SYSTEMATICS, FOSSIL HISTORY, AND EVOLUTION OF THE GENUS *CHRYSEMYS*

W. G. WEAVER, JR.,
Department of Natural Sciences, Florida State Museum
Gainesville, Florida 32601

FRANCIS L. ROSE,
Department of Biology, Texas Technological College
Lubbock, Texas 79409

ABSTRACT

An investigation of skull, shell, and foot osteology of *Chrysemys* showed McDowell's (1964) criteria for the subgenera of *Chrysemys* to be invalid when applied to populations in the southern United States, Mexico, and South and Central America. McDowell's synonymy of *Pseudemys* with *Chrysemys* is valid.

The evidence also indicates that the turtles currently included in *Chrysemys scripta* actually represent three distinct species groups: (1) *C. scripta* including *C. s. scripta, C. s. elegans, C. s. troosti;* (2) *C. gaigeae* including *C. s. gaigeae, C. s. taylori, C. s. hiltoni;* (3) *C. ornata, C. callirostris,* and perhaps *C. dorbigni.*

I. INTRODUCTION

Recently we studied large numbers of fossil and extant specimens of *Chrysemys (Pseudemys).* In order to understand the phylogenetic relationships of the fossil forms, it became necessary to clarify the osteological relationships of the extant turtles of the genus *Chrysemys,* particularly those in the eastern United States. Most previous workers have based their taxonomic allocations of these turtles on color and color patterns; osteological comparisons were usually limited to the skull. The degree of conservatism and parallelism exhibited by turtles militates against the use of a single superficial character, such as color, to determine taxonomic relationships. An ideal taxonomy reflects phylogeny and thus depends on fossil evidence. Color, color patterns, and most soft anatomy are not part of the fossil record. Few workers since Hay (1908) have attempted a comparative osteology of emydine turtles. Because of the lack of such studies, and the fact that large numbers of fossil turtles are now known, our investigation was wholly osteological, dealing with features of the skull, shell, and feet. Most characters used in this study are also present in the known fossil species.

We examined over 20 characters in the following extant and fossil species or races. Fossils are denoted by an asterisk. The number of specimens examined and their geographic origin is shown in parentheses: *Chrysemys concinna suwanniensis* (20, Florida), *C. c. concinna* (1, Georgia), *C. c. hieroglyphica* (1, Tennessee), *C. s. scripta* (20, Florida, Georgia, Alabama), *C. s. elegans* (20, Texas; Coahuila, Mexico), *C. s. troosti* (6, Kentucky), *C. s. gaigeae* (12, Chihuahua, Mexico), *C. s. taylori* (2, Coahuila, Mexico), *C. s. callirostris* (13, purchased), *C. s. ornata* (10, Tabasco, Mexico; Vera Cruz, Mexico; Honduras), *C. p. picta* (9, Georgia, Pennsylvania, New York), *C. p. marginata* (12, Tennessee), *C. r. rubriventris* (10, New Jersey, Massachusetts), *C. alabamensis* (1, Alabama), *C. nelsoni* (20, Florida), *C. platymarginata** (20, Florida), *C. inflata** (6, Florida), *C. carri** (20, Florida), *C. williamsi** (20, Florida), *Echmatemys wyomingensis** (1, Wyoming), *C. floridana peninsularis* (20, Florida).

We are indebted to the Chicago Natural History Museum, U. S. National Museum, University of Kansas Collections, Carnegie Museum, and the University of Florida Collections of the Florida State Museum for specimen loans. The work was partially sup-

ported by a grant from the American Philosophical Society (Penrose Fund) to F. L. Rose. In particular we wish to thank Dr. Walter Auffenberg for his advice and encouragement during this investigation.

II. Character Analysis

Nuchal bone.—The nuchal scute underlap is defined as the length of that part of the nuchal scute lying on the ventral surface of the nuchal bone. In *C. scripta* and *C. nelsoni* the scute sulci are well defined. In *C. floridana* the posterior border is less clear, but the lateral borders are well defined. In *C. concinna* all the ventral sulci are poorly defined and particular care has to be taken not to confuse a more posterior scar marking the skin attachment with that indicating the posterior border of the scute.

These data are compared by dividing the length of the nuchal scute underlay x 100 by the maximum nuchal bone length. The resultant ratios (Fig. 1) show that *C. scripta* has the greatest amount of underlay ($\bar{x}$= 31.7) and *C. concinna* the least ($\bar{x}$=6.7). In this regard *C. nelsoni* is closer to *C. scripta* than to either *C. concinna* or *C. floridana.* The Mexican, Central and South American races of *C. scripta* are more similar to *C. floridana* than *C. scripta* (*C. s. gaigeae,* $\bar{x}$=11.7; *C. s. ornata,* $\bar{x}$=17.5).

The nuchal bones of *Chrysemys scripta* and *C. nelsoni* have a rugose dorsal surface compared with the generally smooth surface in *C. concinna, C. floridana* and *C. picta.* In *C. concinna* the posterior medial edge of the second marginal scute sulcus occurs on the nuchal bone in 85% of the specimens examined. None of the *C. scripta* have the sulcus of the second marginal scute on the nuchal bone; however, it is present on 36% of the *C. nelsoni* and 21% of the *C. floridana.* The scute areas of the nuchal bone in North American *C. scripta* are strongly sculptured (Table 1), those of *C. floridana, C. concinna, C. scripta ornata, C. s. callirostris, C. s. gaigeae* are weakly sculptured.

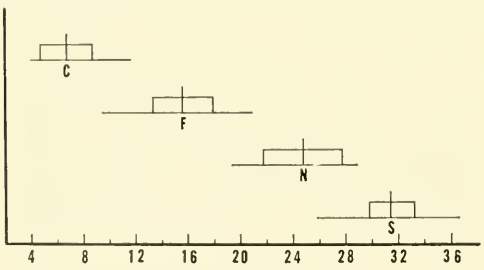

Figure 1. Nuchal scute underlap. **C,** *Chrysemys concinna;* **F,** *C. floridana;* **N,** *C. nelsoni;* **S,** *C. scripta.* The nuchal scute underlap is the length of that part of the nuchal scute lying on the ventral surface of the nuchal bone X 100 divided by the maximum nuchal bone length. Vertical line = mean; horizontal line = range; white rectangle = one standard deviation.

Gular scute overlap.—The gular scute overlap is defined as the length of that part of the gular scute lying on the dorsal surface of the epiplastral lip at the mid-line. When the measurement x 100 is divided by the nuchal bone length there is no significant difference between *C. scripta* and *C. nelsoni* (Fig. 2). However, there is a 49% difference between the means of *C. nelsoni* and *C. floridana. Chrysemys concinna* has the least overlap. The tropical races of *C. scripta* resemble *C. floridana* and *C. concinna* in this respect (i.e, *C. s. gaigeae,* $\bar{x}$=9.3; *C. s. ornata,* $\bar{x}$=5.85).

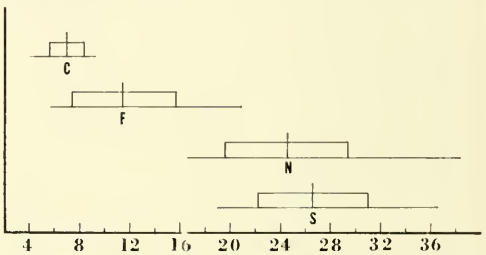

Figure 2. Gular scute overlap. **C,** *Chrysemys concinna;* **F,** *C. floridana;* **N,** *C. nelsoni;* **S,** *C. scripta.* The gular scute overlap is the length of that part of the gular scute lying on the dorsal surface of the epiplastral lip at the midline X 100 divided by the nuchal bone length. Method of presentation as in Figure 1.

Plastron.—The xiphiplastral width is defined as the width of the posterior plastral lobe through the center of the xiphi-hypoplastral junction, divided by the length from the posterior end of the plastron to the sulcus marking the posterior border of the abdominal scute.

The xiphiplastron of *C. scripta* and *C. nelsoni* is wider than that of *C. floridana* or *C. concinna* (Fig. 3). Again, *C. scripta* and *C. nelsoni* are more similar to each other than either is to *C. floridana* or *C. concinna. C. s. gaigeae* is similar to the latter (Fig. 3).

The plastron of *C. concinna* is generally

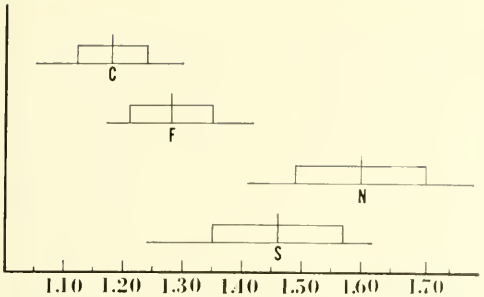

Figure 3. Plastral width/length. **C**, *Chrysemys concinna;* **F**, *C. floridana;* **N**, *C. nelsoni;* **S**, *C. scripta.* Method of presentation as in Figure 1.

flat and turned upward gently at a point even with the axillae. In *C. scripta, C. nelsoni* and *C. floridana* the epiplastron turns abruptly upward and the plastron is convex in the vicinity of the hyo-hypoplastral suture; thus, when placed on a flat surface only a small portion of the plastron touches the surface.

The anterior end of the epiplastron in *C. scripta* and *C. nelsoni* is abruptly truncated and forms a thick epiplastral lip which is overlapped dorsally by the gular scutes. In *C. concinna* and *C. floridana* the anterior end of the epiplastron is rounded and the epiplastral lip is not raised and thick. The Mexican, Central and South American races of *C. scripta* also have poorly developed epiplastral lips.

The posterior end of the xiphiplastron is acutely notched (Table 1) in all the forms examined, except in *C. s. scripta, C. s. troosti, C. s. elegans.* In these and in some *C. picta,* the notch is shallow. The fossil species *C. carri* and *Echmatemys wyomingensis;* living *C. s. scripta, C. s. elegans, C. s. troosti, C. nelsoni, C. rubriventris,* and *C. picta* have a pronounced overlap of the femoral scute onto the dorsal surfaces of the hypo- and xiphiplastra. The femoral scute overlap is restricted in the other species and races.

Pygal projection.—In all of our *C. scripta, C. nelsoni* and *C. picta* the posterior tip of the pygal projects ventrally nearly 90 degrees (Table 1). In 43% of the *C. floridana* and 7% of the *C. concinna* the pygal is ventrally directed, but the inclination is slight, not approaching the 90 degree ventral angle of *C. scripta, C. nelsoni,* and *C. picta.*

The pygal of *C. scripta* is narrow distally. The width of the distal end divided by the width of the proximal end of the pygal shows that *C. scripta* has the narrowest distal width ($\bar{x}$=0.94). The pygal of *C. floridana* ($\bar{x}$=1.44) is more flared than that of *C. concinna* ($\bar{x}$=1.32). *Chrysemys nelsoni* is intermediate between *C. scripta* and *C. floridana* or *C. concinna* (Fig. 4).

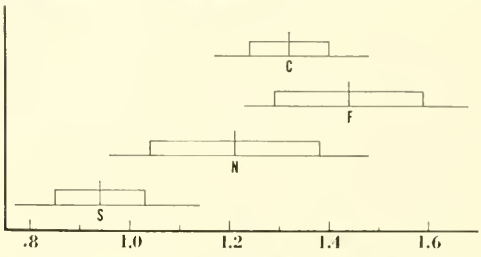

Figure 4. Posterior pygal width/anterior pygal width. **C**, *Chrysemys concinna;* **F**, *C. floridana;* **N**, *C. nelsoni;* **S**, *C. scripta.* Method of presentation as in Figure 1.

Shell weight.—When comparing *C. nelsoni* to *C. rubriventris* we noted a great difference in bone thickness of the respective shells which was reflected in the shell weights. The weight of the dried shell was plotted against the carapace length (Figs. 5 and 6). The shell of *C. nelsoni* proved much heavier than that of comparable sized *C. rubriventris* (Fig. 5). A similar relationship exists between the shell weights of *C. s. gaigeae, C. s. taylori,* and the North American races of *C. scripta,* the latter having a heavier shell (Fig. 6).

Maxilla-quadratojugal junction.—McDowell (1964) stated that members of the *C. floridana* group and *C. nelsoni-rubriventris* group have a strong sutural union between the maxilla and quadratojugal (=McDowell's squamosal) bones; this union being absent in *C. scripta* and *C. picta.* All of the *C. scripta* from North, Central, or South America that we have examined lacked this union; however, 50% of the *C. nelsoni,* 17% of the *C. floridana,* and 30% of the *C. concinna* also lacked this union on one or both sides of the skull.

Width of nares.—The narial opening of *C. picta* and North American *C. scripta* is small compared to the other species of *Chrysemys.* When the narial width x 100 is divided by the skull length (tip of snout to a line even with the posterior tips of the supratemporals) *C. scripta* has an average of

TABLE I
Comparison of Characters in *Chrysemys*

	Chrysemys c. concinna	*C. floridana peninsularis*	*C. ornata*	*C. gaigeae*	*C. s. scripta*	*C. s. elegans*	*C. s. troosti*	*C. p. pieta*	*C. rubriventris*	*C. nelsoni*	***C. platymarginata*	***C. carri*	***C. williamsi*
Long gular scute overlap	—	—	—	—	+	+	+	+	+	+	+	+	—
Wide, thick, rectangular epiplastral lips	—	—	—	—	+	+	+	+	+	+	+	+	—
Humeral-pectoral sulcus behind endoplastron	+	+	+	+	+	+	+	+	+	+	+	+	+
Wide femoral scute overlap	—	—	—	—	+	+	+	+	+	+	+	+	—
Expanded xiphiplastron	—	—	—	—	+	+	+	+	+	+	+	+	—
Acute notch at posterior end of plastron	+	+	+	+	—	—	—	—	+	+	—	+	+
Rugose plastron	—	—	—	—	—	—	—	—	+	+	—	+	—
Long nuchal scute underlap	—	—	—	—	+	+	+	+	+	+	+	+	—
Sculptured scutal areas on nuchal bone	—	—	—	—	+	+	+	—	—	—	+	—	—
Strong peripheral bone notching	+	—	—	+	+	+	+	—	—	—	+	—	—
Acute ventral projection of pygal bone	—	—	—	—	+	+	+	+	+	+	+	+	—
Rugose carapace	—	—	—	—	+	+	+	—	+	+	+	—	—
Wide upper and lower triturating surface	—	—	—	—	—	—	—	—	+	+	—	—	?
Well developed ridge on upper triturating surface	+	+	+	+	+	+	+	—	+	+	?	?	?
Cusps on upper triturating ridge	+	+	—	—	—	—	—	—	+	+	?	?	?
Median symphysial ridge on lower alveolar surface	+	+	—	—	—	—	—	—	+	+	?	?	?
Flat ventral surface of mandible	+	+	—	—	—	—	—	—	+	+	—	—	—
Notched premaxilla	—	—	+	+	+	+	+	+	+	+	?	+	?
Narrow nasal opening	—	—	+	?	+	+	+	+	—	—	?	?	?
Maxilla and squamosal united in more than 50% of specimens examined	+	+	—	—	—	—	—	—	—	—	?	?	?
Number of phalanges in fifth toe	3	2	3	2	2	2	2	2	2	2	?	?	?

** = fossil forms + character present — character not present

13.3%, *C. nelsoni* 16.6%, *C. floridana* 19.3%, and *C. concinna* 20.6%. Again, *C. nelsoni* effectively bridges the gap between *C. scripta* and the other two species (Fig. 7).

Temporal arch length.—The arch length is defined as the distance from the posterior end of the maxilla to the anterior edge of the distal surface (articulating surface) of the quadrate x 100 divided by the skull length. The character is highly variable (Fig. 8). *Chrysemys scripta* has an average of 34.0, *C. nelsoni* 13.2, *C. floridana* 28.2, and *C. concinna* 29.6.

Alveolar shelf.—McDowell (1964) separated the subgenus *Pseudemys* into *floridana* and *rubriventris* sections by the features of

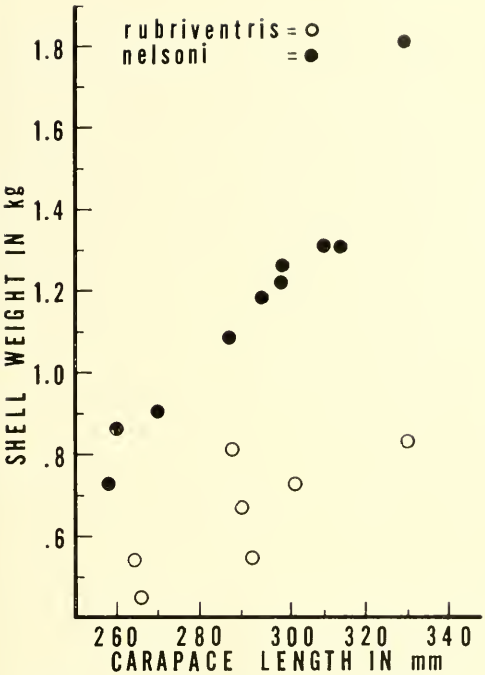

Figure 5. Relative shell weights of *Chrysemys rubriventris* and *C. nelsoni*.

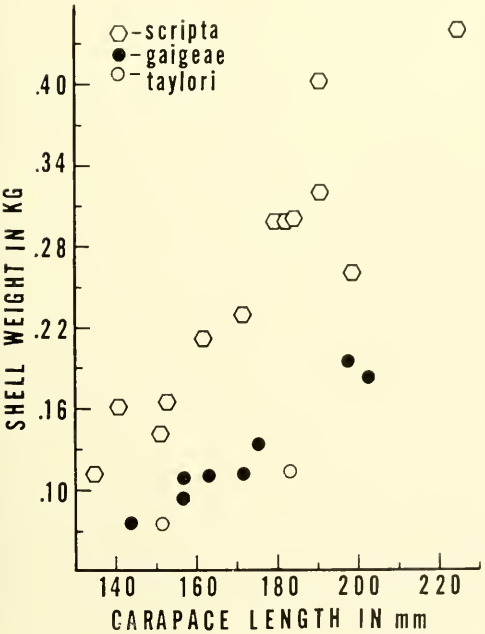

Figure 6. Relative shell weights of *Chrysemys scripta scripta, C. s. gaigeae,* and *C. s. taylori.*

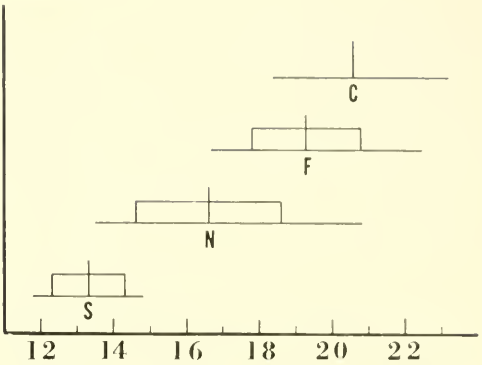

Figure 7. Narial width. **C,** *Chrysemys concinna;* **F,** *C. floridana;* **N,** *C. nelsoni;* **S,** *C. scripta.* Values determined by narial width X 100 divided by skull length. Method of presentation as in Figure 1.

the vomer and the alveolar surface. In the *rubriventris* section, but not in the *floridana* section, the vomer contributes to the upper triturating surface. Essentially this vomerine contribution results in a wider triturating surface. For purposes of comparison the alveolar width was measured from the anterior tip of the premaxilla to the posterior edge of the anterior median triturating surface x 100 divided by the skull length. *Chrysemys nelsoni* has a triturating shelf about 50% wider than that of the other

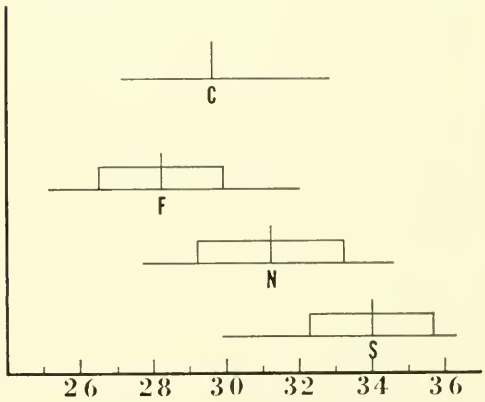

Figure 8. Temporal arch length. **C,** *Chrysemys concinna;* **F,** *C. floridana;* **N,** *C. nelsoni;* **S,** *C. scripta.* Arch length is the distance from the posterior end of the maxilla to the anterior edge of the distal surface (articulating surface) of the quadrate X 100 divided by the skull length. Method of presentation as in Figure 1. Fewer than 20 specimens of *C. concinna* were measured for this character, thus no standard deviation was calculated.

species. In this respect *C. scripta* is closer to *C. floridana* and *C. concinna* than to *C. nelsoni* (Fig. 9). We found a similarly broad triturating shelf which includes the vomer in *Graptemys*. Thus far no exhaustive work has been done on the food habits of *C. nelsoni* or *C. rubriventris* to determine

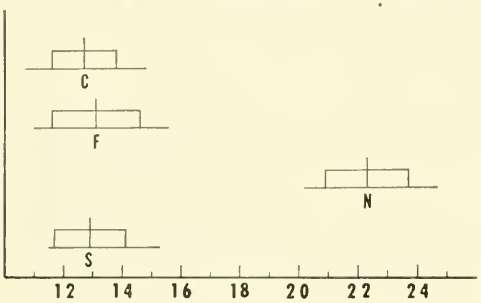

Figure 9. Alveolar width. **C**, *Chrysemys concinna;* **F**, *C. floridana;* **N**, *C. nelsoni;* **S**, *C. scripta.* Alveolar width is the distance from the anterior tip of the premaxilla to the posterior edge of the anterior median triturating surface X 100 divided by the skull length. Method of presentation as in Figure 1.

whether the broad shelf in these species is used for mollusk crushing as in *Graptemys*.

The upper triturating surface has a well developed longitudinal ridge cusped on its anterior end in *C. floridana, C. concinna,* and *C. nelsoni* (Table 1). McDowell uses this as one of the features separating the subgenera *Pseudemys* and *Trachemys*. *Trachemys* usually lacks these cusps. In *C. concinna,* however, the cusp is often reduced, while in *Chrysemys scripta* neither the ridge nor cusps are strongly developed (although by no means entirely absent). In this respect the Neotropical and the North American *C. scripta* are similar to each other.

The lower triturating shelf has a median longitudinal ridge in members of the *nelsoni-rubriventris* section of *Pseudemys* and one lingually positioned in the *floridana* section of *Pseudemys,* and in *Chrysemys,* and *Trachemys*. A ridge from the dorsal anterior tip of the mandibular symphysis back to the median anterior border of triturating shelf occurs in *C. floridana, C. concinna,* and *C. nelsoni. Chrysemys picta,* and both temperate and Neotropical *C. scripta* lack this ridge. *Chrysemys nelsoni* and *C. rubriventris* also have a much wider, lower alveolar surface than in other species of *Chrysemys*.

Shell depth.—Shell depth is defined as the depth of the shell through the center of the third neural bone x 100 divided by the carapace length. Carapace length is defined as the distance along the mid-line from the anterior end of the nuchal bone to the posteriormost end of the carapace. The data show that the shell of *C. concinna* is flatter than that of the other species (Fig. 10).

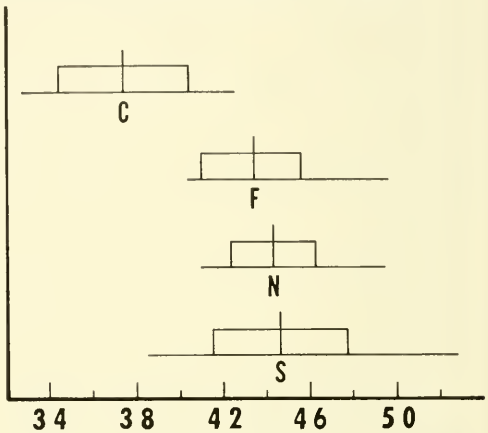

Figure 10. Shell depth. **C**, *Chrysemys concinna;* **F**, *C. floridana;* **N**, *C. nelsoni;* **S**, *C. scripta.* Shell depth is the depth of the shell through the center of the third neural bone X 100 divided by the carapace length.

Carapace peak.—Viewed laterally the carapace rises to a peak on the mid-line before sloping toward the pygal. In *C. concinna* the peak occurs on either the third neural (56%) or the fourth (44%). The peak shifts posteriorly in *C. floridana, C. nelsoni,* and *C. scripta* respectively. In the latter the peak usually is on the fifth neural (60%) (Fig. 11).

Phalanges in the fifth toe.—McDowell's definition of the subgenus *Trachemys* includes the presence of three phalanges on the fifth toe; four in *Pseudemys* (Table 1). We found that the fifth toe of *C. concinna* has three phalanges; *C. floridana,* two; North American *C. scripta,* two or three; *C. picta,* two; *C. s. ornata,* three; *C. terrapin,* two (from Grand Cayman, B.W.I.). The terminal phalanx apparently ossifies late in ontogeny in these turtles. We are investigating the foot architecture of these turtles in more detail.

Posterior pterygoid extension.—The posterior end of the pterygoid extends back to

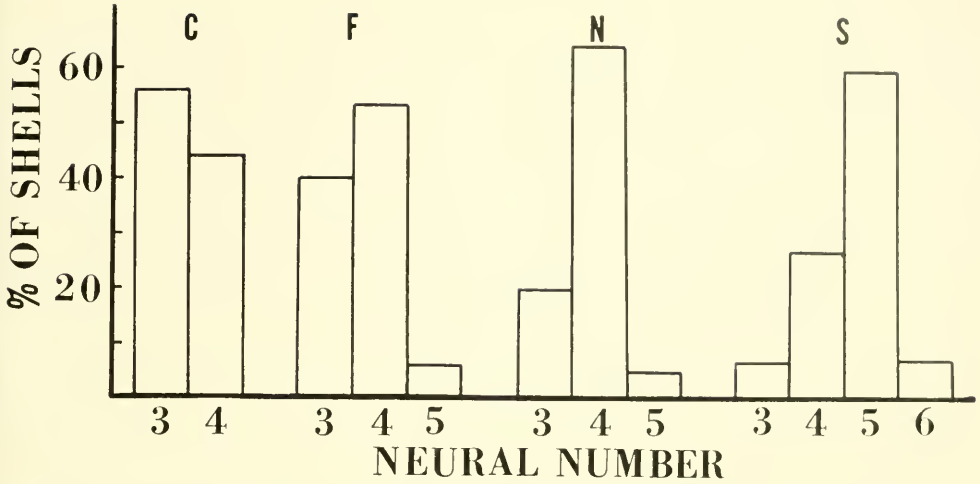

Figure 11. Carapace peak. On the left is the per cent of shells peaking on the neurals indicated at the bottom. **C,** *Chrysemys concinna;* **F,** *C. floridana;* **N,** *C. nelsoni;* **S,** *C. scripta.*

the level of the exoccipital in some *Trachemys,* but not in *Chrysemys* or *Pseudemys.* In all emydines the posterior pterygoid extension increases in length with age, with its most posterior position occurring in large *C. scripta.*

Constriction of first vertebral scute.—An unconstricted first vertebral scute is a feature used by McDowell to separate the subgenus *Chrysemys* from the subgenus *Trachemys.* In our specimens it is unconstricted in 67% of the *C. picta* and 100% of the adult *C. scripta gaigeae.*

III. Discussion

McDowell (1964), in a review of the aquatic Testudinidae, recognized three subgenera under the genus *Chrysemys: Pseudemys,* including the *floridana* and *rubriventris* groups; *Trachemys* (the *scripta* complex), and the monotypic *Chrysemys.* His subgeneric criteria were based on skull osteology and foot architecture. We concur with McDowell that all the species currently listed under *Pseudemys* are best placed in the genus *Chrysemys* on the basis that none of the characters said to separate them (Galbreath, 1948; Hay, 1908) are here considered to be of generic rank. Additionally Zug (1966) showed that the members of *Pseudemys* and *Chrysemys* have a very similar penial morphology.

The close relationship between *C. picta* and *C. scripta* is the best argument for considering *Pseudemys* synonymous with *Chrysemys.* The primary differences between the two species occur in the shell. The carapace of *C. picta* lacks a dorsal ridge and notched posterior peripheral bones. The pleural bones of old individuals of *C. picta* may have a rugose pattern superficially similar to that of North American *C. scripta.* However, the rugosity of *C. picta* consists of thick, deep, longitudinally curved ridges, much more strongly developed and more numerous on the distal portion of the pleural bones than on the proximal portions. In *C. scripta* the ridges are thinner and comparatively equal in development and abundance over all of the pleural bones, giving a rugose appearance to the entire carapace.

Chrysemys scripta and *C. picta* are similar in the nuchal scute underlap, gular scute overlap, femoral scute overlap, number of phalanges on the fifth toe, and general skull features. Apparently the primitive emydine skull was similar to that of *C. picta* or *C. scripta,* and not *C. nelsoni, C. alabamensis,* or *C. rubriventris* as theorized by McDowell. McDowell assumes emydine evolution through forms with wide triturating surfaces such as occur in *C. alabamensis* and *C. nelsoni.* However, we have shown elsewhere (Rose and Weaver, 1966) that *C. nelsoni* arose from a narrow-jawed ancestor. In addition, specimens of the extinct genus *Echmatemys,* here believed ancestral to the remaining North American emydines, have

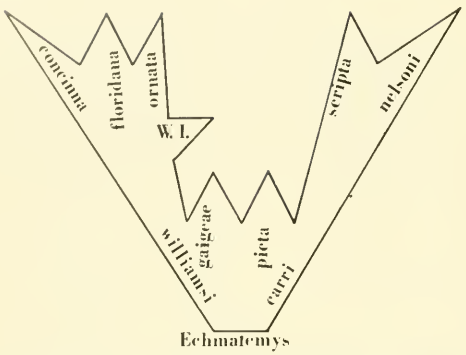

Figure 12. Proposed phylogeny of *Chrysemys*. *Echmatemys*, *Chrysemys williamsi*, and *C. carri* are fossil forms. W.I. indicates the West Indian species of *Chrysemys*.

narrow triturating surfaces. Other skull features we consider primitive include the following: the mandibles lack a median, internal symphysial ridge, are rounded ventrally; and have a narrow triturating surface with a median longitudinal ridge, but no appreciable development of cusps; the maxillae are provided with a narrow triturating shelf to which the vomer does not contribute; the narrow nasal opening; and a notched premaxilla. Most of these features occur in the North American *C. scripta*. The skull of the closely related *C. nelsoni* is modified from this basic design. That it has been modified from a *picta* or *scripta*-like skull is shown by a fossil jaw found within the shell of a specimen of the Pliocene *C. carri* (Rose and Weaver, 1966). This mandible is practically identical to that of large, Recent *C. scripta scripta*.

We feel that the turtles currently placed in *C. scripta* comprise three species groups: (1) *C. s. scripta, C. s. elegans, C. s. troosti*, all of North America; (2) *C. s. gaigeae, C. s. taylori, C. s. hiltoni*, found in the Rio Grande valley and northern Mexico; and (3) *C. s. ornata, C. s. callirostris* and perhaps *C. dorbigni*, found in southern Mexico and Central and South America (also see Williams, 1956). We believe that species groups 2 and 3 are quite distinct from *C. scripta*. In particular our analysis indicates that groups 2 and 3 are more closely related to *C. floridana* and/or *C. concinna* than to *C. scripta*. *Chrysemys scripta ornata* and *C. s. callirostris* are similar to *C. floridana* and/or *C. concinna* in the extent of the nuchal scute underlap and gular scute overlap, the number of phalanges on the fifth toe, the absence of doubly notched posterior peripheral bones, the relatively narrow plastron with a well developed posterior bone, the relatively narrow plastron with a well developed posterior notch, and the shape of the epiplastral lip. Until these populations are studied in greater detail we propose that they be considered distinct at the species level, and be designated as *C. ornata, C. callirostris*, and *C. gaigeae*. Tentatively we include *C. s. taylori* and *C. s. hiltoni* in *C. gaigeae*.

The Pliocene species *C. williamsi* also has many characters in common with its probably derived species, *C. concinna, C. floridana, C. ornata*, and *C. callirostris*. It is quite distinct from contemporary species in the same geographic area, *C. carri* and *C. inflata* (Rose and Weaver, 1966; Weaver and Robertson, 1967). *Chrysemys inflata* is unquestionably a member of the evolutionary line leading to North American *C. scripta*, while *C. carri* is similar to both *C. scripta* and *C. nelsoni*, suggesting an even earlier common ancestor for both *scripta* and *nelsoni* (Rose and Weaver, 1966). Thus the genetic separation between the tropical turtles now considered races of *C. scripta* and extant North American *C. scripta* has existed at least since the Pliocene.

The living *Chrysemys scripta* as defined above, shares with the *nelsoni-rubriventris* group a ventrally projecting pygal bone, long nuchal scute underlap, long gular scute overlap, rugose carapace, keel on posterior neural bones, well defined and truncated epiplastral lip, wide posterior plastron, and notched upper jaw. The two groups differ primarily in posterior peripheral notching and the architecture of the triturating surfaces. The taxonomic question thus resolves itself as to what species or races are to be included in the subgeneric framework provided by McDowell. The features used by McDowell to define the subgenera of *Chrysemys* are invalid. Of the four characters he uses to distinguish the subgenera *Pseudemys* and *Trachemys*, two, the dentary shape and anterior triturating cusp, are sufficiently variable to render their validity as subgeneric criteria questionable. The remaining two characters, the number of phalanges on the fifth toe and the nature of the maxilla-quadratojugal junction, are completely invalid as used by McDowell. A

firm union between the maxilla and quadratojugal does not occur consistently in *C. floridana,* in *C. nelsoni,* or *C. concinna* as claimed by McDowell. Similarly we found members of both subgenera *Trachemys* and *Chrysemys* to have both two and three phalanges in the fifth toe and none with four which McDowell stated for the subgenus *Pseudemys.* Furthermore, McDowell's arrangement is contrary to the fossil evidence showing that *C. nelsoni* and *C. rubriventris* are more closely related to *C. scripta* than to *C. floridana* and *C. concinna.* We feel that present knowledge concerning the Mexican, Central and South American, and West Indian forms is insufficient to delimit accurately subgenera of the genus *Chrysemys.*

Though *C. floridana* and *C. concinna* are presently regarded as separate species (Conant, 1958; Carr, 1952) the data upon which this interpretation rests has never been published. These populations, originally listed as races under *C. floridana,* were raised to species rank by John Crenshaw in an unpublished manuscript (Crenshaw, 1955). Our evidence fully supports this division at the species level. However, we find no evidence of hybridization between *C. concinna* and *C. floridana* as reported by Crenshaw (1955, 1965).

The *gaigeae-taylori* populations of the Rio Grande valley area are more difficult to interpret than populations of the *ornata* complex in South and Central America. Some individuals of *C. gaigeae* resemble *C. scripta (sensu strictu)* by having doubly notched peripherals and a median carapace keel, although the latter is weakly developed. Generally the carapace is smooth, but when ridges do occur they are on the distal ends of the peripheral bones, as in *C. picta. Chrysemys gaigeae* is notable in that the first vertebral scute in all of our specimens is unconstricted, a feature seen elsewhere only in some *C. picta.* The remarkable thinness of the shell of *C. gaigeae* and *C. taylori* also contrasts strongly with the North American *C. scripta* (Fig. 6).

Table 1 summarizes 21 of the characters used in our analysis. Thirteen of these are present in 5 or more of the extant species or races studied. These thirteen are considered to be "primitive," or generalized features of the genus *Chrysemys.* Of these *Echmatemys* has 9; however, the nature of several characters in this extinct genus remains unknown. The Pliocene *C. carri, C. williamsi* and *C. platymarginata* each have 9, 2, and 9 primitive characters respectively. Fossil and Recent *C. picta* and *C. scripta* have 9 and 12, respectively, of these features; fossil and Recent *C. nelsoni,* 11. It is noteworthy that *C. concinna, C. floridana, C. gaigeae,* and *C. ornata* have only 5 or less of these features, attesting to the modifications from the ancestral condition.

Obviously all of the characters used in this study do not have equal value. In addition, some characters are linked to others. For example, the gular scute overlap seems to be linked with the nuchal scute underlap and perhaps the femoral scute overlap with the xiphiplastral width. Our rationale for including such characters lies in the considerable extent we have relied on fossil evidence in our interpretations. Extinct species are often represented by elements that have poorly diagnostic characters. These characters, however, may be linked to others which are known to be highly diagnostic. We feel, however, that most of the characters listed in Table 1 are significant in determining evolutionary trends and relationships within *Chrysemys.* The most significant features, in our opinion, are those shown in Figures 1-10.

These data indicate that there are two major evolutionary lines in the Recent New World Emydinae. *Chrysemys concinna, C. floridana, C. ornata, C. callirostris,* and possibly *C. gaigeae* form an "advanced" line, while North American *C. scripta, C. nelsoni,* and *C. picta* constitute a "primitive" line. The two lines were already distinct by the Pliocene, as witnessed by the presence of *C. williamsi* and *C. carri* in a single deposit in Florida (Rose and Weaver, 1966). The advanced evolutionary line is here referred to as the *floridana* group and the primitive evolutionary line as the *scripta* group.

The large amount of fossil material makes possible a summary of evolutionary trends within *Chrysemys.* A hypothetical phylogeny is shown in Figure 11.

Scutes.—The nuchal scute underlap, gular scute overlap, and femoral scute overlap have become reduced in the *floridana* line. The extant condition was present in the earliest fossil known of that group, *C. williamsi.* The scutal over- and underlaps re-

mained long in members of the *scripta* line (Figs. 1 and 2) as in the fossil *Echmatemys.*

Peripheral bones.—Notching of the posterior peripheral bones (Table 1) appeared in both the *floridana* and *scripta* groups, but was virtually absent in *Echmatemys.* The most pronounced notching occurs in North American *C. scripta,* where peripherals 7-11 on each side are doubly notched. Posterior peripheral bone notching also occurs in the *floridana* group, particularly in *C. concinna,* but the bones are singly notched. The posterior peripherals of the *floridana* group become horizontally flared, and thus provide a streamlined form most highly developed in *C. concinna.* The *scripta* group maintains a primitive unstreamlined shell shape.

Pygal bone.—The sides of the pygal bone are parallel in the Pliocene *C. williamsi* and Recent *C. ornata,* expanded posteriorly in *C. floridana* and *C. concinna.* They are parallel in *C. scripta,* but posteriorly expanded in some *C. nelsoni,* and *C. rubriventris.* In both evolutionary lines median posterior pygal notching became well developed.

Plastron.—Primitively the plastron was expanded laterally both anteriorly and posteriorly, as in *Echmatemys.* Such expansion was maintained in the *scripta* group, but not in the *floridana* group where the plastron became narrow (Fig. 3). In the *scripta* group the plastron tended to become rugose and *C. nelsoni* and *C. rubriventris* developed extreme plastral rugosity (Table 1).

Phalanges.—A reduction from 3 to 2 phalanges on the fifth toe has occurred in both evolutionary lines. Behavioral differences have probably influenced this character.

Carapace Rugosity.—Both evolutionary lines developed a more rugose carapace than their respective fossil ancestors (Table 1). The increase in rugosity became most pronounced in the *scripta* line (Weaver and Robertson, 1967).

Mandible.—The mandible of *Echmatemys* was rounded ventrally and had a narrow triturating surface with a thin longitudinal, lingually positioned ridge. A median, anterior, internal, symphysial ridge was missing. This type of mandible persisted in extant *C. scripta* and *C. picta,* but was profoundly modified in *C. nelsoni* where the triturating surface became greatly expanded and a median symphysial ridge developed. In the *floridana* line *C. ornata* had a lower jaw with a narrow triturating shelf, *C. floridana* and *C. concinna* developed wider triturating surfaces as well as a median symphysial ridge. Ventrally the mandibles of *C. floridana* and *C. concinna* became somewhat flattened as they did in some large North American *C. scripta.* In both lines this represented a modification of the ancestral condition.

Cranium.—The primitive emydine cranium was probably similar to that of *C. scripta* and *C. picta.* In these two species the quadratojugal and maxillary bones are separated by the jugal. Both evolutionary lines evolved a firm union between these bones in some of their members.

A notched premaxillary (Table 1) and a relatively narrow nasal opening were primitive features which were maintained in the *scripta* line.

IV. Summary

In order to determine the phylogenetic significance of recently discovered fossil emydine turtles, over 20 osteological comparisons of 14 extant and fossil species were made. McDowell's subgeneric concept of the genus *Chrysemys* was then compared with the data accumulated. Our results showed that:

(1) McDowell's use of *Chrysemys* to include species currently listed in *Pseudemys* is considered valid.

(2) McDowell's subgeneric classification of *Chrysemys* is shown to be invalid. *Chrysemys scripta* is to be restricted to only the North American races, *C. s. scripta, C. s. troosti, C. s. elegans.* The Mexican, Central and South America turtles previously considered races of *C. scripta* comprise two distinct species groups. In particular, *C. ornata* and *C. callirostris* (of William's *ornata* subseries, 1956) are more closely related to *C. floridana* and *C. concinna* than to *C. scripta. Chrysemys nelsoni, C. rubriventris,* and probably *C. alabamensis* are more closely related to *C. scripta* than to *C. floridana* and *C. concinna.*

(3) Two evolutionary lines occur in *Chrysemys,* an advanced line including *C. concinna, C. callirostris, C. floridana* and *C. ornata* and a conservative line including *C. scripta, C. nelsoni* and *C. picta.* The fossils presently available show that the separation

between these two evolutionary lines has existed since the Pliocene.

V. Literature Cited

Carr, A. F. 1952. *Handbook of Turtles.* Comstock, Ithaca, N. Y., 542 pp.

Conant, Roger 1958. *A Field Guide to Reptiles and Amphibians.* Houghton Mifflin Co., Boston, 366 pp.

Crenshaw, J. W. [MS.] The ecological geography of the *Pseudemys floridana* complex in the southeastern United States. Unpublished Ph.D. dissertation, submitted 1955, University of Florida. A brief summary is available in *Dissert. Abst.* (for 1955), 15(11):2349.

———— 1965. Serum protein variation in an interspecific hybrid swarm of turtles of the genus *Pseudemys*. *Evol.*, 19:1-15.

Galbreath, E. C. 1948. A new extinct emydid turtle from the Lower Pliocene of Oklahoma. *Univ. Kansas Publ. Mus. of Nat. Hist.*, 1:265-280.

Hay, O. P. 1908. The fossil turtles of North America. *Spec. Publ. Carneg. Inst. Washington*, 75:268.

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

Rose, F. L. and W. G. Weaver, Jr. 1966. Two new species of *Chrysemys* (=*Pseudemys*) from the Florida Pliocene. *Tulane Stud. Geol.*, 5(1):41-48.

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

Williams, E. E. 1956. *Pseudemys scripta callirostris* from Venezuela with a general survey of the *scripta* series. *Bull. Mus. Comp. Zool.*, 115:145-160.

Zug, George R. 1966. The penial morphology and the relationships of cryptodiran turtles. *Occ. Pap. Mus. Zool. Univ. Mich.*, (637):1-24.

June 12, 1967