Review of the Fossil Trionychidae (Testudines) from Alabama, Including the Oldest Record of Trionychid Turtles from Eastern North America

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ABSTRACT

Trionychid turtles are currently found throughout much of eastern North America, but their fossil record within this region has not been thoroughly documented. This study reviews previously reported trionychid fossils from Cretaceous to Pleistocene strata of Alabama and makes new additions to that list. The fossils described herein include the first trionychid fossils from the Cretaceous of Alabama and the oldest reported trionychid fossils from eastern North America. The presence of trionychids in Alabama at this time may imply that the family traversed the Western Interior Seaway before it had completely closed off. New trionychid fossil specimens are also reported from the Eocene and the late Miocene of Alabama. A late Miocene (Hemphillian) trionychid specimen, a nearly complete carapace, is here attributed to *Apalone* cf. *A. spinifera* and may represent one of the earliest records of that species known. Several Pleistocene trionychid fossils are described, a few of which are assigned to *A. spinifera*. These Alabama trionychid fossils, while mostly fragmentary, help in the understanding of the evolution of trionychids in the eastern United States and may have further implications for their paleobiology and the paleoecology of Alabama and eastern North America.

INTRODUCTION

Trionychids (Testudines: Trionychidae), soft-shelled turtles, are common turtle fossils recovered from Cretaceous through Quaternary strata in North America. Their fossils are relatively easy to identify to the higher taxonomic level, and these turtles are known to frequently live in ponds, rivers, streams, and other environments that are routinely good for fossilization. Their fossil record in North America dates back to at least the Upper Cretaceous Dunvegan Formation (Cenomanian) of Alberta, Canada, and representatives of this family still exist today (Brinkman, 2003). Trionychids are unique as they lack several features present among other turtles. They lack keratinous scutes, pygals, and an ossified bridge connecting the carapace and plastron, while maintaining a layer of leathery skin that covers their shells (Ernst and Barbour, 1989). The leathery skin is laid over papillose areas of the carapace and plastron known as callosities (Bonin et al., 2006). Their fossils are often easy to identify (to family level) based on texture and surface ornamentation from these callosities.

Today, trionychids can be found in Africa, Asia, the Indo-Archipelago, and North America, and the fossil record indicates they were once present in Australia, Europe, and South America as well (Gaffney and Bartholomai, 1979; Gaffney, 1981; Ernst and Barbour, 1989; Ernst and Lovich, 2009). *Apalone* is the only currently recognized modern trionychid genus from North America, and at least four species, *A. calvata*, *A. ferox*, *A. mutica*, and *A. spinifera* (*A. s. aspera, and A. s. spinifera*), have been reported from Alabama (Buhlmann et al., 2008; Ernst and Lovich, 2009; Guyer et al., in press). These taxa are also the only representatives of the family in eastern North America today.

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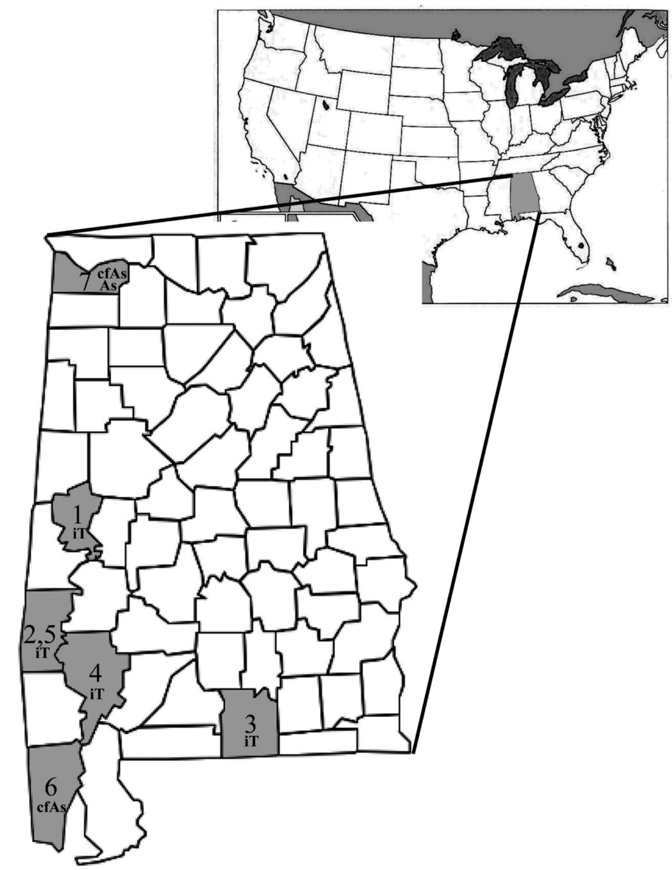

Figure 1. Localities of fossil Trionychidae from counties in Alabama. Abbreviations for fossil sites: 1, Site AGr–43 (Upper Cretaceous); 2, Site ACh–3 (lower Eocene); 3, Site ACov–11 (lower to middle Eocene, and middle Eocene); 4, Site ACl–3 (middle Eocene); 5, Site ACh–21 (upper middle Eocene); 6, Site AMb–1 (upper Miocene); 7, Site ACb–2 (upper Pleistocene). Abbreviations for taxonomic identifications: As, *Apalone spinifera*, cfAs, *Apalone* cf. *A. spinifera*, iT, indeterminate trionychid.

This study offers a review of trionychid fossils from Alabama, providing insight into the poorly known fossil record of trionychids from eastern North America (east of the Mississippi River).

Reviewed here are the stratigraphic distributions of fossil trionychid turtles from Alabama. Specimens from each stratigraphic unit are reviewed by locality, elements present, and morphological features. Key stratigraphic, evolutionary, and/or paleobiological features are discussed in each geologic time interval, such as Cretaceous, Eocene, Miocene, and Pleistocene.

Institutional Abbreviations—MSUVP: Michigan State University Museum (Vertebrate Paleontology Collections), East Lansing, Michigan; **RMM**: Red Mountain Museum (currently the collection is housed at McWane Science Center), Birmingham, Alabama; **UAM**: University of Alabama Museums, Tuscaloosa, Alabama; **USNM**: United States National Museum, Washington, D.C.

MATERIAL AND METHODS

Geologic Setting

Definitive trionychid fossils have been recovered from various localities across Alabama, although most were collected from the western part of the state (Fig. 1). Specimens have been recovered from localities of various ages, which include the Late Cretaceous (site AGr-43), early Eocene (site ACh-3), early to middle Eocene (site ACov-11), middle Eocene (site ACl-3), late middle Eocene (site ACh-21), late Miocene (site AMb-1), and late Pleistocene (site ACb-2) (Fig. 2). In this study, fossils are presented stratigraphically, from oldest to youngest, and by locality. Additional locality information is available to qualified researchers by contacting McWane Science Center in Birmingham or the Alabama Museum of Natural History in Tuscaloosa.

Samples

Literature, museum catalogues, and firsthand specimen examination were used in this study. As much information was recorded as possible for all specimens, including elements present, locality information, geologic units, and measurements. Pictures and descriptions were taken of each specimen when possible.

RESULTS

Cretaceous Trionychids (from Eutaw Formation)

Locality and Stratigraphic Information—Site AGr-43, Greene County, Alabama. Tombigbee Sand Member (upper Santonian to lower Campanian) of the Upper Cretaceous Eutaw Formation.

Material—UAM PV1990.0006.0003, costal fragment (Fig. 3A–B); UAM PV1994.0002.0058, hyoplastron(?) fragment (Fig. 3C–D); UAM PV1994.0005.0034, indeterminate shell fragment (Fig. 3E–F).

Description—The costal fragment (UAM PV1990.0006.0003) measures 19.74 mm anteroposteriorly by 36.08 mm mediolaterally. It is thicker towards its medial portion, and thinner laterally. While there are a few pits that make up the sculpturing medially, the majority of the dorsal surface is covered with numerous rows and furrows (Fig. 3A). The pits are mostly circular, sub-circular, or elongate and the rows, or grooves, are not straight, tending to be generally oriented in an anterolateral to mediposterior direction. There are a few raised areas within the grooves that break up their continuity. Ventrally, the element is quite smooth (Fig. 3B).

UAM PV1994.0002.0058 represents the only plastron

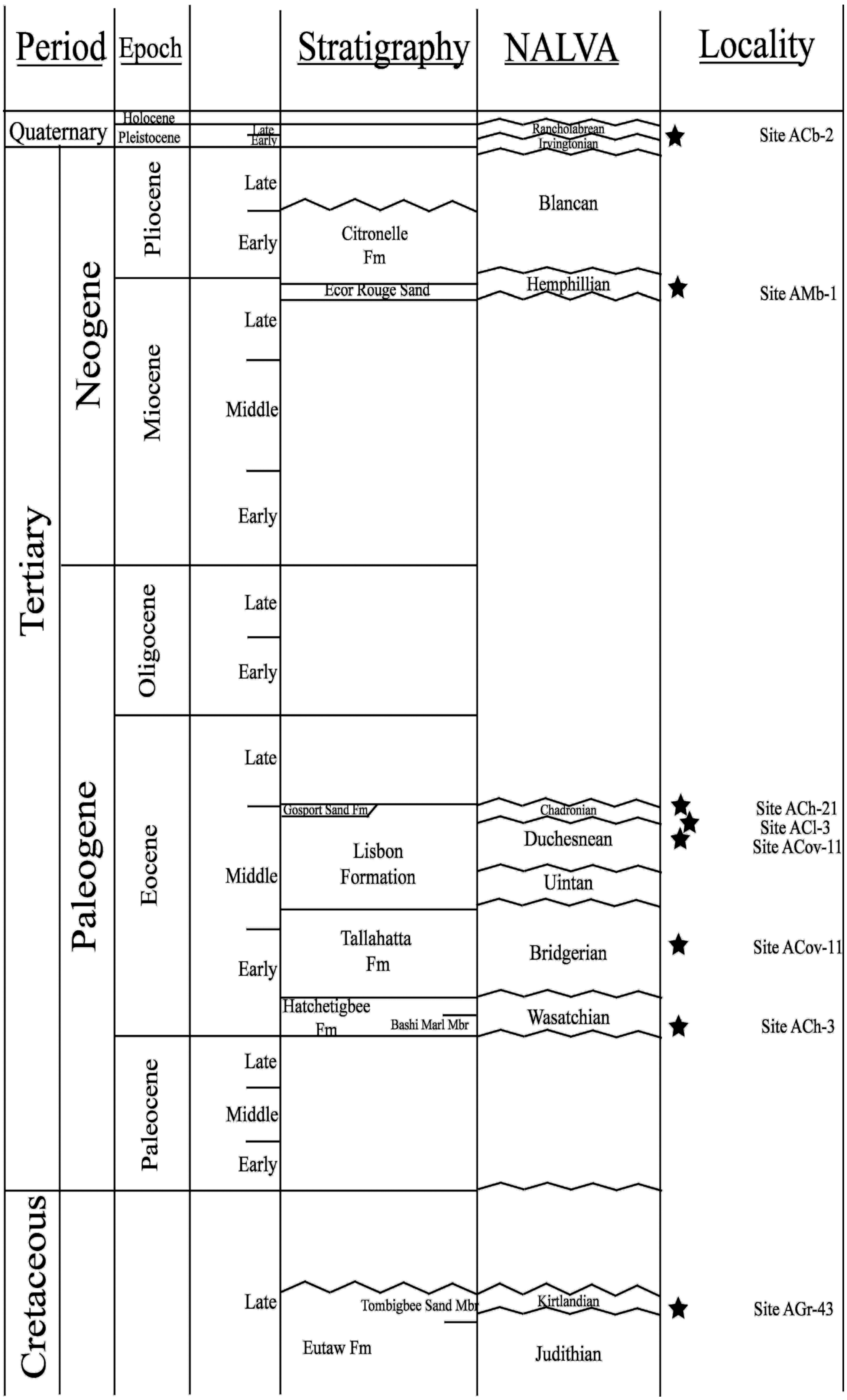

Figure 2. Stratigraphic occurrences of trionychid fossils from Alabama. The star symbol indicates a fossil trionychid occurrence. Site ACov–11 is listed twice for the two layers representing trionychid fossils; one in the Tallahatta Formation and one in the Lisbon Formation. Abbreviations: Fm, formation; Mbr, member, NALVA, North American Land Vertebrate Age.

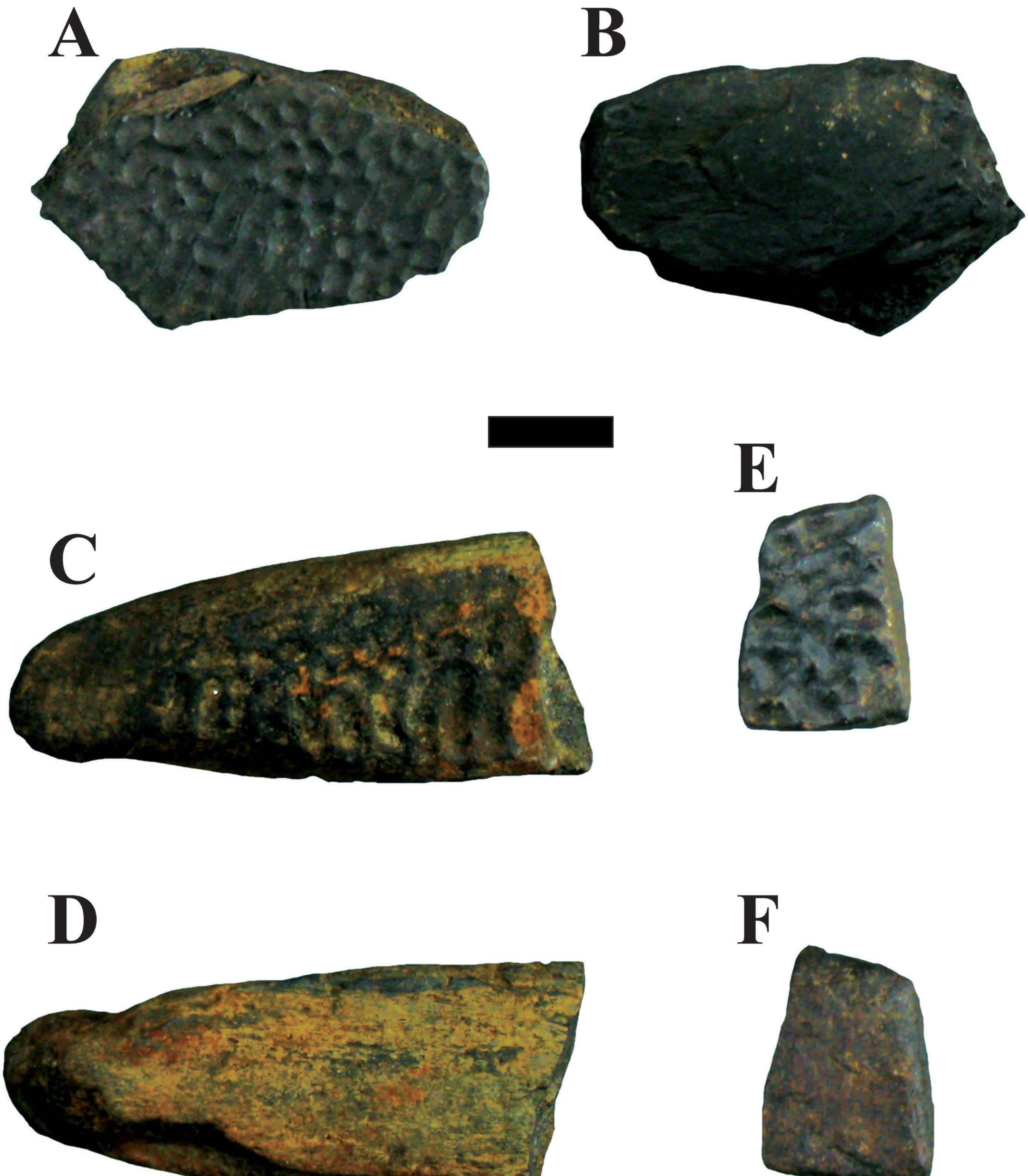

Figure 3. Late Cretaceous trionychid turtles from Alabama. A–B, UAM PV1990.0006.0003, costal fragment in dorsal (A) and ventral (B) views. C–D, UAM PV1994.0002.0058, hyoplastron(?) fragment in ventral (C) and dorsal (D) views. E–F, UAM PV1994.0005.0034, indeterminate shell fragment in external (E) and internal (visceral) (F) views. Scale bar equals 1 cm.

fragment from a Cretaceous trionychid known from Alabama. It is tentatively identified as the anterolateral portion of the hyoplastron. Surface sculpturing is comprised of several crescent grooves separated by numerous ovoid and/or elongate pits, which are particularly prominent towards the lateral edge (Fig. 3C). Distal to the sculptured surface (anteriorly), the element becomes far thinner (8.30 mm versus 11.06 mm) and smooth. Medially and proximally the element is broken. It has a maximum preserved anteroposterior length of 48.01 mm and a maximum preserved transverse width of 20.31 mm, making it quite robust. The element would have belonged to a relatively large individual due to its general size and robustness. Dorsally (viscerally), the element is smooth with no sculpturing (Fig. 3D).

UAM PV1994.0005.0034 is represented by two shell fragments. The larger of the two is very smooth and robust. It does not represent a trionychid but, instead, some other type of turtle with a smooth shell surface such as a member of the Adocidae or Baenidae. However, the smaller is a costal(?) fragment, with a maximum preserved width (transversely) of 14.18 mm and a maximum preserved length (anteroposteriorly) of 18.71 mm, and does represent a trionychid (Fig. 3E). The surface sculpturing of the element is comprised almost entirely of pitting. Similar to UAM PV1990.0006.0003, the pits are almost entirely circular to sub-circular in shape. With so little of the specimen preserved it is not known if there would have been any grooves present, or if they are just not present on this portion of the shell. Ventrally the surface contains no sculpturing (Fig. 3F).

Remarks—The fossils described above represent the first reported trionychid fossils from the Cretaceous of Alabama. All three specimens, however, are too fragmentary to identify to the generic level and are considered indeterminate trionychids. While Puckett (1996) estimated that the Tombigbee Sand Member to be Santonian in age based on ostracode biostratigraphy, Obradovich (1993) suggested the unit spanned the Santonian–Campanian boundary. Becker et al. (2008) later suggested just the base of the unit extended into the uppermost Santonian. The age of the Tombigbee Sand is further discussed below. Considering the unit to be latest Santonian to early Campanian in age, the trionychids from the Tombigbee Sand represent the oldest record of the family from east of the Mississippi River in North America.

Eocene Trionychid (from Hachetigbee Formation)

Locality and Stratigraphic Information—Site ACh-3, Choctaw County, Alabama. Bashi Marl Member (lower Ypresian) of the lower Eocene Hachetigbee Formation.

Material—UAM PV1989.0004.0178, nearly complete left 1st costal (Fig. 4A–B).

Description—UAM PV1989.0004.0178 represents a nearly complete left 1st costal. It has a maximum mediolateral width of 74.05 mm and a maximum anteroposterior length of 38.00 mm. The surface texture is subdued, which appears to be from postmortem taphonomic processes (Fig. 4A). Ornamentation, or sculpturing, on the carapacial surface is comprised of numerous circular pits, most of which have coalesced into jagged grooves. Medially these grooves seem to be mediolaterally-oriented, but laterally they are more anteroposteriorly-oriented. On the ventral surface, the curved, inflated surface that signifies the first costal rib is readily identifiable (Fig. 4B). The element is thicker medially and thinner laterally. It is conservatively identified as an indeterminate trionychid.

Eocene Trionychid (from Tallahatta Formation)

Locality and Stratigraphic Information—Site ACov-11, Covington County, Alabama. Lower to middle Eocene Tallahatta Formation (upper Ypresian to lower Lutetian).

Material—MSUVP 1186, two partial costals and one complete neural.

Remarks—Holman and Case (1988) reported two fragmentary costals and a complete neural from the Tallahatta Formation. They identified the material as an indeterminate trionychine and figured all three elements (Holman and Case, 1988, fig. 1). The authors reported that one costal had sculpturing comprised of pits that were either circular or ovoid in shape, while the other was covered with elongated pits and ridges. Both types of sculpturing may occur on a single complete costal in some fossil trionychids (Holman and Case, 1988; Gardner and Russell, 1994). This is clearly evident for *"Amyda" egregria* (Hay, 1908, 531, fig. 1), which has both the circular and ovoid pattern in the medial parts of its costals, and an elongated pit and ridge pattern in the lateral portions (Holman and Case, 1988). The neural is believed to be a 4th. The larger costal (Holman and Case, 1988, fig. 1B) was thought to be from an individual with a carapacial length of approximately 460 mm based on comparisons with other trionychid material, indicating a relatively large trionychid. Holroyd et al. (2005) agreed with the earlier identification of an indeterminate trionychine. Little else can be noted of the material present. Based mainly on the sculpturing, the identification of Holman and Case (1988) and Holroyd et al. (2005) of an indeterminate trionychine is conservatively maintained.

Eocene Trionychid (from Lisbon Formation)

Locality and Stratigraphic Information—Site ACov-11, Covington County, Alabama. Middle Eocene Lisbon Formation (middle Lutetian to middle Bartonian).

Material—UAM PV1992.0028.0007, an incomplete right 5th(?) costal (Fig. 4C–D); UAM PV1992.0028.0019, plastron fragment, incomplete costal fragment, indeterminate shell fragment (Fig. 4E–J).

Description—UAM PV1992.0028.0007 represents the

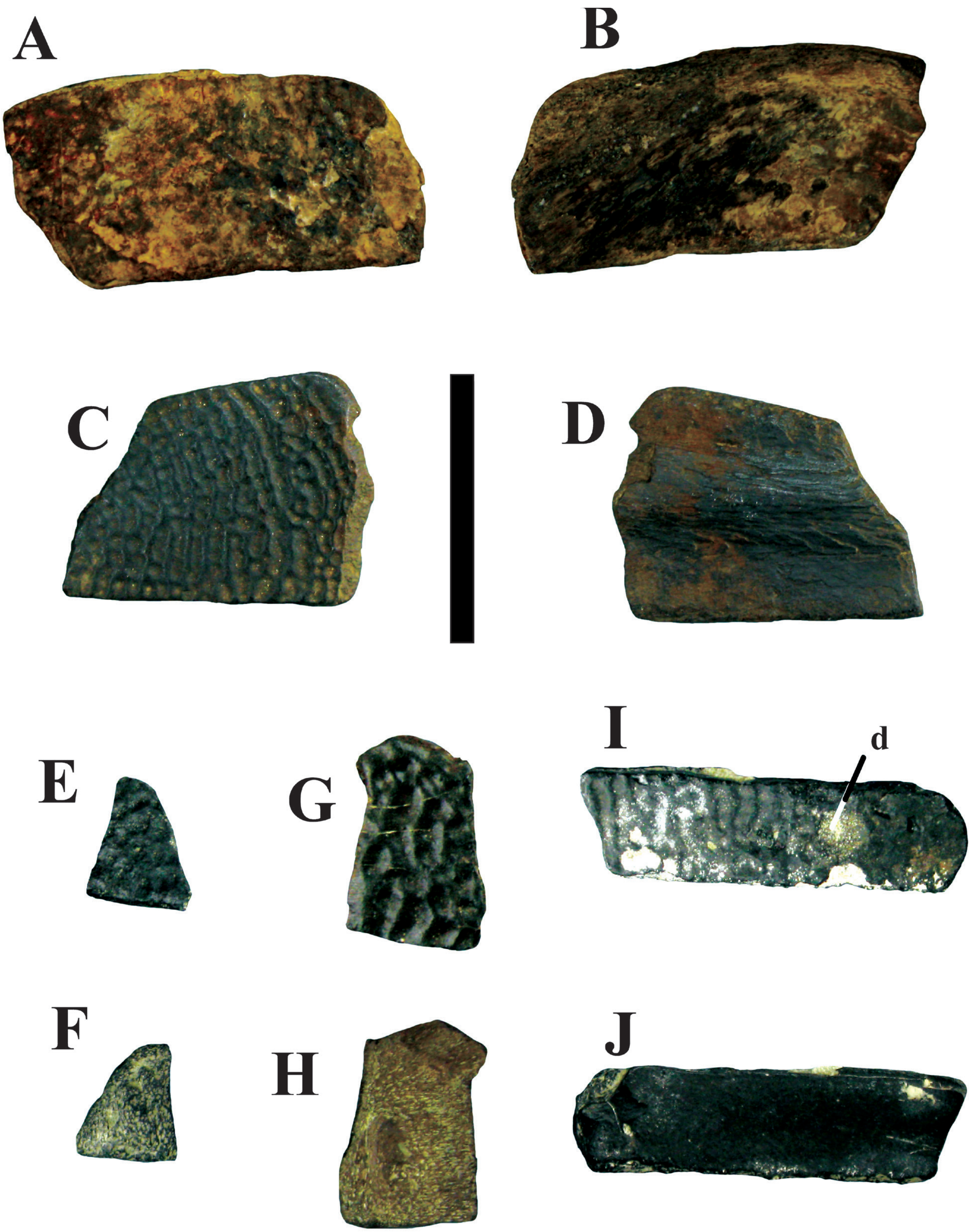

Figure 4. Eocene trionychid turtles from Alabama. A–B, UAM PV1989.0004.0178, nearly complete left 1st costal in dorsal (A) and ventral (B) views. C–D, UAM PV1992.0028.0007, incomplete right 5th(?) costal in dorsal (C) and ventral (D) views. E–J, UAM PV1992.0028.0019, indeterminate shell fragment in external (E) and internal (visceral) (F) views; plastron fragment in ventral (G) and dorsal (H) views; and incomplete costal fragment in dorsal (I) and ventral (J) views. Abbreviation: d, depression. Scale bar equals 5 cm.

distal portion of a right 5th(?) costal. This identification is based partially on its slight anteroposterior asymmetry, along with the ventral inflation for the costal rib. The element flares distally, and the lateral edge is uneven, although partially incomplete. The preserved bone has a maximum anteroposterior length of 43.18 mm at its lateral edge, and a maximum mediolateral width of 53.86 mm at its posterior edge. Dorsally, the surface is comprised of pitting and grooves where the pits have semi-coalesced (Fig. 4C). The pits tend to be circular to ovoid in shape, while the surface texture is slightly subdued due to presumed weathering. Ventrally the element is smooth with little distinct morphology (Fig. 4D).

Of the three shell fragments in UAM PV1992.0028.0019, the smallest represents an indeterminate element. It is sub-triangular in shape, with its three sides measuring 19.49 mm, 21.60 mm, and 26.62 mm, respectively. The visceral surface is not preserved (Fig. 4F), while the external surface is sculptured with numerous pits (Fig. 4E). The plastron fragment is sub-rectangular and measures 35.43 mm mediolaterally and 23.83 mm anteroposteriorly (maximum length). The visceral, or dorsal, surface is only partially preserved towards the medial edge (Fig. 4H). It is believed to be a plastron fragment based partially on the geometry of the preserved portion of the visceral surface. Ventrally, the sculpturing is comprised of numerous pits, some of which have slightly coalesced into small rows or grooves (Fig. 4G). The pits themselves are relatively large and circular to ovoid in shape. The costal fragment is sub-rectangular as well, with an anteroposterior length of 17.44 mm (measured proximally) and a mediolateral width of 64.42 mm. It is broken midway through, missing both its distal end and half its length (along the costal rib). The portion of the ventral surface that is preserved shows part of the inflation for the costal rib (Fig. 4J). Dorsally, numerous pits are present, with a large percentage of them coalesced into grooves or rows. A small depression is present on the dorsal surface that appears broken (Fig. 4Id).

Remarks—The material described from ACov-11 is too incomplete to identify to the generic level and so is here considered indeterminate Trionychidae.

Locality and Stratigraphic Information—Site ACl-3, Clarke County, Alabama. Middle Eocene upper Lisbon Formation (middle Bartonian).

Material—UAM PV2000.0001.0046, incomplete right 3rd(?) costal (Fig. 5A–B).

Description—UAM PV2000.0001.0046 represents the median portion of a costal, questionably identified as a right 3rd. This identification is based on the parallel anterior and posterior edges of the element, paired with the orientation of the inflation for the costal rib on its ventral surface. The costal has a maximum anteroposterior length of 55.61 mm and a maximum preserved mediolateral width of 57.52 mm through where the costal rib is present. Dorsally, the sculpturing is prominent and is

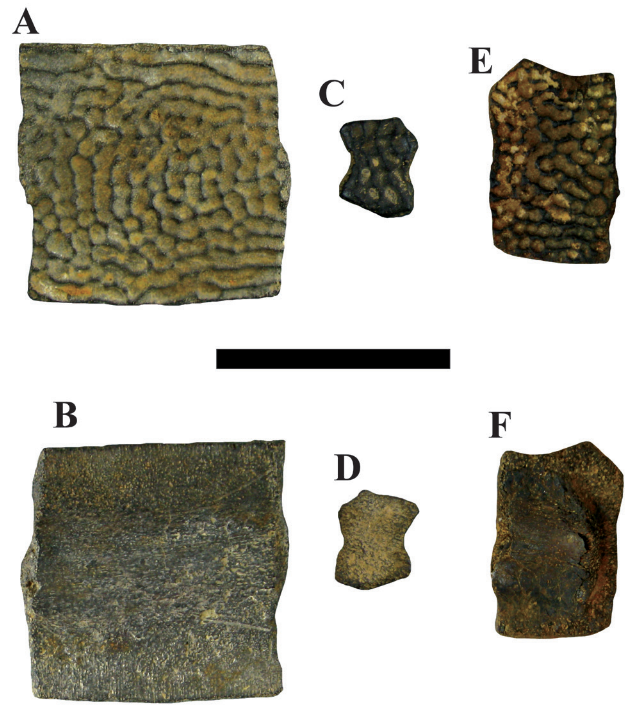

Figure 5. Eocene trionychid turtles from Alabama. A–B, UAM PV2000.0001.0046, incomplete right 3rd(?) costal in dorsal (A) and ventral (B) views. C–F, UAM PV1991.0034.0002, indeterminate shell fragment in external (C) and internal (visceral) (D) views; and proximal portion of right costal in dorsal (E) and ventral (F) views. Scale bar equals 5 cm.

represented by numerous grooves and furrows, with a few pits present toward its edges (Fig. 5A). The pits that are present are circular to ovoid in shape. Ventrally, the inflation for the costal rib is prominent and runs approximately through the middle of the costal (Fig. 5B).

Remarks—The material described from ACl-3 is too incomplete to identify further than being from an indeterminate trionychid.

Eocene Trionychid (from Gosport Formation)

Locality and Stratigraphic Information—Site ACh-21, Choctaw County, Alabama. Upper middle Eocene Gosport Sand Formation (upper middle Bartonian).

Material—UAM PV1991.0034.0002, proximal portion of right costal, indeterminate shell fragment (Fig. 5C–F).

Description—UAM PV1991.0034.0002 represents two different shell fragments. The smaller fragment has maximum measurements of 21.14 mm by 16.82 mm. Dorsally, the sculpturing contains approximately 14 pits, but no true grooves or rows (Fig. 5C). At least two of the sides of the element appear to be sutural surfaces. The element is quite thin, although much of this may be due to the ventral surface not being preserved completely (Fig. 5D). A proximal portion of a right costal is also preserved with UAM

PV1991.0034.0002. Since the anterior and posterior edges are reasonably parallel, this bone probably represents a median costal, potentially the 3rd or 4th. The costal has a maximum anteroposterior length of 41.35 mm, and the preserved mediolateral portion is 26.68 mm wide. While four of the sides of the element are rectangular, the anteromedial surface is angled where the costal would contact an anterior neural. Sculpturing of the dorsal surface contains numerous pits, the majority of which are ovoid in shape, with very few coalesced into grooves or rows (Fig. 5E). Ventrally the element is inflated where the rib would dorsomedially project to contact the dorsal vertebrae (Fig. 5F). The inflated surface is quite wide (28.88 mm).

Remarks—The material described from ACh-21 is too incomplete to identify further than being from indeterminate Trionychidae.

Miocene Trionychids

Locality and Stratigraphic Information—Site AMb-1, Mobile County, Alabama. "Ecor Rouge Sand" (beneath the Citronelle Formation) (Messinian, upper Miocene).

Material—USNM 347929, nearly complete carapace (Fig. 6).

Description—USNM 347929 is a nearly complete carapace from the late Miocene of Alabama (Fig. 6). The posterior of the shell is a bit fragmented, and the nuchal is incomplete. It has an approximate anteroposterior length, or straight carapace length, of 37.05 cm and a mediolateral width of 37.62 cm between the two lateral edges of the costal ribs (through the 4th costals). Seven neurals are present down the midline of the carapace (no preneural present), with 7 sets of costals present lateral to them. The nuchal and 7th costals are broken and fragmented. Ventrally, the carapace is similar to numerous other trionychids, particularly *Apalone*. Dorsally, the sculpturing of the carapace is comprised of various pits and ridges, often coalesced into longer ridges and grooves. The ridges and grooves comprise the vast majority of the carapacial sculpturing.

Remarks—Isphording and Lamb (1971) discussed the age and origin of the Citronelle Formation and inferred the maximum (oldest possible) age for the vertebrate fauna as Hemphillian, based mainly on comparisons of vertebrates recovered from similar sites in Florida. Isphording and Lamb (1971) briefly mentioned trionychid remains from this formation, but later research showed the material came from an informal unit located at the base of the Citronelle known locally as the Ecor Rouge Sand (Hulbert and Whitmore, 2006). Isphording and Lamb (1971) identified the remains as either *Apalone* ("*Trionyx*") *spinifera* or *A. ferox*, but did not provide a catalog number for the specimen. Hulbert and Whitmore (2006) mention that trionychid fossils (identified by the authors as "*Apalone*") are abundant in the Mauvilla local fauna at site AMb-1 in Mobile County, Alabama.

Figure 6. Late Miocene trionychid turtles from Alabama. *Apalone* cf. *A. spinifera* (USNM 347929), nearly complete carapace in dorsal view. Scale bar equals 10 cm.

USNM 347929 does not exhibit any ridging on the anterolateral portion of the carapace (anterior 'marginal' region), which was considered a characteristic of *A. ferox* by Ernst and Barbour (1989). While the nuchal is broken and incomplete in USNM 347929, it is approximately three times wider than long, adhering to a character of *A. spinifera* noted by Meylan (1987). Based on the morphology preserved and sculpturing, the fossil is referable to *Apalone* cf. *A. spinifera*. It is noted that *Apalone calvata*, *A. ferox*, *A. mutica*, and *A. spinifera* are present in Alabama today (Buhlmann et al., 2008; Ernst and Lovich, 2009; Guyer et al., in press).

Pleistocene Trionychids

Locality and Stratigraphic Information—Site ACb-2, Colbert County, Alabama (Wisconsinan, late Pleistocene).

Material of *Apalone* sp.—Zone 1/2: RMM 6805, nine shell fragments; RMM 3709, 27 shell fragments; RMM 3633, 10 shell fragments (Fig. 7); RMM 4858, 22 shell fragments; RMM 4952, 30 shell fragments; RMM 5185, 14 shell fragments. Zone 3: RMM 4186, 12 shell fragments; RMM 4723, two shell fragments; RMM 4644, 20 shell fragments; RMM 5341, 13 shell fragments; Zone 4: RMM 4474, one costal; RMM 4482, three shell fragments (Fig.

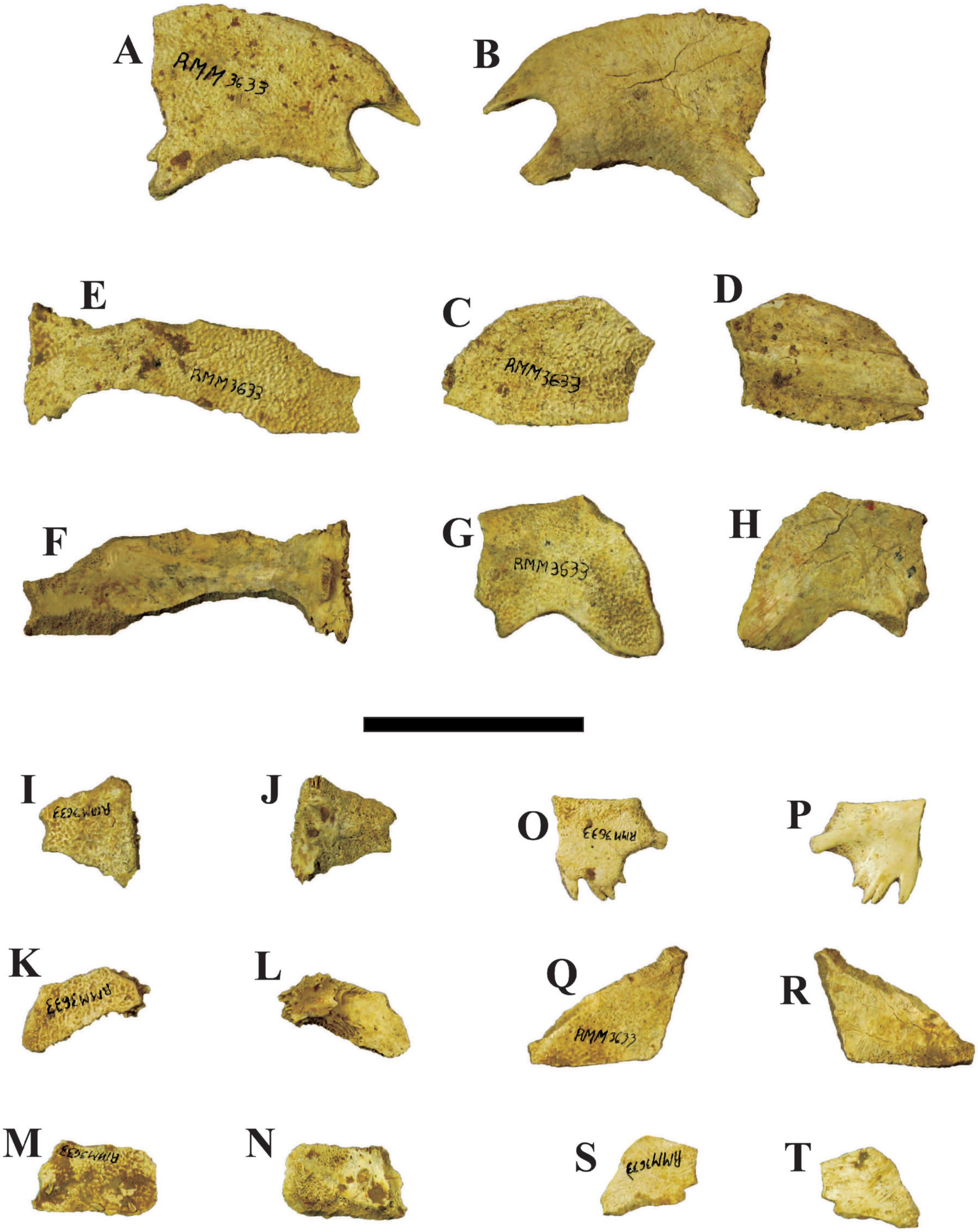

Figure 7. Pleistocene trionychid turtles from Alabama. A–T, *Apalone* sp. (RMM 3633), A–B, incomplete right hypoplastron in ventral (A) and dorsal (B) views; C–D, nearly complete 1st costal in, dorsal (C) and ventral (D) views; E–F, incomplete right 6th(?) costal in dorsal (E) and ventral (F) views; G–H, incomplete xiphiplastron in ventral (G) and dorsal (H) views; I–J indeterminate shell fragment in external (I) and internal (visceral) (J) views; K–L, fused neural and incomplete costal in dorsal (K) and ventral (L) views; M–N, indeterminate shell fragment in external (M) and internal (visceral) (N) views; O–P, plastron fragment in ventral (O) and dorsal (P) views; Q–R, indeterminate shell fragment in external (Q) and internal (visceral) (R) views; S–T, indeterminate shell fragment in external (S) and internal (visceral) (T) views. Scale bar equals 5 cm.

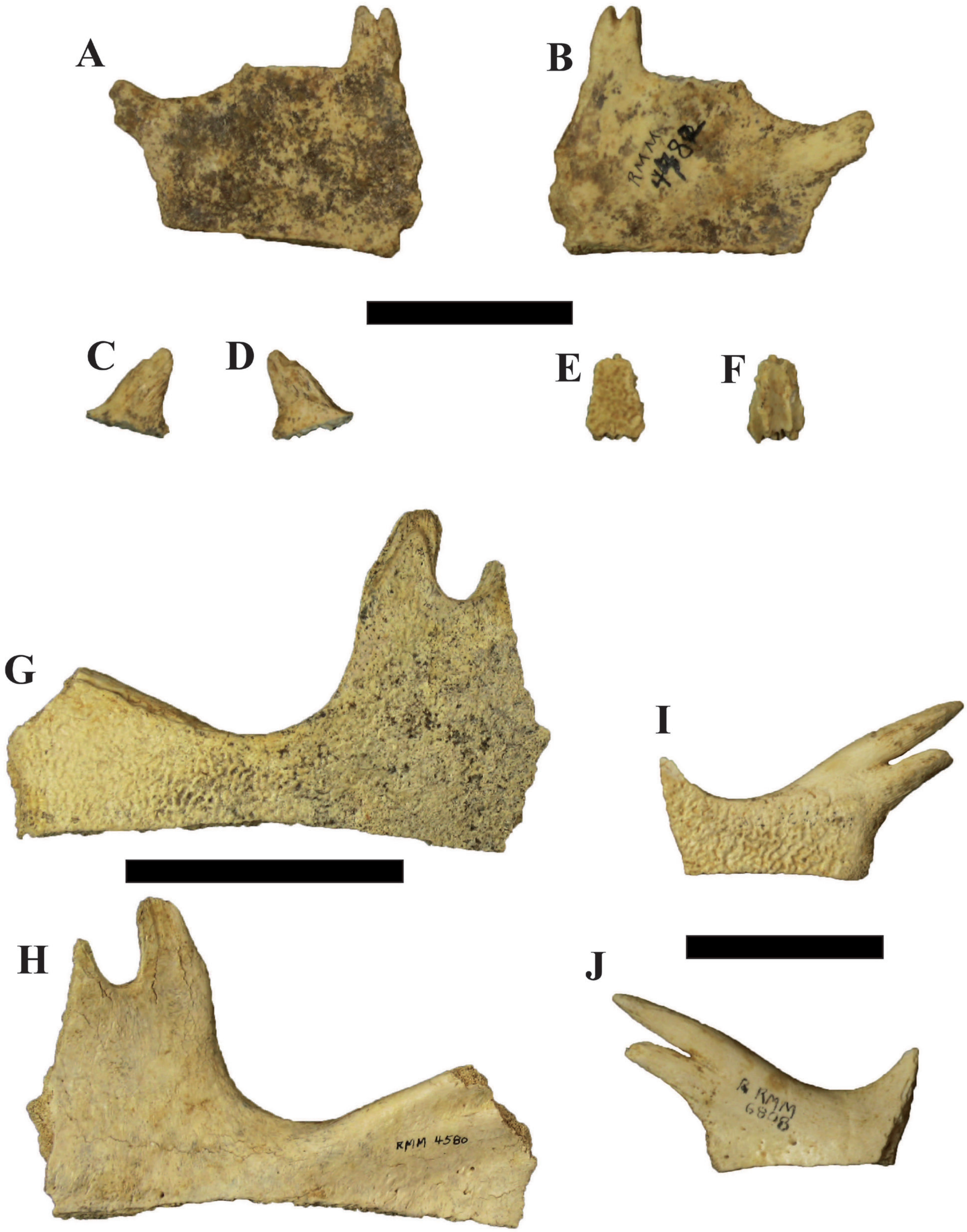

Figure 8. Pleistocene trionychid turtles from Alabama. ***Apalone*** **sp. (RMM 4482), A–F, incomplete left hypoplastron in ventral (A) and dorsal (B) views; plastron fragment in ventral (C) and dorsal (D) views; 3rd(?) neural in dorsal (E) and ventral (F) views.** ***Apalone spinifera*** **(RMM 4580), G–H, nearly complete left hypoplastron in ventral (G) and dorsal (H) views. I–J,** ***Apalone spinifera*** **(RMM 6808), nearly complete juvenile right hypoplastron in ventral (I) and dorsal (J) views. Scale bar equals 2 cm for A–F, I–J; Scale bar equals 5 cm for G–H.**

8A–F); RMM 4916, three shell fragments; RMM 5119, four shell fragments. Disturbed Zone: RMM 3779, one costal fragment. Overlying Clay Cap: RMM 5517, two shell fragments; RMM 5526, one shell fragment.

Remarks—Holman et al. (1990) reported the specimens listed above from site ACb-2, a cave locality in Colbert County, Alabama. Based on radiometric dates, the fossil material recovered from this cave ranged in age from 11,820 ±500 BP for Zone 1 to 26,500 ± 990 BP for Zone 4 (Holman et al., 1990). These specimens represent relatively small trionychids with shell sculpturing commonly comprised of elongate pits that are frequently coalesced into shallow grooves and low ridges, reminiscent of modern *Apalone* shell sculpturing. RMM 3633 (Fig. 7) is represented by various shell fragments, none of which are sufficient to identify lower than genus level. RMM 4482 (Fig. 8A–F), while containing multiple elements as well, is also insufficient to identify past the genus level. In fact, all the material listed here, as noted by Holman et al. (1990), is too fragmentary and incomplete for specific-level identification and is conservatively identified as *Apalone* sp., based primarily on sculpturing.

Material of *Apalone spinifera*—Zone 1: RMM 4580, nearly complete left hypoplastron (Fig. 8G–H); Zone 1/2: RMM 6808, nearly complete juvenile right hypoplastron (Fig. 8I–J).

Description—RMM 4580, a left hypoplastron, is incomplete, missing its medial- and lateral-most portions (Fig. 8G–H). From what is preserved, the bone has a maximum anteroposterior length of 55.09 mm and a maximum preserved mediolateral width of 89.02 mm. RMM 6808, a right hypoplastron from a juvenile, is missing its medial portion (Fig. 8I–J). It has a maximum anteroposterior length of 18.67 mm and a maximum preserved mediolateral width of 32.80 mm, although both measurements would be slightly longer if the bone was complete. Both RMM 4580 (Fig. 8G) and RMM 6808 (Fig. 8I) have sculpturing comprised of inconsistent ridges and grooves, reminiscent of modern *Apalone*. While the juvenile right hypoplastron (RMM 6808) has been figured previously (Holman et al., 1990:fig. 3D), the larger left hypoplastron (RMM 4580) has not.

Remarks—In addition to the aforementioned Pleistocene specimens, Holman et al. (1990), also reported two specimens they identified to the species level, RMM 4580 and RMM 6808. The authors noted that the hypoplastron of *Apalone spinifera* can be distinguished from that of *A. mutica* in “having a much less acute greater xiphiplastral notch and a much shorter lesser xiphiplastral notch” (Holman et al., 1990:524). Based on this characteristic, Holman et al. (1990) identified both RMM 4580 and RMM 6808 as *A. spinifera*. The identification of these two fossils as *A. spinifera* is reaffirmed here based on the xiphiplastral notching and sculpturing. It was also noted that *A. spinifera* occurs throughout Alabama today (Mount, 1975, fig. 348), although no specific records have been found near the cave site (Holman et al., 1990; HerpNet data portal, 2006).

DISCUSSION

Fossil trionychids from Alabama are represented primarily by portions of the carapace and plastron from strata of the Upper Cretaceous, Eocene, Miocene, and Pleistocene. This study marks the first report of trionychid fossils from the Cretaceous of Alabama. These latest Santonian to early Campanian fossils also represent the earliest known occurrence of the family in eastern North America. Previously reported Late Cretaceous trionychid fossils from eastern North America have been confined to either the Campanian (e.g., Miller, 1966, 1967, 1968; Baird and Horner, 1979; Robb, 1989; Manning and Dockery, 1992; Garcia and Hippensteel, 2011; Weems et al., 2011) or the Maastrichtian (e.g., Hay, 1908; Baird, 1986; Weems, 1988; Garcia and Hippensteel, 2011). The Black Creek Formation at Phoebus Landing, North Carolina has been dated to the upper part of the lower Campanian, ranging between 78.5 and 77.1 Ma (Self-Trail et al., 2004).

Previous studies have interpreted the base of the Tombigbee Sand to extend across the Santonian–Campanian boundary (Raymond et al., 1988; Dowsett, 1989; Obradovich, 1993; King and Skotnicki, 1994; Kennedy et al., 1997), with the age of this boundary, according to the International Commission of Stratigraphy, being 83.5 ± 0.7 Ma (Cohen et al., 2012). Obradovich (1993) reported the base of the Tombigbee Sand Member to lie at 84.09 ± 0.40 Ma based on a radiometrically-dated bentonite collected from nearby eastern Mississippi. This suggests the base of the Tombigbee Sand does indeed extend into the latest Santonian with the upper portion of this unit being early Campanian. Thus, the specimens recovered from the Tombigbee Sand at site AGr-43 are slightly older than those recovered from the Phoebus Landing Site in North Carolina, representing the oldest trionychid fossils reported from eastern North America. It seems that trionychids originated in the western part of North America (Brinkman, 2003), and moved east. Trionychids are known to be freshwater turtles, however, there have been specimens recovered from marine deposits as well (Head et al., 1999). The Western Interior Seaway did not partially close until the Maastrichtian in the United States and Canada (Erickson, 1999). This may imply that these turtles were able to traverse the Western Interior Seaway and get to southern Appalachia before the seaway had completely closed off. Nevertheless, the family either quickly traveled north in the eastern part of the continent, migrants from the west simply arrived later in the north, or older geologic units (pre-Campanian) have not yet yielded trionychid fossils from northern Appalachia.

While no Paleocene trionychid remains are known from the state, Eocene remains of trionychids from Alabama have been previously reported by Holman and Case (1988) and Holroyd et al. (2005), although the two papers studied the same specimens, including MSUVP 1186. Holman and Case (1988) and Holroyd et al. (2005) referred to this material as indeterminate trionychine. Vitek (2011) recently reviewed a number of Eocene trionychid specimens from the western United States and established the new genus *Oliveremys*. However, none of the Alabama material is complete enough to be confidently referred to this genus. Conservatively, all the Eocene trionychid material from Alabama is considered indeterminate trionychids in this study until more complete material can be collected. Mancini and Tew (1990) determined the relative ages of the Eocene units discussed herein, including the Hachetigbee Formation as the oldest of the Eocene units, and the Gosport Sand Formation (late–middle Eocene) as approximately coeval with the very top of the Lisbon Formation (see Fig. 2). With so little Eocene trionychid material known from eastern North America, any material can be significant, both for the taxonomic group, and for the potential they have to tell us about the paleoecology. Trionychids are considered freshwater turtles, and their preferred habitats of slow moving water can help elucidate further information on Alabama at the time of deposition.

Although no Oligocene trionychids have been recovered from Alabama, late Miocene trionychid remains from the state have previously been reported by Isphording and Lamb (1971), Thumond and Jones (1981) and Hulbert and Whitmore (2006), the latter of whom mentioned the abundance of these fossil turtles at site AMb-1. Younger Cenozoic trionychid material, including that from the late Miocene, has commonly been thrown into the genus *Trionyx*, which has routinely been treated as a 'waste-basket' taxon (Meylan, 1987). Further investigation into the nearly complete carapace (USNM 347929) described here from the late Miocene confirms a more accurate referral to *Apalone*, and potentially to *Apalone* cf. *A. spinifera*. If this specimen is indeed *A. spinifera*, it would mark one of the earliest occurrences of this species and may show its origins in the southeastern United States. However, Voorhies (1990) discussed the presence, or potential presence, of *A. spinifera* from the Hemphillian of Nebraska, which is still likely the oldest known occurrence of the species. *Apalone spinifera* may have evolved in the midwestern United States, and quickly moved into Alabama and the southeastern part of the country, but more fossils are needed to confirm or refute this hypothesis.

Pleistocene remains of trionychids from Alabama have largely been recovered from caves. Curren (1977), however, reported two carapace fragments he attributed to "*Trionyx* sp." from site F-1 in Pickens County, a stream locality in the Gulf Coastal Plain. Based on radiocarbon dates from an overlying layer of shells, the age of fossils at site F-1 was thought to be older than 4,425 ± 95 B.P., with an estimated age of 8,000 to 12,000 B.P. (Curren, 1977). While specimen numbers were provided ("UAP–40" and "UAP–65") as part of the "University of Alabama Paleontology Collections," official UAM numbers have not yet been given to them. Holman et al. (1990) reported the 17 cave specimens (see list above) from site ACb-2 identified as *Trionyx* sp., but here referred to *Apalone* sp. These specimens tend to exhibit sculpturing similar to that of other specimens of *Apalone*, but are too fragmentary to identify past the generic level. The two specimens identified as *Apalone spinifera* (RMM 4580 and RMM 6808), however, are complete enough to allow specific-level identification. Although the fossil record of *A. spinifera* is generally quite poor in Alabama (Holman et al., 1990), the fossil records of *A. calvata*, *A. ferox*, and *A. mutica* are even less common (or non-existent) in the state (despite modern populations being present in Alabama today). It is currently unknown if the absence of these three species of *Apalone* in the fossil record has any bearing on their evolution, or if it suggests any potential paleobiological or evolutionary implications for the region (namely between 26,000 and 11,000 B.P.). It could be that *Apalone spinifera* was present in the area first, with other species moving in later, or potential implications involving the evolution of *A. calvata*, *A. ferox*, and *A. mutica*. Local extinction could have occurred during glacial times, with *A. spinifera* immigrating back to the area first. It is more likely that not enough material is known or the material is too incomplete and fragmentary to identify to the other taxa.

Following the last glacial and leading to the present, trionychids remained in Alabama. Thurmond and Jones (1981) reported that subfossils of trionychids are not uncommon in Native American sites in the state. Curren (1974), for example, identified *Apalone* sp. ("*Trionyx* sp.") from site lCr8 in Colbert County based on shell fragments. Weigel et al. (1974) identified *Apalone spinifera* ("*Trionyx spinifer*") from Russell Cave in Jackson County, also based on shell fragments. Furthermore, Knight (2010) reported the presence of indeterminate trionychid remains from excavations near Moundville in Hale County. Also, carapace fragments from indeterminate trionychids (UAP V1985.0013.0040 from site F-20 in Montgomery County and UAP V1985.0013.0065 from site F-23 in Wilcox County) are also noted here, although they are both of uncertain ages and are believed to be late Pleistocene/early Holocene in age (Ebersole, 2012, pers. comm.).

CONCLUSIONS

The fossils described here include the first reported Late Cretaceous trionychids from Alabama. These indeterminate trionychids are currently the oldest trionychid fossils from eastern North America; slightly older than various soft-shelled turtle fossils reported from the Campanian of that region. The Cretaceous trionychids from Alabama may also indicate the family traversing the Western Interior Seaway before it was completely closed. The Eocene trionychid material is quite fragmentary, and is also identified as belonging to indeterminate Trionychidae. The late Miocene trionychid fossil reported here, a nearly complete carapace, is identified as *Apalone* cf. *A. spinifera*. If it is confirmed to represent *A. spinifera,* it would be one of the oldest representatives of the species and may have important implications for its evolution in the southeastern United States. Pleistocene trionychid fossils from Alabama have been recovered mainly from caves, and some have been identified as *A. spinifera*. This taxon has a scant fossil record, and its identification in the Pleistocene of Alabama may have paleobiological and paleoecological implications for this species, such as *A. spinifera* immigrating to the region more quickly than other taxa after glacial periods. Although fragmentary, these fossils help advance our understanding of the evolution of trionychids in eastern North America.

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LITERATURE CITED

Baird, D. 1986. Upper Cretaceous reptiles from the Severn Formation of Maryland. The Mosasaur 3:63–85.

Baird, D., and J. R. Horner. 1979. Cretaceous dinosaurs of North Carolina. Brimleyana 2:1–28.

Becker, M. A., D. E. Seidemann, J. A. Chamberlain Jr., D. Buhl, and W. Slattery. 2008. Strontium isotopic signatures in the enameloid and dentine of Upper Cretaceous shark teeth from western Alabama: paleoecologic and geochronologic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 264:188–194.

Bonin, F., B. Devaux, and A. Dupré. 2006. Turtles of the World. John Hopkins University Press, Baltimore, Maryland, 416 pp. [Translated by P. C. H. Pritchard].

Brinkman, D. B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. Canadian Journal of Earth Science 40:557–571.

Buhlmann, K. A., T. D. Tuberville, and J. W. Gibbons. 2008. Turtles of the Southeast. University of Georgia Press. Athens, Georgia, 252 pp.

Cohen, K. M., S. Finney, and P. L. Gibbard. 2012. International Chronostratigraphic Chart. International Commission on Stratigraphy, August, 2012. Available at http://www.stratigraphy.org/ics%20chart/ChronostratChart2012.pdf. Accessed November 1, 2012.

Curren, C. B., Jr. 1974. An ethnozoological analysis of the vertebrate remains, Little Bear Creek site (lCr8). Journal of Alabama Archaeology 20:127–182.

Curren, C. B., Jr. 1977. Paleo Indian and the Pleistocene of Alabama. Unpublished manuscript on file at the Office of Archaeological Research, Moundville, Alabama. 3 13 pp.

Dowsett, H. 1989. Documentation of the Santonian–Campanian and the Austinian–Taylorian stage boundaries in Mississippi and Alabama using calcareous nanofossils. U.S. Geological Survey Bulletin 1884:1–20.

Erickson, J. M. 1999. The Dakota Isthmus – closing the Late Cretaceous Western Interior Seaway. North Dakota Academy of Science, Proceedings 53:124-129.

Ernst, C. H., and R. W. Barbour. 1989. Turtles of the World. Smithsonian Institution Press, Washington D. C., 313 pp.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. The Johns Hopkins University Press, Baltimore, Maryland, 827 pp.

Gaffney, E. S. 1981. A review of the fossil turtles of Australia. American Museum Novitates 2720:1–38.

Gaffney, E. S., and A. Bartholomai. 1979. Fossil trionychids of Australia. Journal of Paleontology 53:1354–1360.

Garcia, W., and S. Hippensteel. 2011. New vertebrate material from the Peedee Formation of Elizabethtown, NC and the Severn Formation of Bowie, MD and the shallow marine vertebrate fauna of the upper Campanian-upper Maastrichtian of eastern North America. Geological Society of America, Abstracts with Programs 43:83.

Gardner, J. D., and A. P. Russell. 1994. Carapacial variation among soft-shelled turtles (Testudines: Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 193:209–244.

Guyer, C., M. A. Bailey, and R. H. Mount. In press. Reptiles of Alabama. University of Alabama Press, Tuscaloosa, Alabama.

Hay, O. P. 1908. The Fossil Turtles of North America. Carnegie Institute of Washington, Publication No. 75, Washington D.C., 568 pp.

Head, J. J., S. M. Raza, and P. D. Gingerich. 1999. *Drazinderetes tethyensis*, a new large trionychid (Reptilia: Testudines) from the marine Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan). Contributions from the Museum of Paleontology, The University of Michigan 30:199-214.

HerpNet data portal. 2006. HerpNET2 Portal. Available at http://herpnet.org. Accessed October 15, 2012.

Holman, J. A., and G. R. Case. 1988. Reptiles from the Eocene Tallahatta Formation of Alabama. Journal of Vertebrate Paleontology 8:328–333.

Holman, J. A., G. Bell, and J. Lamb. 1990. A late Pleistocene herpetofauna from Bell Cave, Alabama. Herpetological Journal 1:521–529.

Holroyd, P. A., J. F. Parham, and J. H. Hutchison. 2005. A reappraisal of some Paleogene turtles from the southeastern United States. Journal of Vertebrate Paleontology 25:979–982.

Hulbert, R. C., Jr., and F. C. Whitmore Jr. 2006. Late Miocene mammals from the Mauvills local fauna, Alabama. Bulletin of the Florida Museum of Natural History 46(1):1–28.

Isphording, W. C., and G. M. Lamb. 1971. Age and origin of the Citronelle Formation in Alabama. Geological Society of America Bulletin 82:775–780.

Kennedy, W. J., W. A. Cobban, and N. H. Landman. 1997. Campanian ammonites from the Tombigbee Sand Member of the Eutaw Formation, the Mooreville Formation, and the basal part of the Demopolis Formation in Mississippi and Alabama. American Museum Novitates 3201:1-44.

King, D., and M. Skotnicki. 1994. Upper Cretaceous stratigraphy and sea level history, Gulf Coast Plain of central and eastern Alabama. Geologic Society of America Special Paper 287:27–41.

Knight, V. J., Jr., 2010. Mound Excavations at Moundville: Architecture, Elites, and Social Order. University of Alabama Press, Tuscaloosa, Alabama, 424 pp.

Mancini, E. A., and B. H. Tew. 1990. Tertiary sequence stratigraphy and biostratigraphy of southwestern Alabama (Geological Society of America Southeastern Section guidebook, Field Trip 1): Geological Survey of Alabama, Tuscaloosa, Alabama, 51 pp.

Manning, E. M., and D. T. Dockery III. 1992. A guide to the Frankstown Vertebrate Fossil Locality (Upper Cretaceous), Prentiss County, Mississippi. Mississippi Office of Geology, Circular No. 4, 43 pp.

Meylan, P. A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186:1–101.

Miller, H. W. 1966. Cretaceous vertebrate fauna from Phoebus Landing, North Carolina [abs.]. Journal of the Elisha Mitchell Scientific Society 82:93.

Miller, H. W. 1967. Cretaceous vertebrates from Phoebus Landing, North Carolina: Proceedings of the Academy of Natural Sciences of Philadelphia 119:219–239.

Miller, H. W. 1968. Additions to the Upper Cretaceous vertebrate fauna of Phoebus Landing, North Carolina. Journal of the Elisha Mitchell Scientific Society 84:467–471.

Mount, R. H. 1975. The Reptiles and Amphibians of Alabama. Auburn University Agricultural Station, Auburn, Alabama, 368 pp.

Obradovich, J. D. 1993. A Cretaceous time scale; pp. 379-396 in W. G. E. Caldwell (ed.), Evolution of the Western Interior Basin. Geologic Association of Canada Special Paper, vol. 39.

Puckett, T. M. 1996. Ecologic atlas of Upper Cretaceous ostracodes of Alabama. Geological Survey of Alabama, Monograph 14:1–176.

Raymond, D., W. Osborne, C. Copeland, and T. Neathery. 1988. Alabama Stratigraphy. Geological Survey of Alabama, Circular 140, Tuscaloosa, 98 pp.

Robb, A. J., III. 1989. The Upper Cretaceous (Campanian, Black Creek Formation) fossil fish fauna of Phoebus Landing, Bladen County, North Carolina. The Mosasaur 4:75–92.

Self-Trail, J. M., R. A. Christopher, D. C. Prowell, and R. E. Weems. 2004. The age of dinosaur-bearing strata at Phoebus Landing, Cape Fear River, North Carolina. Geological Society of America Abstracts with Programs 36:117A.

Thurmond, J. T., and D. E. Jones. 1981. Fossil Vertebrates of Alabama. The University of Alabama Press, Tuscaloosa, Alabama, 244 pp.

Vitek, N. 2011. Insights into the taxonomy and systematics of North American Eocene soft-shelled turtles from a well-preserved specimen. Bulletin of the Peabody Museum of Natural History 52:189–208.

Voorhies, M. R., 1990. Vertebrate biostratigraphy of the Ogallala Group in Nebraska; pp. 115–151 in T. C. Gustavson (ed.), Geologic Framework and Regional Hydrology: Upper Cenozoic Blackwater Draw and Ogallala Formations, Great Plains. University of Texas at Austin, Bureau of Economic Geology, Austin, Texas.

Weems, R. E. 1988. Paleocene turtles from the Aquia and Brightseat formations, with a discussion of their bearing on sea turtle evolution and phylogeny. Proceedings of the Biological Society of Washington 101:109–145.

Weems, R. E., W. C. Lewis, J. H. Murray, D. B. Queen, J. B. Grey, and B. D. DeJong. 2011. Detailed sections from auger holes in the Elizabethtown 1:100,000-scale map sheet, North Carolina: U.S. Geological Survey Open-File Report 2011–1115, 286 p. Available only online at http://pubs.usgs.gov/of/2011/1115.

Weigel, R. D., A. J. Holman, and A. A. Paloumpls. 1974. Part 5: Vertebrates from Russell Cave; pp. 81–85 in J. W. Griffin, Investigations in Russell Cave, Russell Cave National Monument, Alabama. National Park Service Publications in Archaeology 13.