

THE FOSSIL FRESHWATER EMYDID TURTLES
OF FLORIDA

By

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Abstract of Dissertation Presented to the Graduate Council
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Limited fossil evidence shows that a turtle of the genus *Graptemys* lived in peninsular Florida in the Santa Fe River during the Pleistocene. The small sample of available material, including elements of both Rancholabrean and Blancan periods, indicates that this turtle occupied the river throughout most of the Pleistocene before becoming extinct in that drainage. The apparent affinities of this turtle with Recent *G. barbouri* of the Apalachicola River system bring up several geologic and zoogeographic considerations.

Prior evidence of the fossil history of the monotypic genus *Deirochelys* is limited to a single Upper Pleistocene fragment and a number of Subrecent elements from Florida. On the basis of several morphological adaptations unusual among emydine turtles (e.g., neural bone width and rib structure), fossils from twenty Florida sites, ranging from Miocene to Subrecent in age, are referred to the genus *Deirochelys*. Evidence of the gradual evolution of a suite of characters associated with a gape-and-suck method of feeding is presented. The Middle Pliocene representative of the

genus is recognized as a distinct species which, like the Miocene fossils, is intermediate between modern *D. reticularia* and less specialized emydines such as *Chrysemys*.

Reexamination of type and referred materials indicates that *C. carri* Rose and Weaver is indistinguishable from *Chrysemys caelata* (Hay). *Chrysemys caelata* is a characteristic member of Hemphillian faunas of Florida and appears to be immediately ancestral to *C. nelsoni*.

Fossil members of the *Chrysemys scripta* group (subgenus *Trachemys*) in Florida are reexamined and compared to fossil *Chrysemys* from other parts of North America. Designation of the Rancholabrean subspecies *C. s. petrolei* is confusing and biologically unrealistic. Cranial material of *C. platymarginata* affirms the *Trachemys* affinities of this Blancan turtle described from Florida. However, a morphological comparison of *C. platymarginata* with *C. idahoensis*, described from the Upper Pliocene of Idaho, reveals that the two may be conspecific. Additional material from the Great Plains supports this hypothesis. The phylogeny proposed in 1967 by Weaver and Rose, in which the *C. scripta* group is believed to be more closely related to the *C. rubriventris* series than either is to the *C. floridana* series, is rejected in favor of that proposed by McDowell in 1964, in which the last two series are more closely related to each other than either is to the *C. scripta* group.

All pre-Pliocene records of the genus *Chrysemys* are reexamined. Patton's 1969 report of *Chrysemys* from a nonmarine Oligocene deposit in Florida cannot be confirmed. Fragments assigned to the genus by Olsen from a Miocene deposit in the Florida panhandle actually represent a sea turtle and land tortoise. *Chrysemys* is present in the Thomas Farm

Miocene fauna, although some material previously assigned to the genus may represent *Deirochelys*.

INTRODUCTION

The family Emydidae, including nearly 30 living genera and 80 species, is the largest of all turtle families. Its essentially circum-global distribution (excluding Australia and subsaharan Africa) makes it the most widely distributed of all nonmarine turtle families. Emydids are especially well-represented in southeastern Asia and the southeastern United States and are the dominant family of turtles in North America (Auffenberg, 1974; Mount, 1975).

A major step in understanding evolution of the modern chelonian fauna lies with clarification of the relationships and evolutionary processes that have occurred within the Emydidae. Although in the last two decades considerable significant comparative work in this field has been accomplished through the techniques of serology (*e.g.*, McKown, 1972; Merkle, 1975), cytogenetics (*e.g.*, McKown, 1972; Bickham, 1975; Bickham and Baker, 1976), and comparative morphology (*e.g.*, McDowell, 1964; Waagen, 1972; Bramble, 1974), inadequate attention has been paid to the direct evidence provided by the fossil record.

Freshwater emydid turtles in the southeastern United States, and especially those in Florida, are well-represented in vertebrate fossil deposits. This paper attempts to reevaluate, expand, and coordinate our knowledge of these turtles as reflected by their fossil record. In addition to systematic and evolutionary considerations, ecologic and biogeographic implications are discussed. The geographic domain of this paper is Florida, although the relationships of turtles from

this area cannot be meaningfully discussed without comparisons to turtles from other regions of North and Central America.

Although probably originating in the Late Mesozoic, the Emydidae are unknown as fossils before the Tertiary. The family is well-represented in several Eocene formations in Western North America, primarily by the presumably extinct genus *Echmatemys*. Most modern genera remain unknown as fossils until the Miocene or later. The geologic youth of Florida restricts the present work to Oligocene and younger strata; hence, early evolutionary paths within the family will not be found here.

By far the most important early thrust in chelonian paleontology was Oliver Perry Hay's (1908) "Fossil turtles of North America," in which he discussed extensive Pleistocene and older material from Florida. Since then, little work was done in Florida until the late 1950's and 1960's, when there occurred a resurgence of interest in fossil emydids. Most significant are the works of Weaver and Rose (1967) and Weaver and Robertson (1967), which deal with the genus *Chrysemys*, and a series of papers by Milstead and Auffenberg (Milstead, 1956, 1967, 1969; Auffenberg, 1958; Milstead and Tinkle, 1967) on box turtles (*Terrapene*). As the latter have been thoroughly studied, I shall not deal further with *Terrapene*.

The following work consists of five sections each dealing with a distinct taxonomic unit. The first section, details the first known occurrence of *Graptemys barbouri* in the fossil record and the first fossil record of the genus in Florida. The second section describes a remarkable collection of fossils that clearly outline the direction of evolution in the previously poorly known genus, *Deirochelys*. The

third revises the relationships of two Middle Pliocene turtles of the genus *Chrysemys*. The fourth presents a new interpretation of the *Chrysemys scripta* complex based on a comparison of fossils from Florida with those from the midcontinent, and the fifth reexamines the Miocene and Oligocene fossils previously assigned to the genus *Chrysemys*.

As elements of the shell are by far the most frequently found and readily recognizable turtle fossils, it is primarily with these that I have worked. Many adaptive characters are reflected by shell morphology. Cranial material is used when available, although it is unfortunately scarce in most fossil deposits. Chelonian limb elements are generally of little systematic value at the specific level and are very rarely found in association with shells in Florida deposits.

CHAPTER I
A PLEISTOCENE *GRAPTEMYS* (REPTILIA: TESTUDINES)
FROM THE SANTA FE RIVER OF FLORIDA

Prior to this study the genus *Graptemys* has not been reported in the southeastern United States east of the Apalachicola River system in western Georgia and the Florida panhandle. All valid records indicate that the eastern-most species, *G. barbouri*, is presently endemic to the Apalachicola drainage (Cagle, 1952; Carr, 1952; Dobie, 1972; Wharton et al., 1973). Fossil elements from the Santa Fe River in northern peninsular Florida now prove that a turtle of this genus did occur there during the Plio-Pleistocene. The close alliance of this turtle with modern *G. barbouri* suggests the importance of Pleistocene physiographic changes to the distribution of these animals. The discovery of this fossil form adds to our limited knowledge of the fossil history of the genus, previously summarized by McKown (1972).

Description of Fossil Sites

The Santa Fe River in northern peninsular Florida has previously been described by Hellier (1967); it is presently one of the major tributaries of the Suwannee River. All fossils were obtained from two adjacent sites in the Santa Fe at the Columbia/Gilchrist county line (29°50'N, 82°42'W), well downstream from the subterranean portion of the stream's course. Both sites are bottom deposits with reworked bone. Santa Fe I is a heterochronic deposit containing material from both the Rancholabrean (late Pleistocene) and Blancan (Upper Pliocene)

periods; it normally lies under 6 to 8 m of water. Fossils representing the two ages from this site may generally be distinguished by their state of preservation; Blancan elements are often a glossy black in contrast to the coarse brown Rancholabrean material. Santa Fe II, which lies in 2.5 to 3 m of water approximately 100 m downstream from Santa Fe I, contains only Rancholabrean material. Site ages have been well-established on the basis of their mammalian faunas (Hibbard et al., 1965; Webb, 1974).

Description of Fossil Elements

Three elements positively representing the genus *Graptemys* are available: a third neural, a nearly-complete nuchal bone, and the major portion of a mandible (Fig. 1). A right hyoplastron representing either a *Graptemys* or a small *Chrysemys concinna* is also described. All specimens are in the Florida State Museum (UF) and the Timberlane Research Organization (TRO).

Nuchal bone. A nearly-complete nuchal bone (UF 10572) from Santa Fe I was collected by B. Waller and R. Allen in 1963. The very broad, short nuchal scute is characteristic of *Graptemys*. Although the dorsal midline of the bone is conspicuously elevated, the distinct keel usually present in *G. barbouri* is lacking. However, Roger Sanderson (pers. comm.), after examining several hundred *G. barbouri*, believes this character to be of little taxonomic significance. Dimensions of the fossil are width of anterior border--approx. 35.6 mm; max width--approx. 69.8 mm; length of anterolateral border--8.1 mm; max length--47.8 mm; length of nuchal scute--3.6 mm. Estimates based on these measurements place the fossil turtle between 210 mm and 230 mm cara-

pace length (CL), corresponding to a plastron length (PL) of 180 mm to 197 mm; carapace width (CW) is estimated at roughly 190 mm to 200 mm. These dimensions correspond to those of Recent adult female *G. barbouri* although the carapacial width is relatively greater. State of preservation indicates that this turtle is probably Blancan in age.

Neural bone. A large *Graptemys* neural bone (TR0 100) was found in 1961 at Santa Fe II by J. Waldrop and D. Bell. The distinct keel ending abruptly in a blunt knob midway back along the midline of the neural indicates that this is the third neural of a *G. barbouri*-like turtle. Dimensions of the bone are max length--30.6 mm, max width (anterior margin, lateral border)--30.5 mm; min width (posterior margin, lateral border)--18.0 mm; max thickness, lateral border--10.0 mm. Except for the more rapid tapering from anterior to posterior borders, the neural appears to be that of a very large *G. barbouri* (estimated CL = 270 mm to 280 mm; PL = 230 mm to 240 mm).

Mandible. The only available data for the partial lower jaw (US 19161) is the collection site, Santa Fe II. The broad alveolar surfaces as well as the size of the jaw indicate that this turtle had an extremely large head modified for crushing hard food such as mollusks. This structure and habit is characteristic of females of the sexually-dimorphic extant forms, *G. barbouri* and *G. pulchra*. The fossil mandible appears almost identical to that of a Recent adult female *G. barbouri*, except that the alveolar surfaces of the fossil are less expanded posteriorly (possibly a function of ontogenetic change), and the two halves of the jaw meet at a slightly wider angle than in the Recent

form. Dimensions of the fossil elements are approx. max width (excluding articulating surface)--54 mm; max width of alveolar surface--18.6 mm. Comparison with Recent *G. barbouri* yields an estimated carapace length for this individual of 280 mm to 290 mm (assuming skull:shell ratios to be approximately the same in Pleistocene and Recent forms).

Hypoplastron. The only data for the right hypoplastron (UF 19246) is Santa Fe I. The thin, flat nature of the piece, the very narrow zone of scute overlap on the dorsal surface, and the straight anterior border (*i.e.*, the absence of an obvious concavity into which the entoplastron fits, as in most *Chrysemys*) indicate that this element may be from *Graptemys*. However, hypoplastra of some individuals of *Chrysemys concinna*, a common turtle of both the Pleistocene and present in the Santa Fe River, also fit this description, and the element may belong to a small individual of that species. The dimensions of the bone are: max length--62.7 mm; width from midline to anterior, ventral edge of axillary notch--48.5 mm; max thickness along hyo-hypoplastral suture--4.4 mm. State of preservation indicates a probable Blancan age.

Based on available material it is concluded that the Santa Fe *Graptemys* was a sexually-dimorphic form (or forms) very similar to *G. barbouri* in both structure and habits. Maximum adult body size was probably slightly greater than that attained by modern *G. barbouri*. The shell may have been somewhat broader and the keel less pronounced than in extant *G. barbouri*. Pending acquisition of further material which may show the Blancan, Rancholabrean, and Recent forms to represent two or even three distinct forms, all the Santa Fe *Graptemys* are

tentatively referred to *Graptemys* cf. *G. barbouri* Carr and Marchand. Erecting further names for these allochronic forms is presently unwarranted.

Discussion

Accounting for the presence of *G. barbouri* in the Suwanee drainage during the Pleistocene requires consideration of several geologic and zoogeographic phenomena. Mainly because *Graptemys* rarely if ever travels on land (McKown, 1972), endemism to a single river system is characteristic of several species of the genus--*G. versa*, *G. oculifera*, *G. flavimaculata*, and for all intents and purposes, *G. nigrinoda* (Cagle, 1954; Folkerts and Mount, 1969; Conant, 1975). Since Dobie (1972) eliminated Cagle's (1952) apparently-erroneous record for the Escambia River in western Florida, all remaining records indicate that *G. barbouri* likewise developed as an endemic species in the Apalachicola River system. The presence of a Pleistocene turtle, here believed to be conspecific with Recent *G. barbouri* (although the problem remains essentially the same even if it were later shown to be a distinct species of common ancestry), in a drainage system which empties into the Gulf of Mexico approximately 185 km from the mouth of the Apalachicola requires comment. Several explanations are suggested.

The eustatic changes in Plio-Pleistocene sea levels, corresponding to the formation and melting of the Ice Age glaciers, are well-known phenomena. During glacial periods the retreating sea exposed a much larger expanse of the Floridian Plateau (that portion of the continental shelf surrounding Florida and extending far out into the Gulf--Cooke, 1945) than is now above sea level. Frey (1965) has stated that this

eustatic lowering of the sea level reached a maximum of 120 m below present sea level, and during the Wisconsinan glacial episode some 20,000-18,000 years ago exposed up to a 210 km wide stretch of continental shelf (Fig. 2). Donn et al. (1962) have calculated that minimum sea level came even earlier, in the Illinoian glacial period, when the sea dropped to between 140 m and 160 m below its present level. Conceivably such a drop in sea level could bring about the confluence of many rivers which now empty directly into the Gulf. Continuation of the Apalachicola and Suwannee Rivers beyond their present mouths would create a hypothetical junction between them (Swift, 1970) near the expected western-most coastline of Pleistocene central peninsular Florida. However, the absence of large numbers of fish species common to both rivers as well as intervening drainages discredits this idea. Nevertheless, even if convergence of the two rivers did not occur, a lowland marsh between the two could have allowed turtles to migrate from one stream to the other. If this were the case the occurrence of a *G. barbouri*-like turtle in two presently widely separated rivers could thus be explained. Furthermore, if the present absence of *Graptemys* fossils from the Suwannee north of its junction with the Santa Fe reflects a real situation, then it may be that the ancestral (upper) Suwannee was captured by a stream (the present lower Suwannee, including the Santa Fe) eroding eastward from the Gulf of Mexico during the Plio-Pleistocene (Vernon, 1951; Brooks, 1966). Whether this stream was confluent at one time with the Apalachicola is not presently known. Evidence shows that prior to this time the ancestral Suwannee likely emptied into the Gulf south of its present

mouth via connection with the present-day Waccasassa River (Vernon, 1951; White, 1970).

A second possible migratory route which may have been followed by the ancestral *G. barbouri* involves the upper reaches of these rivers. Although *Graptemys* rarely wanders overland it is conceivable that under some conditions (e.g., flooding) a few individuals may move to an adjacent stream. Figure 2 reveals the proximity of the Flint River, a major tributary of the Apalachicola in which *G. barbouri* is known to occur (Cagle, 1952; Wharton et al., 1973; R. Franz, pers. comm.), to the upper reaches of the Withlacoochee and Alapaha Rivers, both of which empty into the Suwannee. The distances may have been even less during the Pleistocene had the waters been significantly higher or the courses of the rivers different than they are now; the latter possibility is especially likely in this area of sand-limestone substrate. Furthermore, certain fishes common to the two drainages suggest direct communication at some time in the past between the upper reaches of these two rivers (C. Gilbert, pers. comm.). Yerger and Relyea (1968) explain the distribution of *Ictalurus serracanthus*--known only from the Apalachicola, Ochlockonee, and Suwannee drainages--by stream piracy following closure of the Suwannee Straits (Plio-Pleistocene). They suggest that stream capture between tributaries of the Ochlockonee (until relatively recently a part of the Apalachicola drainage) and the upper Suwannee may have accounted for a westward migration of this fish from the Suwannee into the Apalachicola. It is likely that stream capture between tributaries of these same rivers or between the Flint and upper Suwannee may account for the occurrence of *G. barbouri* in these two drainages. Its apparent absence (both Pleistocene and Recent)

from the upper Suwannee and Ochlockonee may reflect inadequate collecting or unsuitable habitat.

A third possibility, not necessarily exclusive of either of the preceding two, is that *G. barbouri* has not always been restricted to one or two widely separated rivers but was more widespread than previously thought. The long period of relatively stable environmental conditions during the Blancan may have been conducive to the expansion of *G. barbouri*'s range throughout much of the seemingly favorable limestone-underlain habitat between the two rivers. Thus it is postulated that at various times *G. barbouri* occurred (though perhaps in relatively low densities) in most or all rivers between the Apalachicola and Suwannee. In addition to explaining the presence of this turtle in two widely separated rivers as simply its occurrence at the ends of a nearly-continuous range, the idea also seems compatible with the distribution of the remaining southeastern members of the genus. The occurrence of *G. kohni* in the rivers of eastern Texas and Louisiana (Conant, 1975), *G. pulchra* from the Pearl River to the Escambia and Yellow Rivers in western Florida (Dobie, 1972), and *G. barbouri* from the Apalachicola to the Suwannee River, would provide a nearly-continuous range of large, sexually-dimorphic *Graptemys* of the wide-headed female line (Cagle, 1953; McKown, 1972) in the river systems draining the entire northern shore of the Gulf of Mexico. The only apparent gap is the Choctawhatchee River System between the ranges of *G. pulchra* and *G. barbouri* (Dobie, 1972) (Fig. 2).

Ultimately the solution to this question may lie with the collection of further fossil evidence and with detailed studies of the dis-

tributions of other lotic organisms. Current investigations on fish and snail faunas of these and other river systems in the southeastern United States may help provide an answer.

The reasons for extinction of the Santa Fe *Graptemys* remain speculative. At present the river seems sufficiently similar to Carr and Marchand's (1942) description of ideal *G. barbouri* habitat to support a population of these turtles; this seems to be further indicated by the fact that *Ictalurus serracanthus*, which also seems to prefer rocky, clear streams with moderate flow, still inhabits the Santa Fe today (Yerger and Relyea, 1968). From the paucity of fossil material *Graptemys* was apparently never common in the Santa Fe. In comparison to the few *Graptemys* fossils over 500 elements of *Chrysemys concinna*, *C. nelsoni*, and *C. scripta* have been collected from the same sites. Even though *C. concinna* is abundant in the Santa Fe today its habits are sufficiently distinct (and presumably were in the Pleistocene) from those of *G. barbouri* that significant competition between the two turtles would have been unlikely. More probably, climatic changes or physical changes in the topography of the land or in the river itself made the habitat unsuitable at some time in the past for the small population of *Graptemys*, or possibly for the mollusks upon which the females presumably fed.

Figure 1. Fossil *Graptemys* elements from the Santa Fe River, Florida. (A) nuchal; (B) mandible; (C), (D) third neural dorsal and lateral aspects.

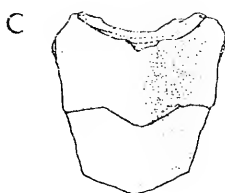
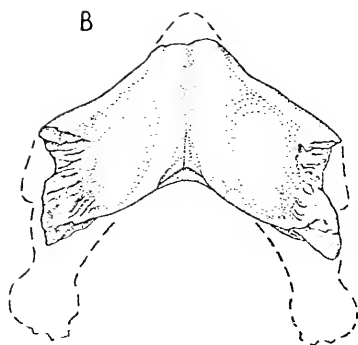
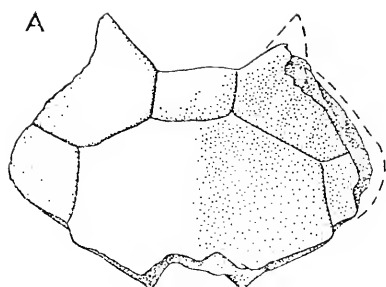
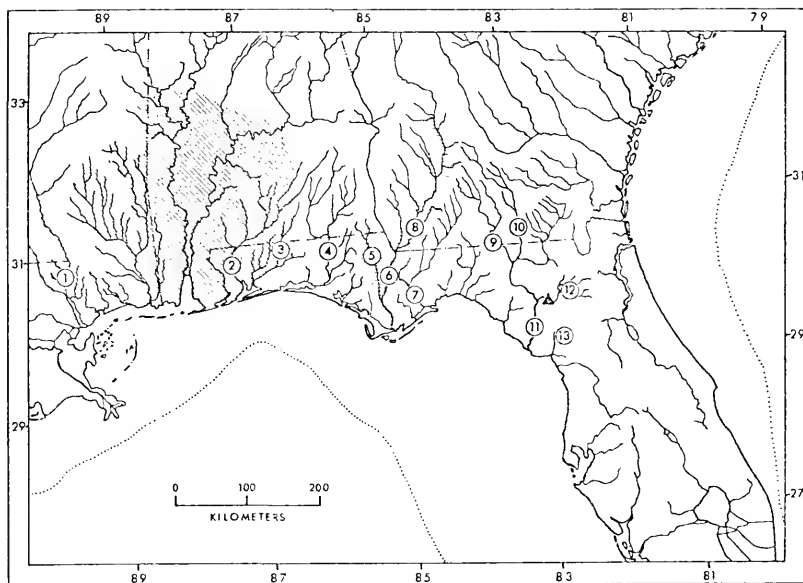


Figure 2. Southeastern United States and Gulf of Mexico, showing range of *Graptemys pulchra* and *G. barbouri*. Diagonal hatching, approximate range of *G. pulchra* (northern boundary indefinite); horizontal hatching, reported range of *G. barbouri*; triangle, Santa Fe River sites I and II; dotted line, 120 - meter contour showing approximate coastline during maximum eustatic lowering of sea level in the Quaternary (after Frey, 1965); rivers mentioned in text:

- | | | |
|-------------------|------------------|----------------|
| 1. Pearl | 6. Apalachicola | 10. Alapaha |
| 2. Escambia | 7. Ochlockonee | 11. Suwannee |
| 3. Yellow | 8. Flint | 12. Santa Fe |
| 4. Choctawhatchee | 9. Withlacoochee | 13. Waccasassa |
| 5. Chipola | | |



CHAPTER II
EVOLUTION AND FOSSIL RECORD OF THE CHICKEN TURTLE
DEIROCHELYS WITH A REEVALUATION OF THE GENUS

The evolutionary history of the monotypic genus *Deirochelys* is one of the more enigmatic chapters in our knowledge of North American emydine turtles. Previous workers (Carr, 1952; Loveridge and Williams, 1957; McDowell, 1964) have generally agreed that *Deirochelys* is a highly specialized derivative of the genus *Chrysemys* (sensu McDowell, 1964). Furthermore, Baur's (1889) suggestion of a close phylogenetic relationship between *Deirochelys* and another North American monotypic emydine genus, *Emydoidea*, has been supported by most subsequent workers (Loveridge and Williams, 1957; Jackson, 1959; McDowell, 1964; Zug and Schwartz, 1971). Recently Waagen (1972) and Bramble (1974) have cast doubt on this idea based on their respective studies of musk glands and shell mechanics.

The fossil record has been of no help in these matters to date. Prior knowledge of the fossil history of the genus *Deirochelys* is limited to description of one partial nuchal bone from the Upper Pleistocene of Florida (Jackson, 1964, 1974a) and to mention of the presence of *D. reticularia* in a Subrecent Florida site (Hirschfeld, 1968). Jackson (1974a) suggested that the Pleistocene element represents a turtle which is conspecific with modern *D. reticularia*. All other fossils assigned to the genus, i.e. *Deirochelys floridana* Hay and *Trachemys jarmani* Hay (Hay, 1908; Weaver and Robertson, 1967), actually represent the genus *Chrysemys* (Jackson, 1964, 1974a).

This paper examines material referable to the genus *Deirochelys* from one Miocene, five Pliocene, twelve Pleistocene, and two Subrecent sites, all in Florida. The Miocene fossils are the oldest known representatives of the genus. Two species of *Deirochelys*, one new, are recognized as fossils. As will be shown the major course of evolution within *Deirochelys* has been the extreme elongation of the head and neck, a condition achieved by only one other emydine genus (*Emydoides*) and presumably developed as a trophic specialization. The accompanying cervical musculature hypertrophy has necessitated further structural modifications of the shell and vertebral column. It is for this reason that in tracing the evolution of the genus I dwell primarily upon this cervico-cranial elongation and associated morphological modifications (e.g., changes in neural bone width and rib and vertebral structures), to which I collectively refer hereafter as a single "character suite."

Materials and Methods

All fossil specimens except those from Waccasassa River and a few from Thomas Farm are part of the vertebrate paleontology collection of the Florida State Museum (UF); the Waccasassa River 1 specimens are from the Timberlane Research Organization (TRO), Lake Wales, Florida, while some of the Thomas Farm fossils are from the collections of the Museum of Comparative Zoology, Harvard University (MCZ). Comparative skeletal material was examined from the herpetology collection of the Florida State Museum (UF), the National Museum of Natural History (USNM), and my personal collection (DRJ). Extant specimens examined were *Deirochelys reticularia*: DRJ 264, 266, 270, 274, 278-280, UF

1420, 7744, 14244, USNM 11610, 11615, 29477, 29584, 62219, 80965, 95789; *Emydoidea blandingii*: UF 14249, 18931; *Chelydra serpentina*: DRJ 253; *Chelys fimbriata*: UF 21977.

A shell thickness index (STI) was determined for most fossils. Thicknesses of fossil shell elements were measured and divided by corresponding measurements of a series (N = 10) of Recent adult *D. reticularia* of corresponding size, or by linear extrapolations to produce such if no modern turtle of sufficient size could be found. As the relationship between shell thickness and body length may be asymptotic rather than strictly linear, the STI values given for the largest fossils may actually be underestimates. There was little individual STI variation among the Recent turtles when corrected for differences in body length. More medial elements (neural bones and proximal ends of pleural bones) generally yielded slightly higher STI values than peripheral elements (peripheral, pygal, and nuchal bones), indicating that increase in shell thickness is not necessarily proportional for all parts of the same shell. Medial edges of peripheral elements were measured to reduce this discrepancy.

An index of free rib length (width of rib canal) was determined by dividing the straight-line distance from the proximal tip of the pleural bone to its union with the rib by the width of the pleural bone at the level of the union. The fragmented condition of most of the fossils necessitated the use of pleural bone width rather than length.

In comparing neural and pleural bones of fossil *Deirochelys* with those of Recent turtles, it is necessary to determine which of the eight neural or pleural bones the fossils represent. The presence

and position of scute sulci as well as the relative proportions of the anterolateral and posterolateral borders of the bones usually make this possible. Because of the relatively great width and frequent anomalies of the posterior neural bones of most emydine turtles, these bones are of little taxonomic value.

All measurements are maximum and given in mm.

Fossil Localities

The appendix provides an annotated list of Florida localities that have yielded fossil *Deirochelys* mentioned in this paper. Reference is made to other publications in which stratigraphy, paleoecology, and correlative age of each of these deposits is described in detail. Figure 3 shows the geographic distribution of these sites.

Systematic Descriptions

All past descriptions of the genus *Deirochelys* (Agassiz, 1857; Baur, 1889; White, 1929; Schwartz, 1956; Jackson, 1959; McDowell, 1964; Zug and Schwartz, 1971) have necessarily been drawn solely from the single extant species, *D. reticularia*. Hence, many characters which would have been more appropriately designated as specific characters, particularly those involving color pattern, have been incorporated into the definition of the genus. Therefore, in order to accommodate the fossil members of the genus it is necessary to relegate many of the generic characters, including all references to color pattern, to specific level. Additionally, an examination of osteological characters through time reveals phylogenetic changes within the genus that

may be used to distinguish certain allochronic forms. For these reasons I find it necessary to give a brief systematic reevaluation of the genus as a prelude to a formal description of the fossil forms. The present chronologically-expanded definition of the genus, like those of Baur (1889), White (1929), Jackson (1959) and McDowell (1964), is based solely on osteological characters. As fossil skull material is unknown, all skull characters are drawn from modern *D. reticularia*. Schwartz (1957) gives a brief but adequate account of the taxonomic history of the genus.

Family Emydidae

Subfamily Emydinae

Genus *Deirochelys* Agassiz

To the generic synonymy given by Zug and Schwartz (1971) should be added the following entry:

Hirochelys Beyer, 1900: 45.

Type. *Testudo reticularia* Latreille.

Referred species. *Deirochelys reticularia*, the only extant species, presently distributed throughout the southeastern United States and known from the Pleistocene of Florida; *Deirochelys carri*, n. sp., Pliocene Alachua clays of Florida, Hemphillian age.

Definition. Shell elongate to subovate in adults; carapace elliptical or cuneiform in outline and usually sculptured with fine parallel ridges or scales (Fig. 4); anterior edge of nuchal bone generally truncate and acuminate; lateral sulci of nuchal scute usually parallel above and below; nuchal scute usually two to three

times longer than wide above, approximately as wide as long below; nuchal bone overlapped only by small corner of first costal scute or not at all; vertebral scutes as wide as long; neural bones hexagonal, short-sided in front; first neural bone circular to subovate in outline; other neural bones generally as wide or wider than long (Fig. 4); peripheral bones unnotched; pygal bone approximately parallel-sided with a shallow mesial notch; ribs dorsally free from pleural bones well below proximal ends of pleurals, their free portions slender and bowed ventrally (Fig. 5) accommodating the enlarged trunk vertebral muscle complex (Shah, 1963).

Plastron usually considerably narrower than carapace, akinetic, and firmly united to carapace by a high bony bridge and plastral buttresses; inguinal scutes large [contrary to Holman's (1967) statement that they are absent]; plastron smooth ventrally or with traces of sculpturing similar to but less pronounced than that of carapace; entoplastron usually anterior to humeropectoral sulcus and overlapped by gular scutes for approximately one third of length.

Skull and second through seventh cervical vertebrae elongate; neural spines of anterior thoracic vertebrae laterally compressed as vertical sheets (Fig. 6); triturating surfaces of maxilla and mandible narrow, without ridges; beak never hooked; interorbital width very narrow, less than one-half diameter of orbit; palate decidedly flat; posterior palatine foramina much larger than foramina orbito-nasale (Gaffney, 1972) (= anterior palatine foramina of Hoffman, 1890); temporal arcade complete; quadrate nearly enclosing stapes; hyoid apparatus strongly developed, lateral horn length at least as great as skull width; cervical musculature as described by Shah (1963).

A specialization of the genus almost certainly related to the elongate neck and hypertrophied vertebral musculature is the modification of the spinal column. The differences between *Deirochelys* and more primitive emydines (*Chrysemys*, *Echmatemys*), summarized in Table 1 and Figure 6, are most conspicuous in the first four thoracic vertebrae. In both forms ribs attach intercentrally and the thoracic vertebrae are united by their neural spines to the overlying neural bones. The net effect of these modifications in *Deirochelys* has been to move the rib attachment ventrally (away from the carapace), allowing for the hypertrophied trunk vertebral musculature without changing the distance of the spinal cord from the ventral surface of the carapace.

Deirochelys reticularia (Latreille)

Chicken Turtle

The only addition to the species synonymy listed by Zug and Schwartz (1971) is:

Hirochelys reticulata Beyer, 1900:45.

Type: The type was formerly in the collection of the French Museum National d'Histoire Naturelle but is now considered lost (Schwartz, 1956). Schwartz (1956) described a neotype and neoallotype from the vicinity of the original type locality.

Type locality. Restricted by Harper (1940) to the vicinity of Charleston, South Carolina.

Diagnosis: A *Deirochelys* characterized by relatively low length: width ratios for third through fifth neural bones (means, 0.6 to 0.7;

Table 1. Comparison of the thoracic vertebrae of
Deirochelys and *Chrysemys*.

Character	<i>Chrysemys</i>	<i>Deirochelys</i>
Neural spines	low and robust	laterally compressed as vertical sheets
Centra	narrowest ventrally; not compressed	narrowest dorsally; dorsoventrally compressed; ventral surfaces wide and flattened
Site of rib attachment to vertebra	expanded dorsal region of centra	expanded ventral region of centra

Fig. 7) and relatively great length of free portions of dorsal ribs (Fig. 8); coloration as described by Schwartz (1956) with notation that the yellow forelimb band is usually but not always wide; neck nearly as long as plastron; usual pattern of cervical central articulation (perhaps a generic character): (2((3((4))5))6))7((8) (Williams, 1950; Jackson, 1974b).

Description of fossil material. The following fossils, listed in reversed chronologic order by site, are here assigned to *D. reticularia*.

Nichol's Hammock: contains more *D. reticularia* than any other post-Pliocene site; 75 carapacial elements (UF 20892), a cervical vertebra (UF 20904), and a supraoccipital crest (UF 20905) represent 12 to 20 individuals ranging from 65 mm to 195 mm carapace length (CL); many additional elements from this deposit, particularly plastral and peripheral bones which lack diagnostic features, probably represent *D. reticularia* as well; fossils from the site are indistinguishable from modern *D. reticularia*, their shallow rugosity probably reflecting their relatively small size; STI 0.95 to 1.05.

Warm Mineral Springs: To date, 35 elements - one nuchal, seven neural, one suprapygal, six pleural, 13 peripheral, and five plastral bones, plus a scapula and broken femur - all assigned field number WMS 19352 and representing five to ten individuals of CL 138 to 184, have been removed from this site. The bones are similar to those from Nichol's Hammock and have an average STI of 1.15.

Vero: A large number of plastral and carapacial elements, including at least two nuchal, two neural and two pleural bones (all recently

acquired by the Florida State Museum as part of the former Florida Geological Survey collection and as yet uncatalogued) are virtually indistinguishable from modern *D. reticularia*; STI 0.85-0.95.

Waccasassa River I: Two second neural bones (TR0 101, 102) and a third neural bone (TR0 103), representing three individuals of 130 to 210 CL (Fig. 9); STI 1.1 to 1.3.

Waccasassa River V: A lightly-sculptured nuchal bone, UF 16271 (Fig. 9): greatest length 30.5, greatest width 35.5, estimated CL 135; proximal end of a pleural bone, UF 16275; STI 1.1.

Waccasassa River VI: A distinctly grooved nuchal bone, UF 21906: greatest length 39.8, greatest width 42.3, estimated CL 170; STI 1.1.

Reddick IIC: A first neural bone (UF 21955) from an adult turtle (estimated CL 180) and the proximal end of a fourth pleural bone from a juvenile; STI 1.1.

Coleman IIIC: Four elements (UF 15186E) representing at least three individuals: a longitudinally rugose, relatively deeply notched pygal bone (length 21.5); a left epiplastron (interepiplastral suture length 13.6); a characteristically rugose left xiphiplastron missing its distal portion (hypo-xiphiplastral suture length 40.7); and a distinctly sculptured right hypoplastron (interhypoplastral suture length 58.4); STI 1.3.

St. Petersburg, Catalina Gardens: Lower two thirds of a right fifth pleural bone (UF 19248): greatest width 30.0, estimated length 60, estimated CL 220; STI 1.3.

Seminole Field: A deeply sculptured fragment of a right second pleural bone (UF 9927) with rib attachment - width at rib level 28.0, thickness at rib level 5.9, estimated CL 210; fragment of a left hypoplastron (UF 9927) with deep longitudinal grooves on ventral surface, estimated CL 210; STI 1.4.

Bradenton 51st Street: A characteristically sculptured fragment of a nuchal bone (UF 2482): estimated CL 210, STI 1.25.

Kendrick 1A: A sixth neural bone (UF 19250) with a pronounced, scale-like sculpturing and a low, rounded keel - greatest length 19.3, greatest width 33.2, greatest thickness 6.0, estimated CL 250, STI 1.3; a deeply grooved partial nuchal bone (UF 9292) possibly from the same individual and described previously by Jackson (1964): estimated CL 250, STI 1.1 to 1.6; (Fig. 10).

Wall Company Pit: Proximal halves of two broken pleural bones (UF 5026): a second left (estimated CL 175, STI 1.6) and a deeply rugose fourth right (estimated CL 220, STI 1.5) with rib distance: pleural width ratios of 0.84 and 0.80, respectively.

Haile XVI: 38 elements representing at least 15 individuals of CL 116 to 240: a nuchal bone (UF 20896), length 40.0, estimated CL 182; a second neural bone contiguous with the second and third right pleural bones (UF 20888; Fig. 11), and the first left and second right peripheral bones (UF 20889) almost certainly from the same individual, estimated CL 230; fifteen fragmentary pleural bones (UF 20895; UF 20898) and seven peripheral bones (UF 21970); a hypoplastron (UF 21969) and

partial hypoplastron (UF 21968); contiguous second, third and fourth neural bones (UF 20893) from a turtle of 227 CL; and the third (UF 20897), fourth (UF 21971), two fifth (UF 20894 and UF 20898), and sixth (UF 20898) neural bones from five turtles with CL of 240, 140, 225, 160 and 220, respectively. Neural length: width and rib distance: pleural width ratios are included in Figs. 7 and 8; STI of neural bones 2.0 to 2.2.

Haile XV: A fifth neural bone (UF 19249), the dorsal surface of which is extremely flat but moderately sculptured: greatest length 20.2, greatest width 32.0, estimated CL 210; an anterior fragment of a nuchal bone (UF 19168), estimated CL 230; STI 1.5; (Fig. 12).

Discussion of fossil material. All of the Rancholabrean and Subrecent material is clearly referable to *D. reticularia*. With the exception of shell thickness, relative dimensions of individual fossils show no significant differences from corresponding measurements of extant turtles. The Blancan and Irvingtonian material, as well as the Kendrick nuchal, indicate that this species reached a slightly larger maximum size during the Late Pliocene and Pleistocene than at present. The blunt median keel on the Kendrick neural, although not typical of most extant *D. reticularia*, occurs posteriorly in a few individuals. Though tending to be more pronounced in the Pleistocene, shell rugosity patterns are within the range of variation of modern *D. reticularia*.

The single consistent difference between Pleistocene and Recent *D. reticularia* is that of shell thickness. The STI of Pleistocene *D. reticularia* is 1.1 to 2.2 times that of Recent turtles. The trend

towards shell thickness reduction appears roughly chronoclinal since at least the Irvingtonian (Table 2), though the absence of material from some glacial and interglacial periods may conceal unseen fluctuations. Similar trends in post-Pliocene shell thickness reduction have been suggested, though less well supported by a time-transgressive series of fossils, for *Chrysemys* (Preston, 1966, 1971), *Emydoidea* (Taylor, 1943), *Graptemys* (Chapter 1), *Kinosternon* (Fichter, 1969), *Trionyx* (Wood and Patterson, 1973) and *Geochelone* (Auffenberg, 1963b). Although shell thickness alone is inadequate as a basis for taxonomic separation, it is not a simple function of turtle size as Auffenberg (1958) states for *Terrapene*. From Middle Pleistocene to the present, the shell of *D. reticularia* has become progressively thinner. Gaps in the STI-time curve may reflect our incomplete sampling of the fossil record. Nevertheless, the possibility of sexual and ontogenetic polymorphism in this character, as well as hidden fluctuations in the curve, could complicate the matter. Unfortunately, sample sizes from most fossil sites are inadequate for a thorough treatment of the data.

The Irvingtonian (Haile XVI) fossils differ from younger material in two additional ways: a higher length: width ratio for the second and third neural bones (Fig. 7) and a slightly more proximal site of rib juncture with the second and third pleural bones (Fig. 8). These characters do not exhibit allometry in Recent adult turtles, and there is thus no reason to suspect it in Pleistocene populations. In these respects Irvingtonian *Deirochelys* are morphologically intermediate between the later Pleistocene and the Middle Pliocene turtles discussed below. The near identity of the Blancan neural (UF 19249) with that of

Table 2. Shell thickness index (STI) of fossil *Deirochelys* from 16 Florida sites listed chronologically by faunal periods.

Age and Site	STI	Age and Site	STI
Arikareean		Rancholabrean, cont.	
Thomas Farm	1.9	Bradenton	1.25
Hemphillian		Kendrick	1.3
Love	1.6-2.1	Seminole Field	1.4
Mixson	1.8	Catalina Gardens	1.3
Haile VI	1.9	Coleman IIIC	1.3
Blancan		Waccasassa I	1.1-1.3
Haile XV	1.5	Waccasassa V	1.1
Irvingtonian		Subrecent	
Haile XVI	2.0-2.2	Warm Mineral Spring	1.15
Rancholabrean		Nichol's Hammock	0.95-1.05
Wall Co. Pit	1.5-1.6		

an Irvingtonian one (UF 20894) suggests that little shell evolution was experienced between these periods.

The differences between modern and Upper Pliocene to Middle Pleistocene *Deirochelys* are real and might justify taxonomic distinction were it not for the intermediate Rancholabrean material. Such time-related changes are, however, to be expected within a chronocline lineage, as shown previously by Milstead (1967) with *Terrapene*. The modern subspecies of *D. reticularia* are distinguished by coloration and shell shape (Schwartz, 1956) and consequently can not be compared to these fossils. Furthermore, *D. reticularia* likely varied geographically during the Pleistocene as it does now. For these reasons I refrain from erecting subspecific epithets for any of the Pleistocene or Upper Pliocene fossils and simply refer them all to the species *Deirochelys reticularia*.

The existence of certain morphological differences, reflected in carapacial osteology, of specimens referred above to *D. reticularia* and all earlier representatives of the genus (Figs. 7 and 8) is accentuated by the absence of Late Hemphillian fossils. This gap in a gradually evolving lineage creates a convenient (though admittedly artificial) point of division between morphologically distinct forms. I therefore designate the turtle represented by the Middle Pliocene fossils as

Deirochelys carri new species

Etymology. Named in honor of Archie F. Carr for his extensive contributions to our knowledge of Recent turtles and to herpetology in general.

Holotype. UF 20908, a fragmented but nearly complete carapace lacking only the nuchal bone, first neural bone, and anterior peripheral bones (Fig. 13A); a partial plastron consisting of the left hyoplastron, hypoplastron, and xiphiplastron apparently represents the same individual (Fig. 13B).

Type locality and horizon. Alachua Clay, Love Bone Bed, near Archer, Alachua County, Florida, Early Hemphillian, Middle Pliocene.

Referred material. All from four Florida sites producing Hemphillian faunas:

Mixson's Bone Bed: a fourth neural bone, UF 20890 (formerly Florida Geological Survey V-2599), assigned previously by O. P. Hay (1916) to *Chrysemys caelata*: estimated CL 290, STI 1.8.

McGehee Farm: a complete (UF 19204) and two partial (UF 20891 and UF 20903) nuchal bones - measurements of UF 19204: length 57.1, width 60.8, corresponding to a CL of approximately 263; right hypoplastron, ninth right peripheral bone, and left and right xiphiplastral fragments (UF 20899).

Haile VI: contiguous second neural bone fragment and proximal portion of left second pleural bone, (UF 20887); estimated CL 253, STI 1.9; contiguous pygal bone and eleventh left peripheral bone, (UF 6485a); anterior end of third cervical vertebra (lacking zygapophyses), UF 6485b (Fig. 14); five peripheral bones, UF 6485c; first neural bone, (UF 6485d); seventeen pleural bone fragments, (UF 6485e); many other

elements and fragments from this site may represent either *D. carri* or *Chrysemys caelata* (Chapter III).

Love Bone Bed: Although excavation is incomplete, this deposit is already the richest source of fossil *Deirochelys* known. At the time of this writing over 400 carapacial elements and half as many plastral elements of *Deirochelys* have been removed. Other than the holotype, only two sets of associated carapacial bones have been found (UF 24100 and UF 20900, Fig. 15). The less water-worn carapacial elements display the distinct scale-like sculpturing characteristic of the genus (Fig. 16). Many elements represent turtles of exceptionally large size for *Deirochelys*: the largest nuchal bone (UF 20906) measures 59.8 (length) x 61.8 (width). The average STI range is 1.6 to 2.1.

Diagnosis. *Deirochelys carri* differs from *D. reticularia* in having relatively narrower neural bones (mean length: width ratio of third through fifth neural bones 0.8 to 0.9; Figs. 7, 13A) and a more proximal site of emergence of the ribs from the pleural bones (Figs. 8, 15). Elongation of cervical vertebrae and patterns of shell rugosity are similar in these species, but the carapace of *D. carri* appears to be relatively broader.

Shell rugosity and width of first vertebral scute of *D. carri* are like those of *Chrysemys caelata* and *C. williamsi*, respectively, also from the Florida Pliocene (Chapter III); nevertheless, other generic characters distinguish these species from *D. carri*. Neural bones of *D. carri* are similar in shape to those of the Florida Pliocene *Chrysemys inflata* (Weaver and Robertson, 1967), yet distinguished from them by

absence of the pronounced keel and deeply excavated surface of the latter.

Description. With the exception of the less developed character suite previously alluded to, *D. carri* is, in most respects, similar to *D. reticularia*. Nevertheless, many of the fossils indicate that the former reached a greater size than *D. reticularia*, perhaps as large as 320 mm CL, compared to approximately 250 mm CL today (Carr, 1952). The shell of *D. carri* is about twice as thick as that of extant *D. reticularia* but not unlike that of Blencian and Irvingtonian representatives of the modern species (Table 2). Additionally, the reconstructed holotype shell is relatively broad and flat compared to Recent chicken turtles. In this respect, as well as in the flaring of the posterior peripheral bones, *D. carri* is reminiscent of some members of the genus *Chrysemys* and appears to have been more streamlined than *D. reticularia*. One fairly constant difference between *D. reticularia* and *D. carri* is that the anterior edge of the fourth vertebral scute (incised at the fifth neural bone) of *D. reticularia* projects forward to form a sharp anteriorly-directed V, whereas that of *D. carri* projects forward only slightly (and more bluntly) or not at all (Fig. 13A). The plastron of *D. carri*, like that of *D. reticularia*, is narrow. The anal notch in the plastron associated with the holotype of *D. carri* is twice as deep as that of *D. reticularia*. There is no significant morphological variation among *D. carri* from the four sites. Measurements and qualitative observations of all material from Haile VI, McGehee Farm, and Mixson's Bone Bed fall within the range of variation of elements from the Love Bone Bed.

Discussion. *Deirochelys carri* is similar in most respects to its presumed descendant *D. reticularia*. The major differences are modifications associated with the further development of the specialized elongate neck and head in *D. reticularia*. In this respect both *D. carri* and *D. reticularia* surely represent segments of a single chronological lineage. The neural spines and dorsal rib heads of *D. carri* are typical of the genus and only slightly more robust than those of *D. reticularia*. The single cervical vertebra (UF 6485b) referable to *D. carri* (Fig. 14) is likewise slightly more robust than the corresponding vertebra of *D. reticularia*; additionally the posterolateral flanges on the modern centrum, which must serve as muscle attachment surfaces, are lacking in the fossil (the possibility of wear is unlikely). Although it is impossible to determine accurately the length of the Pliocene vertebra from the Haile VI fragment, it appears that the characteristic cervical elongation and development of associated modifications in *Deirochelys* had already approached present levels by Middle Pliocene. Nevertheless, *D. carri*'s narrower neural bones and more proximal rib union with the pleural bones relative to *D. reticularia* imply a shorter free rib between the pleurals and vertebral column and a correspondingly less developed set of cervical extensor muscles in the former. A slightly shorter or less powerful neck in the Pliocene species therefore seems likely. Certainly any future finds of *Deirochelys* skull and cervical material in the Love Bone Bed would be particularly valuable.

Although the Love Bone Bed provides us with an exceptionally fine series of *Deirochelys* fossils, far older than any previously known

for the genus, we can trace the evolutionary record of this turtle back still one step further - to the Miocene.

The Thomas Farm *Deirochelys*

The only emydid turtle previously recognized from the Florida Miocene (Thomas Farm) is a species *Chrysemys* of uncertain status (Williams, 1953; Rose and Weaver, 1966). In an effort to determine the relationships of this turtle, I examined the holdings of the Florida State Museum for additional material. Among the elements retrieved were a faintly sculptured neural bone (UF 21949) only slightly narrower than those of *D. carri*, and the proximal fragment of a pleural bone (UF 21950) with a rib juncture scar too low for that of *Chrysemys* (Fig. 17). Comparisons with Recent and fossil *Deirochelys* and *Chrysemys*, including "typical" *Chrysemys* elements from Thomas Farm, leave no doubt that the two fossils represent *Deirochelys*. Curvature of the scute sulcus, relative length of the anterolateral borders, and extreme lowness of the neural spine all indicate that the neural bone is a fifth, while the relative proportions of the medial borders of the pleural bone in addition to the position of the sulcus indicate that it is probably the second pleural bone from the left side. As with the Pliocene *Deirochelys*, the shell is relatively thick (STI, 1.9).

In addition to the two fossils described above, I tentatively refer to *Deirochelys* the following elements from Thomas Farm: one complete epiplastron (UF 21932) and the medial half of another (UF 21939), the posterior part of a right xiphiplastron (UF 21946), the major part of an entoplastron (UF 21942), and the proximal end of a

pleural bone (UF 21951). Additionally, one complete and two fragmentary nuchal bones (MCZ 3432; see Fig. 4 in Williams, 1953, and Fig. 2B in Rose and Weaver, 1966), although probably representing *Chrysemys*, may be *Deirochelys*. The width of the first vertebral scute and shape of the nuchal scute are like those of both *Deirochelys* and *Chrysemys ornata*.

Both the shape of the neural bone (length: width ratio, 0.94, Fig. 7) and the point of juncture of the rib with the pleural bone (rib distance: pleural bone width ratio, 0.41, Fig. 8) indicate that, in terms of cervical hypertrophy, the Thomas Farm *Deirochelys* was even more primitive (less specialized) than *D. carri*. Remains of the very low neural spine fused to the neural bone confirm this. Hence, I believe that the limited Thomas Farm material represents a turtle distinct from *D. carri*. However, any taxonomic assignment of the Thomas Farm fossils other than to genus must await additional and preferably associated material. More important at present is that in the Thomas Farm Miocene we find an important link in the gradual evolutionary sequence from a generalized emydine ancestor (cf. *Chrysemys*) into the more specialized *D. carri* and its highly specialized descendant, *D. reticularia*.

Discussion

The material now available shows that the genus *Deirochelys*, instead of being an evolutionary enigma, possesses possibly the most complete evolutionary record of any modern turtle genus. Evolution of *Deirochelys* has been by specialization of a generalized emydine stock (presumably *Chrysemys*). The earliest fossils are, in fact, difficult to distinguish from *Chrysemys*. We may estimate by extrapolation at

what point the two genera would be no longer distinct--i.e., the time at which a generalized turtle began its initial shift to a new adaptive zone in response to selective pressure. The elongated neck (and presumably skull) as well as associated muscular (Shah, 1963) and osteological modifications of *Deirochelys* had already developed by Middle Pliocene. This character suite is already conspicuous in hatchling *D. reticularia*, so that phylogenetic recapitulation must occur very early during ontogenetic development if it occurs at all. The divergence from a more generalized aquatic emydine stock (moderately short neck, long neural bones, weak hyoid apparatus, robust ribs emerging from very near the proximal ends of pleural bones, limited trunk vertebral musculature, and a relatively broad shell, as in the genus *Chrysemys* and some members of the Eocene genus *Echmatemys*) had certainly begun by the Miocene. Extrapolations based on an average rate of evolution from such a generalized ancestor suggest an Oligocene origin of the genus (Fig. 18). This character suite almost certainly evolved as a peculiar trophic structure; *Deirochelys* utilizes a "pharyngeal" method of feeding (Bramble, 1973) for capturing prey capable of quick movements (primarily aquatic arthropods). Arguments such as those of Webb and Johnson (1972), in which cervical elongation is held to represent a thermoregulatory device, seem at most of secondary significance in this case, particularly in light of the hypoertrophied hyoid skeleton.

The thick shell of *D. carri* and the Thomas Farm *Deirochelys*, as well as of Blancan and Irvingtonian *D. reticularia* (Table 2), suggests that until Late Pleistocene, *Deirochelys* was a moderately thick-shelled turtle. Pleistocene reduction in weight and volume of the shell may

have allowed faster pursuit and increased maneuverability necessary for capturing fast-moving prey (author's unpublished data) on which *Deirochelys* had come to specialize. Loss of armor (if the thick shell served this purpose) may have been offset by crypsis and behavioral immobility (unpublished observations). In addition to changes in shell thickness, general reduction in body size, accompanied by relative elongation and heightening of the shell, seems to have occurred from at least Hemphillian to Rancholabrean times.

Relationships

Baur (1889) was the first to hypothesize a close relationship between *Emydoidea* and *Deirochelys* on the basis of similar skull and rib specialization. Although Carr (1952) believed the similarity between *Emys* (= *Emydoidea*) *blandingii* and *D. reticularia* to be "purely fortuitous," most subsequent workers supported Baur's idea. Bramble (1974) summarizes the situation:

Williams (in Loveridge and Williams, 1957) presented a forceful case for a relationship between *Emydoidea* and *Deirochelys*. Although *Deirochelys* possesses no plastral hinge and on many points of shell morphology closely approaches certain members of the genus *Chrysemys* (McDowell, 1964), it does, as Williams noted, share with *Emydoidea* a number of specializations of the skull, cervical vertebrae and neck musculature. On these grounds Williams suggested that *Emydoidea* was a derivative of *Deirochelys* and only convergent with *Emys*. This view has been widely adopted by later workers (Tinkle, 1962; McDowell, 1964; Zug, 1966; Pritchard, 1967; Milstead, 1969; Ernst and Barbour, 1972), some of whom (Tinkle, 1962; Zug, 1966) have presented additional evidence in support of it. McDowell (1964: 275) found no 'significant cranial differences between *Deirochelys* and *Emydoidea*' and accordingly placed both genera in a *Deirochelys* Complex within the Emydinae. (p. 724)

However, Bramble's (1974) study of shell kinesis and other osteological and myological characters indicates instead that *Emydoidea* is a "close phyletic associate of *Emys* and *Terrapene*" as well as of *Clemmys* (the four genera comprising the *Clemmys* Complex), and that these genera may be distinguished as a group from *Deirochelys* and McDowell's (1964) *Chrysemys* Complex. Waagen (1972) formed an identical opinion from his analysis of musk glands in Recent turtles. On the basis of fossils discussed in this paper I agree with the conclusions of Waagen (1972) and Bramble (1974) that *Deirochelys* shares a close relationship with the genus *Chrysemys*, and that similarities between *Emydoidea* and *Deirochelys* are "undoubtedly the result of convergent feeding system" (Bramble, 1974). In fact, most of the modifications used to substantiate a close relationship between *Deirochelys* and *Emydoidea* (elongated ventrally-bowed free ribs, widened neural bones, elongated cervical vertebrae, and a greatly hypertrophied cervical musculature) are also present in the totally unrelated (at least at the familial level) cryptodire genus *Chelydra* as well as the pleurodire genus *Chelys*. They are, moreover, all modifications associated with the pharyngeal method of feeding (Bramble, 1973) employed by these turtles. Hence, the taxonomic use of this particular character suite, so clearly convergent among members of three distinct families, should be treated cautiously in attempts to determine intrafamilial relationships. This paper has presented evidence of the gradual development of these adaptations as a unit of functional morphology (Wilson, 1975) within one of these phyletic lines.

Pleistocene and Late Pliocene fossils of *Emydoidea*, which are clearly referable to the modern species *E. blandingii* (Taylor, 1943;

Preston and McCoy, 1971), show no special resemblances to Late Tertiary *Deirochelys*, other than the convergent character set already discussed, and hence do not support a theory of their divergent evolution. Neither the fossil records nor the present distributions (Carr, 1952; Preston and McCoy, 1971; Zug and Schwartz, 1971; McCoy, 1973; Jackson and Kaye, 1974) give any indication that the two genera were ever sympatric, although the southern extension of the range of *Emydoidea* in the Late Pleistocene (Jackson and Kaye, 1974) closely approaches the present northern limit of *Deirochelys* in Mississippi. Further ecological studies might help to determine if this allopatric relationship reflects a Gause-type competitive relationship or a difference in thermal requirements.

Distribution and Paleoecology

The genus *Deirochelys* is endemic to the southeastern United States, and it is therefore not surprising that the first extensive evidence of its fossil history should be from Florida. All vertebrate fossil sites known to contain *Deirochelys* (Fig. 3) occur within the range of the modern subspecies *D. reticularia chrysea* or its zone of intergradation with *D. r. reticularia* (Schwartz, 1956; Zug and Schwartz, 1971).

Deirochelys reticularia usually inhabits quiet, shallow bodies of freshwater throughout its range although it occasionally enters the quieter portions of streams (Pope, 1939; R. Webb, 1950; Carr, 1952; Schwartz, 1956; Campbell, 1969) and perhaps rarely saltwater (Neill, 1948; Martof, 1963). Personal observations in north-central Florida

indicate that the densest populations of *Deirochelys* occur in shallow (less than one meter) ponds with abundant basking logs, emergent bushes (e.g., *Cephalanthus*), and an extensive *Lemma-Wolffiella* surface mat. From a structural standpoint, the relatively short limbs, long nuchal scute underlap, and absence of streamlining (as compared to a lotic form such as *Chrysemys concinna*) reflect its evolution as a quiet-water form. The turtle also shows a proclivity for overland wandering (Neill, 1948; Carr, 1952; Gibbons, 1969, 1970). Its typical association with the Southeastern Coastal Plain (Mount, 1972; Mount and Folkerts, 1968) implies adaptation to a warm temperate climate. The presence of *Deirochelys* and associated fauna [*Lepisosteus*, *Amia*, *Alligator*, *Chrysemys caelata* (Chapter III), *Trionyx* cf. *T. ferox*] in Hemphillian sites thus indicates the existence of quiet freshwater (e.g., sinkhole ponds or sluggish streams) and a warm, equable climate in the Florida Middle Pliocene.

Even in the most favorable habitats *Deirochelys* today rarely reaches densities comparable to those of sympatric emydine turtles (e.g., *Chrysemys nelsoni*, *C. floridana*, *C. scripta*). This relationship appears to hold also in the Pliocene; in the only Pliocene deposit containing large numbers of *Deirochelys* (Love Bone Bed), *Chrysemys caelata* elements outnumber those of *D. carri* approximately four to one. In what presumably was a suboptimal habitat for *Deirochelys* at McGehee Farm the ratio is even more disparate. This indicates that populations of *Deirochelys* may be more restricted by limiting factors than are other emydines.

All fossil records for *Deirochelys* from sites near the present coastline of Florida (Fig. 3) are either Subrecent or Late Rancholabrean.

All other sites except those in the Waccassassa River are in presently well-drained localities 21 to 37 m above present sea level; these include all sites assigned to the Hemphillian, Irvingtonian, Blancan, and early Rancholabrean periods.

Webb and Tessman (1968) have presented vertebrate faunal evidence supporting conclusions based on physiographic evidence (Alt and Brooks, 1964; Alt, 1967) that sea level dropped and rose again as much as 30 meters during Hemphillian (middle Pliocene) time. McGehee Farm (early Hemphillian) was thus very near the Pliocene coastal shoreline during its time of deposition and its fauna clearly reflects an estuarine influence, although nearby Mixson's Bone Bed, which occurs at the same elevation, does not (Webb, 1964; Webb and Tessman, 1968). Additionally, the Late Pliocene and Middle Pleistocene interglacial deposits containing *Deirochelys* were much nearer to coastal shorelines during deposition than they are today. It seems probable that since at least the Pliocene *Deirochelys* has been associated primarily with lowland habitat, as was the Pleistocene box turtle subspecies *Terrapene carolina putnami* in Florida (Auffenberg, 1958). Distribution of these turtles in the Florida peninsula and along the Gulf coast must have fluctuated with the advance and retreat of the Pleistocene sea. The proclivity of the genus for overland wandering has probably been instrumental in maintaining or reestablishing inland populations at higher elevations in the abundant "perched" lakes (bodies of water which are completely above the piezometric surface and sometimes subject to spontaneous drainage) common throughout much of the peninsula today. The present inland populations may be relicts of higher sea levels or terrestrially-reestablished populations.

Figure 3. Fossil sites in peninsular Florida containing *Deirochelys*. Site ages are given in Appendix.

- | | |
|---------------------------|--------------------------|
| 1. McGehee Farm | 9. Seminole Field |
| 2. Haile sites | 10. Catalina Gardens |
| 3. Love Bone Bed | 11. Bradenton |
| 4. Wall Company Pit | 12. Warm Mineral Springs |
| 5. Mixson's Bone Bed | 13. Nichol's Hammock |
| 6. Kendrick 1A | 14. Reddick 11C |
| 7. Waccasassa River sites | 15. Thomas Farm |
| 8. Coleman 111C | 16. Vero |

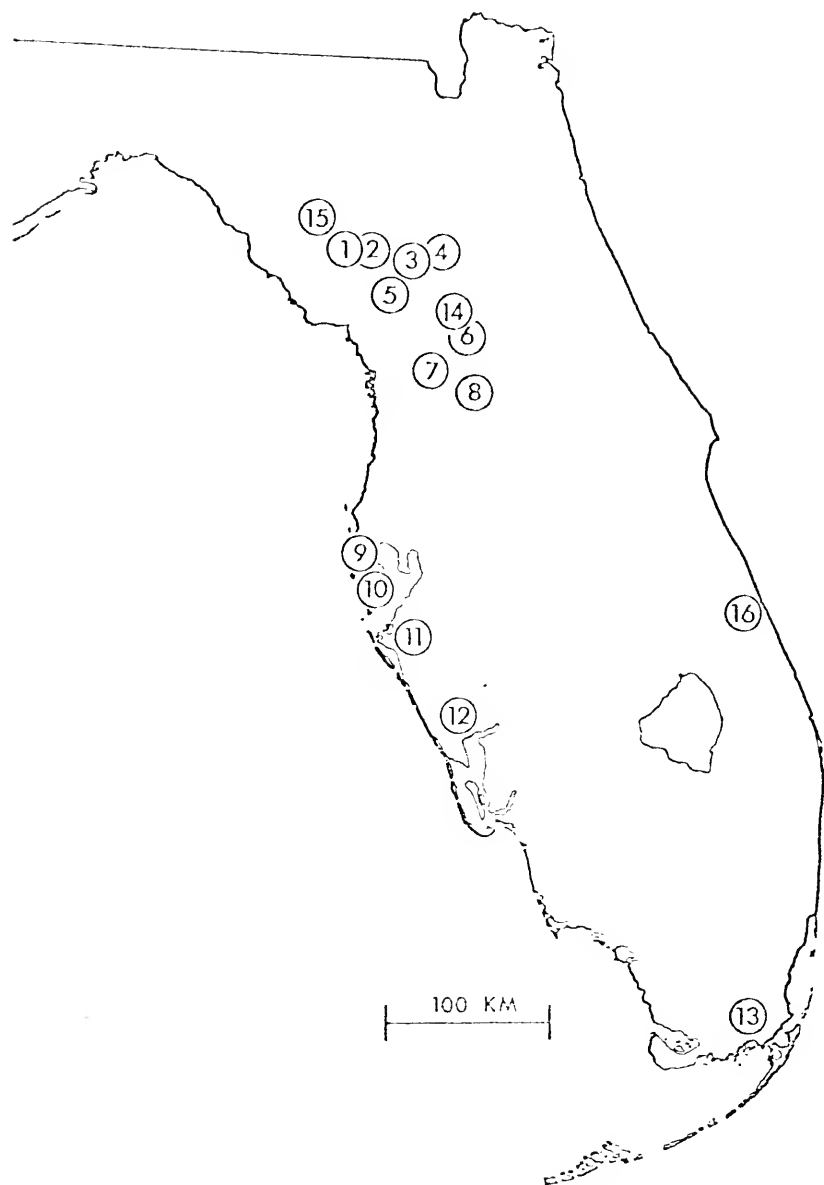
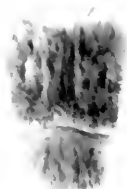


Figure 4. Third neural bones of *Chrysemys floridana* (A) and *Deirochelys reticularia* (B); note greater width and characteristic sculpturing of latter.

Figure 5. Frontal aspects of third pleural bones of *Chrysemys concinna* (A) and *Deirochelys reticularia* (B), showing dorsal ribs.

A



B



A



B



Figure 6. Lateral (A, C) and frontal (B, D) aspects of third neural bones and associated vertebrae of *Diagonolepis reticulata* (A, B) and *Ginyserys nelsoni* (C, D): c, centrum; s, neural spine.

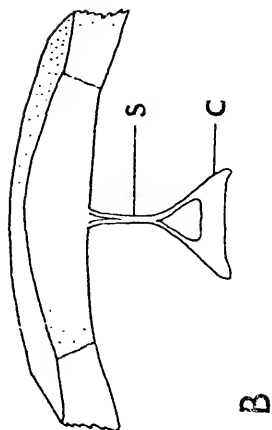
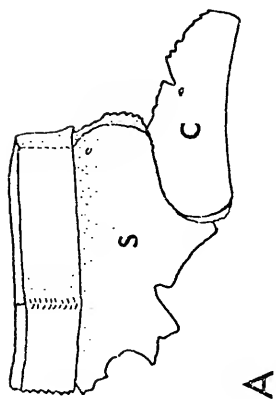
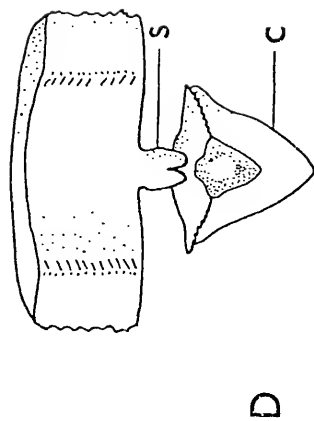
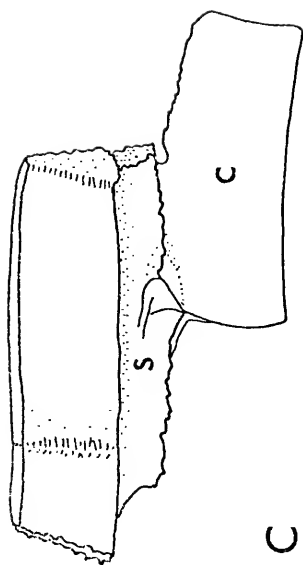


Figure 7. Length: width ratios of second through sixth neural bones of Recent (closed circles), Irvingtonian (stars), Hemphillian (triangles - Love; square - Haile VI; asterisk - Mixson's), and Arikareean (open circle) *Deirochelys*. Dice - Leraas diagrams depict mean, range, and two standard errors; numbers above and below bars represent sample sizes.

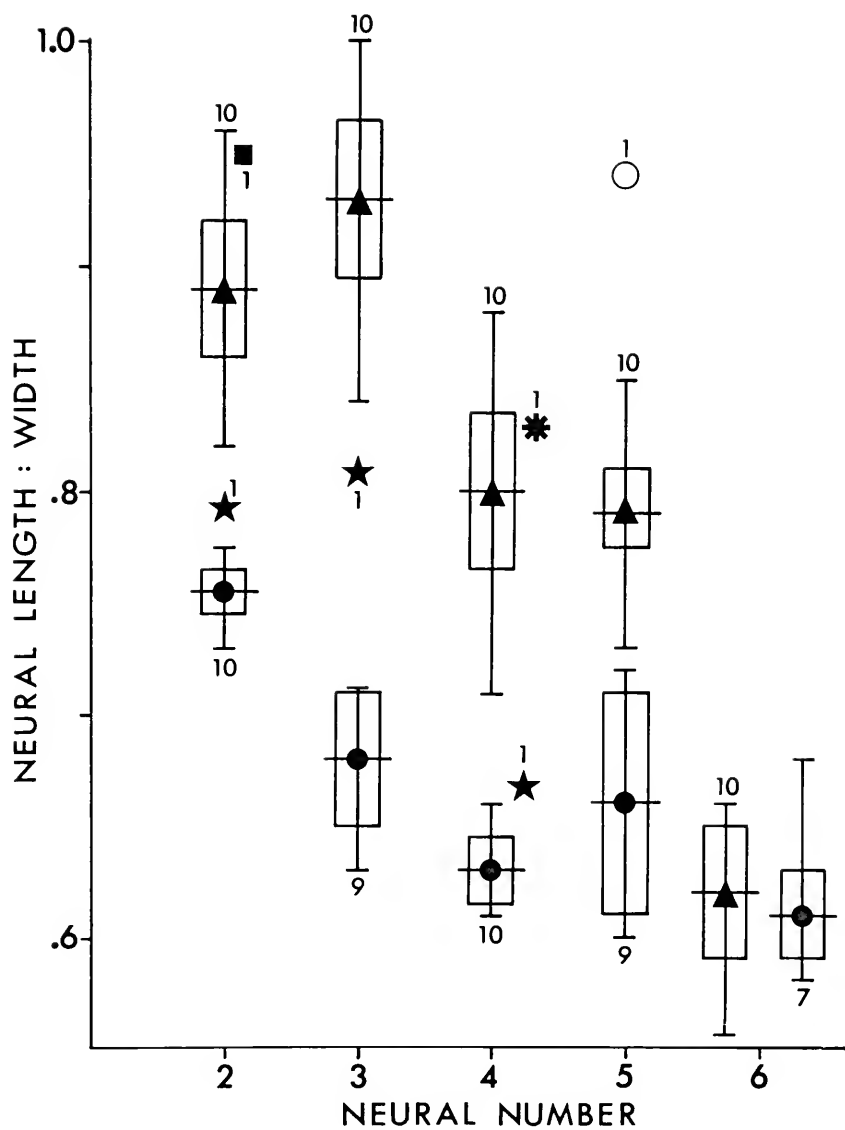


Figure 8. Rib distance: pleural bone width ratios for Recent, Pleistocene, and Pliocene *Deirochelys*; all symbols as in Fig. 7.

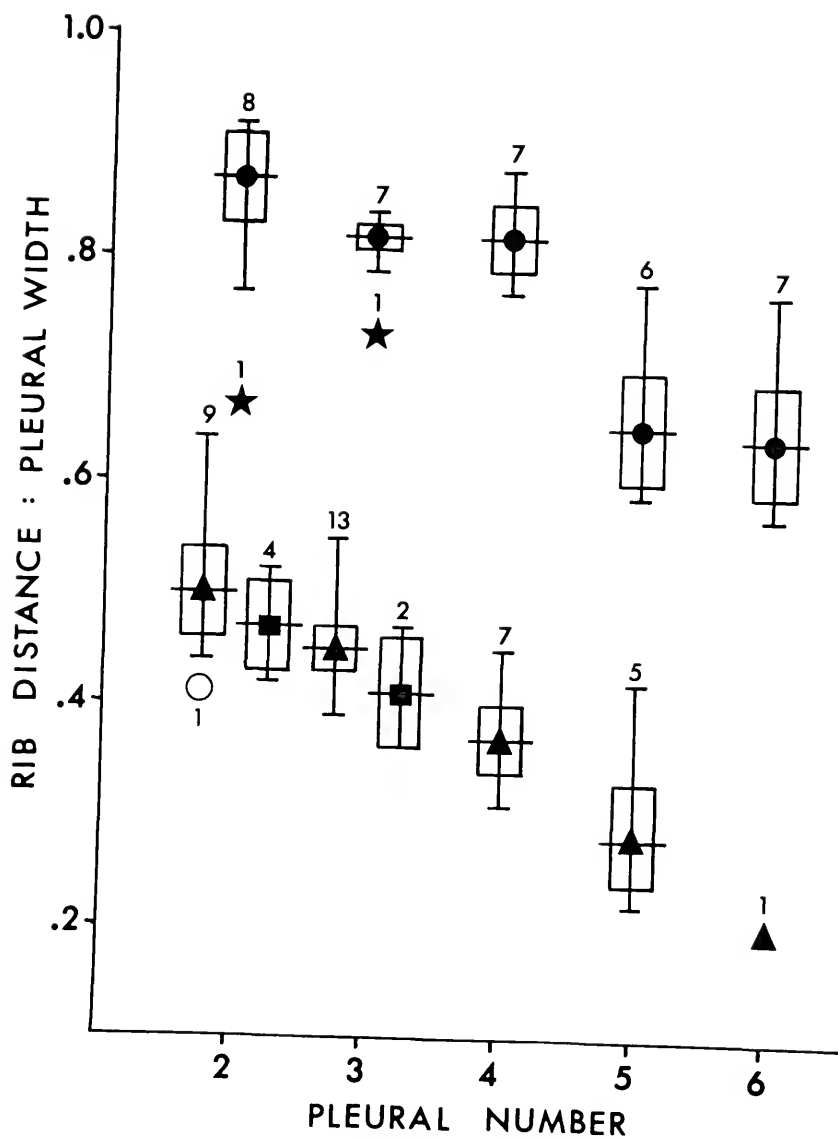


Figure 9. Nuchal (UF 16271) and three neural bones (TRO 101-103) of Rancholabrean *Deirochelys reticularia* from Waccasassa River V and I, respectively.

Figure 10. Distinctly sculptured nuchal bone (UF 9292) and sixth neural bone (UF 19250) of *Deirochelys reticularia* from Kendrick 1A.



Figure 11. Dorsal (A) and ventral (B) surfaces of carapace fragment (UF 20888) of Irvingtonian *Deirochelys reticularia* (Haile XVI). Note sculpturing, neural bone width, and rib junctures.

Figure 12. Fifth neural bone (A, UF 19249) and nuchal bone fragment (B, UF 19168), of Blacan *Deirochelys reticularia* (Haile XV), showing broad nuchal scute underlap.

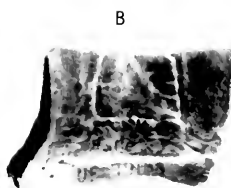
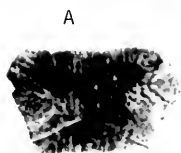
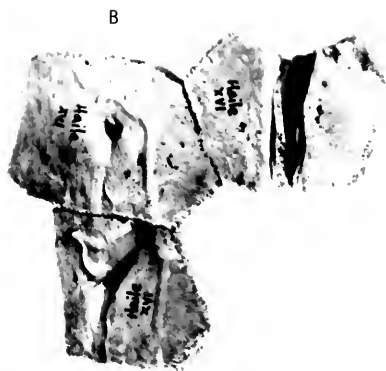


Figure 13A. *Deirochelys carri* holotype, UF 20908, dorsal aspect of carapace. Hatched areas missing from fossil.

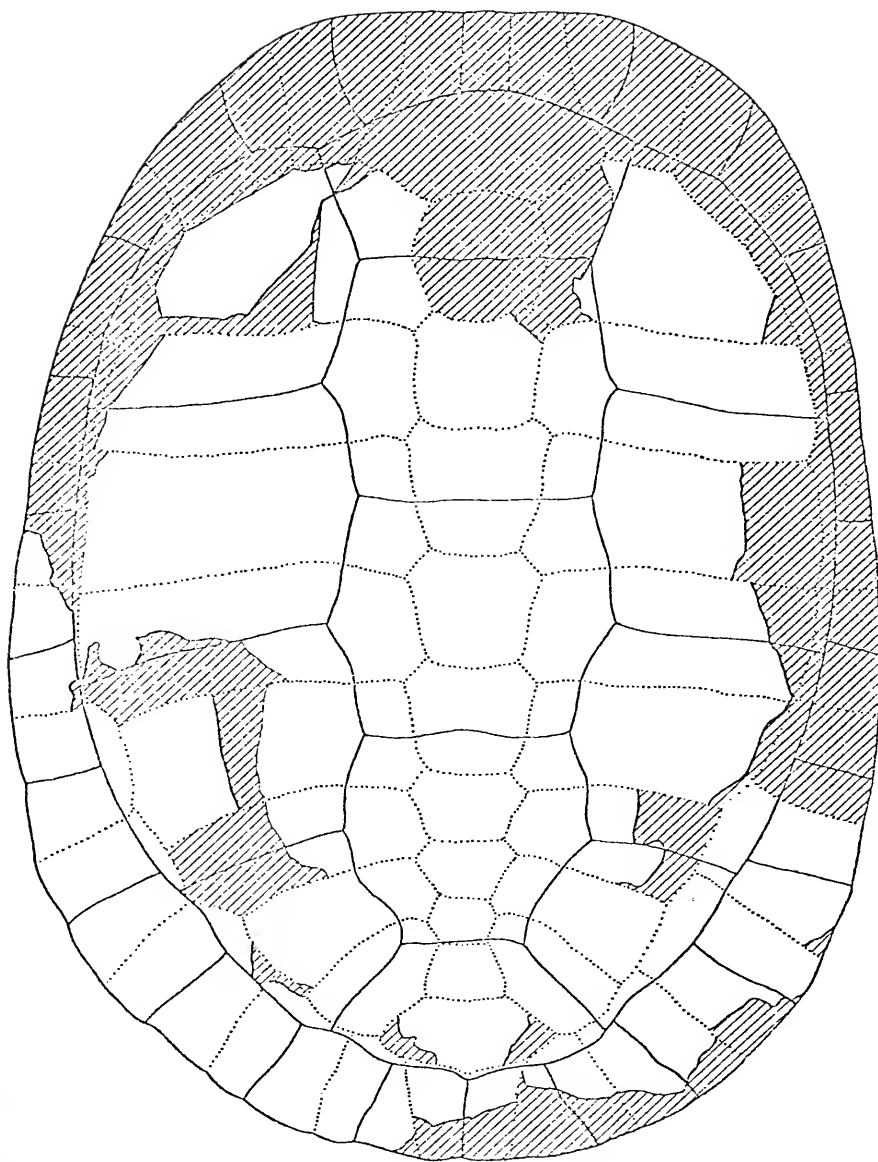


Figure 13B. *Deirochelys carri* holotype, UF 20908, ventral aspect of
plastron. Hatched areas missing from fossil.

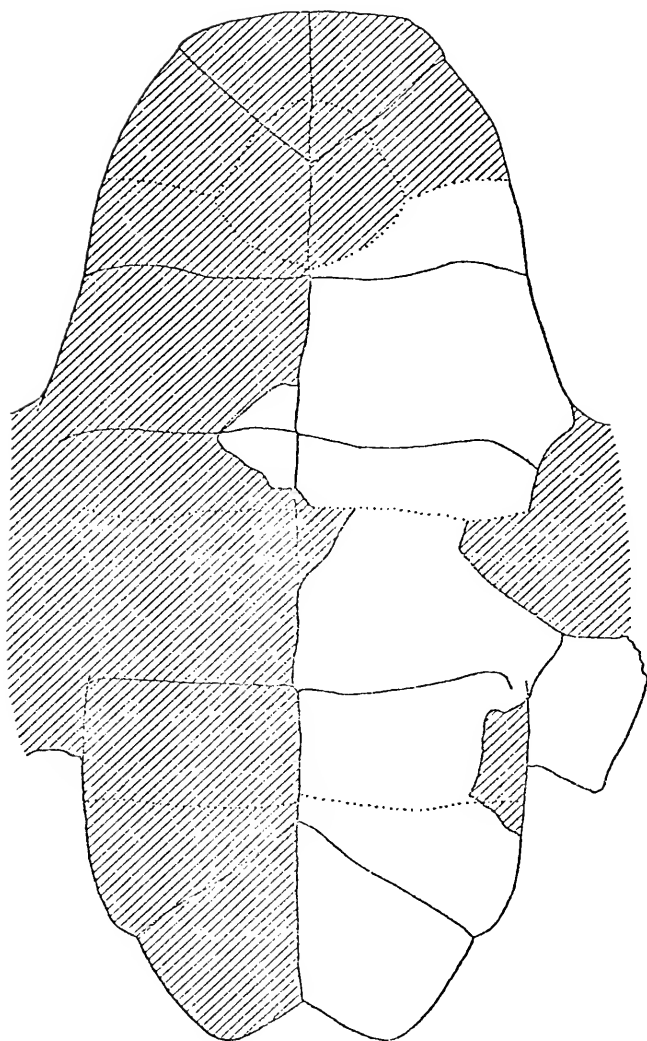


Figure 14. Third cervical vertebrae of *Deirochelys carni* (A) and *D. reticulata* (B).

Figure 15. Ventral surface of posterior region of *Deirochelys carni* carapace, UF 20900, showing rib junctures with pleural bones. Arrows indicate where junctures would occur in *D. reticulata* of equivalent size.



Figure 16. A distinctly sculptured nuchal bone (A) and posterior peripheral bone (B) of *Deirochelys carri* from the Love Bone Bed (x 1.15).

Figure 17. *Deirochelys* fossils from the Thomas Farm Miocene (X 2.25). (A) Neural bone, (B) visceral surface of pleural bone fragment showing rib juncture scar.

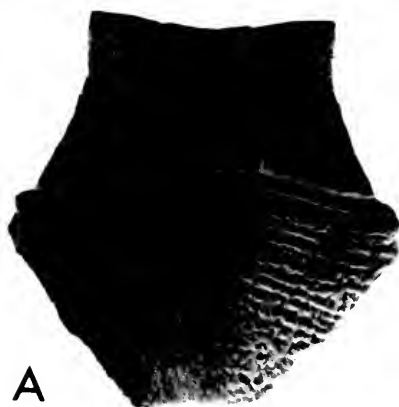
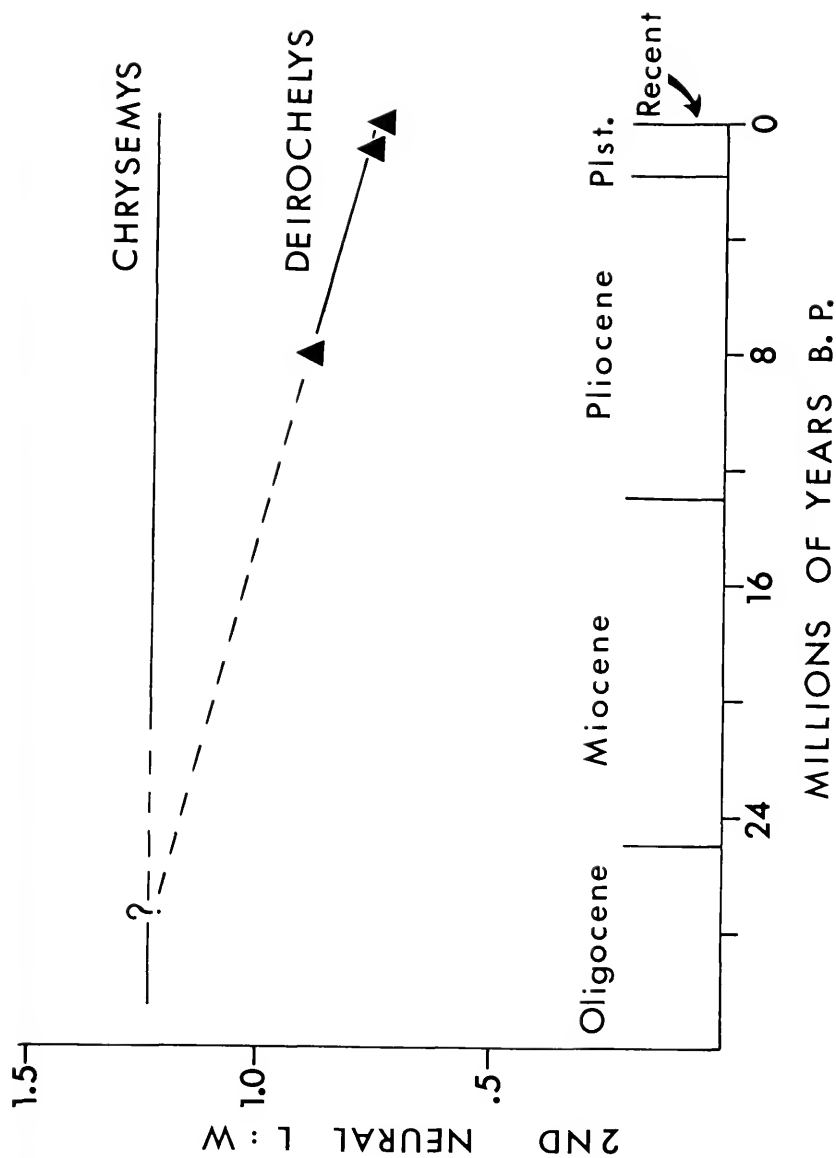


Figure 18. Extrapolation through time of second neural bone length: width ratio of *Deinoceratops*, indicating hypothetical point of divergence from a more generalized emydine line.



CHAPTER III
THE STATUS OF THE PLIOCENE TURTLES
CHRYSEMYS CAELATA (HAY) AND *CHRYSEMYS CARRI* ROSE AND WEAVER

Three non-*Trachemys* species of *Chrysemys* (sensu McDowell, 1964) have been described from the Pliocene of Florida. Hay (1908) described *C. caelata*, largely on the basis of shell sculpturing, from Mixson's Bone Bed,* Levy County. Hay considered this site Pleistocene in age although it had previously been recognized as Pliocene (Dall and Harris, 1892; Leidy and Lucas, 1896) and was so reassigned by Simpson in 1929. Rose and Weaver (1966) examined shells of *Chrysemys* from McGehee Farm in adjacent Alachua County and described both a smooth-shelled species (*C. williamsi*) and a rugose species (*C. carri*) yet made no reference to *C. caelata*. Both sites are Pliocene deposits within the Alachua Formation (Simpson, 1929a; Rose and Weaver, 1966; Hirschfeld and Webb, 1968). The occurrence of two rough-shelled species in approximately equivalent strata only 34 km apart prompted me to investigate their taxonomic status. All specimens are in the collections of the U.S. National Museum (USNM), Florida State Museum (UF), and Florida Geological Survey (FGS).

*Uncertainty surrounds Hay's designation of the type locality of *C. caelata*, as it does much of the early Mixson material (Simpson, 1929a). In conjunction with the original description, Hay (1908) gave the locality as "'Mason's bone bed,' somewhere in Levy County, Florida," but later (1916) referred the site only to "somewhere in Levy County, Florida." The data with the USNM specimens read "Levy County, Florida, 1885, L. C. Johnson." As this is the period when Johnson and other representatives of the U.S. Geological Survey were originally investigating Mixson's Bone Bed (Simpson, 1929a), and as the material exhibits the same condition of preservation as known Mixson material, I suggest that "Mason's" is a liberal orthographic interpretation of "Mixson's."

Taxonomic Considerations

Chrysemys caelata was described by Hay (1908) on the basis of 11 unassociated elements; of these he considered 10 (USNM 2508) as probably representing one large individual and a single pleural (USNM 6064) a smaller specimen. The nuchal bone was designated as the type. My examination of this material reveals that probably no more than two bones represent any single individual. However, the entire series appears to represent one species. The two posterior peripherals to which Hay (1908) referred are a tenth and eleventh from the right side. In his original description (1908) he wrongly referred to the seventh right peripheral as a third left, but corrected this error in 1916. As Hay gives adequate measurements and detailed accounts of the sculpturing on most of the bones, a redescription of the material is unnecessary.

Hay (1908) placed great emphasis on the characteristic sculpturing of the shell of *C. caelata*, which he said "resembles that of *Trachemys scripta*" (= *Chrysemys*). The sculpturing bears an even stronger resemblance to that of *C. nelsoni*, which, like *scripta*, occurs in Florida today. Having only limited material from which to describe the sculpturing, Hay did not appreciate the range of intraspecific variation to which this character is subject. Other specified diagnostic characters include a well-developed epiplastral lip and absence of notches along the posterior carapace edge.

Rose and Weaver (1966) described *Chrysemys carri* from a series of incomplete shells (holotype UF 9427 and nine paratypes). They diagnosed it as "a species of *Chrysemys* with a rugose carapace and plastron, a slight median posterior keel, long nuchal scute underlap..., moderate

gular scute overlap..., un-notched peripherals," large epiplastral lip, "and a clearly notched and rectangular pygal bone."

I have examined and compared the type series of both *C. carri* (except UF 11083 which could not be located) and *C. caelata*. Patterns of surface rugosity and scutellation of the individual elements of *C. caelata* are well within the range of and often virtually identical to sculpturing and scutellation patterns of corresponding elements of *C. carri* (Figs. 19 and 20). Measurements of the type nuchal bones show no significant differences in proportions (Table 3). The long nuchal scute underlap of *C. carri*, which distinguishes this turtle from *C. williamsi* and *C. concinna* (Rose and Weaver, 1966), is also evident in the type of *C. caelata* (Fig. 19, D and E). Examination of more than 100 nuchal bones of *C. carri* reveals that the length/width ratio of the nuchal scute underlap varies from 1.0 to 2.3. The ratio for the type of *C. caelata* is 1.0, within the limits of variation in the McGehee series. Sulci on the dorsal surface of the *caelata* nuchal are aberrant (Fig. 19A); these measurements are of little value. The moderate gular scute overlap of *C. carri*, a character stressed by Rose and Weaver (1966) as highly diagnostic, is not significantly different from that on the type epiplastron of *C. caelata* (Fig. 20, A and C). The epiplastral lip is pronounced in both *C. carri* and *C. caelata* (Fig. 20), although within the large McGehee series the shape and size of this lip are clearly variable. In both *C. caelata* and *C. carri* the peripherals, and hence the carapacial margins, are un-notched. Furthermore, in both descriptions the authors characterize the posterior peripherals as horizontally flared (i.e., with a concave upper surface). Finally, all of the

Table 3. Maximum measurements (mm) of holotype nuchal bones of *Chrysemys caelata* and *C. carri*.

	<i>caelata</i>	<i>carri</i>
length	46.6	44.6
width	53.3	52.0
anterior border	23.3	23.0

elements assigned to *C. caelata* represent turtles within the size range of *C. carri* (largest plastron in McGehee series, 295 mm; estimated carapace length, 338 mm).

I am unable to compare the remaining diagnostic characters of *C. carri*--the slight median posterior keel and the notched rectangular pygal bone--with *C. caelata* as Hay's (1908) type series includes neither neurals nor pygal. Hay (1916) later erroneously assigned the neural (FGS V-2599 = olf 3425) of a *Deirochelys* to *C. caelata*; the impact of this error was discussed in Chapter II.

There appear to be no significant morphological differences between *C. caelata* and *C. carri*. Furthermore, considering the geographic proximity of the type localities (34 km) and the approximate stratigraphic equivalence (Webb, 1964; Hirschfeld and Webb, 1968) of the horizons, the names undoubtedly refer to the same species. *Chrysemys carri* Rose and Weaver is therefore a synonym of *Chrysemys caelata* (Hay).

Relationships

Patterns of shell sculpture, scutellation and shell morphology of *C. caelata* are similar to those of *C. nelsoni*; the two species are surely closely related if not synonymous. Nevertheless, they may usually be distinguished by the shapes of the entoplastron and first suprapygals (Fig. 21). In addition differences in the ratios of maximum gular scute length/epiplastral lip width (*caelata* \bar{x} , 0.66; *nelsoni* \bar{x} , 0.80) and posterior width of first suprapygals/greatest width of second suprapygals (*caelata* \bar{x} , 0.63; *nelsoni* \bar{x} , 0.44) are significant (Student's t-test, $p < 0.025$). Also, the pygal bone of *C. caelata* is more truncate, less

deeply notched, and usually less deeply overlapped by the fifth vertebral scute than that of *C. nelsoni*.

Rose and Weaver (1966) assigned two mandibles (UF 11086 and UF 11095) from McGehee Farm to *C. caelata*. Based on its flattened ventral surface, which is nearly continuous with the scar marking the insertion on the dentary of the *M. occipito-squamoso-maxillaris* [(= *Temporalis* of Wiedemann, and *M. temporalis* of Bojanus, Stannius, Cuvier, and Owen) Hoffman, 1890], mandible UF 11095 is similar to that of *C. nelsoni* and hence may represent *C. caelata*. There are no indications of the serrated cutting edge, bicuspid notching, or broad alveolar surface characteristic of jaws of *C. nelsoni*. However, mandible UF 11086 is less flattened ventrally, the muscle scar does not come close to reaching the ventral surface, and the entire jaw is foreshortened (hence, wider) relative to *C. nelsoni*; these conditions are similar to those of *C. concinna* (as well as *C. floridana*) and the jaw likely represents its predecessor, *C. williamsi*. For the present, as no skull material positively referable to *C. caelata* is known, this species must be considered specifically distinct from *C. nelsoni*.

Further study is also needed to clarify the relationship of *C. caelata* with other Pliocene and Early Pleistocene *Chrysemys*, particularly *C. idahoensis* from Blancan beds in Idaho (Gilmore, 1933; Rose and Weaver, 1966) and *C. hillii* of the Kansas Lower Pliocene. The latter has been associated by most authors with the *Trachemys* line (Cope, 1878; Hay, 1908; Adler, 1968; F. Rose, pers. comm.), and certain characters (e.g., notching of pygal and peripheral bones) would seem to distinguish it from *C. caelata*.

Discussion

Chrysemys caelata is now known from a large series of nearly complete shells from McGehee Farm in addition to the few original elements from Mixson's Bone Bed. The characteristics described by Rose and Weaver (1966) may be added to those listed by Hay (1908) to give us an improved definition of this species. Other than these two descriptions, *C. caelata* has been mentioned few times in the literature. Of the 12 additional Mixson elements Hay (1916) assigned to this species, at least the neural and probably the epiplastron represent *Deirochelys*. Four of these, including the epiplastron (which, however, is pictured), must tentatively be considered lost. I have examined the remainder and, except for the neural, agree with Hay's assignment (although the peripheral he refers to as the second left is actually a first left). Gilmore's recognition of *C. caelata* from Melbourne, Florida (Hay, 1923, 1927), which Hay believed to be Aftonian (Late Blancan) but now generally considered Rancholabrean (Hibbard et al., 1966; Webb, 1974), is extremely doubtful. I have seen only *C. scripta* from this site. All other references to *C. caelata* (Auffenberg, 1955, 1963; Goin and Auffenberg, 1955) refer to a series of elements from Haile VI, another Florida Pliocene site only 3 km east of McGehee Farm. Many of these elements (a neural and the proximal ends of several pleurals) actually represent the genus *Deirochelys* (Chapter II). Allocation of the remaining fragments (mostly peripherals and distal ends of pleurals) is difficult; tentatively I consider at least some of them to represent *C. caelata*. Recent excavation of a newly discovered Pliocene site (Love Bone Bed) at Archer, Alachua County, Florida (29°33'N, 82°31'W; sec. 9, T11S, R18E) has yielded large quantities

of turtle material, much of which can be definitely assigned to *C. caelata*; to date, two partial shells (UF20869 and 20870) as well as numerous unassociated elements representing this species have been removed.

Chrysemys caelata, then, is a rugose *Chrysemys* presently known from four Pliocene sites encompassing a total area of only 47 square kilometers in adjacent Alachua and Levy Counties, Florida. Recent workers (Auffenberg, 1963; Hirschfeld and Webb, 1968; Webb, 1969 and pers. comm.) have assigned all four sites to the Alachua Formation. Although the "formation" is time-transgressive, including sediments ranging in age from early Miocene through Recent, fossils representing distinct faunas within it are often unmixed (Simpson, 1930; Cooke, 1945; Vernon, 1951; Auffenberg, 1963; Puri and Vernon, 1964; Hirschfeld and Webb, 1968). I therefore conclude that *Chrysemys caelata* is indicative of early Hemphillian faunas (Hirschfeld and Webb, 1968; Webb, 1969) of the Alachua Formation.

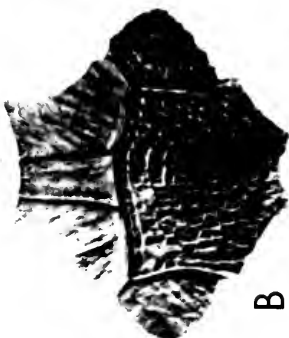
Morphologically, *C. caelata* appears to be ancestral to *C. nelsoni*, a relatively common turtle of both Pleistocene and Recent Florida. Like *nelsoni*, *caelata* was probably characteristic of still or slow-moving water. Likewise, *caelata*'s coeval at McGehee Farm, *C. williamsi* (Rose and Weaver, 1966), appears, on the basis of shell morphology, to be the Pliocene forerunner of *C. concinna*, a stream-inhabitant (Crenshaw, 1955) of Pleistocene and Recent Florida. These two lines (*floridana-concinna* species group and *rubriventris* species group, including *C. nelsoni*) within the subgenus *Pseudemys* (sensu McDowell, 1964) were therefore distinct in north peninsular Florida by Middle Pliocene. Nevertheless, Crenshaw (1955, 1965) indicates that in rare instances in the southeastern United States reproductive isolation of the two groups has either

partially broken down or not yet fully developed. That *C. caelata* and *C. williamsi* were found in separate concentrations within the McGehee deposit (Rose and Weaver, 1966) suggests that although sympatric they may have been predominantly allotopic (as are *C. nelsoni* and *C. concinna* today in this region). Sedimentology and associated faunas in the same deposits (Webb, 1964; Hirschfeld and Webb, 1968) support this hypothesis.

Figure 19. Dorsal (A, B, C) and ventral (D, E) aspects of nuchal bones of the type of *Chrysemys caelata* (A, D), McGehee Farm *C. carri* UF20882 (B) and UF 20883 (E), and *C. caelata* from Love Bone Bed, UF 20870 (C). (x 1.0).



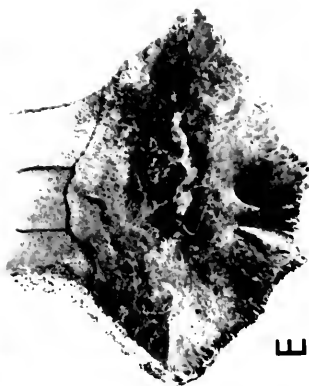
C



B



A



E

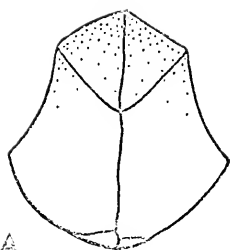


D

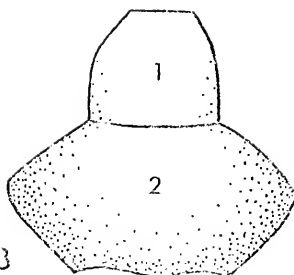
Figure 20. Left epiplastra of *Chrysemys caelata* USNM 2508
(A, dorsal; B, ventral) and *C. carini* UF 20066
(C, dorsal; D, ventral). (x 1.0).



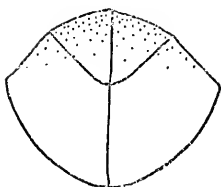
Figure 21. Ventral surfaces of entoplastra (A, C) and dorsal surfaces of suprapygals (B, D) of *Chrysemys nelsoni* (A, B) and *C. caelata* (C, D).



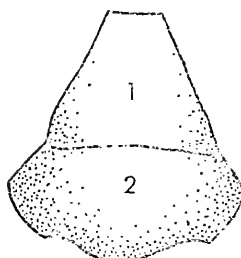
A



B



C



D

CHAPTER IV
A REEXAMINATION OF THE *CHRYSEMYS SCRIPTA* GROUP BASED ON
FOSSIL EVIDENCE

The systematic status and relationships of *Chrysemys scripta* and its close relatives have been a major center of controversy among turtle evolutionists. Most early workers (Agassiz, 1857; Gray, 1870; Hay, 1908; Gilmore, 1933) assigned the *C. scripta* complex full generic standing as the genus *Trachemys*, although Boulenger (1889) included it in *Chrysemys*. Subsequent workers (Carr, 1952; Williams, 1956; Loveridge and Williams, 1957) incorporated the group into the genus *Pseudemys* (as had Cope, 1878) but made few statements about intrageneric relationships above the species level. It was not until 1964 when McDowell considered *Pseudemys* and *Chrysemys* (*sensu stricto*) congeneric that subgenera were formally recognized. The subgenus *Trachemys* included all members of the *C. scripta* complex; the subgenus *Pseudemys* included two series of turtles--the *floridana* series (*C. floridana* and *C. concinna*) and the *rubriventris* series (*C. rubriventris*, *C. alabamensis* and *C. nelsoni*)--both more closely related to each other than either is to *Trachemys*; finally, the type species of the genus, *C. picta*, was considered a third distinct subgenus, *Chrysemys*.

Weaver and Rose (1967) examined the ideas of McDowell (1964) using fossil and extant material and concluded that his subgenera were invalid. They developed a new phylogeny for the genus in which they considered the North American *C. scripta* group to be more closely related to the *C. rubriventris* complex, and the West Indian, Mexican, Central and South

American turtles previously considered races of *C. scripta* to be more closely related to *C. floridana* and *C. concinna*. Their failure to recognize the importance of convergence of specific adaptations, as well as the false premises on which they delineated "ancestral characters," leave their conclusions suspect.

One of the major drawbacks to a vertical study of the *C. scripta* complex has been the absence of skulls of extinct forms; in fact, only two fossil emydid skulls from all of North America have been previously reported (Hay, 1908; Gilmore, 1933), and the identities of these are ambiguous. McDowell's (1964) conclusions, drawn almost entirely from cranial characters, have therefore been nearly impossible to apply to fossil forms, the taxonomy of which has necessarily been based almost exclusively on shell osteology. In this paper I report previously unrecognized skull material from the Florida Pliocene which casts new light on some of these problems. Furthermore, only very limited attempts have been made to relate fossils from Florida to those from the Great Plains; this must be done if paleontological species are to have biological meaning. My purpose, therefore, is not to revise the genus again, but to analyze all available fossils to point out problems with some of the earlier schemes, and to reinterpret intrageneric relationships accordingly. Of primary interest here is the relationship of the *C. scripta* complex to other members of the genus. The term "North American *C. scripta*," as used in this paper, includes only those turtles occurring in the continental United States. All fossils, unless otherwise noted, are in the vertebrate paleontology collection of the Florida State Museum (UF).

Trachemys in the Pleistocene

Probably due to their abundance in the Pleistocene of Florida and Texas and the ease with which they may be recognized, fossils of the *C. scripta* group (i.e., *Trachemys*) have been known longer and studied more extensively than those of most other southeastern emydid turtles. Hay (1908, 1916) recognized eight extinct species from Pleistocene deposits in Florida and Texas that he assigned to this group: *Trachemys euglypha* (Leidy), *T. sculpta* Hay 1908, *T. ? jarmani* Hay 1908, *T. petrolei* (Leidy), *T. bisornata* (Cope), *T. trulla* Hay 1908, *T. ? delicata* Hay 1916 and *T. ? nuchocarinata* Hay 1916. Weaver and Robertson (1967) correctly placed six of these names in synonymy with *C. scripta* and incorporated them, as well as other Florida Rancholabrean material, in their new combination *C. s. petrolei*. The remaining two names represent fossils incorrectly assigned to *Trachemys*: *T. nuchocarinata* = *Terrapene carolina* (Auffenberg, 1958) and *Trachemys jarmani* = *C. nelsoni* (Chapter 11). The only other *Trachemys* recognized by Hay was *T. hillii* (Cope) from the Pliocene Loup Fork beds of Kansas; it is discussed further below.

Because of intraspecific variation within Recent, Rancholabrean, and Irvingtonian *C. scripta*, the utility of *C. s. petrolei* as a reliable stratigraphic tool in Florida is meager. Justification for giving the Rancholabrean fossils separate taxonomic status must be questioned. Weaver and Robertson (1967) distinguish *C. s. petrolei* from all other *C. scripta* by only two characters: its larger average size and greater carapacial rugosity. They admit, however, that these are "minor distinctions." They also state that "the extensive rugosity and

sculpturing of the Rancholabrean fossils is often present in large, extant specimens of *C. s. scripta*." Furthermore, they add that "an additional series of fossils from Ichatuckenee Springs" shows "a size gradation from typically large Rancholabrean nuchals to smaller ones which, in the absence of mineralization, are *indistinguishable* from those of extant *C. s. scripta*" (italics mine).

Neither of the two characters used to diagnose *C. s. petrolei* is reliable. Although the shells of Rancholabrean *C. scripta* are often more rugose than their modern counterparts, the character is subject to extreme variability in both temporal groups. It is not uncommon to find, in peninsular Florida, living *C. scripta* whose shells are more rugose and more deeply insculpted than those of many fossil *C. scripta*.

The second and chief character by which Weaver and Robertson (1967) define *C. s. petrolei*--larger average size than extant *C. scripta*--seems to me insufficient to serve alone as the basis for a separate taxon. The larger average size of turtles in the Pleistocene versus those today is not unique to *C. scripta*. It can be documented not only in other species of *Chrysemys* in Florida but also in most other genera; e.g., *Deirochelys* (Chapter 11), *Graptemys* (Chapter 1), and *Terrapene* (Auffenberg, 1958). Many reasons can be speculated to account for larger size in the Pleistocene: climatic differences as they affect heat loss and retention by poikilotherms; size-selective predation by man or other predators; and, nutritional differences in diet, etc. Body size is a complex phenomenon and should not be used as the sole criterion for establishing additional taxa.

The designation of a temporal subspecies must be made with extreme caution (see Mayr, 1969). Although the concepts of temporal and geographic

subspecies are not necessarily equivalent, they must nonetheless be compatible when applied to one species. The designation of a temporal subspecies that might in itself encompass more than one geographic subspecies is more apt to cause confusion than to increase understanding. This is precisely the case with *C. s. petrolei*, as pointed out previously by Preston (1971). Two distinct subspecies occupy the purported range of *C. s. petrolei* (Florida to Atascosa County, Texas) today: *C. s. elegans* in the west and *C. s. scripta* in the east. The possibility certainly exists that more than one race of *C. scripta* occupied this region during late Pleistocene, so that *C. s. petrolei* in Texas may have been subspecifically distinct from *C. s. petrolei* in Florida. Essentially the same problem arose when Preston (1966, 1971) recognized *C. s. bisornata* (by which he meant *C. s. elegans*-like turtles from the Irvingtonian mammalian age) from both Florida and Texas.

It is unfortunate that the diagnoses of the modern subspecies of *C. scripta* rely almost entirely upon color pattern, as they thus cannot be compared directly with the fossils. The osteological characters used by Preston (1966) to distinguish these forms have some value--particularly the development of the middorsal keel and the relief of the nuchal lamina--though intrasubspecific variation is too great to consider them infalible.

Interestingly, *C. scripta* from Irvingtonian deposits in Florida and Texas appear to differ osteologically in the same way that the subspecies *C. s. scripta* and *C. s. elegans* differ in these regions today. Thus, a nearly complete shell (MUVF 4546) from the early Irvingtonian Seymour Formation, Burnette Ranch, Knox County, Texas, lacks a pronounced

middorsal keel and has a relatively flat nuchal scute and low profile. A partial shell (UF 21802) from Coleman IIA, Sumter County, and a series of elements from Haile XVI, Alachua County--both Irvingtonian deposits in Florida--display the raised nuchal scute, pronounced middorsal keel, and slightly higher profile characteristic of *C. s. scripta*. It appears, therefore, that these two modern subspecies became established no later than early Pleistocene. Any scheme that assigns these fossils subspecific standing distinct from modern forms seems to me biologically unrealistic and an artifact of choosing one's own lifetime as a significant point of reference in geologic time.

I suggest, as implied by Preston (1971), that until we achieve a better understanding of the *C. scripta* group (possibly through the discovery of more fossils), the recognition of fossil subspecies is unwarranted and can only lead to further confusion. Fossils resembling *C. s. elegans* or *C. s. scripta* should be referred to the species and their apparent affinities with modern subspecies discussed, but assignment of temporal subspecific names is presently premature.

Pleistocene fossils of *C. scripta* provide us with information on the species' former distribution and the occurrence of subspecies. However, for knowledge of the evolution of *Trachemys* we must look back to at least the Pliocene.

Trachemys in the Upper Pliocene

Systematics

Weaver and Robertson (1967) described *Chrysemys platymarginata* as a member of the *Trachemys* group from Haile XVA, Alachua County, Florida.

Although the fauna of this site was then thought to be Irvingtonian (Pleistocene), Robertson (1976) has since reinterpreted it as Blancan (latest Pliocene). Other peninsular Florida sites of Blancan age also contain *C. platymarginata* (Weaver and Robertson, 1967). Based on shell morphology (doubly-toothed peripheral bones, extensive gular scute overlap and nuchal scute underlap, highly sculptured nuchal bone, and well developed median keel on the carapace), Weaver and Robertson properly assigned *C. platymarginata* to the *C. scripta* complex (subgenus *Trachemys*). They believed no skull material of *C. platymarginata* was available. However, a small box of cranial fragments from Haile XVA, collected in 1964 by S. D. Webb, J. Robertson, and R. Allen, contains parts of the skulls of this species, and a chelydrid and trionychid. The fragmentary material was reassembled and compared to literature descriptions (Hay, 1908; Gilmore, 1933; McDowell, 1964; Weaver and Robertson, 1967) and Recent specimens. Much of the cranial anatomy of the fossil emydids can be observed from three partial skulls (UF 21888, 21892, and 21963); UF 21888 includes both dentaries as well. Unassociated fragments (UF23920 and 23921) from several other skulls are also available. Since other emydids (e.g., *Chrysemys concinna* and *Deirochelys*) are also present in the Haile XVA fauna, the emydid skull fragments must be examined closely before specific assignment is made.

McDowell (1964) diagnoses the genus *Chrysemys* by the following cranial characters: "trituration surface of maxilla with sharply defined middle ridge; anterior edge of inferior process of parietal thin; posterior end of pterygoid usually not in contact with exoccipital." Examination of the Haile XVA skulls confirms their identity as *Chrysemys* as defined by McDowell (1964).

Additionally, according to the criteria set forth by McDowell (1964) and modified by Weaver and Rose (1967), the skulls are clearly associated with the *Trachemys* line within the genus. McDowell characterizes the subgenus as follows: ventral surfaces of dentary relatively rounded, middle ridge of upper triturating surface lacking an anterior cusp, maxilla not sutured to quadratojugal (= McDowell's squamosal), pterygoid extending back near the exoccipital, and crista praetemporalis heavier than in other *Chrysemys*. The Haile XVA skulls are clearly assignable to the *Trachemys* line within the genus *Chrysemys* and may thus be confidently referred to *C. platymarginata*, the shell of which also reflects its *Trachemys* affinities. Two other cranial characters that I find consistent with extant *Trachemys* are the recessed vomer, which does not participate in the alveolar surface (unlike the *C. rubriventris* complex), and the broad pterygoids (0.31 to 0.32 times skull width, as compared to 0.23 to 0.28 for species of the *C. rubriventris* group and 0.32 to 0.38 for *C. scripta*; Fig. 22A. A symphyseal ridge on the mandibular alveolar surface appears to be consistently absent or inconspicuous in all living and fossil *Trachemys*. Finally, the posterolateral region of the dentary of *C. platymarginata*, as in *C. scripta*, rises abruptly to meet a relatively higher coronoid bone than is present in either the *C. rubriventris* or *C. floridana* series.

In the above, as well as most other characters, the skull of *C. platymarginata* differs little from that of its presumed descendant, *C. scripta*. Certain differences, presumably adaptive, do exist, however. Most obvious are the much broader maxillary surfaces of *C. platymarginata* (Fig. 22B); this is principally due to expansion of the posterior part

of the alveolar surface medial to the longitudinal maxillary ridge. Alveolar expansion is present in all Haile XVA maxillae but seems most highly developed in the largest individuals. The alveolar surface incorporates a lateral projection of the palatine bone as it does in extant members of the *scripta*, *floridana* and *rubriventris* groups. The supraoccipital of *C. platymarginata* appears slightly larger than in Recent *C. scripta*, though *C. platymarginata* cranial material is insufficient to test this statistically. This feature, coupled with greater lateral expansion of the parietal roof in *C. platymarginata*, would provide additional surface area for attachment of the adductor mandibulae externus musculature (Gaffney, 1972).

Most of these morphological features indicate adaptation to coarser or harder foods than those eaten by the omnivorous *C. scripta*. In particular, they suggest a turtle with feeding habits similar to modern *C. nelsoni* (unpublished data show post-hatchling *C. nelsoni* to be entirely herbivorous). The broad pterygoids indicate that animal food may still make up a significant part of the diet, however.

With knowledge of the skull of *Chrysemys platymarginata*, its relationships to other species in the genus can now be studied. Other than Rogers' (1976) report of *C. scripta* from Texas, the only Blancan turtle known which may be a member of the *C. scripta* group is *Chrysemys idahoensis*. Described by Gilmore (1933) from the Hagerman lake beds (Upper Pliocene) of Idaho, the species is based not only on an entire (though partially crushed) shell, but also on a remarkably preserved and excellently illustrated skull (USNM 12059). Although unsure of its generic identity (whether *Pseudemys*, *Trachemys*, or *Graptemys*), Gilmore

believed the skull, with its broad alveolar surfaces, bore closest resemblance to *C. rubriventris*. He pointed out, however, that the skull differs from *C. rubriventris* by its broader pterygoids and less pronounced median alveolar ridge with finer denticulations. These features are diagnostic of the *Trachemys* group. Hay's (1908) improper description of the lower jaw of that group led Gilmore to say that *C. idahoensis* could not belong to *Trachemys*. Rose and Weaver (1967) noted the strongly notched peripheral bones of *C. idahoensis*, but nonetheless concurred with Gilmore's opinion of its affinities with the *C. rubriventris* series. Zug (1969) correctly points out that the cranial characteristics and geographic distribution of *C. idahoensis* are actually more similar to *C. scripta* than to the *C. rubriventris* line. The primary feature by which previous authors associated *C. idahoensis* with the *C. rubriventris* lineage is the broad alveolar surfaces of their jaws. Broad alveolar surfaces have occurred in the *C. scripta* lineage in the past, however, as noted above in *C. platymarginata*. This characteristic is an adaptive trophic feature which should not be employed per se to distinguish the two groups. Additionally, in all Recent species assigned to the *C. rubriventris* group (*C. rubriventris*, *C. nelsoni*, and *C. alabamensis*), the vomer forms an integral part of the alveolar surface; the vomer of *C. idahoensis*, like that of *C. scripta*, is recessed. All other features used earlier to assign *C. platymarginata* to the *Trachemys* group are also present in *C. idahoensis*. Gilmore (1933) points out the occurrence of carapacial rugosity in the paratype of *C. idahoensis* and the wide pterygoids of the type skull, both characteristic of *C. scripta*. The posterior tapering of the shell and elevated (tent-like) pygal bone of the holotype,

considered as a species characteristic by Gilmore (1933) are probably artifacts of post-mortem compression; both features are more nearly "normal" in the paratype.

Although Zug (1969) contends that the broad alveolar surfaces, coupled with robust inferior parietal processes, indicate molluscivory, I disagree. For reasons stated earlier I believe that these characteristics in the genus *Chrysemys* are adaptations for herbivory.

The type skull figured by Gilmore (1933) appears at first glance extraordinarily large for *Chrysemys* and particularly for *Trachemys*. Comparison with Recent *C. nelsoni* and extrapolations for Recent *C. scripta* of equivalent size (*C. scripta* does not reach this size today) reveals that the skull of *C. idahoensis* is not significantly longer than that of *C. scripta* or *C. nelsoni* though it is proportionately wider. The skull of *C. idahoensis* rises abruptly posterior to the fronto-parietal suture, effectively creating a higher and deeper supraoccipital crest. Whether this is an artifact of illustration or preservation, an aberrancy, or a real adaptation allowing for attachment of hypertrophied jaw musculature, remains to be determined upon collection of additional cranial material.

I conclude that *C. idahoensis* is a valid member of the *C. scripta* group; it is known from the Upper Pliocene of south-central Idaho, by Gilmore's (1933) original material and by six additional elements described by Zug (1969).

Two extinct species, *C. idahoensis* and *C. platymarginata*, both clearly represent the *Trachemys* group. Both occur in Upper Pliocene (Blancan) deposits, but their type localities are 3345 km apart. The

question arises as to whether these two turtles represent contemporaneous but distinct lineages within the *C. scripta* group, or whether they might actually represent two populations of a single widespread species. Were it to be based only on records from Idaho and Florida, the latter hypothesis could be seriously questioned on geographic grounds alone. However, Zug (1969) identified the anterior half of a plastron (UMMP V-42609) from the late Hemphillian Wolf Canyon area of Meade County, Kansas as *C. idahoensis*. Additionally, among material collected by J. A. Holman at Devil's Nest Airstrip, Knox County, Nebraska, are an eleventh left peripheral bone (MSU VP842) and a small xiphiplastron (MSU VP832) which represent *Trachemys* and are indistinguishable from *C. idahoensis*. The material from this site is tentatively believed to be Hemphillian (J. A. Holman, pers. comm.). Finally, a series of approximately 30 elements (MUVF 9267), including four nuchal bones, from the Upper Pliocene (Blancan) Beck Ranch local fauna in Scurry County, Texas, were assigned by Rogers (1976) to *C. scripta*. These fossils are here reassigned to *C. idahoensis* on morphological (e.g., peripheral bone rugosity and flare) and temporal grounds. The Kansas and Nebraska localities fall approximately midway between the type localities of *C. idahoensis* and *C. platymarginata*, roughly 1400 km from the former. Its additional occurrence in Texas suggests *C. idahoensis* must have occupied much of midcontinental North America during the Pliocene.

Today only a single polytypic species of *Trachemys*, *Chrysemys scripta*, occurs along the Atlantic Coast from Virginia to northern Florida, westward to southern Texas, and northward to northern Kansas, Missouri, and Illinois (Conant, 1975). Thus, it is not unusual for species of this

group to be distributed over extensive areas and wide latitudinal ranges. From a geographic standpoint, therefore, it would not be surprising if *C. platymarginata* and *C. idahoensis* represent a single widespread late Pliocene species.

Morphologically *C. idahoensis* and *C. platymarginata* are similar. Both are large turtles (max CL greater than 300 mm) with a faintly rugose carapace, notched peripheral bones, incised nuchal scute, and extensive plastral scute overlap. The skulls of both are like *C. scripta* but with a more extensive parietal roof, larger supraoccipital, and broader alveolar surfaces. The distinct double-notching of the posterior peripheral bones characteristic of *C. scripta* is evident in *C. platymarginata*; although less pronounced, the condition does occur in some peripheral bones of *C. idahoensis* (Zug, 1969; Rogers, 1976). Likewise, the mid-dorsal keel and carapacial sculpturing are more pronounced in *C. platymarginata* than *C. idahoensis*. However, these differences are no greater than those existing between the Recent subspecies of *C. scripta*--*C. s. elegans* and *C. s. scripta*. Where such minor differences do occur, *C. idahoensis* more closely resembles the northern and western *C. s. elegans*, and *C. platymarginata* the southeastern *C. s. scripta*. Should *C. idahoensis* and *C. platymarginata* actually represent a single species, the evolution of what we recognize as subspecific differences may have begun by at least the late Pliocene.

I suggest that *Chrysemys idahoensis* (Gilmore) and *Chrysemys platymarginata* Weaver and Robertson represent a single widespread species of the *C. scripta* group. This is supported by their morphological similarity, approximate contemporaneity, and existence of geographically

intermediate populations. *Chrysemys platymarginata* should therefore be placed in the synonymy of *C. idahoensis*. Based on present subspecies distributions and minor morphologic differences in the Pliocene, it is likely that populations from Idaho and the Great Plains were subspecifically distinct from those in Florida.

Based on minor cranial and carapacial differences, *Chrysemys idahoensis* is considered distinct from *C. scripta* (see Weaver and Robertson, 1967, for carapacial differences). The carapace of *C. idahoensis* is generally less rugose and more posteriorly flared, and the upper triturating surface and parietal roof are more extensive than those of *C. scripta*. These and other minor differences may be chronoclinal, and the point in time at which we separate the species must necessarily be in part an arbitrary decision. An examination of *Trachemys* fossils from five Irvingtonian deposits (Coleman IIA, Haile XVI, Inglis IA, Pool Branch II, and Punta Gorda) and six Blancan deposits (Haile IA and XVA, Port Charlotte, and Santa Fe River I, IB, and VIII) in peninsular Florida, and one early Irvingtonian site (Burnette Ranch, Seymour Formation, Knox County) in Texas, reveals almost exclusively *C. scripta* phenotypes in the Irvingtonian and predominantly *C. idahoensis* phenotypes in the Blancan; some phenotypic mixture as well as integradation occurs in both. The shift from *C. idahoensis* to *C. scripta* is therefore believed to have occurred from late Blancan to very early Irvingtonian.

Paleoecology

Chrysemys idahoensis was a large, mostly herbivorous, polytypic species that represented the *C. scripta* group over much of North America

during the Upper Pliocene. Its great latitudinal range may suggest a more homogeneous climate in North America at this time, although *C. scripta* today is adapted to a wide variety of climatic regimes. The presence in the Hagerman fauna of mammals with extant southern distributions likewise indicates that winters must have been milder than at present (Zakrzewski, 1969). Fossils of otters (Bjork, 1970), beavers and voles (Zakrzewski, 1969), large numbers of fish (Miller and Smith, 1967), frogs, water snakes (Holman, 1968), water and shore birds (Brodkorb, 1958; Feduccia, 1967; Murray, 1967), as well as the pollen record (Leopold in Weber, 1965), suggest a slightly wetter climate and greater abundance of fresh water in the Hagerman area during deposition than at present (Zakrzewski, 1969). Chantell (1970) concludes from the frog fauna that Hagerman was probably a warm, well-vegetated floodplain habitat. In light of this evidence, the occurrence of a *C. scripta*-like turtle in Idaho is not surprising.

Pleistocene glaciation must have exterminated the northernmost populations of *C. idahoensis*. Failure of the species (or of its presumed descendant *C. scripta*) to reestablish northern populations may have been due to establishment of lower (harsher winter) temperatures coupled with development of more xeric conditions. Drainage changes that must have occurred (Miller, 1965; Taylor, 1966) would have had profound effects on the distributions of all aquatic vertebrate populations. Reestablishment may have been further hindered by the successful invasion of another aquatic emydid turtle, *C. picta*, although *C. picta* and *C. scripta* coexist extensively today.

Populations of *C. scripta* in the Florida peninsula (as far south as Palm Beach County) also disappeared later in the Pleistocene. Here,

competition with several, more efficient large herbivorous congeners (*C. floridana*, *C. nelsoni*, *C. concinna*) may have been the determining factor. Alveolar surface width reduction and related changes between *C. idahoensis* and *C. scripta* may indicate a shift from more specialized herbivory to generalized omnivory in response to the immigration or evolution of superior competitors. The shift towards increased carnivory may have necessitated the reduction in body size which has occurred in the *C. scripta* line during late Pleistocene and Recent times. Should this be the evolutionary strategy that led to modern *C. scripta*, the species' abundance over most of its large range today attests to its marked success.

Systematic Conclusions

McDowell's (1964) characters defining the subgenus *Trachemys* are, as pointed out by Weaver and Rose (1967), either invalid or insufficient, although some (dentary shape, anterior triturating cusp and maxillary-quadratojugal junction) are helpful when used in conjunction with other characters. However, rather than redefine McDowell's subgenera, Weaver and Rose (1967) state that his subgeneric groupings are totally invalid. They contend that North American *C. scripta* (including fossil forms) are actually more closely related to the *C. rubriventris* series than either is to the *C. floridana* series. I cannot agree with their interpretation for several reasons.

Firstly, they accepted the opinion of most previous authors (Hay, 1908) that the Eocene emydid fossil turtles from the Bridger and Uinta Formations, assigned to the genus *Echmatemys*, were ancestral to most North American emydid genera, including *Chrysemys*. Characters of the

skull and shell of *Echmatemys* were accordingly considered to represent ancestral conditions where they occurred in *Chrysemys* spp. Unfortunately, their basic premise is probably incorrect. Many of the shells, and also the only known skull, of *Echmatemys* appear to represent the Neotropical emydid genus *Rhinoclemys* (= *Callopsis* of Smith et al., 1976), considered by McDowell (1964) to be the only New World genus in the subfamily Batagurinae. Characters of "*Echmatemys*" are thus of little value in determining relationships within the genus *Chrysemys*.

The second problem with the interpretation of Weaver and Rose (1967), as well as of McDowell (1964) in some instances, is the failure to recognize morphological convergence due to ecological adaptation. Such characters as shell shape, alveolar surface width, and scute overlap and underlap reflect specific adaptations to the environment and not necessarily phylogenetic relationships. In aquatic turtles, for example, narrow scute overlap and underlap, by decreasing turbulence of a submerged turtle, are adaptations to lotic environments (as witness their occurrence in such distantly related riverine turtles as *Graptemys*, *Podocnemis*, *Chrysemys concinna*, *Trionyx*, etc.). The fact that *C. scripta* and *C. nelsoni* have greater scute overlaps does not imply a close phylogenetic relationship but rather reflects evolutionary responses to similar ecologies (occupation of more lentic habitats). Alveolar surface width has already been shown to vary between closely related forms (*C. scripta* and *C. idahoensis*) and must therefore be treated very cautiously as a phylogenetic character. Such characters as strong peripheral bone notching have surely arisen independently in *C. scripta* and *C. concinna* and can therefore not be regarded as primitive to the entire genus.

Finally, as I have shown previously (Chapter III), fossil evidence does not indicate a close relationship of *C. scripta* to the *C. rubriventris* series as stated by Rose and Weaver (1967) and Weaver and Rose (1967). Furthermore, structure of the choanae imply a distinct dichotomy between the *C. scripta* series and all members of the *C. floridana* and *C. rubriventris* series (Parsons, 1960).

For these reasons the phylogeny proposed by Weaver and Rose (1967) should be rejected. McDowell's (1964) concept of the genus seems more realistic. Whether his subgenera would be better considered distinct genera must await study of the fossil record of *C. picta*.

With knowledge of the Upper Pliocene *Trachemys* described in this paper and that of Gilmore (1933), I present the first diagnosis of the group that incorporates characters of both the shell and skull as they have evolved through time. This diagnosis does not attempt to include Mexican, Antillean, and Central and South American forms as their relation to the *C. scripta* complex remains unclear (Weaver and Rose, 1967).

Characters clearly associated with all known North American *Trachemys* are pterygoids broad and extending posteriorly to exoccipitals; alveolar maxillary ridge without cusps or strong serrations; vomer not participating in alveolar surface; mandibular symphyseal ridge absent or inconspicuous; anterior and posterior peripheral bones notched (some doubly); nuchal scute sulci incised deeply on nuchal bone; medial longitudinal keel present at least posteriorly; carapace but not plastron usually with some longitudinal wrinkles; gular and femoral scutes broadly overlapping plastron; and nuchal scute underlap longer than wide. The number of phalanges is unknown in fossil forms.

Further Problems

Chrysemys idahoensis is clearly not the progenitor of the *Trachemys* line; it appears too late in the fossil record and already shows most of the diagnostic characteristics, such as the doubly toothed peripherals, of modern *C. scripta*. *Chrysemys hillii* (Cope), as expanded by Adler (1968) to include *C. limodytes* (Galbreath, 1948), is known from the early Pliocene of Oklahoma and Kansas. Adler (1968) points out a number of similarities of *C. hillii* to *C. scripta*, including slight notching of the posterior peripheral bones; he speculates that the fossil species may be ancestral or closely related to *C. scripta*. Cope (1878) himself suggested such a relationship and was followed by Hay (1902, 1908), who referred the species to *Trachemys*. I have not yet seen the types of either *C. hillii* or *C. limodytes*; however, from Hay's (1908) excellent photograph and Galbreath's (1948) illustration, I am inclined to agree with Adler's (1968) hypothesis.

The presumably middle Pliocene *Chrysemys inflata* (Weaver and Robertson, 1967), still known only from peninsular Florida, remains ambiguous. Until further material is discovered I will follow Weaver and Robertson's (1967) suggestion that "it was a specialized or aberrant species characterized by an extreme development of *Trachemys* features and not representative of the main evolutionary sequence leading to recent *C. scripta*." (p.65) I additionally hypothesize that *C. inflata* represents a pre-Blancan isolate from *C. idahoensis* stock that, by genetic drift or perhaps in response to unique environmental stresses, developed its massive, gothic shell. Its failure to persist, as well as its subsequent replacement in the peninsula during the Pleistocene by more conventional

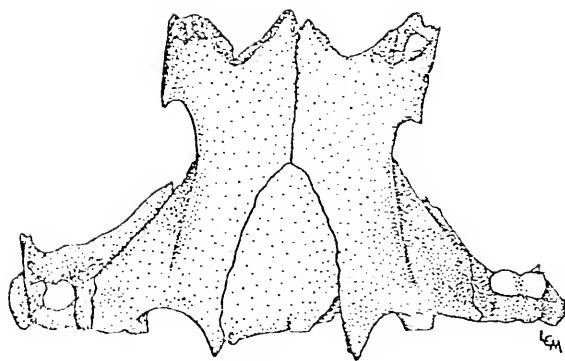
C. scripta stock, may indicate overspecialization or maladaptiveness to a changing environment. It is not surprising that *C. inflata* is known only from peninsular Florida, where *C. idahoensis* (*platymarginata*) appears to have developed the largest and most massive shell within its range. I predict that *C. inflata* will not be found elsewhere.

The recent discovery of James L. Dobie (pers. comm.) of the nearly complete carapace of a *Chrysemys scripta* (TMM 31081-280) from Bee County, Texas, in the collections of the Texas Memorial Museum, is confusing. The shell is reportedly from the Goliad Formation (late Miocene-early Pliocene). It is, however, remarkably similar to Middle and Upper Pleistocene *C. scripta*, particularly MUV4546 (Texas Irvingtonian). I suspect that, through a data mix-up or depositional quirk, the shell may be Pleistocene. The alternative is that *C. scripta* existed as early as Middle Pliocene (perhaps including *C. hillii*), and that turtles assigned to *C. inflata* and *C. idahoensis* represent a now extinct second line of *Trachemys* in North America.

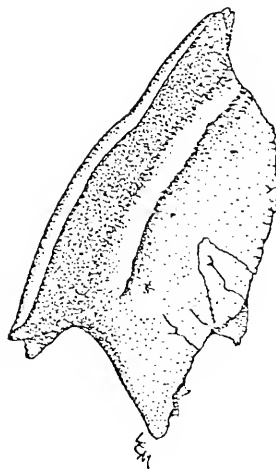
Finally, the status and relationships of the several Mexican, Central and South American, and Antillian extant forms assigned to the *C. scripta* complex (Williams, 1956; McDowell, 1964; Weaver and Rose, 1967; Moll and Legler, 1971) remain to be determined. As shown previously many of the relationships suggested by Weaver and Rose (1967) are based on inadequate characters; hence, their conclusions regarding the relationships of the Neotropical turtles in this complex must be reexamined. Unfortunately, these turtles are essentially unknown as fossils. I suggest that they be retained provisionally as members of the *C. scripta* complex as put forth by Williams (1956).

Figure 22A. Posterior palatal surface of skull (UF 21963) of
Chrysemys idahoensis from Haile XV.

Figure 22B. Alveolar surface of right maxilla (UF 23921) of
C. idahoensis from Haile XV.



A



B

CHAPTER V
PRE-PLIOCENE RECORDS OF THE GENUS *CHRYSEMYS*

Emydid turtle fossils have been reported from only two of the several Miocene deposits known from Florida (Olsen, 1964b)--Thomas Farm in Gilchrist County (Williams, 1953) and the Seaboard Air Line Railroad Company in Leon County (Olsen, 1964a). The fossils from both sites were referred to the genus *Chrysemys* (sensu McDowell, 1964) and, in conjunction with its presence in an Oligocene deposit (Patton, 1969), mark the earliest known occurrence of the genus. In light of its wide distribution and significant role in the North American turtle fauna, these early records of the genus *Chrysemys* are of considerable importance. After examining fossils from these sites I find that a reappraisal of the material is necessary.

Materials and Methods

I examined all previously described Thomas Farm fossils from the Museum of Comparative Zoology (MCZ) as well as additional undescribed material from the Florida State Museum (UF). The Seaboard fossils, formerly housed by the Florida Geological Survey, are now also in the Florida State Museum, as are the I-75 fossils. Comparative skeletal material was examined from the Florida State Museum (UF) herpetology collection as well as the author's (DRJ) personal collection (the latter to be incorporated into the UF collection).

Site Records for *Chrysemys*I-75

Patton (1969) lists the occurrence of "*Pseudemys* sp." in this site, the only known nonmarine Oligocene deposit in Florida. Unfortunately, some of the vertebrate fossils from this site have been lost (T. Patton, pers. comm.). Of the chelonian fossils available (UF 16897-16899), the only identifiable fragments represent land tortoises.

Seaboard Air Line Railroad Company, Switchyard B

Olsen (1964a) recognizes "pieces of the plastron and carapace of the terrapin *Pseudemys* sp. idet." from this Lower Miocene deposit in the Florida panhandle. Having examined all of the turtle material from this site, I find no fossils that can be assigned to any emydid genus. Several fragments labeled "*Pseudemys* hypoplastron" proved, upon reconstruction, to be a large posterior peripheral bone of a sea turtle (UF 21952). The only other fossils labeled *Pseudemys* are actually fragments of a xiphiplastron (UF 21953) and pleural bone (UF 21954) from two small tortoises (Testudinidae). As Olsen (1964) reports the presence of the tortoise *Geochelone* and four genera of marine fishes, neither reassignment contradicts his conclusions about the stratigraphy and paleoecology of the site.

Having eliminated the Oligocene and one of the two Miocene reports of *Chrysemys*, we must now examine the remaining Miocene record more closely.

Thomas Farm

Williams (1953) first noted the presence of emydid turtle fossils in the Thomas Farm Lower Miocene fauna and tentatively assigned them to

the *Chrysemys floridana* group. Rose and Weaver (1966) affirmed the generic designation but reassigned the fossils to the *C. rubriventris* group. However, none of these workers realized the antiquity of the fossil record of the genus *Deirochelys* (Chapter II), nor did they have any reason to suspect its occurrence in the Thomas Farm fauna. Confirmation of the presence of *Deirochelys* in this fauna (Chapter II) therefore necessitates a reexamination of all emydid material from this site.

The inclusion of *Chrysemys* as a member of the Thomas Farm fauna, based only upon the original material (MCZ 3432), would be questionable were it not for two adjacent neural bones (UF 21933) collected since Williams' paper. The two neural bones (Fig. 23), though possessing an anomalous common sutural border dorsally, are clearly the second and third neural bones of a relatively small *Chrysemys* (estimated carapace length 220). They are longer than wide (length:width ratios of 1.2 and 1.1, respectively), unlike *Deirochelys* (Chapter II), and possess no middorsal keel. Their dorsal surfaces are finely rugose, and the neural spines are low and robust. A posterior neural bone (UF 21935) almost certainly representing *Chrysemys* further indicates the absence of a strong keel. The lack of a keel or of any gross surface sculpturing is characteristic of McDowell's (1964) subgenus *Pseudemys* and the *C. ornata* group of the subgenus *Trachemys*.

With the occurrence of *Chrysemys* in the Thomas Farm Miocene thus reaffirmed, we may suspect that most of the emydid fossils probably do represent this genus. However, until complete material represents both genera in the Miocene, it will be difficult to assign many of the individual Thomas Farm bones to either genus with certainty. Nevertheless, as all of the unworm peripheral and pleural bones from the site

exhibit a finely to moderately rugose surface, we may conclude with some assurance that the Thomas Farm *Chrysemys* possessed a rugose carapace similar to that of *C. nelsoni* and the Pliocene *C. caelata* (Chapter III).

Because of the importance placed on the nuchal bone by most chelonian paleontologists, I am obligated to comment on the Thomas Farm nuchals. Without knowledge of the presence of *Deirochelys* in Thomas Farm, both Williams (1953) and Rose and Weaver (1966) naturally assumed them to represent *Chrysemys*. Rose and Weaver pointed to the resemblance of the nuchal scute underlap of the complete nuchal bone (see their Fig. 2B) to that of *C. nelsoni* and the Pliocene *C. caelata* (their *C. carri*; see Chapter II). The similarity also holds for the two fragmentary nuchals, but, more importantly, equivalent nuchal scute underlaps for all three may be found in *Deirochelys* as well (e.g., UF 7744; DRJ 300, 305). Furthermore, Rose and Weaver (1966) overlooked the importance of the laterally expanded first vertebral scute (see Williams, 1953, Plate 4B), evident on both nuchal bones in which the sulci can be seen. Only in *Deirochelys* and the Pliocene *C. williamsi* among Florida emydids is the first vertebral scute regularly this wide. This condition occurs as an uncommon variant in both *C. nelsoni* (e.g., DRJ 225) and *C. floridana* (e.g., DRJ 255). However, the nuchal scute underlap is much longer than that of *C. williamsi*. In conclusion, the nuchal bones represent either *Deirochelys* or an undescribed species of *Chrysemys* that combines features of two Pliocene species, *C. caelata* and *C. williamsi*. Interestingly, this combination of characters is common today in the Central American turtle, *C. ornata*.

Discussion

Williams (1953) tentatively assigned the Thomas Farm *Chrysemys* to the *floridana* group on the basis of shell rugosity and other unspecified details. Rose and Weaver (1966) rightly pointed out that the pleural bone rugosity bore stronger resemblance to that of *C. nelsoni* and *C. caelata* and, based on this and two other characters that must be questioned on the grounds that they may have been drawn from *Deirochelys*, referred the Thomas Farm fossils to the *nelsoni-rubriventris* complex.

It is not yet clear which of these two viewpoints is correct. Indeed, there is no evidence to indicate that these two lines within the subgenus *Pseudemys* (i.e., *nelsoni-rubriventris* and *floridana-concinna*) had diverged by the Miocene. (For reasons given in Chapter IV, I cannot agree with Rose and Weaver's [1966] hypothesis of a close relationship between *C. nelsoni* and *C. scripta*.) In fact, an Oligocene or early Miocene turtle like that at Thomas Farm, with strong resemblance to *C. ornata*, would seem sufficiently generalized to give rise not only to both lines of *Pseudemys* (*rubriventris* and *floridana*) but to *Trachemys* as well.

A final paleoecological note may be added. Among freshwater emydid turtles, a rugose carapace and relatively long nuchal scute underlap seem to be associated with occupation of quiet waters, and a smooth carapace and short nuchal scute underlap with more strongly flowing water (these are only two of what appears to be a complex of habitat-related morphological characters). Regardless of generic affiliations, the nuchal scute underlap and carapacial rugosity of the Thomas Farm emydid fossils therefore imply that the Lower Miocene environment of Thomas Farm included slow-moving or still water, as previously suggested by Auffenberg (1963).

Figure 23. Dorsal and visceral surfaces of second and third neural bones (UF 21933) of *Chrysemys* from Thomas Farm (x 2.2).



APPENDIX
FOSSIL LOCALITIES CONTAINING *DEIROCHELYS*

Miocene: Arikareean site

Thomas Farm, Gilchrist County.

Auffenberg (1963a) reviews the geology and literature pertinent to this site in addition to discussing its ophidian fauna. He interprets the site as representing a lower Miocene fissure fill and points out biotic evidence for the presence of slow-moving or still water during that time.

Pliocene: Hemphillian sites

Haile VI, Alachua County.

One of a series of Pliocene sites assigned to the "Alachua Formation" of Florida, parts of its paleoherpetofauna have been treated by Auffenberg (1955, 1963a), Goin and Auffenberg (1955), and D. Jackson (Chapter III). Auffenberg (1963a) discusses the stratigraphy of the deposit and states that it represents an ancient stream bed. The site lies approximately 26 m above present sea level.

Love Bone Bed, Alachua County.

This previously unreported site (29°33'N, 82°31'W; Sec. 9, T11S, R18E) near Archer, Alachua County, Florida, is named for Ronald Love who discovered it in 1974; it is now being excavated by the Florida State Museum under the supervision of S. David Webb. Preliminary stratigraphic studies reveal that the deposit represents the "Alachua clays" which were

laid down in an ancient stream bed cut into uplifted Eocene Ocala limestone.

The presence of the horses *Hipparion plicatile* Leidy and *Nannippus ingenuus* (Leidy), an early *Osteoborus* dog, the artiodactyls *Synthetoceras* and an advanced *Cranioceras*, and an early saber-cat of the genus *Barbourofelis* (S. D. Webb, pers. comm.), as well as the turtle *Chrysemys caelata* Hay (Chapter III), indicates an early Hemphillian fauna roughly equivalent to that of McGehee Farm and Mixson's Bone Bed.

McGehee Farm, Alachua County.

An early Hemphillian site in the Alachua Formation (Rose and Weaver, 1966; Hirschfeld and Webb, 1968), McGehee Farm is the type locality of the Pliocene emydid turtle *Chrysemys williamsi* (Rose and Weaver, 1966), the tortoise *Geochelone alleni* (Auffenberg, 1966), and the chelydrid *Macroclemys auffenbergi* (Dobie, 1968), and has additionally yielded abundant material representing *Chrysemys caelata* (Chapter III) and *Trionyx* sp.

Mixson's Bone Bed, Levy County.

The first known Pliocene deposit (Dall and Harris, 1892; Leidy and Lucas, 1896) within the type section of the Alachua Formation (Simpson, 1929a) of Florida, Mixson's Bone Bed is the type locality of Hay's (1908) *Chrysemys caelata* (Chapter III).

Pliocene: Blacan site

Haile XVA, Alachua County.

This deposit represents a former sinkhole filled with alternating coarse sands and clays. The fauna, assigned to the Aftonian interglacial,

is characterized by a rich assortment of aquatic and terrestrial vertebrates, including the turtle *Chrysemys platymarginata* (Weaver and Robertson, 1967) for which the site is the type locality. Although now 24 m above present sea level the presence of marine vertebrates in the fauna indicates higher sea level during deposition and a decided estuarine influence (Kinsey, 1974; S. Webb, 1974). Robertson (1976) presents a detailed account of the stratigraphy and the mammalian fauna of the deposit.

Pleistocene: Irvingtonian site

Haile XVI, Alachua County.

An undescribed pit (29°40'40"N, 82°34'20"W; Sec. 25, T9S, R17E) in the Haile limestone quarries (Ligon, 1965) excavated by the Florida State Museum under the supervision of S. David Webb in May, 1973. The fauna appears to be interglacial, of Irvingtonian age, and may represent the first known Yarmouthian deposit in Florida. A more detailed discussion of the deposit will accompany reports of faunal studies presently being conducted.

Pleistocene: Rancholabrean sites

Bradenton 51st Street, Manatee County.

A coastal marsh 3 m above present sea level (S. Webb, 1974), the site is discussed by Simpson (1930a, b) and Auffenberg (1958; 1963a) and is now known to represent the Sangamonian interglacial (S. Webb, 1974).

Coleman IIIC, Sumter County.

An undescribed deposit (Sec. 7, T20S, R23E) of Rancholabrean age (S. D. Webb, pers. comm.), this site, like previously reported Coleman

deposits (Martin, 1974), represents a filled sinkhole in the late Eocene Ocala Limestone; its surface lies approximately 24 m above present sea level.

Kendrick 1A, Marion County.

A sinkhole-fissure fill near Kendrick, the deposit lies approximately 24 m above present sea level. Kurten (1965) and Brodkorb (1959) assign the fauna to the Illinoian or early Sangamonian although Auffenberg (1958) and S. Webb (1974) believe it to represent the Wisconsinan.

Reddick 11C, Marion County.

Approximately 24 m above present sea level, this inland deposit represents a Pleistocene sinkhole or fissure fill containing a Rancho-labrean fauna (S. D. Webb, 1974).

St. Petersburg, Catalina Gardens, Pinellas County.

A small, previously-unreported deposit (Sec. 12, T32S, R16E) at approximately present sea level, its fauna is apparently Rancho-labrean in age (S. D. Webb, pers. comm.).

Seminole Field, Pinellas County.

A Pleistocene coastal marsh three meters above present sea level, Simpson (1929a), Auffenberg (1958) and Kurten (1965) assign this site to the Wisconsinan glacial period. Cooke (1926) and Simpson (1929a) give accounts of the stratigraphy of the deposit. Simpson (1929a, b, 1930b) lists the mammalian fauna, and Gilmore (1938), Brattstrom (1953) and Auffenberg (1963a) the snake fauna.

Vero, Indian River County.

Only three meters above present sea level, this site is considered by most recent authors (Weigel, 1962; Auffenberg, 1963a; Webb, 1974) to represent the late Wisconsinan glacial period. Weigel (1962) discusses its stratigraphy and vertebrate fauna (but does not include *Deirochelys*) and reviews the extensive literature pertaining to the site.

Waccasassa River I, V, and VI, Levy County.

Although S. Webb (1974) includes site VI in his chronology of Florida Pleistocene localities, neither of the other deposits which have yielded *Deirochelys* (I, Sec. 20 and V, Sec. 32, T13S, R16E) has been mentioned. The sites are 6 m to 7 m above present sea level and contain Rancholabrean faunas (S. D. Webb, pers. comm.).

Wall Company Pit, Alachua County.

The stratigraphy of this small fissure deposit is briefly discussed by Auffenberg (1963a). Auffenberg (1958) tentatively assigns the deposit to a time between the Illinoian glacial maximum and the Sangamonian interglacial maximum.

Subrecent sites

Nichol's Hammock, Dade County.

Hirschfeld (1968) describes the geology, paleoecology, and vertebrate fauna of this solution hole site. Her herpetofaunal list includes *Deirochelys reticularia*.

Warm Mineral Springs, Sarasota County.

Ferguson et al. (1947) describe the hydrology and topography of this spring (Sec. 25, T39S, R20E, less than six meters above present sea

level) under the name of Warm Salt Spring. Clausen et al. (1975) present a detailed description of the geology of the deposit for which they report a radiocarbon age of approximately 10,000 years. Fossils are currently being excavated by the Florida Department of State under the direction of W. A. Cockrell.

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BIOGRAPHICAL SKETCH

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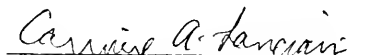
He is a member of the American Society of Ichthyologists and Herpetologists, American Society of Naturalists, American Society of Zoologists, American Association for the Advancement of Science, and the National Audubon Society.

He is unmarried, has no children to his knowledge, and is now seeking happiness rather than fortune.

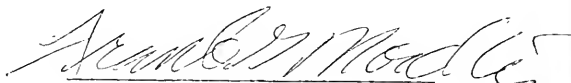
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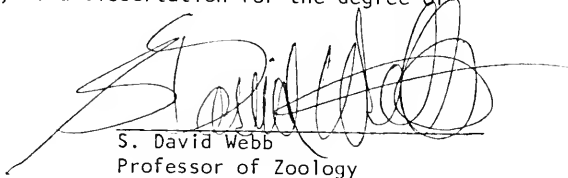
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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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