Turtles of the Lee Creek Mine (Pliocene: North Carolina)

George R. Zug

ABSTRACT

Eleven taxa of turtles have been recovered from the Lee Creek Mine: a sideneck turtle (Bothremys); six seaturtles (Caretta, ?Chelonia, Lepidochelys, Procolpochelys, Syllomus, and Psephophorus); two pond turtles (probably Pseudemys and Trachemys); a softshell turtle (trionychid); and a giant tortoise (Geochelone). The fossils are largely disassociated skeletal elements and fragments derived from spoil piles created by drag-line mining of phosphate. The mining removes and discards the Yorktown Formation (Pliocene) and processes much of the Pungo River Formation (middle Miocene), hence the Lee Creek Mine turtles are mainly from the lower Pliocene. The turtle fauna appears to be a natural assemblage of extant and extinct taxa. Caretta and Syllomus are the most abundant fossils; a few specimens of each had some adherent Yorktown matrix. Geochelone fossils are next in abundance, although an order of magnitude less than Caretta and Syllomus. The other genera are each represented by fewer than 10 fragments or elements. Cranial and carapacial differences indicate that the Lee Creek Caretta represents a new species, C. patriciae. The Geochelone also differs from its eastern North American Pliocene contemporaries by its larger size and unique plastral morphology. The fossils of the other taxa are too few and fragmentary to identify reliably to species or genus.

Introduction

The middle Miocene to early Pliocene faunas of the central Atlantic coast and coastal plain of North America included a variety of marine, freshwater, and terrestrial turtles. Marine species dominated the turtle fauna, and at least one species each of the sideneck turtle *Bothremys*; the three hard-shelled seaturtles *Chelonia*, *Procolpochelys*, and *Syllomus*; and the leatherback seaturtle *Psephophorus* have been reported. Other Miocene turtles from this region included a terrestrial tortoise, *Geochelone*, and a softshell turtle (freshwater trionychid). Additional hard-shelled seaturtles (Table 1) have been described from the central Atlantic and adjacent regions, but close examination (Weems, 1974) of these fossils has shown these taxa to be synonyms of *Syllomus aegyptiacus* (Lydekker). Representatives of these seven genera of turtle occur in the Miocene marine deposits of New Jersey, Maryland, and Virginia (Table 3). These turtles and the extant taxa of southeastern North America provided the comparative base for the identification and analysis of the temporally and geographically close fossil turtles of the Lee Creek Mine.

The Lee Creek Mine turtles appear to derive primarily from the Yorktown Formation and, thus, are a more recent fauna than the turtles from the Calvert Formation of Virginia and Maryland. The mining operation, however, penetrates and discards the top of the Pungo River Formation (temporally equivalent to the Calvert Formation), so there is a possibility that a few Calvert-aged (middle Miocene) turtles are mixed in with this predominantly (early to middle Pliocene) Yorktown fauna (see Gibson, 1983, for age and stratigraphy of mid-Atlantic coastal deposits). The mining operation scatters the fossils from the numerous beds of the Yorktown Formation, resulting in fewer associations of skeletal elements with one another or with their stratum of origin in the Lee Creek Mine fauna as compared to the Calvert fauna. This lack of positive association is unfortunate because the Lee Creek seaturtle fauna is diverse and straddles a faunal transition between a middle Tertiary and the Holocene fauna.

My primary objective has been to identify the Lee Creek Mine turtles and briefly describe their fossil remains. This task has forced me to make taxonomic decisions on isolated bony elements, and in some instances the amount of comparative material has been limited. These necessarily tenuous decisions must be and can be confirmed only with less fragmented and better associated fossils from Yorktown deposits.

ACKNOWLEDGMENTS.—All fossil specimens described herein are in the vertebrate paleontological collection of the National Museum of Natural History (NMNH, which houses collections of the former United States National Museum (USNM)). Some of the USNM catalog numbers cited herein represent lots rather than individuals due to the quantity of disassociated ele-

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Taxon	Citation	Type locality	Current name
Suborder PLEURODIRA			
Family PELOMEDUSIDAE	CONTRACTOR OF STREET, S		
Taphrosphys miocenica	Collins and Lynn, 1936:155	Calvert County, Maryland	(=Bothremys miocenica)
Suborder CRYPTODIRA			
Family CHELONIIDAE			
Chelonia grandaeva	Leidy, 1851:329	Salem County, New Jersey	(=Procolpochelys grandaeva)
Chelonia marylandica	Collins and Lynn, 1936:162	Calvert County, Maryland	(=Syllomus aegyptiacus)
Peritresius virginianus	Berry and Lynn, 1936:176	Westmoreland County, Virginia	(=Syllomus aegyptiacus)
Syllomus crispatus	Cope, 1896:139	Pamunky River, Virginia	(=Syllomus aegyptiacus)
Family DERMOCHELYIDAE			
Psephophorus calvertensis	Palmer, 1909:370	Calvert County, Maryland	
Family TESTUDINIDAE			
Testudo ducateli	Collins and Lynn, 1936:166	Calvert County, Maryland	(=Geochelone ducateli)
Family TRIONYCHIDAE			
Trionyx cellulosus	Cope, 1868:142	Charles County, Maryland	

TABLE 1.-Miocene turtles described as new species from the central Atlantic coast of North America.

ments received from the mine. My use of this collection was aided by Robert Purdy and Clayton Ray (both NMNH). Gladwyn Sullivan (NMNH) prepared and assembled the better-associated fragments. Victor E. Krantz (NMNH) photographed all of the specimens.

A number of individuals assisted in this study: Robert Weems (U.S. Geological Survey), Eugene Gaffney (American Museum of Natural History), and Rainer Zangerl (Rockville, Indiana) broadened my narrow outlook on this fossil assemblage, and I hope improved my interpretation of it, and they reviewed early drafts of the manuscript; more recent versions benefitted from the comments of D. Bohaska (NMNH), C. Crumly (Academic Press), K. Dodd (U.S. Geological Survey), C. Ernst (George Mason University), R. Estes (deceased), W.R. Heyer (NMNH), A. Holman (Michigan State University), and R. Weems. I thank all of the above for their assistance.

Seaturtle Identification

The Lee Creek Mine turtle fossils are predominantly hardshelled seaturtle fragments, and many of these cannot be identified to species or even to genus. Having worked with these fossils intensely in the early 1970s and then only episodically until the final preparation of this manuscript in 1988, I discovered that my ability to assign taxonomic names with confidence was directly proportional to my current immersion in seaturtle osteology. To assist my memory, I developed diagnoses for the main fossil skeletal elements and include them herein to assist others in the identification of seaturtle elements and fragments. These diagnoses also document my criteria for the assignment of taxonomic names to the Lee Creek Mine fossils. The diagnoses are not complete; they emphasize the type and nature of the Lee Creek Mine fossils. For example, I describe only the tip of the dentary because only that part of the lower jaw has been recovered, and in Psephophorus, only osteoderms are known. The diagnoses also tend to state differences as absolutes when some of the differences are more subtle and subjective.

The major features for distinguishing the various genera of extant cheloniid seaturtles are summarized in Table 2. A partial skull of *Caretta* (USNM 186731; Figures 3, 4) was reassembled from fragments. The two critical features for identifying this skull as *Caretta* are the exclusion of the frontal from the orbit and the absence of vomerine-premaxillary contact on the secondary palate. The frontal also enters the orbit in *Procolpochelys* and *Syllomus*.

Dentaries can be differentiated by the nature of the ridges on the triturating surface. Syllomus has a complex pseudodont surface (Figure 7A) with a high, denticulate symphyseal ridge extending across the entire width of the dentary; a high, sharp-edged denticulate ridge on the lingual edge; and cone-shaped denticles along the labial border (Weems, 1980, fig. 2c). The dentary surface is nearly as complex in Chelonia; a high symphyseal ridge extends across the entire width of the dentary; a high, sharp-edged ridge is slightly inset along the entire lingual border; and the labial border is sharp-edged and occasionally faintly denticulate. In Eretmochelys a low symphyseal ridge occurs on the posterior half of the dentary's triturating surface and enlarges near the labial border to form a large, pyramidal protuberance; a lingual ridge is often evident, although weakly developed. The triturating surface in Caretta and Lepidochelys is a smoothly concave surface curving gently to a sharp labial edge. The labial and lingual borders are sharp-edged but low. Some Caretta have a low, sharp-edged symphyseal ridge across the entire width of the dentary. Juvenile Lepidochelys kempii (Garman) have a low pyramidal protuberance (Figure 7B) at the posterior end of the symphysis and occasionally have a faint lingual ridge; the protuberance and lingual ridge are not evident in adult L. olivacea (Eschscholtz). The dentary of Procolpochelys is unknown.

Of the many carapacial fragments, it is possible to distinguish the linked osteoderm (=epithecal ossicle) shell of dermochelyids from the typical testudine shell of cheloniids. The osteoderms of *Psephophorus* are large, thick, irregular polygons (Figure 7c), in contrast to the small, thin, irregular polygons of *Dermochelys*. The osteoderms forming the dorsal ridges of the

Cranial characteristics Cc LCs Cm Ei Lk Lo Frontal in orbit _ + + + + _ Strong temporal emargination + _ _ + + + Supraoccipital ridge blade-like dorsally + _ _ ± _ Premaxillary-vomer contact on secondary palate + _ -+ + Trochlear process of pterygoid elongate and thin + +? _ _ _ Articular surface of quadrate broad + _ _ _ _ + Triturating surface of dentary strongly ridged + ±

TABLE 2.—Comparison of cranial characteristics of Holocene cheloniid seaturtles and the Lee Creek Mine seaturtle skull. Abbreviations: Cc, *Caretta caretta* (Linnaeus); Cm, *Chelonia mydas* (Linnaeus); Ei, *Eretmochelys imbricata* (Linnaeus); Lk, *Lepidochelys kempii*; Lo, *Lepidochelys olivacea*; LCs, Lee Creek skull; +, structure present or as described; -, absent or not as described; ±, present or absent.

carapace in *Dermochelys* are as large in circumference as those of *Psephophorus* but are thinner. The reticulated external surface of the *Syllomus* carapace is unlike the surface texture of any other cheloniid, although the surface texture might be confused with that of trionychids. The shell elements are distinctly thinner (absolutely and relatively) in *Syllomus* than they are in any of the other Lee Creek Mine cheloniids.

Neurals are found frequently. In most cheloniids, the neurals are elongate hexagons with the posterior segment two to three times longer than the anterior segment (i.e., casket-shaped). Only in Procolpochelys are the neurals regular hexagons; the neurals also are proportionately thicker in Procolpochelys than they are in any of the other seaturtles except Psephophorus. The neural series in Caretta and Lepidochelys appears to be evolutionarily undergoing fragmentation and size reduction. Regular polygonal neurals lie between elongate ones in these two taxa. In addition to their unique surface texture, Syllomus neurals often bear a longitudinal ridge along the entire length of each neural; the ridge ranges from a faint indication to a distinctly elevated (~5 mm), sharp-edged keel. Young Caretta and Lepidochelys (of extant species) also have keeled neurals; in the small juveniles, the middorsal ridge is continuous only in the youngest individuals. The ridge has five spines or knobs extending well above the keel. These spines are most evident in small (carapace length (CL) <25 cm) Lepidochelys; in larger juveniles (CL >40 cm) only the second spine may persist, and none remains in adults. In L. kempii the spines occur at the posterior edge of each vertebral scute, hence on neurals 1, 4, 7, and 10 (neural number may differ slightly because of tendency for neural fragmentation in carettine seaturtles) and on the posterior suprapygal. The reduction or loss of spines appears to occur from posterior to anterior, with the second spine being the last to disappear, and the external surface of all neurals flattens with increasing carapace length. This external surface is planar in all size classes of Chelonia and Eretmochelys.

Costal fragments are unidentifiable for most genera, although the surface texture of the *Syllomus* carapace is unique and readily identifies even small fragments. Peripherals also are difficult to assign to genus, other than those of *Syllomus*. In general, the larger ninth, tenth, and eleventh peripherals with distinct, serrate borders were identified as *Caretta* peripherals. The pygals of carettine turtles characteristically show a wide, deep, medial V-shaped notch posteriorly (this notch is small or absent in *Procolpochelys*) and have medially slanted peripheral-pygal articular surfaces. The cheloniine pygal has a narrow, shallow notch posteriorly and nearly parallel peripheral-pygal articular surfaces. These differences emphasize the extremes, and pygal morphology in cheloniids forms a continuum.

The most numerous limb bones are humeri, and their morphology appears generically diagnostic in most cases. The *Syllomus* humerus (Figure 1C,E; Weems, 1974, pl. 3: figs. 1–3) is the most distinctive; however, rather than describe the entire humerus of each genus sequentially, a comparative description of each part of the humerus is offered. Humeral morphology terminology follows that proposed by Zug et al. (1986); the major difference from previous use is the recognition that the cheloniid humerus possesses both a radial (lateral) process and a deltopectoral ridge.

The ulnar (medial) process of seaturtles is elongate and extends proximally. This process is greatly elongated and pointed in *Syllomus* (Figure 1C,E) and extends proximally well beyond the humeral head (roughly the width of the head beyond); this elongation produces an attenuated appearance, although the *Syllomus* humerus is proportionately of the same width as that of the other genera. In *Caretta, Lepidochelys,* and *Procolpochelys* the ulnar process is rounded and extends only slightly beyond the head proximally. This process is intermediate in length and is somewhat acute in *Chelonia* and *Eretmochelys*.

The radial (lateral) process is low and lies distal to the level of the humeral head (Figure 1). In *Chelonia, Eretmochelys,* and *Syllomus* the process forms a narrow ridge extending nearly two-thirds across the ventral surface of the shaft. This ridge is broader in *Caretta, Lepidochelys,* and *Procolpochelys* and extends across no more than one-half of the shaft.

The articular (cartilage-supporting) surface of the humeral head is ellipsoidal in all cheloniids (Figure 1). This surface in *Syllomus* is narrower and more elongate than in the other five genera and is moderately pointed at its pre- and postaxial ends. This surface is usually continuous with the radial process in *Caretta, Lepidochelys,* and *Procolpochelys,* continuous or separate in *Eretmochelys,* usually separate in *Chelonia,* and always separate in *Syllomus.* The head appears to extend farther off the diaphysis in *Chelonia* and *Syllomus.*



FIGURE 1.—Morphology of cheloniid right humeri. A, ventral view of a Holocene *Chelonia mydas* humerus (USNM, uncataloged); B,D, ventral and dorsal views, respectively, of a Holocene *Caretta caretta* humerus (USNM 235590); C,E, ventral and dorsal views, respectively, of a *Syllomus aegyptiacus* humerus (USNM 433179). Abbreviations: dc, deltopectoral crest or ridge; ef, ectepicondylar foramen; if, intertubercular fossa; re, radial epicondyle; rp, radial process; ue, ulnar condyle; ur, ulnar process. (Scale bar=1 cm.)

In Syllomus the deltopectoral crest is a cone-like tubercle projecting strongly beyond the preaxial surface. In the other genera the crest extends longitudinally along the preaxial surface, and it is continuous (or nearly so) with the lesser trochanter in all cheloniids except Syllomus, where it is separated from the radial process by a deep, U-shaped groove. In Caretta and Lepidochelys the crest is truncate and moderately projecting, and it is flattened and slightly projecting in Chelonia and Eretmochelys.

The Syllomus humerus differs strikingly from that of the other genera (Figure 1). Using the deltopectoral crest to divide the humerus into proximal and distal segments, these segments are subequal in length in Syllomus, and the proximal segment is one-third to three-eighths the length of the distal segment in the other five genera. The condylar surface has distinct trochlear and capitellar ridges in Syllomus; these articular ridges are low and rounded or are absent in the other genera.

Ulnae are fairly abundant. The ulna of *Syllomus* differs from the ulnae of other cheloniids by its robustness and shape. It is proportionately shorter; has a deep, concave, proximal articular surface facing postaxially; a raised, sharp-edged postaxial crest; and a broad, radial articular surface.

The cheloniid femur is similar in all of the Lee Creek Mine genera, with subtle differences that allow some differentiation of the taxa. The head is round (nearly circular in outline) in Chelonia, Eretmochelys, and Syllomus and is ellipsoidal in Caretta, Lepidochelys, and Procolpochelys. The greater (posterior) trochanter is large and angular, forming a broad surface anterior to the head in Chelonia, Eretmochelys, Caretta, and Lepidochelys. In Syllomus this trochanter is equally large, but the anterior border is curved and extends proximally beyond the head; it also is hook-shaped above the intertrochanteric fossa (Weems, 1980, pl. 1: figs. 7, 8). The greater trochanter of Procolpochelys is narrow and straight-edged relative to the diaphysis. The lesser (anterior) trochanter is large and protruding in Chelonia, Eretmochelys, Caretta, and Lepidochelys. It is about the same size in Syllomus, but the preaxial border is enlarged and rugose. It is only moderately protruding in Procolpochelys. The condylar surface bears distinct articular ridges only in Syllomus.

Turtle Fauna

Family PELOMEDUSIDAE (sideneck turtles)

Bothremys

FIGURE 2

Collins and Lynn (1936) described the sideneck turtle Taphrosphys miocenica from an anterior lobe of a plastron. Later, Gaffney and Zangerl (1968) reassigned this fossil to Bothremys; however, they were reluctant to confirm its specific identification owing to the incompleteness of the fossil. They did emphasize that this piece of plastron represented the only unquestionable sideneck turtle from the Tertiary of North America. Later, Gaffney (1975) noted that the type material of *T. miocenica* was too incomplete to provide a reliable diagonsis, hence this species is a nomen dubium.

Several pieces of carapace and plastron match the *Bothremys* material. A single hexagonal nuchal (USNM 186773; Figure 2A,B) is 59 mm long at its midline, 47 mm wide anteriorly, and 84 mm wide posteriorly. The nuchal is thin (ll mm at thickest region) and possesses smooth dorsal and ventral surfaces. The scute sutures are lightly etched on the surface. A cervical scute is absent. Sutures of the left and right first marginals, left and right first pleurals, and first vertebral scutes are present dorsally on the nuchal. No scute sutures are visible ventrally. The ventral scute surface occupies the anterior third of the nuchal. The nuchal's shape and the absence of a cervical scute identify it as a pelomedusid element.

Four fragments are from the plastron. Three of these (USNM 358462A (Figure 2C), 358747, 358784) are xiphiplastral fragments with pubic or ischial articular scars (fusion of pelvic girdle to plastron is characteristic of pleurodires), and the remaining fragment (USNM 358462B) is unidentifiable to plastron location. A small fragment of a costal (USNM 425594) has the texture of the other Lee Creek pleurodiran fragments.

A complete left humerus (USNM 358316; Figure 2D,E) is assigned to *Bothremys*. It is a short, robust humerus with a widely flaring greater trochanter, a squat, rugose lesser trochanter, and an ectepicondylar canal on the anterodorsal edge of the diaphysis (canal does not intersect the condylar articular surface). It shares some of the features of the humerus of *Taphrosphys sulcatus* (Leidy) (Gaffney, 1975, fig. 12C,D).

Family CHELONIIDAE (hard-shelled seaturtles)

I recognize five species of cheloniid and one species of dermochelyid seaturtles in the Lee Creek Mine fauna. *Caretta* and *Syllomus* are represented by hundreds of elements, the other seaturtles are represented by many fewer elements.

A partial skull and mandibular fragments match the morphology of these elements in *Caretta*. Numerous carapacial fragments (particularly posterior peripherals) and humeri possess the carettine morphology and also are assigned to *Caretta*. These fossil elements show sufficient differences to indicate that they represent a species distinct from extant *Caretta caretta*.

Caretta patriciae, new species

FIGURES 3-6

HOLOTYPE.—USNM 186731, a partial skull lacking basioccipital, basisphenoid, and left quadrate-squamosal complex through and including left jugal. Collected by J.H. McLellan, 17–20 Jul 1972.

TYPE LOCALITY.—North Carolina, Beaufort County, Lee Creek Mine (35°23'N, 76°47'30"W; United States Geological



FIGURE 2.—Fossil remains of the sideneck turtle *Bothremys* from Lee Creek Mine. A,B, dorsal and ventral views, respectively, of a nuchal (USNM 186773); c, dorsal view of a fragmented xiphiplastron (USNM 358462A), showing a pelvic girdle attachment scar. D,E, dorsal and ventral views, respectively, of a humerus (USNM 358316). (Scale bar=1 cm.)

Survey quadrangle map, 7.5-minute series, Bath, North Carolina, quadrangle), south side of Pamlico River, near Aurora; from a spoil pile.

HORIZON AND AGE.—Presumably from the Yorktown Formation, lower Pliocene.

ETYMOLOGY.—The specific epithet is a patronym in honor of my wife, Patricia, for her years of support and love. It is proposed as a noun in the genitive case.

DEFINITION.—A cheloniid seaturtle with frontals excluded from orbits by prefrontal-postorbital contact, maxillary contact on secondary palate separating premaxillae from vomer, slight temporal emargination, and deep pterygoid grooves. Triturating surface of dentary smoothly concave, with or without a low symphyseal ridge. Carapace morphology carettine, with strongly serrate posterior border, pygal widely and deeply notched posteriorly; neural series in adults bearing large, projecting spines or knobs on neurals 1, 4, 7, 10, and posterior suprapygal; suprapygal spine very large.

DESCRIPTION OF HOLOTYPE.—Most of the dorsal surface of the skull is present (Figures 3, 4A). The skull roof has a slight transverse arch and an equally slight longitudinal arch. Together, the parietals are trapezoidal and are 91 mm long, 50 mm



FIGURE 3.—Cranial skeleton of *Caretta patriciae*, new species. A,B, dorsal and ventral views, respectively, of a skull (USNM 186731, holotype). (Scale bar=1 cm.)



FIGURE 4.—Cranial skeleton of *Caretta patriciae*, new species. A, lateral view of a skull (USNM 186731, holo-type); B–D, dorsal, lateral, and ventral views, respectively, of a dentary (USNM 186730). (Scale bars=1 cm.)

wide anteriorly, and 98 mm wide posteriorly. The frontals have a pentagonal outline, are 29 mm long medially, and are excluded from the orbits by the prefrontals and the postorbitals. The nasals are truncated anteriorly and are 20 mm long medially and 42 mm long laterally.

The anterior palatal region of the skull lacks only the right maxilla and left premaxilla. The triturating surface and adjacent secondary palatal surface are flat and smooth. There is a slight depression in the premaxilla for the tip of the mandible. Posteriorly, the left side of the skull is represented by the articular process of the quadrate and the adjacent part of the pterygoid. The articular surface is ellipsoidal with no distinct medial constrictions, and the surface is inclined only slightly anteriorly. The pterygoid groove is deep and is bordered laterally and medially by well-developed ridges.

ADDITIONAL SPECIMENS.—Numerous fossil elements possess characteristics of *Caretta* or carettine seaturtles and are referred to *C. patriciae*. The morphology of the carapace is based entirely on these isolated elements (Figures 5, 6), even though their association with the skull is uncertain. A few elements are described below.

Parts of a supraoccipital and right opisthotic are present. In addition to unidentified skull fragments, pieces of a right jugal and right quadratojugal are recognizable. The skull fragments



FIGURE 5.—Carapacial elements of *Caretta patriciae*, new species. A,B, dorsal and ventral views, respectively, of a nuchal (USNM 186687); C,D,E, dorsal views of a first neural (USNM 451940), a third or fourth neural (USNM 186683), and a suprapygal (USNM 358420), respectively, of adults; F,G,H, same specimens, lateral views. (Scale bar=1 cm.)

are derived from two individuals; the pieces represent two right jugals and two left pterygoids. Five dentaries are recognizable. The largest piece of dentary (USNM 186730; Figure 4B–D) comprises nearly the entire left half, with only the anterior tip and coronoid extension missing. The triturating surface is broad and smooth. There are no raised labial or tomial ridges. The sulcus cartilaginis meckelii is deep, and anteriorly the dorsal wall overhangs the ventral one. Two fragments are anterior dentary tips (USNM 187101, 358792); each possesses a mucronate outline and a smooth, concave triturating surface with a low symphyseal ridge; anteroposterior widths are 21 and 26 mm, respectively.

Eighteen left and 32 right *Caretta* humeri have been identified from entire specimens or proximal ends. They were differentiated from those of other seaturtles by the diagonistic features listed earlier. Because I found no feature to differentiate



FIGURE 6.—Carapacial elements of *Caretta patriciae*, new species. A,B,D, dorsal views of a right eighth peripheral (USNM 186708), a left eleventh peripheral (USNM 186714), and a left twelfth peripheral (USNM 186703), respectively; c, dorsal view of a pygal (USNM 186688). (Scale bars=1 cm.)

unquestionably the humeri of *Caretta* and *Lepidochelys*, the latter taxon may be represented in this collection of humeri; however, the preponderance of *Caretta* cranial skeletal elements suggests a similar preponderance of postcranial elements. I also identified 15 femora as *Caretta*. Cheloniid ulnae (with the exception of the *Syllomus* ulna) and other appendicular skeleton elements in the Lee Creek Mine collection cannot be identified to genus.

Carettine carapace fragments are the most numerous turtle fossils from Lee Creek Mine. There are hundreds of carapace pieces. Many of the peripherals and neurals are complete or nearly so; costals are invariably highly fragmented; nuchals are rare and incomplete. The similarity of C. patriciae and C. caretta peripherals suggests that shell shape and size of both species are similar and that the posterior margin of the carapace in both was distinctly serrate. Pygals are numerous; 54 were identified as Caretta, and all show a strong notch on the posterior margin. The difference in carapace morphology is the smooth middorsal surface of C. caretta and the presence of a middorsal series of spines or knobs in C. patriciae. The spine-bearing neurals are 1, 4, 7, and 10 based on a comparison of neural outlines and vertebral scute-suture positions in juvenile and adult C. caretta and juvenile Lepidochelys kempii. The spines are variably developed on the neurals but clearly persisted in adult C. patriciae and could be quite large (Figure 5C,D,F,G); the suprapygal (Figure 5E,H) bears proportionately the largest spine, which remains sharply pointed even in the large adults. The largest nuchal fragment (Figure 5A,B) is the anteromedial part of the bone, which bears the anterior lip of the carapace and, ventrally, the bony process for the attachment of the eighth cervical vertebra. This bony process lies less than its longitudinal length from the anterior edge of the nuchal. This position is common in *Caretta*, whereas in the other extant cheloniids the process tends to be posterior.

?Chelonia

A single right humerus (USNM 186749, proximal end) appears to represent this genus. There are numerous other fossils that might also derive from *Chelonia*, but distinguishing characteristics are lacking for reliable identifications.

Lepidochelys

FIGURE 7B

A nearly complete left dentary (USNM 425612; Figure 7B), broken to the right of the symphysis, resembles closely the dentaries of juvenile *Lepidochelys kempii*. The fossil dentary is 17 mm wide at the symphysis, and a large symphyseal pyramid rises from the posterior edge of the triturating surface. This surface is deeply concave in the symphyseal area, gradually becoming more planar toward the articular end. The dentary is slightly deformed by a constriction extending diagonally from the middle of the ventral surface upward and posteriad to the coronoid process.

A small left humerus (USNM 508056) matches closely the humeral morphology of extant juvenile *Lepidochelys*.



FIGURE 7.—Fossil remains of Lee Creek Mine seaturtles. A,B, dorsal views of *Syllomus aegyptiacus* (USNM 427790) and *Lepidochelys* (USNM 425612) dentaries, respectively; C, dorsal view of three osteoderms (USNM 214649) from the carapace of a *Psephophorus;* D,E, pygals (USNM 358461, 358457, respectively) of *Syllomus aegyptiacus*. (Scale bar=1 cm.)

Procolpochelys

A piece of a left hyoplastron (USNM 214648; principally the medial and posterior portion) possesses a strong xiphiplastral notch, which is covered ventrally by a bony shelf and projects from the midline at about a 30° angle. The shape and depth of this notch matches well plastral fragments of juvenile *Procolpochelys* from the Calvert fauna. Several neurals match Calvert *Procolpochelys* neurals in shape and thickness.

Syllomus aegyptiacus

FIGURE 7A,D,E

Syllomus is represented by numerous fragments. The distinctive surface texture of its carapace allows even the most fragmentary carapacial elements to be recognized. Neurals are numerous; most have distinct longitudinal keels. Eight pygals (two figured; Figure 7D,E) have been found, and all but the largest one bear an attenuate tip with a distal bifurcation. Humeri are extremely abundant, with 44 left and 56 right humeri recognized from either entire elements or proximal halves. One humerus (USNM 187122) contained a small amount of matrix, and sedimentological analysis of this matrix indicates that the humerus was derived from the Yorktown Formation. Thus, *Syllomus* survived into the Pliocene and probably was a contemporary of *Caretta patriciae*. Only six femora have been found.

Family DERMOCHELYIDAE (leatherback seaturtles)

Psephophorus

FIGURE 7C

Three articulated carapacial osteoderms (USNM 214649; Figure 7C) represent this genus. They are 10 mm thick, and the largest plate has a maximum length of 39 mm. Each of the three plates is of a different size and shape. There are eight other isolated osteoderms, and most of these are derived from a keeled area of the carapace. The three articulated osteoderms are darker and more mineralized than are most Lee Creek Mine fossils and may derive from the Pungo River Formation.

> Family EMYDIDAE (pond turtles)

Chrysemys complex

FIGURE 8

A few emydid shell fragments represent the *Chrysemys* complex. Over the past three decades, the contents of this complex have been variously considered to be members of one genus or of two or three genera; the number of species has remained essentially static. Herein, I follow the three-genera concept

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FIGURE 8.—Carapacial and plastral elements from turtles of the *Chrysemys* complex. A, ventral view of a *Pseudemys* left hyoplastron (USNM 187104); B,C, dorsal views of a *Trachemys* posterior peripheral (USNM 358314) and pygal (USNM 186774), respectively. (Scale bar=1 cm.)



(Ward, 1984; Seidel and Smith, 1986): *Chrysemys*, monotypic with *picta; Pseudemys*, containing the *floridana* and *rubriven*-*tris* species groups; and *Trachemys*, containing the *scripta* species group.

The Lee Creek Mine emydine fragments appear to derive from both *Pseudemys* and *Trachemys*. An emydine plastron is represented by a left hyoplastron (USNM 187104; Figure 8A). This hyoplastron lacks most of the bridge buttress, but the hypoplastral and hypoxiphiplastral sutures and the position of the abdominofemoral sulcus are distinct. The element is 39 mm long and 33 mm wide, approximately the size of a hyoplastron of an adult *Chrysemys picta;* however, its morphology is more similar to that of a juvenile *Pseudemys*. A piece of left hyoplastron (USNM 358315A) and a smooth-edged ninth or tenth right peripheral (USNM 358315B) also appear to be derived from a *Pseudemys*. Two pygals (USNM 186774 (Figure 8C), 359009) and a tenth or eleventh left peripheral (USNM 358314; Figure 8B) bear deep notches that have the serrated border of a *Trachemys* carapace.

Family TESTUDINIDAE (tortoises)

Geochelone

A giant tortoise is represented by a complete shell (USNM 336458; Figure 9) and miscellaneous shell fragments, principally peripherals. The complete shell has an estimated carapace length (CL) of 88 cm and an estimated plastron length (PL) of 70 cm. The costals and neurals have collapsed into the body cavity but retain their alignment. The shell was high-domed, with a smooth surface and distinct but lightly incised scute borders. In outline, the shell is slightly obovate, wider posteriorly than anteriorly; the peripherals possess a slight lateral flare. The plastron is smaller than the shell opening and bears a well-developed epiplastral lip, which extends beyond the anterior margin of the carapace. The plastral surface is very lightly etched with scute outlines.

Three lineages of tortoises are known from the late Tertiary of eastern North America: Geochelone (Caudochelys), Geochelone (Hesperotestudo), and Gopherus. The Lee Creek Mine tortoise is large, has a narrow nuchal scute, parallel-sided costals, and a plastron smaller than the carapace opening, traits that ally it to Geochelone. Two species of Geochelone, G. ducateli (Collins and Lynn) (Calvert Formation, Maryland) and G. tedwhitei (Williams) (Hawthorne Formation, Florida), occur in Miocene faunas (Auffenberg, 1974). Both of these species are moderate-sized tortoises of less than 40 cm PL and are considered to be members of the subgenus Caudochelys. Larger tortoises of the subgenus Hesperotestudo have members in midcontinental Miocene faunas but do not appear in Atlantic coast faunas until the Pliocene and then only in the Southeast. The Lee Creek Mine tortoise fossils do not closely match either of these two species groups. Although some of the isolated peripherals fall within the size range of G. ducateli, the Lee Creek Mine peripherals are proportionately thinner. The epiplastral lip of the shell also is more angular and projecting than that of G. ducateli. As in many Hesperotestudo, the fossil's humeropectoral scute border lies on the hyoplastron immediately posteriorad to the entoplastron; however, the pectoroabdominal border is widely separated from the humeropectoral border (pectoral/abdominal midline lengths, 0.30%). This feature distinguishes the Lee Creek Mine tortoise from the Hesperotestudo lineage, and this separation also is greater than in Caudochelvs.

Of the eastern Pliocene Geochelone, only G. (Caudochelys) hayi (Sellards) is a large species, encompassing the size of the Lee Creek Mine tortoise. Both G. (Hesperotestudo) alleni Auffenberg and G. (H.) turgida (Cope) have plastron lengths of less than 25 cm and large plastra filling their shell openings. The Lee Creek Mine tortoise may be G. hayi; however, without additional comparative material, such an identification is tentative. The type of G. hayi (USNM 8815) has a carapace of equivalent size but has a proportionately larger plastron with broader epiplastra and a deeper xiphiplastral notch. The type



FIGURE 9.—Ventral view of the complete shell (USNM 336458) of the Lee Creek Mine *Geochelone*. A, shell resting in a plaster jacket (ruler on right=15 cm); B, reconstruction of the plastron proportionately matching the lengths and widths of the fossil elements. (Scale bar=15 cm.)

also has strongly flaring posterior peripherals, which flared only slightly in the Lee Creek Mine specimen.

Family TRIONYCHIDAE (softshell turtles)

Genus undetermined

Three carapacial fragments are referable to trionychid turtles. All possess the strongly pitted and ridged surface texture of the trionychid shell. A proximal end of a costal (USNM 186677) is extremely thick, with the thickness about 25% of the width. A neural (USNM 508057) is of equal thickness. These elements are darker and more mineralized than are most other Lee Creek Mine fossils and perhaps are derived from the Pungo River Formation.

The extant North American softshell turtles represent a monophyletic group (*Apalone*; Meylan, 1987) of three species. Although the Lee Creek Mine fragments likely represent *Apalone*, shell fragments, indeed entire carapaces or plastrons, are insufficient for the differentiation of *Apalone* from its Asian relatives.

Family incertae sedis

A nearly complete right ilium, USNM 187103, lacking the distal sacral border, is indeterminate. It is a small (~40 mm long), stout element with a straight anterior edge and a fan-shaped posterior edge. It possesses the stoutness of a *Chelydra* ilium and the shape of an *Emydoidea* one.

A heavily mineralized right parietal (USNM 187100), \sim 45 mm long and unquestionably turtle, cannot be reliably assigned to genus. Its manner of fossilization suggests that it came from the Pungo River Formation.

Discussion

The Lee Creek Mine fauna has 11 recognizable turtles: a sideneck turtle, six seaturtles, two pond turtles, a softshell turtle, and a giant tortoise. This fauna derives principally from the Yorktown Formation, although the mining operation may have introduced some elements from the Pungo River Formation. Both of these formations are marine, yet the fauna has representatives of marine, freshwater, and terrestrial turtles. None-theless, it seems likely that both faunal components derive from the waters and land immediately adjacent to the depositional site. None, in my opinion, requires a long-distance transportation hypothesis.

The turtles occurring in the two Miocene and one Pliocene marine deposits of the mid-Atlantic coast are summarized in Table 3. Only three species have been recovered from the New Jersey Miocene, and the "*Chelonia*" is almost certainly from an Eocene deposit. This small number probably reflects a lack of good collecting localities rather than a depauperate fauna. The Calvert and the Lee Creek faunas are similar in size and content, sharing six taxa: *Bothremys, Procolpochelys, Syllomus, Psephophorus, Geochelone,* and a trionychid.

The freshwater and terrestrial taxa are all extant taxa, although only the pond turtles occur in the Lee Creek Mine area today. The fragmentary nature of the fossil pond turtles allows only a statement of their presence in the fauna, not their specific identity or ecological significance. Their presence is not unusual because both are known from other late Tertiary and Quaternary faunas. Trachemys is both common and widespread in Cenozoic faunas east of the Rocky Mountains and has a temporal distribution from the early Miocene (Williams, 1953, pl. 4; Jackson, 1988) to the present in eastern North America. Williams (1953) also pictured a Pseudemys floridana-like turtle from an early Miocene deposit in Florida. Specific identification of the Lee Creek Pseudemys and Trachemys will require more complete specimens from Lee Creek Mine and a more comprehensive examination of the fossil history of the Chrysemys complex. The Lee Creek Mine specimens extend the geographic occurrence of these taxa in the Pliocene into the mid-Atlantic region.

Trionychids occurred at the Lee Creek site. Today, they are not present in that area or adjacent to the other two mid-Atlantic fossil sites, yet fragmentary fossils of the trionychids demonstrate their Pliocene or Miocene occurrence (Table 3) in the rivers of the mid-Atlantic coastal plain.

Geochelone also is a common member of late Tertiary and Quaternary faunas of North America. Four of the previously known species (G. ducateli, G. tedwhitei, G. alleni, G. turgida) from eastern Miocene–Pliocene faunas are much smaller tortoises. Some Lee Creek tortoise fossils match the size of these species, but they are too fragmentary to discern whether they represent a second, smaller species in the Lee Creek Mine fauna or represent juveniles of the giant tortoise. The complete shell and many fragments show the Lee Creek Geochelone to be a giant tortoise, the first from the mid-Atlantic Tertiary. It may be G. hayi, but comparative material is inadequate for confirmation.

The pelomedusid *Bothremys* is considered to be a marine sideneck turtle. The presence of the xiphiplastra with girdle scars confirms its presence in the Lee Creek Mine fauna. Its occurrence is important because it may extend the temporal range of this genus from the Calvert Formation through the Yorktown Formation. Without precise stratigraphic data, however, the Lee Creek sideneck turtle must be assigned questionably to the Pliocene. Whether Miocene or Pliocene, the Lee Creek Mine occurrence confirms the presence of sidenecks in the North American Tertiary.

Procolpochelys and *Psephophorus* are very rare in the Lee Creek Mine assemblage, perhaps because they are from the Pungo River Formation; however, *Psephophorus* was recently discovered (Dodd and Morgan, 1992) in a Pliocene deposit in central Florida. They are assumed to be highly pelagic species. Although this pelagic behavior may account for their relative rarity, *Dermochelys*, the modern day counterpart of *Psephophorus*, seasonally migrates along the Atlantic coast (Shoop,

Taxon	Miocene fauna of New Jersey	Calvert fauna of Maryland and Virginia	Lee Creek Mine fauna of North Carolina
Family PELOMEDUSIDAE			
Bothremys	-	+	+
Family CHELONIIDAE			
Caretta	-	-	+
Chelonia	?	?1	+
Lepidochelys	-	-	+
Procolpochelys	+	+	+
Syllomus	-	+	+
Family DERMOCHELYIDAE			
Psephophorus	-	+	+
Family EMYDIDAE			
Chrysemys complex	-	-	+
Family TESTUDINIDAE			
Geochelone	-	+	+
Family TRIONYCHIDAE			
cf. Apalone	+	+	+

TABLE 3.—Occurrence of Miocene and Pliocene turtles in marine deposits of the central Atlantic coastal plains of North America. Symbols: +, species occurs in fauna; –, species absent from fauna; ?, occurrence doubtful.

¹Cope (1868) considered two fragments to represent *Chelonia*; Weems (1974) believed them to be from *Syllomus* and *Procolpochelys*, respectively.

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1987), regularly enters the larger estuaries (e.g., Chesapeake Bay; Musick, 1988), although briefly and in small numbers, and strands regularly on Atlantic beaches (Prescott, 1988). I suspect that the rarity of *Psephophorus* is not because they are pelagic and their carcasses were lost at sea, but because the Lee Creek depositional environment was estuarine, equivalent to today's Albemarle and Pamlico Sounds. Stranding on high energy ocean-front beaches destroys carcasses and provides little opportunity for fossilization. This destruction occurs to all seaturtles, whether they are near-shore or pelagic species.

Extant Caretta caretta and Lepidochelys kempii use the estuaries, bays, and sounds of North America (south of Cape Cod) as summer feeding grounds for juveniles and often occur in high densities in these areas. The abundance of Syllomus and Caretta patriciae suggests that the Lee Creek area was similarly used by these extinct species. This suggestion is further strengthened by the numerous limb bones of juvenile Caretta and Syllomus. To extend this suggestion into speculation, I note that juvenile Caretta caretta, Chelonia mydas, Eretmochelys imbricata, and Lepidochelys kempii are year-around residents in some Florida bays and sounds (Ehrhart, 1983). During the winter, they burrow into the bottom of these bays and possibly hibernate (Ogren and McVea, 1982). It seems likely that the Lee Creek Caretta and Syllomus also were year-around residents of the Pliocene Lee Creek estuary. The abundant fossils of the latter two seaturtles might be attributed to cold-stunning (K. Dodd, pers. comm., 1991), a regular event in some estuaries (Meylan, 1986; Witherington and Ehrhart, 1989) that kills many resident seaturtles.

Without stratigraphic control, suggestions on the origin of the Lee Creek vertebrate fauna are speculative. The commonness of tortoises and juvenile seaturtles and the types of seaturtles present argue for a shallower, near-shore deposition. The teleost fish data is less precise, indicating a "deposition at 60 to 100 m, but could in fact have been much shallower or a great deal deeper" (Fitch and Lavenberg, 1983:527).

The similarity of the Caretta patriciae skull to that of C. caretta indicates a similar diet, dominated by mollusks and crustaceans (Mortimer, 1982; Plotkin, 1989). The skull of Syllomus is more elongate (Weems, 1980) and generally resembles that of Eretmochelys, so it may have shared a preference for sponges (Meylan, 1988) as well. One of the more striking features of Syllomus, however, is its humeral morphology, which is unlike that of any modern seaturtle. Syllomus undoubtedly swam with the aquatic flight locomotor pattern, but the proportional and shape differences of the humerus suggest a modification of the typical pattern, perhaps a more rapid or powerful stroke. Rather than eating sponges, was it capable of chasing and capturing fish or squid? Another peculiarity of Syllomus is the surface texture of the carapace, suggesting a different type of epidermal covering. Scutes were present, but they may have been softer, less keratinized, perhaps similar to the scutes of Natator depressa (Garman). The relationships of these two taxa require closer examination.

The abundance of *Caretta* fossils in the Lee Creek Yorktown deposits and their absence from the Calvert Formation indicate a Pliocene arrival to the mid-Atlantic coast. *Caretta* has been reported from faunas as early as the Eocene and questionably the late Cretaceous (Mlynarski, 1976). These early fossils (Cretaceous and Eocene) are suspect, and their identities must be confirmed.

Zangerl and Turnbull (1955) placed the Miocene Procolpochelys grandaeva Leidy in the cheloniid tribe Carettini. They considered Procolpochelys to be a pelagic divergent and not ancestral to the extant carettines, Caretta and Lepidochelys. The presence of Caretta in the Lee Creek Mine assemblage is additional evidence against Procolpochelys as an ancestor of extant carettines. Carapace structure of these two is similar in two characteristics. Both lack surface sculpturing and possess costoperipheral fontanelles; however, the extent of fontanelle development can not be determined from the present Lee Creek Mine fragments. The fontanelles probably never closed in Procolpochelys. In extant Caretta, closure does occur but apparently only after sexual maturity. The extent of closure, its timing, and intra- and interpopulational variation remain undocumented. Some of the peripherals from Lee Creek Caretta are equivalent in size to those of extant, reproductively active Caretta, and these peripherals lack costoperipheral sutures. Further, the shape of the largest (and clearly adult) posterior suprapygal indicates the presence of large costoperipheral fontanelles in the posterior aspect of the carapace.

Conclusions

Examination of the turtle fossils from the Lee Creek Mine reveals the following: (1) The Pliocene turtle fauna of the mid-Atlantic coast and coastal plain contained extinct and modern genera. The marine or estuarine taxa were Bothremys, Caretta patriciae, ?Chelonia, Lepidochelys, Procolpochelys, Syllomus, and Psephophorus. The freshwater taxa were two pond turtles (probably Pseudemys and Trachemys) and a trionychid, and there was a single terrestrial taxon, Geochelone. (2) The estuarine/near-shore nature of the Lee Creek Mine deposit and the abundance of Caretta and Syllomus indicate that these two taxa were regular residents of the estuaries and coast of the Albemarle Embayment. Juveniles and adults are represented, so the area likely included both feeding grounds and nesting beaches, just as it does for Caretta caretta today. (3) The Pliocene Caretta is morphologically distinct from the modern species and is recognized as a new species, C. patriciae. (4) The Lee Creek Geochelone is the earliest Cenozoic record of a giant tortoise from the mid-Atlantic coast of North America. This tortoise also appears to be morphologically distinct from previously known Miocene-Pliocene Geochelone. (5) The presence of xiphiplastral fragments with pelvic girdle articular scars confirms the presence and likely extends the temporal range of pleurodiran turtles in North America.

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