

EVOLUTION AND FOSSIL RECORD OF THE CHICKEN TURTLE
DEIROCHELYS, WITH A RE-EVALUATION OF THE GENUS

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ABSTRACT

Prior evidence of the fossil history of the monotypic genus *Deirochelys* is limited to a single upper Pleistocene fragment and a number of sub-Recent elements from Florida. On the basis of several morphological adaptations unusual among emydine turtles (e.g., neural bone width and rib structure), fossils from 20 Florida sites, ranging from Miocene to sub-Recent in age, are referred to the genus *Deirochelys*. Evidence of the gradual evolution of a specialized suite of characters associated with pharyngeal feeding is presented. The middle Pliocene representative of the genus is recognized as a distinct species (*Deirochelys carri*, sp. nov.) intermediate between Recent *D. reticularia* and less specialized emydines such as *Chrysemys*. *Deirochelys* fossils from the Thomas Farm Miocene are more primitive than *D. carri* and further bridge the morphological gap between *Chrysemys* and *Deirochelys*.

The evolutionary history of the monotypic genus *Deirochelys* is one of the more enigmatic chapters in our knowledge of North American emydid 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; C. 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 (C. Jackson, 1964, 1974a) and to mention of the presence of *D. reticularia* in a sub-Recent Florida site (Hirschfeld, 1968). Crawford Jackson (1964) found that the Pleistocene element represents a turtle conspecific with Recent *D. reticularia*. All other fossils previously assigned to the genus, i.e., *Deirochelys floridana* Hay and *Trachemys jarmani* Hay (Hay, 1908; Weaver and Robertson, 1967), actually represent the genus *Chrysemys* (C. Jackson, 1964, 1974a).

This paper examines material referable to the genus *Deirochelys* from one Miocene, five Pliocene, 12 Pleistocene, and two sub-Recent 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 (*Emydoidea*) 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),

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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 I specimens are from the Timberlane Research Organization (TRO), 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, 300, UF 1420, 7744, 14244, USNM 11610, 11615, 29477, 29584, 62219, 80965, 95789; *Emydoidea blandingii*: UF 14249, 18931; *Chelydra serpentina*: DRJ 253; *Chelus 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 approximate such if a Recent specimen of sufficient size were unavailable. As the relationship between shell thickness and body length may not be strictly linear, the STI values given for the largest fossils may actually be underestimates. There was little individual STI variation among the Recent specimens 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 specimens, 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 millimeters.

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 1 shows the geographic distribution of these sites.

SYSTEMATIC DESCRIPTIONS

All past descriptions of the genus *Deirochelys* (Agassiz, 1857; Baur, 1889; White, 1929; Schwartz, 1956; C. 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), C. Jackson (1959) and McDowell (1964), is based solely on osteological characters. As fossil skull material is presently unknown, all skull characters are drawn from Recent *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, at present distributed throughout the southeastern United States and known from the Pleistocene of Florida; *Deirochelys carri*, new species, middle 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. 2); 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 by only small corner of first coastal 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. 2); 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. 3) 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

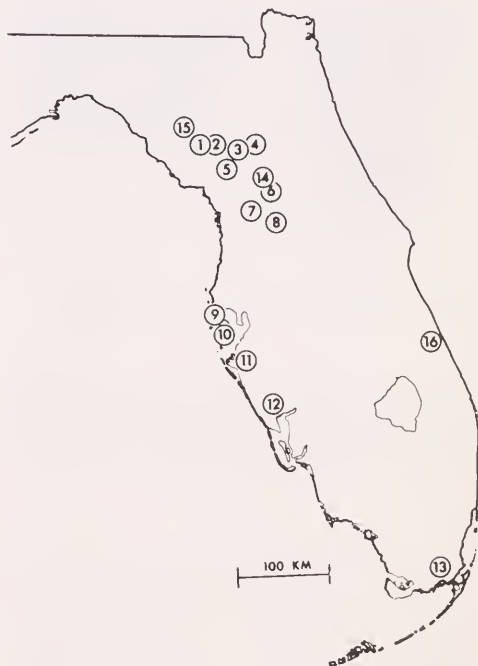


Fig. 1. Fossil sites in peninsular Florida containing *Deirochelys*. Site ages are given in Appendix.

1. McGehee Farm
2. Haile sites
3. Love Bone Bed
4. Wall Company Pit
5. Mixson's Bone Bed
6. Kendrick IA
7. Waccasassa River sites
8. Coleman IIC
9. Seminole Field
10. Catalina Gardens
11. Bradenton
12. Warm Mineral Springs
13. Nichol's Hammock

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.

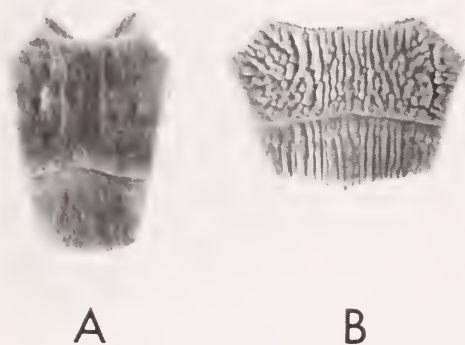


Fig. 2. Third neural bones of *Chrysemys floridana* (A) and *Deirochelys reticularia* (B); note greater width and characteristic sculpturing of latter.

Skull and second through seventh cervical vertebrae elongate; neural spines of anterior thoracic vertebrae laterally compressed as vertical sheets (Fig. 4); 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; coronoid relatively low; 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 (e.g., *Chrysemys*), summarized in Table 1 and Fig. 4, 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 neallotype 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; Fig. 5) and relatively great length of free portions of dorsal ribs (Fig. 6); coloration as described by Schwartz (1956) with notation that the yellow forelimb band is



Fig. 3. Frontal aspects of third pleural bones of *Chrysemys concinna* (A) and *Deirochelys reticularia* (B), showing dorsal ribs.

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 veter	expanded dorsal region of centra	expanded ventral region of centra

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; C. 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 195mm 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 extant *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 5 to 10 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 (TRO 101, 102) and a third neural bone (TRO 103), representing three individuals of 130 to 210 CL (Fig. 7); STI 1.1 to 1.3.

Waccasassa River V: A lightly-sculptured nuchal bone, UF 16271 (Fig. 7); 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 IA: 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 C. Jackson (1964): estimated CL 250, STI 1.1 to 1.6; (Fig. 8).

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. 9), 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); second left pleural bone and first four 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. 5 and 6; STI of neural bones 2.0 to 2.2.

Haile XVA: A fifth neural bone (UF 19249), the dorsal surface of which is extremely flat but moderately sculptured: greatest length

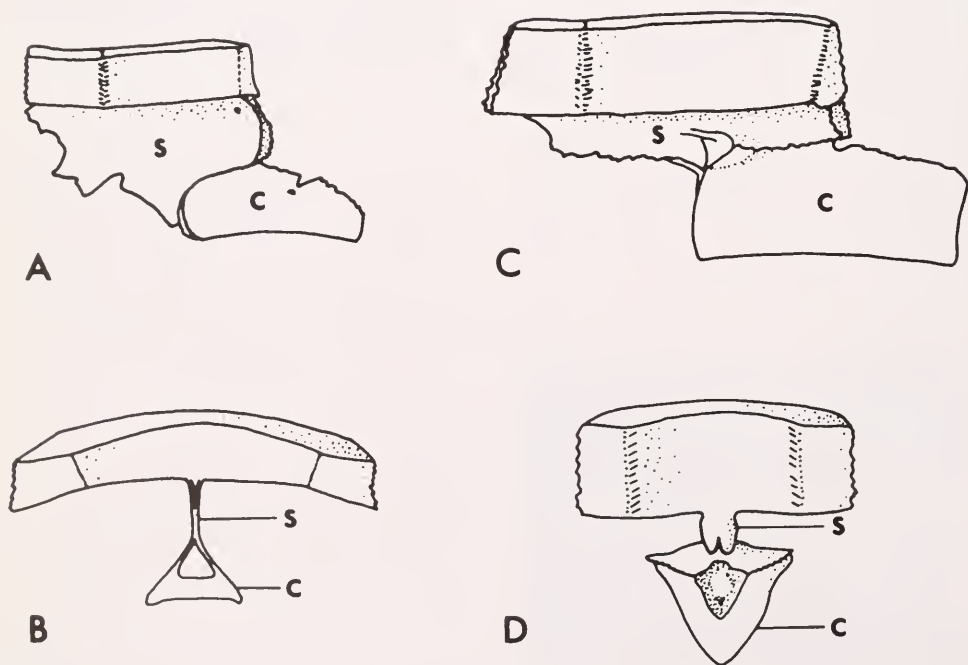


Fig. 4. Lateral (A, C) and frontal (B, D) aspects of third neural bones and associated vertebrae of *Deirochelys reticularia* (A, B) and *Chrysemys nelsoni* (C, D); c, centrum; s, neural spine.

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. 10).

Discussion of fossil material. All of the Rancholabrean and sub-Recent 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

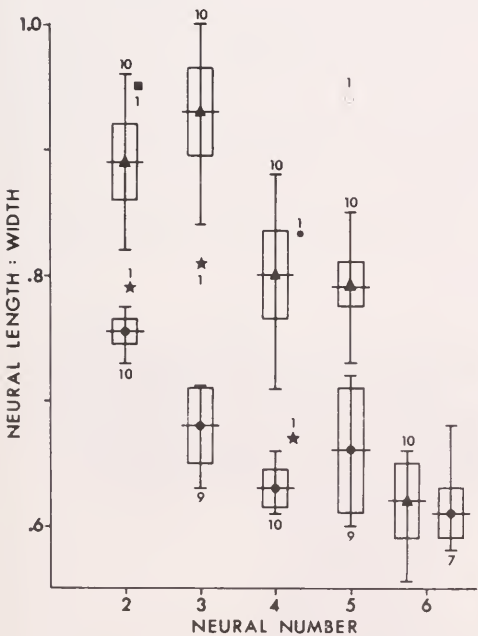


Fig. 5. Length: width ratios of second through sixth neural bones of Recent (circles), Irvingtonian (stars) and Hemphillian (triangles — Love; square — Haile VI; asterisk — Mixson's) *Deirochelys*. Dice — Leraas diagrams depict mean, range, and two standard errors; numbers above and below bars represent sample sizes.

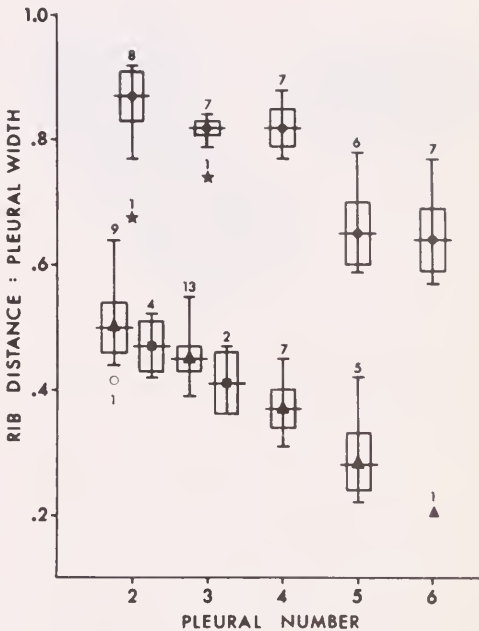


Fig. 6. Rib distance: pleural bone width ratios for Recent, Pleistocene, and Pliocene (*Deirochelys*; all symbols as in Fig. 5).

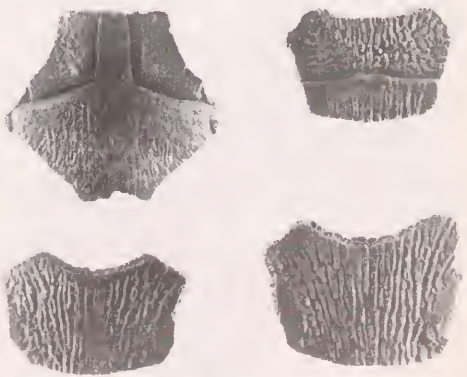


Fig. 7. Nuchal bone (UF 16271) and three neural bones (TRO 101-103) of Rancholabrean *Deirochelys reticularia* from Waccasassa River VA and I, respectively.



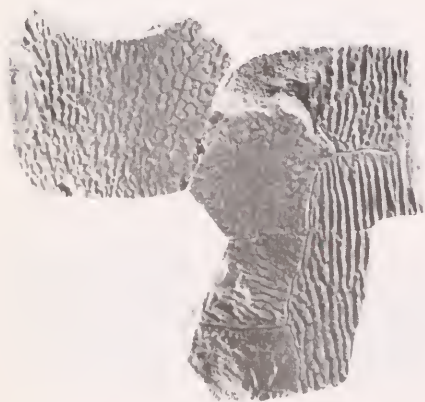
Fig. 8. Distinctly sculptured sixth neural bone (UF 19250) of *Deirochelys reticularia* from Kendrick IA.

few individuals. Though tending to be more pronounced in the Pleistocene, shell rugosity patterns are within the range of variation of extant *D. reticularia*.

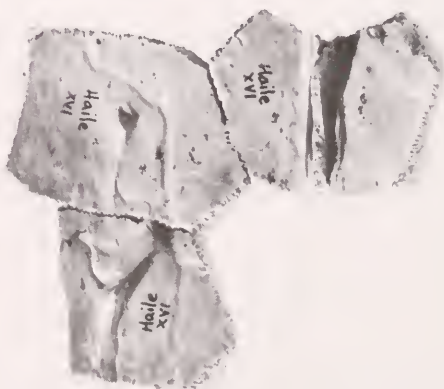
The single consistent difference between Pleistocene and Recent *D. reticularia* is that of shell thickness. The STI of Pleistocene *D. reticularia* is 1.1 to 2.2 times that of Recent specimens. The trend towards shell thickness reduction appears roughly chronoclinal since at least the Irvingtonian (Table 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* (D. Jackson, 1975), *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. 5) and a slightly more proximal site of rib juncture with the second and third pleural bones (Fig. 6). These characters do not exhibit allome-



A



B

Fig. 9. Dorsal (A) and ventral (B) views of part of carapace (UF 20888) of Irvingtonian *Deirochelys reticularia* from Haile XVI. Note characteristic sculpturing, neural bone width, and rib junctures.

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

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

try in Recent adult specimens, 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 an Irvingtonian one (UF 20894) suggests that little shell evolution was experienced between these periods.

The differences between Recent 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 sub-specific 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. 5 and 6) 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, Jr. 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. 11A); a partial plastron consisting of the left hyoplastron, hypoplastron, and xiphiplastron apparently represents the same individual (Fig. 11B).

Type locality and horizon. Alachua Clay, Love Bone Bed, near Archer, Alachua County, Florida; early Hemphillian, middle Pliocene.

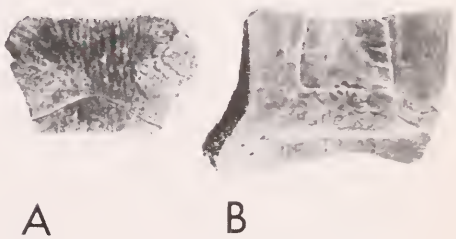


Fig. 10. Blancan *Deirochelys reticularia* from Haile XVA; (A) fifth neural bone (UF 19249) and (B) nuchal bone fragment (UF 19168) showing broad nuchal scute underlap.

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

Mixon's Bone Bed: a fourth neural bone, UF 20890 (formerly Florida Geological Survey V-2599), assigned previously by 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 hypoplas-tron, 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 (lack-

ing zygapophyses) (UF 6485b, Fig. 12); five peripheral bones UF (6485c); first neural bone, (UF 6485d); 17 pleural bone frag-ments (UF 6485e); many other elements and fragments from this site may represent either *D. carri* or *Chrysemys caelata* (D. Jackson, 1976).

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. 13). The less water-worn carapacial elements display the distinct scale-like sculpturing characteristic of the genus (Fig. 14). Many elements represent turtles of exceptionally large size for *Deirochelys*: the largest nuchal bone (UF

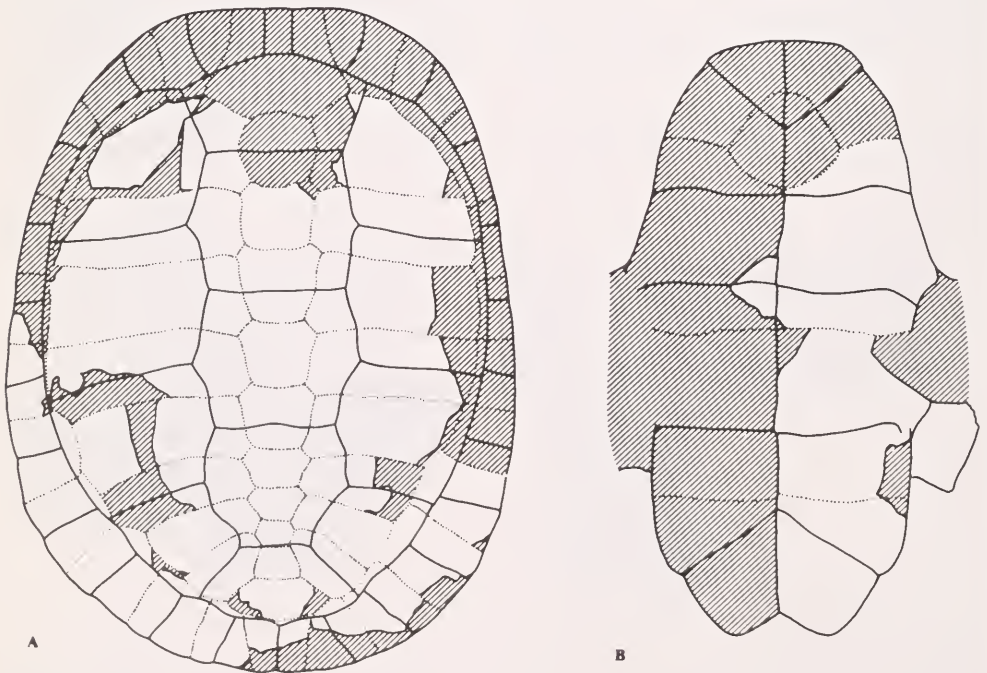


Fig. 11. *Deirochelys carri* holotype, UF 20908. (A) Dorsal aspect of carapace; (B) Ventral aspect of plastron. Hatched areas missing from fossil.

20906) measures 59.8 (length) x 61.8 (width). 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. 5, 11A) and a more proximal site of emergence of the ribs from the pleural bones (Figs. 6, 13). 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 (*D. Jackson*, 1976); 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.

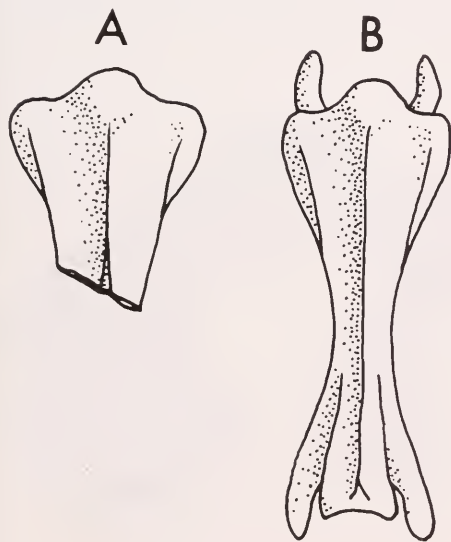


Fig. 12. Ventral surfaces of third cervical vertebrae of (A) *Deirochelys carri* (UF 64856) and (B) *D. reticularia* (DRJ 300) (x2.2).

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 Blaccan 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. 11A). 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.

Comment. *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 chronocline 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 64856b) referable

to *D. carri* is likewise slightly more robust than the corresponding vertebra of *D. reticularia* (Fig. 12). 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, the narrower neural bones and more proximal rib union with the pleural bones in *D. carri*, compared with *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 an exceptionally fine series of *Deirochelys* fossils, far older than any previously known for the genus, one can trace the evolutionary record back one step further — to the Miocene.

THE THOMAS FARM *DEIROCHELYS*

The only emydine turtle previously recognized from the Florida Miocene (Thomas Farm) is a *Chrysemys* species 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 *Deirochelys carri*, and the proximal fragment of a pleural bone (UF 21950) with a rib juncture scar too low for that of *Chrysemys* (Fig. 15). 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 probably is the second pleural bone from the left side. As

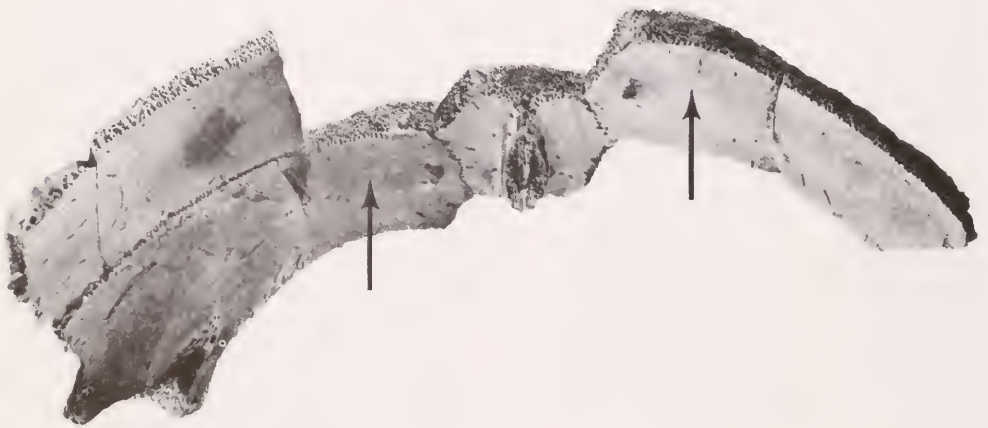


Fig. 13. Ventral surface of posterior region of *Deirochelys carri* carapace, UF 20900, showing rib juncture with pleural bones. Arrows indicate where junctures would occur in a *D. reticularia* of equivalent size.

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. 5) and the point of juncture of the rib with the pleural bone (rib distance: pleural bone width ratio, 0.41, Fig. 6) 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 materi-

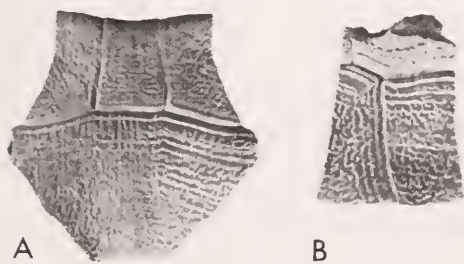


Fig. 14. A distinctly sculptured nuchal bone (A) and posterior peripheral bone (B) of *Deirochelys carri* from the Love Bone Bed.

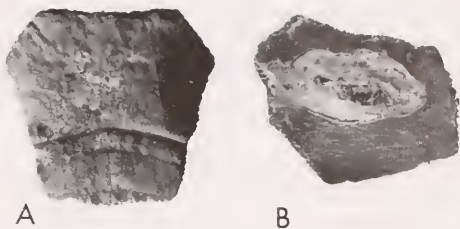


Fig. 15. *Deirochelys* fossils from the Thomas Farm Miocene (x 1.1); (A) neural bone, (B) visceral surface of pleural bone fragment showing rib juncture scar.

al. 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 one of the most complete evolutionary records of any Recent turtle. 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*) had certainly begun by the Miocene. Extrapolations based on an average rate of evolution from such a generalized ancestor suggests an Oligocene origin of the genus (Fig. 16). 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 G. J. W. 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 hypertrophied 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.

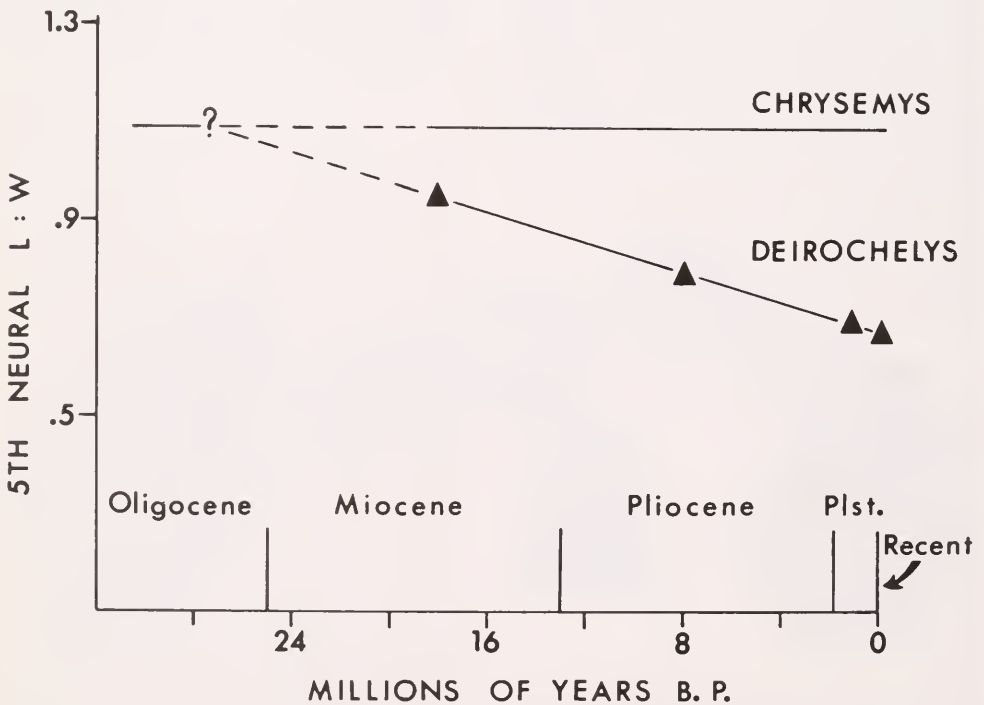


Fig. 16. Extrapolation through time of fifth neural bone length: width ratio of *Deirochelys*, indicating hypothetical point of divergence from a more generalized emydine line.

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.

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 *Chelus*. 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 extant 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. The fossil records and present distributions (Carr, 1952; Preston and McCoy, 1971; Zug and Schwartz, 1971; McCoy, 1973; C. Jackson and Kaye, 1974) indicate that the two genera have remained essentially allopatric, although the southern extension of the range of *Emydoidea* in the late Pleistocene (C. Jackson and Kaye, 1974) just touches the present limit of *Deirochelys* in northeastern Mississippi (C. Jackson and Fortman, 1976). 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. 1) 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 salt-water (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 *Lemna-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 and Folkerts, 1968) implies adaptation to a warm temperate climate. The presence of *Deirochelys* and associated fauna (*Lepisosteus*, *Amia*, *Alligator*, *Chrysemys caelata* [D. Jackson, 1976], *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. 1) are either sub-Recent 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.

S. D. 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 (S. 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 of Mexico 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.

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APPENDIX

FOSSIL LOCALITIES CONTAINING
DEIROCHELYS

Miocene: Hemingfordian 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. Formerly considered Arikarean by most workers, the fauna has recently been reinterpreted as medial Hemingfordian (Patton, 1969; Tedford and Frailey, 1976). Thomas Farm is the type locality of *Geochelone tedwhitei* (Williams, 1953).

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 (1976). 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* (D. Jackson, 1976), 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 emydine 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* (D. Jackson, 1976) 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* (D. Jackson, 1976).

Pliocene: Blacn 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 III C, 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 IA, 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 IIC, Marion County.

Approximately 24 m above present sea level, this inland deposit represents a Pleistocene sinkhole or fissure fill containing a Rancholabrean 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 Rancholabrean in age (S. D. Webb, pers. comm.).

Seminole Field, Pinellas County.

A Pleistocene coastal marsh 3 m 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 3 m 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 - 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.

Sub-Recent 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 6 m 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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