AMPHIBIANS AND NONMARINE TURTLES FROM THE MIOCENE CALVERT FORMATION OF DELAWARE, MARYLAND, AND VIRGINIA (USA)

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ABSTRACT—Two amphibian taxa are reported for the first time from the lower to middle Miocene shallow-marine Calvert Formation. These are Batrachosauroides aff. B. dissimulans (a large proteoid salamander) and cf. Notophthalmus robustus (a small newt). Four kinds of identifiable nonmarine turtles were reported previously from this formation. These are Bairdemys miocenica (a pleurodri), Kinosternon sp. (a musk turtle), Hesperotestudo ducateli and Hesperotestudo wilsoni (tortoises). Four additional taxa reported here are Chrysemys isoni n. sp. (a painted turtle), Trachemys sp. (a pond turtle), Floridemys hardi n. sp. (a small tortoise), and Apalone lina (a softshell turtle). Most of these taxa are known from elsewhere in the Atlantic and Gulf Coastal Plains from New Jersey to Texas. The regional widespread occurrence of many of these taxa indicates that they represent a modestly diverse community of amphibians, fresh water turtles, and land turtles that were endemic to the Atlantic and Gulf coastal regions of the United States during the late early and early middle Miocene. Their pattern of distribution is similar to that of eastern American land mammals during this time interval, indicating that the Atlantic and Gulf coastal plains of the southeastern United States then lay within a single climatic zone that constituted a distinctive and long-lived faunal province throughout the early and middle Miocene (Hemingfordian through Barstovian land mammal ages).

INTRODUCTION

The Calvert Formation is a marine deposit that accumulated in shallow to middle continental shelf environments. As currently defined, the Calvert Formation is restricted to Delaware, Maryland, and Virginia, but age-equivalent strata are widespread and known from New Jersey (Kirkwood Formation), North Carolina (Pungo River Formation), and southern South Carolina, Georgia, and Florida (Marks Head and Coosawhatchie Formations) (see Fig. 1 for regional setting). Calvert Formation strata range in age from mid-Burdigalian (late early Miocene) to mid-Serravalian (early middle Miocene) (Fig. 2).

Remains of sea turtles are fairly common in the Calvert Formation and represent three taxa. These are the dermochelyid Psephophorus calvertensis Palmer 1909, the primitive chelonoid Procolopchelys grandaeva (Leidy 1851), and the advanced chelonoid Trachyspis lardyi Meyer 1843 which is the senior synonym of Syllomus crispatus Cope 1896, Peritresius virginianus Berry and Lynn 1936, and Chelonia marylandica Collins and Lynn 1936 (Weems, 1974; Lapparent de Broyin, 2001; Chesi et al., 2007).

In contrast to the abundant sea turtle remains, nonmarine turtles are rare. The first two species to be recognized were described by Collins and Lynn (1936). Their specimens came from Shattuck’s Zone 10 along the northern Calvert Cliffs in Calvert County, Maryland (Figs. 1, 2). One specimen belonged to a side-neck turtle and was described as a new species, *Taphrophys mosiocienca* Collins and Lynn 1936. This species recently was shown to pertain to the genus Bairdemys (Weems and Knight, 2012) and is now designated Bairdemys mosiocienca (Collins and Lynn, 1936). The other specimen belonged to a moderately large tortoise and was described as a new species, *Testudo ducateli* Collins and Lynn, 1936. It later was reassigned to the genus Hesperotestudo (Gaffney and Meylan, 1988) and is now designated Hesperotestudo ducateli (Collins and Lynn, 1936). Since the paper by Collins and Lynn, only Holman (1998) has described new nonmarine turtle material from the Calvert Formation in Delaware. That material, none of it illustrated, was identified and described as *Kinosternon* sp., Chrysemys complex indeterminate, and ‘Geochelone’ cf. ‘G.’ wilsoni Auffenberg 1964 (now Hesperotestudo wilsoni).

Four additional species of nonmarine turtles (two of which are new species) and two amphibians are reported for the first time from the Calvert Formation, and the material described by Holman (1998) is illustrated. Collectively, this material provides a greatly expanded glimpse of what onshore turtles and amphibians were like in the Delaware-Maryland-Virginia region during early and middle Miocene time.

SYSTEMATIC PALEONTOLOGY


Class Amphibia Linnaeus, 1758
Order Caudata Oppel, 1811
Family Batrachosauroidae Auffenberg, 1958
Genus Batrachosaurusindae Auffenberg and Hesse, 1943
Batrachosauroides aff. B. dissimulans

Figure 3.1–3.8

Material.—USNM 464090, right dentary; USNM 464091, anterior trunk vertebra; USNM 464097, USNM 540754, USNM 540755, three trunk vertebrae. Collectors: Gaffney; D. Bohaska, S. Swelson, and P. Kroehler. Description.—External surface of dentary (Fig. 3.5) nearly smooth, traversed by a broad, relatively deep, longitudinal channel that becomes narrower and deeper anteriorly and wider and shallower posteriorly; at least 14 teeth were present (Fig. 3.6). Vertebrae large; centrum longer than high, up to 10 mm in length, ophisphoceous (Fig. 3.2) but the large notochord canal in the

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center of the cotyle gives the vertebrae a superficially amphicoelous appearance (Fig. 3.1).

**Occurrence.**—Pollack Farm fossil site near Cheswold, Kent County, Delaware in strata belonging to the upper Fairhaven Member (Fairhaven C) of the Calvert Formation, upper lower Miocene (Burdigalian).

**Remarks.**—Two species of amphibian, one large and one small, were found at the Pollack Farm site. Both are represented by opisthocoelous vertebrae, which are characteristic of the families Salamandridae and Batrachosauroididae (Estes, 1981). Vertebrae of the larger species, described here, all have anterior condyles with a large, regular unossified center or notochordal pit that gives the condyle a distinctive ring-like shape in anterior view (Fig. 3.1). Although a small, irregular notochordal pit is found in some salamanders, a large and regular pit is found only in two batrachosauroidid genera, *Opisthotriton* (Upper Cretaceous–Paleocene) and *Batrachosauroides* (Eocene–Miocene). The relatively massive build of these vertebrae, their relatively rounded neural arches, and also their Miocene age all indicate assignment to *Batrachosauroides* (Auffenberg, 1958; Estes, 1981; Albright, 1994).

The specimens found at the Pollack Farm site are morphologically indistinguishable from comparable elements of *Batrachosauroides dissimulans* found in its type area in the late Barstovian (middle Miocene) Fleming Formation of San Jacinto County, Texas (Auffenberg, 1958). The specimens described here are significantly older (late Hemingfordian, early Miocene) so they might represent an earlier and somewhat different species of this genus. This suspicion is reinforced by the observation by Albright (1994) that none of the early Miocene vertebrae of *Batrachosauroides* known from Texas or Florida are as large as the largest type-area middle Miocene vertebrae, which can be up to 15 mm in length (Auffenberg, 1958). This is also true for the early Miocene vertebrae described here. Therefore, the material illustrated here is associated with *B. dissimularis* but not firmly assigned to that species.

The amphibians in the Pollock Farm borrow pit site in Delaware co-occur with the most abundant and diverse assemblage of early Miocene land mammal remains found north of Florida (Emry and Eschelman, 1998). Therefore, the unique occurrence in the Calvert Formation of amphibians at this locality probably can be attributed to its proximity in the early Miocene to a strong current of fresh water from a major river, perhaps the ancestral Susquehanna and/or Delaware rivers. *Batrachosauroides* is a relatively large amphibian that apparently went extinct around the end of the middle Miocene (Wolfe, 1994; Zachos and others, 2001; Böhme, 2003). It probably had reduced limbs, lived in low energy coastal plain streams, and was an active and voracious predator (Holman, 1977; Estes, 1981; Albright, 1994).
**Suborder** Salamandroidea Noble, 1931  
**Family** Salamandridae Gray, 1825  
Genus *Notophthalmus* Rafinesque, 1820  
*cf. Notophthalmus robustus*

**Material.**—USNM 464092, trunk vertebra.

**Description.**—Centrum length of vertebra slightly less than 2 mm, opisthocoelous, small projecting anterior condyle set apart from body of centrum by a prominent constriction.

**Occurrence.**—Pollack Farm fossil site near Cheswold, Kent County, Delaware in strata belonging to the upper Fairhaven Member (Fairhaven C) of the Calvert Formation, upper lower Miocene (Burdigalian).

**Remarks.**—Like *Batrachosauroides*, this vertebra is opisthocoelous. Unlike *Batrachosauroides*, it has a smoothly arcuate anterior condyle that lacks a notochordal pit, so it pertains to the family Salamandridae. Two salamandrid genera are known from the Miocene of North America, *Notophthalmus* and *Taricha*. This specimen could be assigned to either of these genera based only on the few preserved character states, but all known specimens of *Taricha* have been found west of the Great Plains and all known specimens of *Notophthalmus* have been found east of that region. The centrum of this vertebra is quite similar to the type material of *Notophthalmus robustus*, described from the lower Miocene (upper Hemingfordian) Thomas Farm locality in Gilchrist County, Florida (Estes, 1981), but the neural arch of the Pollack Farm specimen is missing so any more detailed comparison is impossible. Because this vertebra is virtually identical in age and size with the type material from the Thomas Farm locality, there is no reason to disassociate this specimen from that species. However, a firm recognition of *N. robustus* in the Calvert Formation must await the discovery of more complete material.

*Notophthalmus robustus* was reported previously from the lower Miocene of Texas and Florida (Estes, 1981; Hulbert, 2001), and its likely occurrence in the Calvert extends its range northeastward to Delaware. There are three living species of *Notophthalmus*, all of which inhabit aquatic and damp forest floor habitats in coastal environments from southeastern Canada through the eastern United States to northeastern Mexico. These species all might be descended from *N. robustus*, because the time of their initial divergence is estimated to be not before the middle Miocene (Reilly, 1990). Because all of the living species have poisonous skins (and two have bright colors to warn away predators), it is likely that their common ancestor had at least the first and possibly both of these traits as well.

**Class** Reptilia Laurenti, 1768, emend. Gauthier, Kluge, and Rowe, 1988  
Order Testudines Linnaeus, 1758  
Suborder Cryptodira Cope, 1868  
Family Kinosternidae Hay, 1892  
Subfamily Kinosterninae Hay, 1892  
Genus Kinosternon Spix, 1824  
*Kinosternon* sp.

**Material.**—One complete and one fragmentary sixth left costal, three peripherals (third left, fifth right, tenth left), two right and
one left hypoplastron; two left and one right hypoplastron (USNM 483389). Material collected by G. Simonson, D. Bohaska, R. Eschelman, and R. Purdy.

**Description.**—Carapace fragments thick; presence or absence of a median neural keel unknown but lateral costal keels definitely absent; anterior musk duct groove on the third peripheral inferentially extends forward onto the unknown second and backward onto the unknown fourth peripheral; plastron has a well developed hinge line on the anterior border of the hypoplastron; entoplastron absent; presence or absence of a hinge

**Figure 3**—Amphibian remains from the Calvert Formation of Delaware. 1–4, Batrachosauroidea aff. B. dissimulans, trunk vertebra (USNM 540755) in anterior, dorsal, right lateral, and posterior views, respectively; 5, 6, Batrachosauroidea aff. B. dissimulans, right dentary (USNM 464090) in external and internal views, respectively; 7, 8, Batrachosauroidea aff. B. dissimulans, anterior trunk vertebra (USNM 464091) in dorsal and left lateral views, respectively; 9, 10, Notophthalmus cf. N. robustus, trunk vertebra (USNM 464092) in dorsal and ventral views (anterior to right), respectively.
line on the posterior border of the hypoplastron uncertain; xiphiplastra inferred to be narrow.

**Occurrence.**—Pollack Farm fossil site near Cheswold, Kent County, Delaware in the upper Fairhaven Member (Fairhaven C) of the Calvert Formation, upper lower Miocene (Burdigalian).

**Remarks.**—The presence of a musk duct groove on the third peripheral (marked by arrow on Fig. 4.15) is a distinctive characteristic of the Kinosternidae. The plastral elements of the small turtle discussed here include hyoplastra that anteriorly have a hinge-line joint with the epiplastra, a feature only found among kinosternids in *Kinosternon*. Mobility along a hinge-line joint is possible in *Kinosternon* only because the entoplastron has been lost, transforming the irregular, interlocking, and immobile geometry among the hyoplastra, the epiplastra, and the entoplastron into a linear geometry between the hyoplastra and the epiplastra that bears a potential for flexibility. There are strong constrictions of the hyoplastron and hypoplastron near their distal ends (marked by arrows on Figs. 4.1, 4.3, 5.1, 5.3, 5.5, 5.7). These constrictions form the narrowest part of the plastral bridges, a feature also typical of kinosternids. Holman (1998) considered the presence or absence of a posterior hinge line groove between the hyoplastron and the xiphiplastra to be uncertain and in this we concur.

The contact between the hyoplastron and xiphiplastra is narrow, indicating that the xiphiplastra were narrower than in most species of *Kinosternon*. The carapace and plastron elements are distinctly thicker than elements of comparable size in the three species of *Kinosternon* that live today in the central and eastern United States (*K. baurii*, *K. subrubrum*, and *K. flavescens*), and the obtuse angle of the fifth right peripheral from the plastral bridge region, as seen in lateral view (Fig. 4.11),
indicates a carapace that was more highly arched than in most living species of *Kinosternon*. No neurals are known, so it is indeterminate if this species had a median keel. Enough costal material is present, however, to demonstrate that the carapace did not bear lateral keels.

As noted by Holman (1998), the thick-shelled turtle represented by this material is not referable to any living species of *Kinosternon*, nor is it a plausible ancestor for any of the three thin-shelled species of *Kinosternon* found today in the eastern or central United States. This applies as well to the hypoplastron from the early Miocene of Florida (Bourque, 2012). Therefore, the phylogeny of kinosternid turtles in the eastern United States is more complex than previously appreciated. Because two sixth left costals, two right hypoplastra, and two left hypoplastra are present, this material belongs to more than one individual. Because no specimen was found in association with any other, it is possible though not probable that more than one species is represented.

A late Paleocene specimen referable to the family Kinosternidae is the oldest record of this family in the southeastern United States (Hutchison and Weems, 1999). A kinosternine turtle (*Xenochelys floridensis*) recently has been described from the late Oligocene of Florida (Bourque, 2012). The Pollack Farm specimens (Holman, 1998) and a single hypoplastron from Florida (Bourque, 2012), all from the early Miocene, provide...
the oldest record of the extant genus *Kinosternon* in the southeastern United States.

Family **Emydidae** Gray, 1873, emend. Mertens and Wermuth, 1955
Genus **Chrysemys** Gray, 1844

**Chrysemys isoni** new species

*Figure 6.1–6.3*

**Diagnosis.**—Anterior region of nuchal greatly thickened, with an anterior border strongly constricted and deeply crenulated; lateral borders with adjacent first peripherals distinctly concave;
cervical scute large and elongate on both dorsal and ventral sides, ventral side much longer than dorsal side.

**Etymology.**—This species is named for its discoverer, Ron Ison.

**Holotype.**—One largely complete nuchal element (CMM-V-4664).

**Occurrence.**—Found in a small side gulley of the Pamunkey River in the region where the Pamunkey forms the boundary between King William and New Kent counties, Virginia. This specimen was found in float material, but its densely phosphatized preservation, dark color, and the area in which it was recovered all strongly indicate derivation from the upper Fairhaven Member (Fairhaven C) of the Calvert Formation in strata equivalent in age to the Popes Creek Sand Member of Gibson (1983) (=the lower "Newport News unit" of Powars and Bruce, 1999).

**Remarks.**—The combination of a constricted anterior margin and a cervical scute that is much longer than wide characterizes this nuchal as belonging to an emydid turtle (Fig. 6.1–6.3). The strongly constricted and deeply crenulated anterior border, distinctly concave lateral borders with adjacent first peripherals, and very elongate cervical scute as seen in both dorsal and ventral views, make this nuchal specifically referable to the genus *Chrysemys* (Fig. 6, bottom left). It differs from the nuchal of the only other described species in this genus, *Chrysemys picta*, in two important characteristics. First, *C. isoni* is much thicker anteriorly than *C. picta*. Second, *C. isoni* has a cervical scute that is much longer on the ventral side than on the dorsal side. In *C. picta* the cervical scute is oppositely proportioned, being slightly longer on the dorsal side than it is on the ventral side.

Among living emydid turtles, all North American members of the subfamily Emydinae (except *Emydoidea blandingii*) have cervical scutes that are distinctly shorter on the dorsal surface of the nuchal than they are on the ventral surface. This produces a ratio of less than one between the length of the dorsal surface and the length of the ventral surface (Fig. 7). In contrast, all members of the subfamily Deirochelyinae (except *Chrysemys picta*) have cervical scutes that are distinctly longer on the dorsal surface of the nuchal than they are on the ventral surface, resulting in a ratio...
considerably greater than one. The relative proportions of the length and width of the cervical scute in dorsal view in *Chrysemys isoni* are close to the cervical scute proportions of *Chrysemys picta*, but the relative proportions of the cervical scute between its dorsal and ventral sides are most similar to *Emydoidea hutchisoni* and *Clemmys gutata* (Fig. 7). The latter ratio would seem to argue for emydine affinities in *C. isoni*, but all other morphological characteristics show strong affinity with *C. picta*. It is notable in this regard that the modern species *Emydoidea blandingii* also has a relatively shorter ventral cervical scute as compared to its late Miocene ancestor or relative *E. hutchisoni* (see arrows on Fig. 7). Both lineages seem to have followed a similar trend in this regard.

**Genus Trachemys Agassiz, 1857**

*Trachemys* sp.  
Figure 8.1–8.3

**Material.**—One posterior right peripheral (CMM-V-4663). Collected by R. Ison.

**Description.**—Peripheral element with a strongly bifurcated external margin, posterior lobe much more elongated than anterior lobe. Sulcal grooves clearly visible.

**Occurrence.**—Found in a small side gulley of the Pamunkey River in the region where the Pamunkey forms the boundary between King William and New Kent counties, Virginia. The specimen was found in float material, but its densely phosphatized preservation, color, and the area in which it was recovered all strongly indicate derivation from the upper Fairhaven Member (Fairhaven C) of the Calvert Formation.

**Remarks.**—Very narrow, serrated posterior peripherals occur in several genera of deirocheline emydid turtles (*Graptemys*, *Pseudemys*, and *Trachemys*). The external margin of this specimen is too strongly bifurcated and has too much contrast between the length of its anterior and posterior marginal lobes to assign it to *Graptemys* or *Pseudemys*, so it can pertain only to the genus *Trachemys*. This specimen almost certainly does not pertain to a living species because of its great age, but even so it is far from sufficient to erect a new species. Several specimens from the Lee Creek Mine near Aurora, North Carolina were referred by Zug (2001) to *Trachemys*, but it is not certain if that material came from the lower Miocene Pungo River Formation (age equivalent to the lower Calvert) or from the lower Pliocene part of the Yorktown Formation (Sunken Meadow Member). A posterior peripheral among the Lee Creek Mine material is similar to the peripheral illustrated here, so it seems likely that at least some of the Lee Creek emydid material came from the Pungo River Formation.
“Chrysemys Group”
Figure 8.4–8.6

Material.—One posterior peripheral (USNM 483390). Collected by G. Simonson.
Description.—Narrow and elongate posterior peripheral, with sulcal grooves narrow and readily discernable and only a slight notching of the distal rim margin.
Occurrence.—Pollack Farm fossil site near Cheswold, Kent County, Delaware in strata of the upper Fairhaven Member (Fairhaven C, Calvert Formation, upper lower Miocene (Burdigalian).
Remarks.—The three genera that comprise this group (Chrysemys, Pseudemys, Trachemys) are closely related and often difficult to distinguish based on isolated elements. That is especially true for specimens recovered from deposits as old as the early Miocene, because it is not at all clear how much these genera had diverged from each other by then in their skeletal characteristics. The posterior peripheral illustrated here (Fig. 8.11–8.13), described but not figured by Holman (1998), does not have a strongly scalloped margin. For this reason it almost certainly does not pertain to Trachemys. It may well pertain to Chrysemys isoni but, in the absence of any associated carapace material, assignment to Pseudemys cannot be precluded.

Family Testudinidae Gray, 1825
Subfamily Xerobatinae Agassiz, 1857
Genus Hesperotestudo Williams, 1950
Hesperotestudo (Caudochelys) ducateli
(Collins and Lynn, 1936)
Figure 9.1–9.3

Material.—Fourth left peripheral (CMM-V-4665). Collected by G. Grimsley.
Description.—Peripheral narrow and high, angle between dorsal and ventral portions about 120°, marked by a faint ridge that is more strongly developed anteriorly. Dorso-lateral portion elongate and nearly vertical in orientation, ventral portion wider than long. Narrow sulcal grooves readily visible.
Occurrence.—Plum Point, Calvert County Maryland, from bluff face above beach in the lower part of Shattuck’s Zone 11, Plum Point Member (Plum Point B), Calvert Formation, lower middle Miocene (Langhian).
Remarks.—The great height, high angle of curvature, and anteroposterior narrowness of this element is characterized testudinid. Based on its size relative to the type, this specimen appears to pertain to a juvenile individual that otherwise is quite comparable to the same element in the type of H. ducateli. It is too narrow to pertain to Floridemys, and the strong elongation of the dorsal portion of the peripheral relative to its ventral portion also is typical of Hesperotestudo and unlike Floridemys. Based on known specimens, this peripheral is too small and occurs too high in the Calvert Formation to belong to H. williamsi.

Earlier assignments of this species to Testudo (and then later to Geochelone) were based on an assumption that all large land tortoises were closely related to each other. This concept has been debunked by a recent molecular phylogenetic analysis (Le et al., 2006), which demonstrates that at least four independent clades are represented among these turtles. As a result, only the Asian species G. platynota and G. elegans remain in the genus Geochelone. A phylogenetic analysis of the Testudinidae by Meylan and Sterrer (2000) demonstrated that fossil North American testudinids are more closely related to the living North American species Gopherus polyphemus than they are to Geochelone or any other testudinid genus living today outside of North America. For this reason, Hesperotestudo now is included with Gopherus, Manouria, and the extinct genus Stylemys in the subfamily Xerobatininae. The genus Hesperotestudo is divided into two subgenera (Gaffney and Meylan, 1988): Hesperotestudo (Williams, 1950) and Caudochelys (Auffenberg, 1963). Both species from the Calvert Formation pertain to the subgenus Caudochelys (Auffenberg, 1974).

This specimen was found in the bluff in a subtly exposed horizon in which bones are somewhat concentrated, about four feet above typical Shattuck Zone 10 lithology. The type of H. ducateli came from a temporary exposure of Shattuck’s Zone 10 about one-fourth mile west of the Calvert Cliffs (Collins and Lynn, 1936). The specimen reported here provides a slight upward range extension for this taxon within Plum Point B to lower Shattuck Zone 11.
Hesperotestudo (Caudochelys) wilsoni (Auffenberg, 1964)

Figures 10, 11

Material.—Two neurals (USNM 540747 and USNM 483391), two partial costal elements (USNM 483391 and USNM 540751), posterior portion of left hypoplastron (USNM 483391), right humerus (CMM-V-4667). Neurals collected by G. Simonson and R. Eshelman, costals collected by G. Simonson; humerus collected by R. George.

Description.—Neurals wider than long, dorsal surface faintly rugose. Costals narrow, long, and preserved segments nearly straight. Humerus large with a robust, stout, and only slightly sigmoidal shaft.

Occurrence.—Neurals and costal fragment from Pollack Farm fossil site near Cheswold, Kent County, Delaware. Humerus from the Pamunkey River where it forms the boundary between King William and New Kent counties, Virginia. All specimens are from the Fairhaven Member (Fairhaven C) of the Calvert Formation, upper lower Miocene (Burdigalian).

Remarks.—All of these elements pertain to a large tortoise referable to the genus Hesperotestudo. Neural and costal remains from the Pollock Farm site in Delaware (Fig. 10) are indistinguishable from the species Hesperotestudo wilsoni, and the scute impressions on the posterior part of the hypoplastron are especially similar to the pattern found on that element in H. wilsoni (Holman, 1998). No humerus was associated with the type material of either H. ducateli or H. wilsoni, so no direct comparisons can be made to that element in either species. However, the large size of this humerus (Fig. 11), and the fact that all of the larger tortoise material comes from Fairhaven C of the Calvert Formation, makes it likely that this humerus came from H. wilsoni. The humerus of a more distantly related small species, Hesperotestudo bermudae from the Pleistocene of Bermuda, has been described and figured by Meylan and Sterrer (2000). The humerus of this species was only about 20 percent as long as the humerus here referred to H. wilsoni. H. bermudae has a narrow humeral shaft that is distinctly sigmoidal in shape, a small caput, and an elongate neck between the caput and the shaft. In contrast, the humerus illustrated here has a wide and thick humeral shaft that is nearly straight, a large caput, and a very short neck relative to the shaft. All of these differences relate to the much larger and more massive build of H. wilsoni relative to H. bermudae.

Hesperotestudo wilsoni is closely related to H. ducateli, but H. ducateli apparently was smaller and certainly was found in a distinctly younger part of the Calvert Formation (Plum Point B; Fig. 2). Another species of Hesperotestudo, described from the early Miocene Thomas Farm site in Florida (H. tedehitiei), also is similar in age but represents a species different and smaller than the material discussed here from the Calvert Formation (Williams, 1953).

Genus Floridemys Williams, 1950

Floridemys hurdi new species

Figure 12.1–12.5

Diagnosis.—On the dorsal surface, the cervical scute of F. hurdi is about twice as long as wide, while the cervical scute of F. nanus is about as long as wide. Anterior border of the first pleural scutes reach onto the posterior borders of the nuchal of F. nanus but are posterior to the nuchal in F. hurdi. The nuchal of F. hurdi pertains to a turtle about 30 percent larger than F. nanus, but both species are much smaller than Hesperotestudo or Gopherus. Anterior nuchal border of both Floridemys species also is much narrower than in Hesperotestudo or Gopherus (Fig. 12, bottom).

Description.—Nuchal of Floridemys hurdi is thickest along a ventral transverse ridge located two-fifths of the way behind the front of the element; posterior border is thin and distinctly concave on the medial ventral side (Fig. 12.2, 12.4, 12.5). Dorsal surface is faintly rugose (Fig. 12.3). Cervical scute on dorsal surface narrow and located far forward on the nuchal; on ventral surface cervical widens markedly into an irregular hexagon (Fig. 12.1, 12.5).

Etymology.—This species is named for its discoverer, Chris Hurd.

Holotype.—A well preserved nuchal (CMM-V-4666).

Occurrence.—Float material found on the beach beneath Randle Cliff, Calvert County, Maryland. The cliff includes strata belonging to Shattuck zones 4–11 (Plum Point A and B). All other land turtle remains from this interval so far have come from zones 10 and 11, so Plum Point B is the likely interval of derivation.

Remarks.—The dorsal surface of the nuchal of F. nanus somewhat resembles the nuchal element of emydid turtles in its constricted anterior border and narrow but elongated cervical scute (Fig. 12.3). However, the great lateral expansion of the cervical scute on the ventral side of the nuchal (Fig. 12.1, 12.5) belies emydid assignment and is compatible only with assignment to the family Testudinidae. Similarly, the arrangement of the costals, alternately wide and narrow at their distal ends, is a characteristic found in testudinid but not emydid turtles. The nuchal in both species of Floridemys is about as wide as long and narrow along the anterior border. This is quite different from the nuchals of Hesperotestudo and Gopherus, which are both much wider than long and have long anterior borders (Fig. 12, bottom). The type specimen of Floridemys was described by Hay (1916) as Bystra nana. That generic name was preoccupied, so the replacement name Floridemys was proposed by Williams (1950). Hay originally believed that the type came from Pliocene strata, but it since has been determined that it probably came from lower Miocene (or possibly upper Oligocene) strata (Auffenberg, 1974; Hulbert, 2001, p. 132). Whether F. nanus and F. hurdi co-existed along different parts of the Miocene Atlantic coast line, or whether the two species are different in age and one species was the ancestor of the other, cannot be determined given what little we know about the stratigraphic provenance of the type of F. nanus.

Family Trionychidae (Fitzinger, 1826). Bell, 1828

Genus Apalone Rafinesque, 1832

Apalone lima (Cope, 1869)

Figure 13

Material.—Three small to large carapace fragments (CMM-V-4661 (two pieces), USNM 540752), one left xiphiplastron fragment (USNM 540753). Pollack Farm material collected by G. Simonson; Pamunkey River material collected by R. Ison.

Description.—Thick, flat costal elements with rounded distal edges. Dorsal surface bears rather high and narrow ridges running across the bone, separated by grooves that are somewhat wider than the ridges. Summits of the ridges are uneven. Connecting ridges are rare, but occasionally a ridge divides or abruptly comes to an end. Proximally the ridges are somewhat irregular in their course, distally they are narrow and much interrupted. There is no evidence of sulcal grooves.

Occurrence.—One carapace fragment (USNM 540752) and xiphiplastron fragment (USNM 540753) are from the Pollack Farm Fossil site near Cheswold, Kent County, Delaware. Two costal fragments (CMM-V-4661) are from the Pamunkey River where it forms the boundary between King William and New Kent counties, Virginia. All specimens are from the upper Fairhaven Member (Fairhaven C) of the Calvert Formation, upper lower Miocene (Burdigalian).

Remarks.—The combination of a ridge and groove sculpture pattern on the external surface of these elements, the absence of any sign of peripheral sutures on distal costal elements, and the absence of any indication of sulcal grooves all readily characterize this material as pertaining to the family
FIGURE 10—Neural and costal elements referable to *Hesperotestudo wilsoni* (Auffenberg, 1964). 1, 2, costal fragment (USNM 483391) in dorsal and lateral views, respectively; 3–5, neural (USNM 483391) in ventral, posterior, and dorsal views, respectively; 6–8, neural (USNM 540747) in ventral, posterior, and dorsal views, respectively.
Trionychidae. The two specimens from Virginia (Fig. 13.5–13.8) are thick and have a ridge and groove sculpture pattern indistinguishable from *Apalone lima* (Cope, 1869). Not all parts of the carapace and plastron have this pattern, so small fragments with a less organized pattern (Fig. 13.3, 13.4) also can pertain to this species. The xiphiplastron fragment (Fig. 13.1, 13.2) has short ridge segments arranged in an irregular pattern.

This species originally was assigned by Cope (1869) to the genus *Trionyx*, which in the nineteenth century was a catch-all generic designation for most fossil trionychid material found in...
**Figure 12**—1–5, top, holotype nuchal of *Floridemys hurdi* new species (CMM-V-4666) in anterior, posterior, dorsal, left lateral, and ventral views, respectively; bottom, comparison of the nuchals of *Floridemys hurdi*, *Floridemys nanus*, *Gopherus polyphemus*, and *Hesperotestudo williamsi* in external (dorsal) view, all to same scale. *Floridemys nanus* drawn from photograph of type specimen nuchal, *Hesperotestudo williamsi* from Auffenberg, 1964, *Gopherus polyphemus* from Auffenberg, 1976.
North America. Modern taxonomic analysis restricts the genus *Trionyx* to the African softshell turtle *T. triunguis* (Meylan, 1987), so it is no longer plausible to place the species *lima* in that genus. Generic taxonomy within the family Trionychidae depends heavily on cranial and plastral anatomy, and none of the type material or the material figured here and ascribed to *Apalone lima* includes cranial or diagnostic plastral elements. Therefore, generic assignment for this taxon cannot be proven at this time, even though the species *lima* seems readily recognizable. All modern soft-shell turtles in eastern North America are referable to the genus *Apalone*, and the living species *A. ferox* has a pattern of ridges along the outer half of its mid-costals that is somewhat similar to that of *A. lima*. Miocene material from the Lee Creek Mine in North Carolina was considered by Zug (2001) to be

![Figure 13](image_url)
probably (though not certainly) referable to *Apalone*. Because the Lee Creek Mine specimens came from the Pungo River Formation, which is identical in age to the lower Calvert Formation, it is likely that they pertain to *A. lima*. The thick-shelled trionychid material described from the lower Miocene Fleming Formation of Texas by Albright (1994) also may pertain to *A. lima*, but again no definitive identification is possible. Because there is no evidence to refute the assignment of this Miocene material to *Apalone*, the species *lima* is referred to that genus until such time as any evidence comes to light demonstrating the presence of any other genus of softshell turtle in the Neogene or Quaternary of North America.

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DISCUSSION

The specimens described and illustrated here expand our knowledge of early to middle Miocene nonmarine turtles in the Calvert Formation from four to eight taxa and provide the first evidence for amphibians. Even so, this new material offers only a limited glimpse into the overall skeletal anatomy of these animals, for their remains are rare and almost always fragmentary. In our current state of knowledge, it is still possible to argue that there was a diverse early to middle Miocene amphibian and nonmarine turtle fauna in what is now the southeastern United States that mostly remains undiscovered. If so, however, it is remarkably well hidden across a very large region (Table 1).
Based on pollen from the Pollack Farm fossil site, Groot (1998) concluded that the coastal region near Delaware was heavily forested during the early Miocene, basing that interpretation on the relative scarcity of herbaceous pollen. He also concluded that the climate was much like that of northern Florida and Georgia today. The pollen spectrum is heavily dominated by pine and oak, however, and although this could represent a commonly occurring bias toward preservation of these two types of pollen in offshore marine strata, it also could reflect a real preponderance of these two kinds of trees in the early-middle Miocene landscape. Pine, especially, is prone to attracting lightening strikes, starting ground fires, and then surviving the subsequent burn of ground cover. This disjunct equilibrium environment is typical of the “Pine Barrens” of New Jersey today and greatly impedes the development of dense brush in the relatively upland areas away from stream bottoms (Forman, 1998). Such an environment would tend to restrict amphibians and reptiles (except tortoises) to areas near streams and stream bottoms.

Land mammal remains are rare in the Calvert Formation, but even so many taxa have been identified. Within the lower part of the Calvert Formation, where all amphibian and nonmarine turtle remains have been found, the Pollack Farm site has produced the most diverse mammalian assemblage. This includes an insectivore (Plesiosorex), possible hedgehogs (unidentified genera), a vesper bat (unidentified genus), two kinds of beavers (Architheriomys and “Monosaulax”), a pocket mouse (Proheteromys), a jumping mouse (Pleiosomithus), two kinds of raccoons (unidentified genera), a bear (“Hemicyon”), two kinds of bear dogs (Amphicyon and Cynelos), two kinds of canids (both Tomarctus), three kinds of horses (Archaeohippus, Architherium, Parahippus), a chalicothere (Tyoelopehalonyx), a rhinoceros (unidentified genus or perhaps genera), two kinds of peccary (Cynorca and Desmatophyus [or Hesperhyus]), a possible anthracothere (unidentified genus), an oreodont (unidentified genus), and a musk deer (Blastomeryx) (Emry and Eschelman, 1998). Based on the presence of beaver remains, Emry and Eshelman (1998) argued that the early Miocene climate was relatively wet. However, they did not entertain the possibility that beaver remains could be from animals that seasonally lived in brackish water environments rather than the fresh water habitats usually preferred by beavers. A number of modern cases have been documented wherein beavers live for prolonged intervals of time in brackish water and even build dams there, so the beavers from the Miocene Calvert Formation could have been adapted to living along the back edges of coastal marshes during the dry part of a seasonally dry climate. Although Groot (1998) did not find much evidence for grasses and herbs, the relative abundance and diversity of horses led Emry and Eshelman (1998) to postulate the presence of at least some open grassy areas in apparent contradiction to the pollen spectrum profile. This interpretation is compatible with a pine-barrens environment.

The relative abundance and diversity of tortoises, compared to all other nonmarine turtle remains, supports a conclusion that the early-middle Miocene climate was at least seasonally dry. It is noteworthy in this regard that many of the freshwater turtles that are present (Bairdemys, Apalone, and Trachemys) could have relied during dry seasons on coastal back barrier marshes that were brackish rather than truly fresh. Bairdemys was certainly salt-water tolerant (Weems and Knight, 2012), some species of Pseudemys (closely related to Trachemys) today inhabit brackish coastal rivers in Florida (Holman, 1998), and the Florida soft-shell turtle (Apalone ferox) sometimes is found today in brackish water (Ernst and Barbour, 1989). Remains of alligators are extremely rare in the Calvert Formation, consisting of only a few scutes from the Pollack Farm site. Similarly, amphibian remains are rare and of very limited diversity in the Calvert Formation and age-equivalent strata throughout the Atlantic Coastal Plain. This could be the result of spotty collecting of fossil remains of nonmarine animals, but it also could be that habitually freshwater vertebrates simply were not common at that time in the southeastern United States and thus were unlikely to be introduced into the shallow marine depositional environments of the Calvert Formation.

The wide geographic occurrence of most of these taxa throughout the Atlantic and Gulf coastal plains in the early and middle Miocene indicates that this area was a fairly homogenous climatic belt that harbored a uniform and widespread fauna. Only Dermatemys is restricted to the far southwestern part of this area (Albright, 1994), but this is consistent with its modern range which is only in wetter areas of southern Mexico and Central America. At the end of the middle Miocene, global climatic cooling put an end to this homogenous climatic belt and it became subdivided into more localized environments and faunas.

The discovery of Floridemys in the Calvert Formation is intriguing. This is an unusually small tortoise that existed in a landscape with quite large mammals. While large Hesperotes-tudo obviously could survive around large mammals without being readily crushed, it is harder to understand how such a small form as Floridemys could have survived underfoot. It is also curious that an obviously terrestrial tortoise like Floridemys has only been found (and only rarely) in marine sediments in Maryland and Florida. Although testudinids are not uncommon finds in the Miocene deposits of the Great Plains (Hay, 1907) no Floridemys material is reported from there. In view of the unusually small size of this genus, in comparison with species of the closely related tortoises Hesperotes-tudo and Gopherus, and its known occurrence only in marine sediments within the southeastern coastal region of the United States, it is proposed here that Floridemys was adapted to life along Miocene barrier islands along the coast of the southeastern United States. The related species Hesperotes-tudo bermudae Meylan and Sterratt (2000) was able to colonize Bermuda from North America across more than one thousand kilometers of the Atlantic Ocean during the Pleistocene, so colonization of near-shore barrier islands by Floridemys should not have been difficult. Prior to the Quaternary, barrier island deposits in the southeastern United States were almost never preserved in the fossil record (but see Weems and Sanders, 1986 for a rare Oligocene exception). Thus, fossils of a Miocene barrier island tortoise only would be likely found in marine sediments offshore of its barrier island habitat when individuals were occasionally swept out to sea, perhaps during hurricanes. Similarly, even though the small area of most barrier islands encourages insular dwarfism in any normally large animal that takes up life in this environment (e.g., dinosaurs: Benton et al., 2010; elephants: Poulakakis et al., 2006; hominids: Aiello, 2010), the isolated habitat of barrier islands at the same time would tend to protect these animals and dwarf tortoises from large predators that on the mainland would readily prey on them. The generally high sea level stands during the early and middle Miocene were conducive to the development of extensive barrier island systems, but the fabric of this system was severely altered near the beginning of the late Miocene when a significant world-wide drop in sea level occurred due to a prolonged accumulation of polar glacial ice. It is likely that this event, with the concurrent widespread destruction of barrier island systems, caused the extinction of Floridemys.
Another striking feature of this fauna is the complete absence so far of any turtle remains referable to the family Chelydridae. Chelydrids are known from the western interior of North America as far back as the late Paleocene (Erickson, 1973), but the oldest chelydrids from the southeastern United States are *Macrolemys auffenbergi* from the late Miocene of Florida (Hulbert, 2001, p. 123) and *Chelydra* sp. from the late Miocene or possibly early Pliocene Gray Fossil Site in eastern Tennessee (Bentley et al., 2011). Chelydrids are tolerant of brackish water, so a complete aversion to salt water cannot explain their absence in the lower and middle Miocene fossil record of the southeast. Although their absence may be an artifact of incomplete collecting, it seems more likely that they truly were not present. The only obvious explanation is that, before the late Miocene, the presence of *Bairdemys* in the coastal plain rivers kept chelydrid turtles from spreading into this environment. Once *Bairdemys* went extinct in North America, probably at the end of the middle Miocene or early in the late Miocene, chelydrids then had opportunity to move into their vacated ecological niche.

Nonmarine turtles so far have been found in the Calvert Formation at only two levels, the upper middle portion of the Fairhaven Member (Fairhaven C—Popes Creek Sand /Newport News beds interval) (ca. 18 Ma) and in Shattuck’s zones 10 and lower 11 of the Plum Point Member (Plum Point B) (ca. 14 Ma). In both cases, it seems likely that the deposits preserved in these intervals formed in relatively shallow marine water. It also may be that there was an exceptional local influx of fresh water, at least seasonally, from the continental interior at those times. Enough time separates these two horizons to place them in two different North American Land Mammal Stages, the early Hemingfordian and the early Barstovian (Emry and Eshelman, 1998), and the presence of two distinctly different species of *Hesperoptestudo* (Caudochelys) at these two horizons suggests at least some significant evolutionary change occurred among turtles across this time interval. Similarly, the amphibian *Batrachosauroidea* increased considerably in size from the early Miocene to the middle Miocene (Albright, 1994). Otherwise, there is little indication of significant change in the complexion of nonmarine turtle or amphibian populations throughout this time interval. As is also the case for sea turtles from the Calvert Formation, the late early and early middle Miocene along the southeastern U.S. seaboard apparently was a time of only gradual change as seen from the perspective of amphibian and reptile populations.

The transition from the middle to the late Miocene, however, probably witnessed considerable climatic and related evolutionary changes that accompanied global cooling and significant Antarctic glacier growth (Wolfe, 1994; Zachos and others, 2001; Böhme, 2003). By the later late Miocene (Messinian), the amphibian *Batrachosauroidea*, the side-neck turtle *Bairdemys*, and the emydid turtle *Chrysemys isoni* apparently had become extinct in the southeastern United States. Also toward the end of the late Miocene (Messinian), a chelydrid (*Macrolemys*) first appears in this region and the amphibian and turtle faunas of the southeastern United States begin to acquire their modern complexion.

**Acknowledgments**

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**References**


