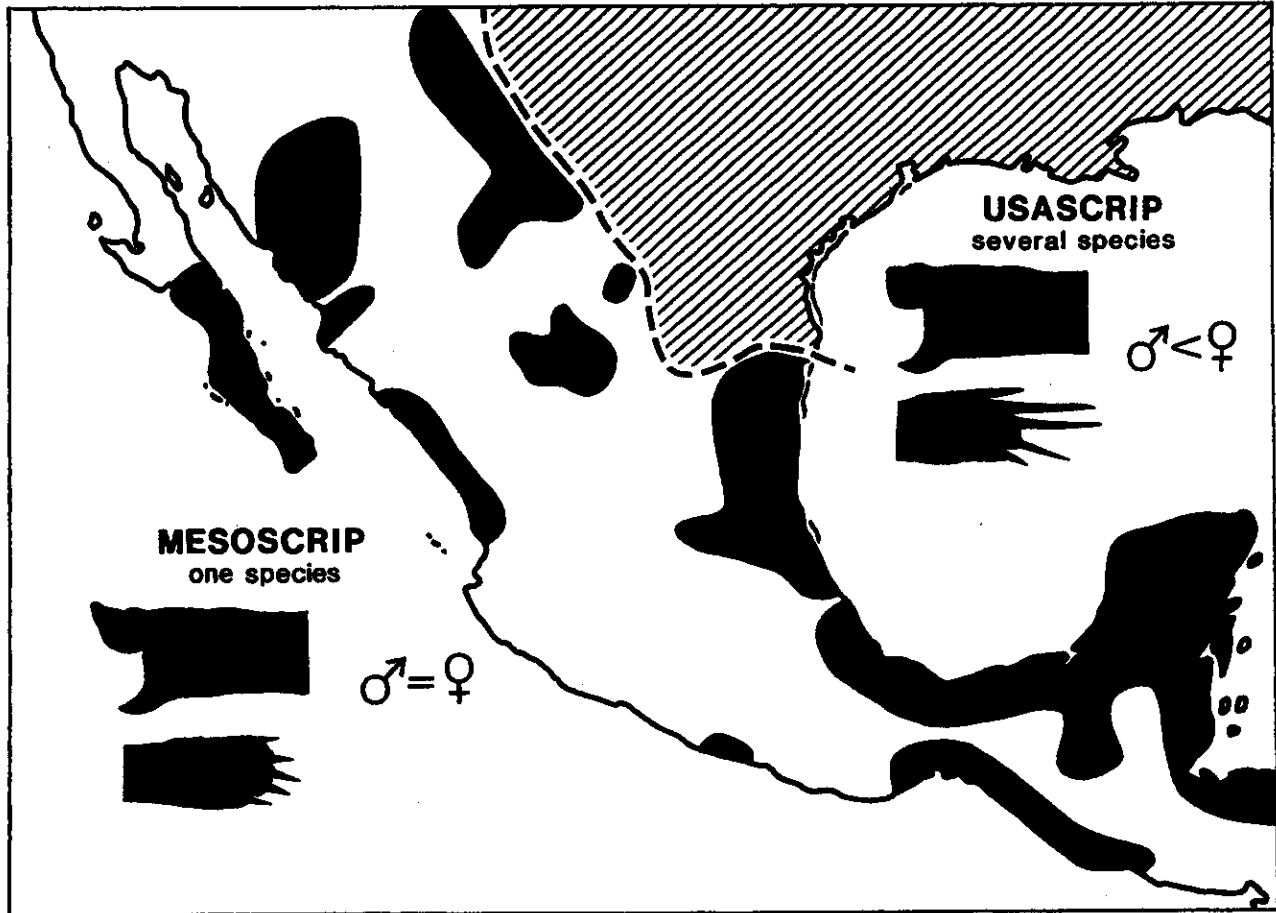
FIGURE 7.12.   Map showing distributions of Mexican species (MESOSCRIP) and a diagonally shaded area indicating where more than one species of *Pseudemys* (USASCRIP) occurs. South and west of the Rio Grande, *Pseudemys scripta* is the only emydine and the only turtle with stripes. In the area of sympatry, males are smaller than females, lack a pointed snout, and have elongated foreclaws. In the area of nonsympatry, males are about the same size as females, have a pointed snout, and lack the elongated foreclaws.

have been selected for in this zone of sympatry where many striped species occur.

6. These sexually dimorphic characters do not have a high selective advantage in MESOSCRIP. There is virtually no emydine sympatry in the entire range of MESOSCRIP; *Pseudemys* is the only striped aquatic turtle and the only basking emydid in the entire region. *Pseudemys* can mate without chance of error.

TIME OF ORIGIN

The Northern Isolates and the subspecies *hiltoni* and *nebulosa* have differentiated more than other subspecies of *Pseudemys scripta* (perhaps to the point logically expected in full species). I attribute much of this differential divergence to isolation and genetic drift. In known instances of secondary overlap (e.g., *taylori* and *elegans*), interbreeding

occurs (this has simply been noted, not studied). This secondary overlap has not resulted in character displacement, and no isolating mechanisms seem to have evolved (but see discussion of *grayi* and *venusta* in Pacific Population of Mexico, above). Differentiation in the other subspecies is closer to that expected in geographic races. An intensive ecological study by Moll and Legler (1971) showed few life history modifications when populations in Panama were compared with those of *elegans* in the United States.

All that I have learned of the relationships and ecology of Mesoamerican *Pseudemys scripta* bespeaks relatively recent colonization and differentiation. The origin of some populations in Mexico can be logically associated with Pleistocene events. I conclude that it is unnecessary to invoke Tertiary events to explain what we see in *Pseudemys scripta*. It is more reasonable to think in terms of recency than of antiquity.

Epilogue

Although the distribution of *Pseudemys scripta* has the appearance of being largely natural and congruent with fairly recent drainage histories, there is no zoogeographic scenario presented here that could not have occurred as a result of human introduction. All *Pseudemys* are bright and attractive as juveniles (witness the German, *"Schmuck . . ."* = jewel; Obst, 1985), but they become less attractive and more difficult to keep as they grow larger. Disenchanted turtle owners commonly release their pets (usually *P. s. elegans*). This has probably happened in every state of the United States, in the Canal Zone, and sporadically on all other continents except Antarctica. Turtles are commonly carried and used by humans for food; this practice occurs now (pers. obs.) and certainly occurred in prehistoric times (Tamayo and West, 1964). Human introduction is a serious alternative hypothesis for the dispersal of *P. s. nebulosa*, some Antillean populations, and some South American populations.

Acknowledgments