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Cover photo: The Santonian-Campanian Mooreville Chalk Formation of Alabama, USA. Photograph taken by ADG.

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The first report of *Toxochelys latiremis* Cope 1873 (Testudines: Panchelonioidea) from the early Campanian of Alabama, USA

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Toxochelys latiremis Cope, 1873 is currently thought to be one of the oldest members of the clade originating from the last common ancestor of all extant species of marine-adapted turtles (Chelonioidea). Fossil material of this species has been reported from numerous lower Campanian marine formations across North America; however, reported occurrences have been conspicuously absent from the upper Santonian-to-lower Campanian Mooreville Chalk of Alabama and Mississippi, USA, the type stratum for the only other valid species within the genus, *Toxochelys moorevillensis* Zangerl, 1953. The apparent absence of *T. latiremis* from the Mooreville Chalk, and from the southern expanse of the Mississippi Embayment, has made *T. latiremis* one of the few outliers in previously proposed paleobiogeographic models for marine turtles in the Late Cretaceous Western Interior Seaway. This absence also confounded attempts at reconciling the distribution and phylogeny of these taxa. Here we report the first material of *T. latiremis* identified from the Mooreville Chalk of Alabama, which represents the southern-most occurrence of this taxon. The discovery of this species in the Mooreville Chalk of Alabama helps to reconcile the previously hypothesized paleobiogeography of North American Late Cretaceous chelonoids with their fossil occurrence and provides the first evidence for overlapping ranges of the only two currently recognized species of *Toxochelys*.

Keywords: Marine turtle, Western Interior Seaway, Mississippi Embayment, Mooreville Chalk, fossil

INTRODUCTION

Toxochelys latiremis Cope, 1873 is arguably the earliest unambiguous total group chelonoid (Joyce 2007, Anquetin 2012, Joyce et al. 2013). Though predated by the protostegids, a cosmopolitan clade of marine-adapted turtles that includes well known taxa such as *Archelon ischyros* Wieland, 1896 and *Protostega gigas* Cope, 1872, recent studies suggest the protostegids represent an independent Jurassic radiation of cryptodiran marine turtles that do not share a marine ancestor with neritic Late Cretaceous forms such as *T. latiremis* or extant chelonoids (for further discussion see Cadena and Parham 2015). *Toxochelys latiremis* has been reported from Coniacian to Campanian formations as far north as modern-day Manitoba and as far south as Tennessee (Hirayama

1997), making it the most widely-distributed species of Late Cretaceous stem chelonoid in North America (Nicholls and Russell 1990).

Based on the occurrence of fossil chelonoids and various other marine tetrapod taxa, Nicholls and Russell (1990) divided the Late Cretaceous Western Interior Seaway (WIS) of North America into Northern and Southern faunal subprovinces. The Northern Interior Faunal Subprovince (NIFS), which extends from southern Canada to the border of Kansas and Texas, is characterized as having low vertebrate diversity dominated by plesiosaurs and the mosasaur *Platecarpus* Williston, 1898, while the Southern Interior Faunal Subprovince (SIFS), spanning much of what is now the southeastern United States, is described as having much higher vertebrate diversity dominated by sharks and turtles (Nicholls and Russell 1990). Despite the distinctions between these subprovinces, the authors noted a broad overlap between the faunas, especially in regards to turtles.

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The majority of the fossil turtle taxa indicative of the SIFS are known from the upper Santonian-to-middle Campanian Mooreville Chalk in Alabama, USA (9 of 11 genera *sensu* Nicholls and Russell 1990). Characterized by highly diverse, marine vertebrate fossil assemblages (see Ikejiri et al. 2013), surface exposures of the Mooreville Chalk make up the southern border of the Late Cretaceous Mississippi Embayment (ME) of the WIS (Mancini et al. 1996, Mancini and Puckett 2005). The warm, shallow waters within the ME appear to have been an ideal habitat for marine turtles, as evidenced by a higher diversity and relative abundance of fossil chelonoids within the Mooreville Chalk than in any other marine formation of equivalent age in North America (Table 1, Nicholls and Russell 1990). The Mooreville Chalk exposures in Alabama have been particularly productive in terms of marine turtle diversity with six currently recognized genera identified (Zangerl 1953, 1960, Hirayama 1997, Ikejiri et al. 2013). Many of these genera also occur within the Niobrara Chalk and Pierre Shale of Kansas as well as the Pierre Shale of Wyoming and South Dakota; however, several taxa including *Toxochelys moorevillensis* Zangerl, 1953, *Thinochelys lapisossea* Zangerl, 1953 and *Ctenochelys acris* Zangerl, 1953 appear to have been endemic to the ME (Zangerl 1953, Gentry 2016). Conversely, only two late Santonian-to-early Campanian fossil chelonoid species known from the WIS have not previously been reported from the Mooreville Chalk, *Porthochelys laticeps* Williston, 1901 and *T. latiremis*. Of these, only the latter is known from multiple specimens.

Historically, remains of *T. latiremis* have been found primarily within the NIFS (Nicholls and Russell 1990) with the only exceptions being a single specimen from the Marlbrook Marl of Arkansas (FMNH P27047; Schmidt 1944) and a partial plastron from the Ripley Formation of Tennessee (UT K20; Zangerl 1953) tentatively referred to *T. latiremis*. The apparent absence of *T. latiremis* from the Mooreville Chalk in both Alabama and Mississippi has been perplexing as fossils belonging to the only other recognized species within the genus, *T. moorevillensis*, are quite common within this unit. Given the greatly expanded range and more functionally advanced marine adaptations of *T. latiremis* relative to *T. moorevillensis* (i.e., better developed forelimb paddles, reduction in carapacial ossification [see Zangerl 1953]), the absence of *T. latiremis* from the Mooreville Chalk has not been readily explainable. In addition, the assumed close evolutionary relationship between these two species, the optimal environmental conditions for marine-adapted turtles in the ME during the Late Cretaceous, and the

Table 1. List of chelonoid genera from Campanian marine formations of North America. Data from the Anderson River, Pembina, Sharon Springs, and Niobrara Chalk formations derived from Nicholls and Russell (1990). Mooreville Chalk data from Ikejiri et al. (2013) and personal observations from the lead author (ADG). Taxonomy follows Hirayama (1997).

Anderson River	Pembina	Sharon Springs	Niobrara	Mooreville Chalk
--	<i>Toxochelys</i>	<i>Toxochelys</i>	<i>Toxochelys</i>	<i>Toxochelys</i>
--	--	--	<i>Ctenochelys</i>	<i>Ctenochelys</i>
--	--	--	<i>Porthochelys</i>	<i>Prionochelys</i>
--	--	--	--	<i>Peritresius</i>
--	--	--	--	<i>Corsochelys*</i>
--	--	--	--	<i>Thinochelys*</i>

previously observed trends in North American chelonoid paleobiogeography, all suggest that *T. latiremis* should be present within the southeastern portions of the ME.

Here we report two specimens of *T. latiremis* from the Mooreville Chalk of Alabama (Fig. 1), representing the first occurrences of this taxon from the southern expanses of the ME. In addition to describing these new specimens, we discuss their implications with respect to the paleobiogeography of North American chelonoids during the Late Cretaceous.

MATERIAL AND METHODS

The turtle specimens described in this study are from the collections housed at the McWane Science Center (MSC) in Birmingham, Alabama, USA. Specimens of *T. latiremis* (McWane specimens RMM 5614 and 5615) were prepared and cleaned using manual preparation techniques and water. When necessary, broken elements were repaired using B-76 butvar. The specimens were photographed using a Nikon D3300 camera and processed using Adobe Photoshop version 2014 software as part of the production of the figures. Osteological terminology follows Zangerl (1953) and higher taxonomic rankings follow Joyce et al. (2004). For the purpose of site protection, the sited locality, ASu-11, is referenced by its Alabama State site number. More detailed information regarding this locality is available to qualified researchers and is on file at MSC.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York City, New York, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; KUVF, University of Kansas Museum of Natural History, Lawrence, USA; MSC, McWane Science Center, Birmingham, Alabama, USA; RMM, Red Mountain

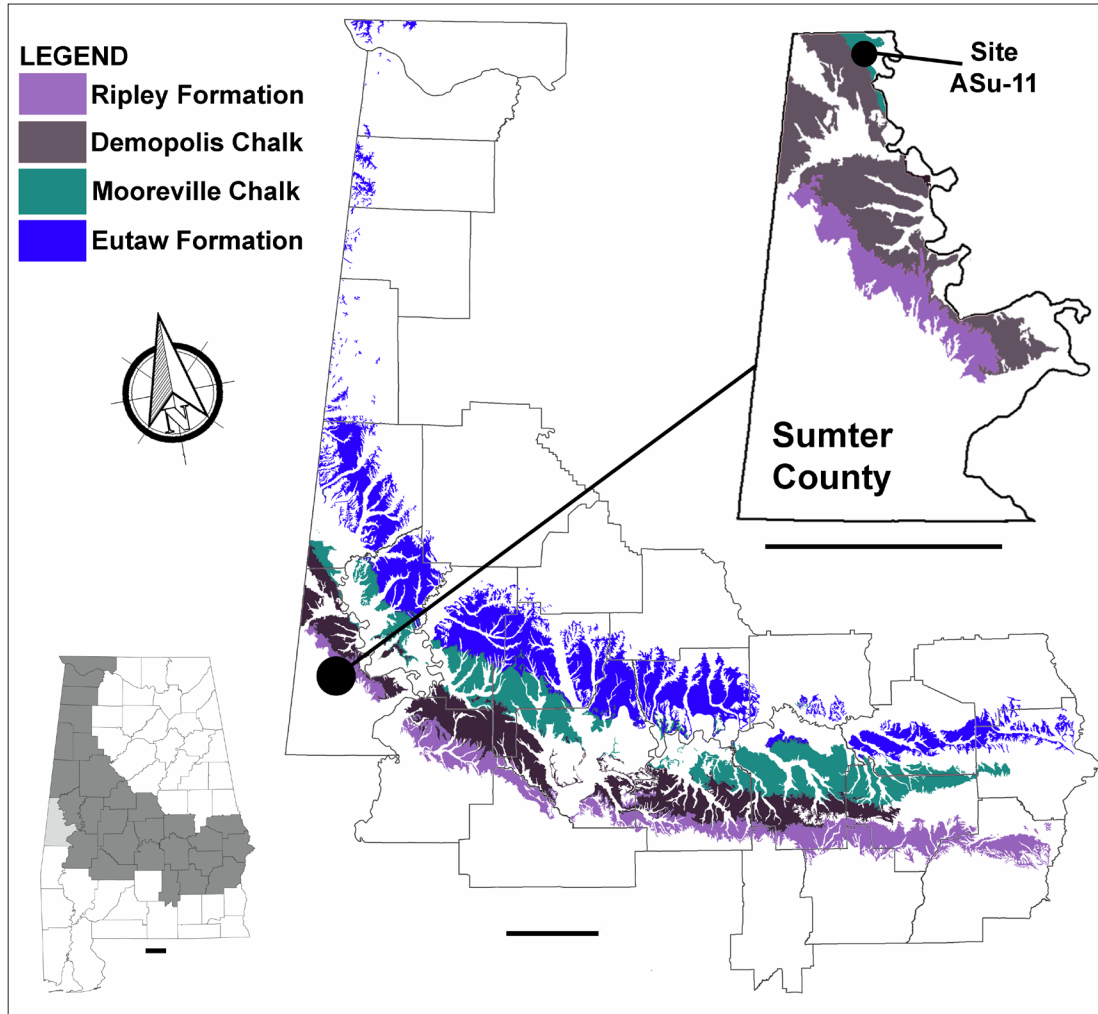


Figure 1. Map showing Santonian and Campanian surface exposures in Alabama and the location of site ASu-11. Scale bars=30 km.

Museum, Birmingham, Alabama (collections now at MSC); **ROM**, Royal Ontario Museum, Toronto, Canada; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

SYSTEMATIC PALEONTOLOGY

TESTUDINES **BATSCH, 1788**

CRYPTODIRA **COPE, 1868**

AMERICHELYDIA **JOYCE, PARHAM, LYSON, WARNOCK, AND DONOGHUE, 2013**

PANCHELONIOIDEA **JOYCE, PARHAM, AND GAUTHIER, 2004**

TOXOCHELYS **COPE, 1873**

Toxochelys latiremis **COPE, 1873**

FIGS. 3–5

Toxochelys latiremis sp. nov. **COPE, 1873**, p. 10.

Toxochelys serrifer **COPE, 1875**, p. 299.

Toxochelys brachyrhinus **CASE, 1898**, p. 378.

Porthochelys browni **HAY, 1905**, p. 183.

Phylemys barberi **SCHMIDT, 1944**, p. 66.

Toxochelys browni **ZANGERL, 1953**, p. 197.

Toxochelys barberi **ZANGERL, 1953**, p. 193.

Type species—*Toxochelys latiremis* **Cope, 1873**, Campanian Pierre Shale, Kansas, USA. AMNH 2362, left ramus of the lower jaw, and partial coracoid.

Referred specimens—RMM 5614, nearly complete nuchal, one neural, one peripheral, and the proximal half of the left humerus collected from the lower Mooreville Chalk. RMM 5615, partial carapace including multiple peripheral and costal fragments, one partial neural, three cervical vertebrae, incomplete left ilium, and the right scapula missing the acromial and scapular processes collected from the lower unnamed member of

the Mooreville Chalk.

Locality and Geological Setting—The specimens identified in this study were collected from site ASu-11, located in Sumter County, Alabama, USA (Fig. 1). This locality is comprised of several acres of exposed Mooreville Chalk gullies, and repeated collecting at this site has produced numerous species of Late Cretaceous fishes, sharks, mosasaurs, and marine turtles. In Alabama, the aerial extent of the Mooreville Chalk forms an arcuate belt that extends from east to west across the central portion of the state (Cicimurri and Ebersole 2014) (Fig. 1). Although surface exposures of this formation are abundant in central and western Alabama, the Mooreville Chalk is replaced by the stratigraphically equivalent Blufftown Formation in the eastern part of the state (Raymond et al. 1988).

The Mooreville Chalk represents the stratigraphically lowest unit within the Campanian/Maastrichtian Selma

Group. The Mooreville Chalk is divided into two members, the upper Arcola Limestone Member and a lower unnamed member that makes up the lower 1.5 meters of the unit (Raymond et al. 1988, Liu 2007; Fig. 2). The exposures at site ASu-11 are comprised of both the lower portion of the Mooreville Chalk and the lower unnamed member. The lithology of the Mooreville Chalk consists of a compact yellowish-gray, fossiliferous chalk and chalky marl. The lower unnamed member is comprised of a fossiliferous chalky sand that is highly glauconitic and contains abundant phosphate pellets and invertebrate steinkerns (Raymond et al. 1988). Overall, the Mooreville Chalk and lower member are thought to represent a calm, middle-shelf environment with dysoxic bottom conditions (Wylie and King 1986, Prieto-Márquez et al. 2016).

In Alabama, the contact between the Mooreville Chalk and the underlying Tombigbee Sand Member of the Eutaw Formation is time-transgressive, with the contact


Period/ Epoch	Stage	Substage	West Alabama Stratigraphy	Central Alabama Stratigraphy	Planktonic Foram Zone	Age (mya)	
Upper Cretaceous	Campanian	Upper	Ripley Formation	Ripley Formation	<i>Globotruncana aegyptiaca</i> I.Z.	75	
			Bluffport Marl Mbr.	Bluffport Marl Mbr.	<i>Globotruncanella havanensis</i> P.R.Z. <i>Globotruncanita calcarata</i> T.R.Z.		
		Middle	Demopolis Chalk	Demopolis Chalk	<i>Globotruncana ventricosa</i> I.Z.		
			Demopolis Chalk				
		Lower	Mooreville Chalk	Mooreville Chalk	<i>Globotruncanita elevata</i> P.R.Z.		80
							
	Santonian	Upper	Tombigbee Sand Member	Tombigbee Sand Member	<i>Dicarinella asymetrica</i> T.R.Z.	85	
		Middle					
		Lower	Eutaw Formation (in part)	Eutaw Formation (in part)	<i>Dicarinella concavata</i> I.Z.		

Figure 2. Generalized Santonian through Campanian surface stratigraphy of west and central Alabama. Planktonic foraminiferal zones after Caron (1985). Turtle icon represents the stratigraphic position of the specimens reported in this study.

traversing the Santonian/Campanian boundary (Puckett 2005). Prior studies of the planktonic foraminifera present within the Mooreville Chalk have shown that at localities in central Alabama, the base of the unit falls within the *Dicarinella asymerica* (Sigal, 1952) Taxon Range Zone, with the last occurrence of this taxon marking the Santonian/Campanian boundary (Puckett 1994; Mancini et al. 1996). At localities in western Alabama, the base of the Mooreville Chalk, which includes the entirety of the lower unnamed member, lies at the base of the lower Campanian *Globotruncanita elevata* Brotzen, 1934 Partial Range Zone (Puckett 2005). The combination of both the lower portion of the Mooreville Chalk and the lower member being exposed at site ASu-11, and the location of this site in western Alabama, provides an early Campanian age for the specimens examined in this study.

Description

Carapace—The carapacial elements preserved with both RMM 5614 and RMM 5615 are indistinguishable from previously described, adult *T. latiremis* specimens (KUVF 1244, YPM 3602, Zangerl 1953; ROM 28563, Nicholls 1988). The nuchal preserved with RMM 5614 clearly exhibits the large, well-developed posteromedial nuchal fontanelles characteristic of other Late Cretaceous chelonoid *sensu stricto* taxa (i.e., *Ctenochelys* Zangerl, 1953; *Prionocheilus* Zangerl, 1953). The sulcus of the broad cervical scale is visible on the dorsal surface of the nuchal (Fig. 3A), a feature identical to that seen on YPM 3602 (see Zangerl 1953, fig. 74). The nuchal emargination is deeply embayed and receives a small contribution from the left and right 1st peripherals. The size of the posterior nuchal fontanelles, the width of the cervical scale, and the embayment of the nuchal emargination can all be used to easily distinguish the nuchal of *T. latiremis* from that of *T. moorevillensis* (Fig. 4).

The peripherals of RMM 5615 decrease in width from the 1st peripheral to the 4th and increase in width posteriorly (Fig. 5A). The width of the most complete posterior peripheral of RMM 5615 (left 10th peripheral) is roughly 60% of its length, while the width of the single peripheral of RMM 5614 equals nearly 75% of its length. Unlike the only other currently recognized species of *Toxochelys*, *T. moorevillensis*, the width of the posterior peripherals of *T. latiremis* never exceeds their length (Nicholls 1988; see Table 2). The peripherals preserved with RMM 5615 have moderately convex lateral margins and exhibit the same smooth, unserrated outline typical of *Toxochelys*. On RMM 5615, adjacent to each costal are large, lateral fontanelles that are nearly 50% as wide as the associated

costal plates (Fig. 5A). The unkeeled neurals on both RMM 5615 and RMM 5614 are posteriorly elongate and possess a distinct ventral boss that served as the site of articulation with the thoracic vertebrae (Fig. 3B, 5A).

Girdle material—Preserved with RMM 5615 is the medial portion of the right scapula. Although the ends of the articular and scapular processes are not preserved, the angle formed by these two processes appears to have been greater than 90° (Fig. 5C). Also preserved with RMM 5615 is the majority of the left ilium (Fig. 5D). The posterior iliac process is mostly intact and is proportionally similar in size to that of adult specimens of *Ctenochelys stenoporus* Zangerl, 1953 (see Matzke 2007, text-fig. 15). The pubic facet is considerably larger than the ischiatic facet, both of which are smaller than the acetabular area.

Humerus—The large, proximal end of the left humerus preserved with RMM 5614 (Fig. 3D) is only the third humerus described for *T. latiremis* and the first from a putative adult. The other described humeri referred to *T. latiremis* are preserved with FMNH PR123 (Zangerl 1953, p. 183, fig. 72) and ROM 28563 (Nicholls 1988, p. 182, fig. 1), both of which are juvenile or subadult specimens. The proximal head is roughly 6.5 cm wide, proportionally larger than the single known humerus of *T. moorevillensis* (Zangerl 1953, p. 165, fig. 69). The medial process extends anteriorly beyond the level of the lateral process and is more broadly circular than that of both juvenile *T. latiremis* and adult *T. moorevillensis*, though the element has undergone some degree of distortion due to compression. The lateral process is only slightly distal to the caput humeri, a feature typical of Cretaceous stem chelonoids (Hirayama 1997).

Vertebrae—The remains of three cervical vertebrae are preserved with RMM 5615, and although all have been distorted by various degrees of compression, one of the vertebrae (Fig. 5B) is nearly intact and better preserved than the others. Though its precise position in the neck cannot be accurately determined, one key feature that can be identified on this particular vertebra is the weak ventral keel running along at least the posterior half of the centrum. The pre- and postzygophyses are missing, as are the transverse processes. All three vertebrae appear to be procoelous.

DISCUSSION AND CONCLUSIONS

Despite both specimens in our sample being represented by only partial skeletal remains, they can be definitively assigned to *Toxochelys latiremis* based on the proximal position of the lateral humeral process, the deeply embayed nuchal with large posteromedial

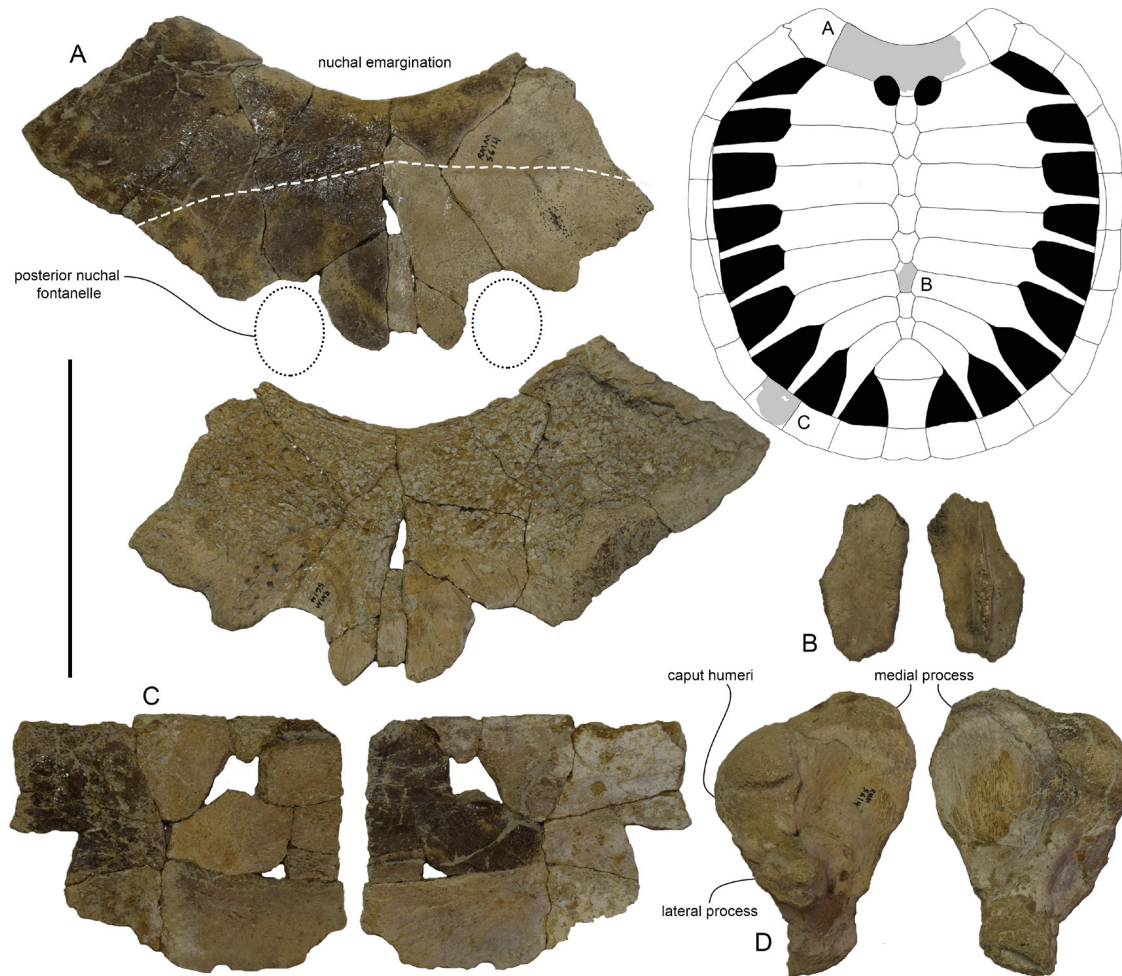
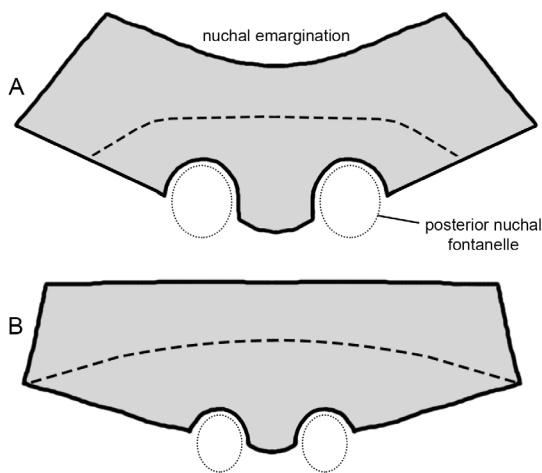


Figure 3. *Toxochelys latiremis*, RMM 5614. **A.** Nuchal in dorsal (top) and ventral (bottom) views. **B.** Neural in dorsal (left) and ventral (right) views. **C.** Peripheral in dorsal (left) and ventral (right) views. **D.** Proximal head of the left humerus in ventral (left) and dorsal (right) views. Dashed lines represent the sulcus of the cervical scale. Scale bar=10 cm. Drawing shows position in carapace of the elements A–C (gray).

Figure 4. Comparison of the nuchals of *Toxochelys latiremis* (**A**) and *Toxochelys moorevillensis* (**B**) in dorsal view. Dashed lines represent the sulcus of the cervical scale.



fontanelles, an absence of peripheral serrations, posterior peripherals whose width never exceeds their length, and the presence of posteriorly elongate, roughly hexagonal, unkeeled neurals (see Zangerl 1953, Nicholls 1988). Given these features, RMM 5614 and RMM 5615 align more closely with unambiguously referred specimens of *T. latiremis* (YPM 3602 and ROM 25863) than with any chelonoid taxon currently recognized from the Mooreville Chalk (see Table 2). Based on variations in cranial metrics, there is some doubt regarding the species level definition of *T. latiremis* as defined by Nicholls (1988) and the subsequent synonymy of the Pierre Shale and Niobrara specimens referred to *T. latiremis* by Carino 2007 (Don Brinkman *pers. communication* 2017) as none of the skulls he described are associated with any post-cranial remains. The diagnostic carapacial features of *T. latiremis*, however, are not in question, and RMM

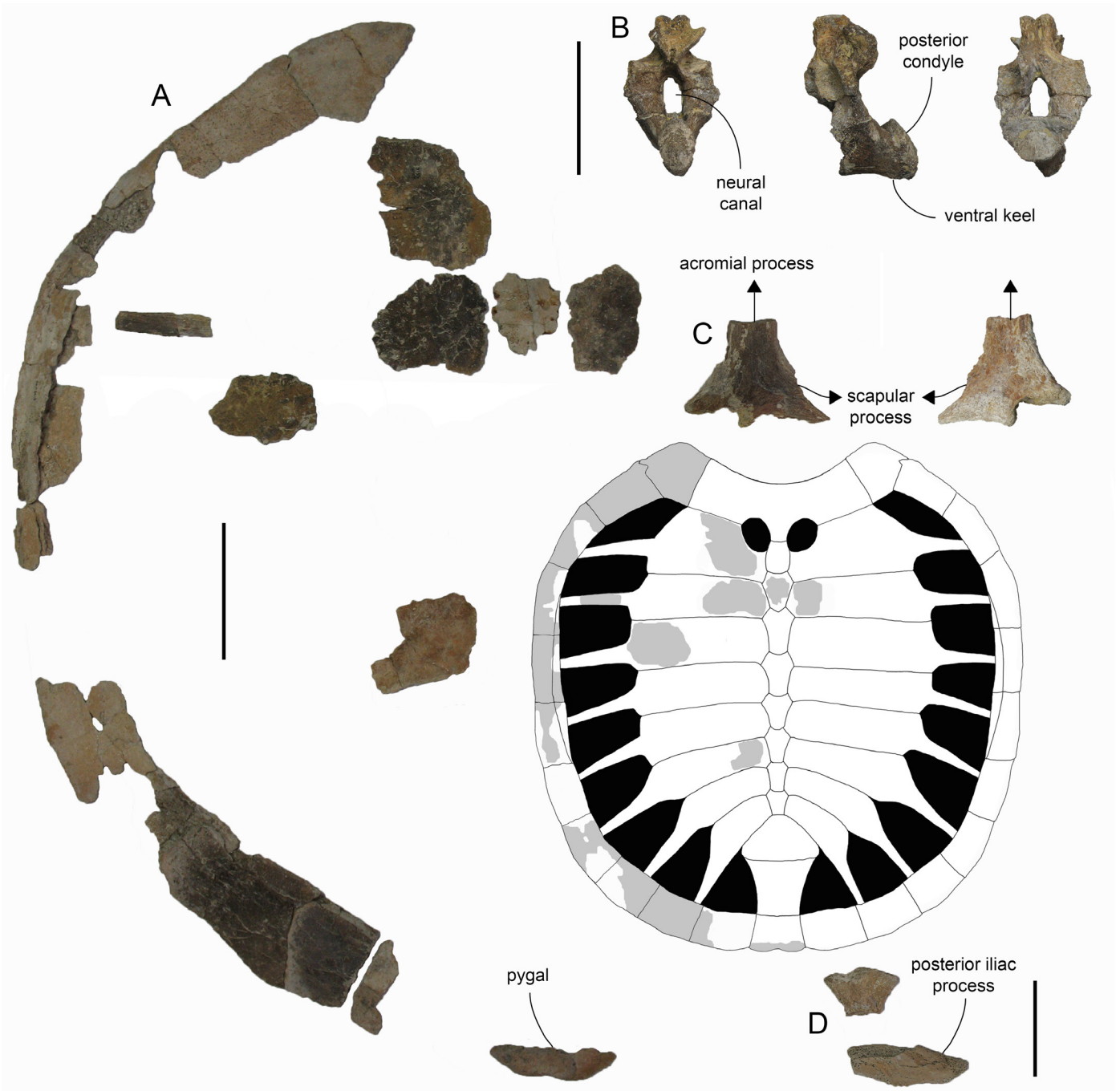


Figure 5. *Toxochelys latiremis*, RMM 5615. **A.** Carapacial elements in dorsal view. The positions of the carapacial elements are shown in gray. Scale bar=10 cm. **B.** Cervical vertebra in posterior (left), lateral (middle), and anterior (right) views. **C.** Preserved portion of the right scapula in anterior (left) and posterior (right) views. **D.** Left ilium in medial view. Scale bars=5 cm. Elements in **B–D** are not highlighted in the drawing.

5614 and RMM 5615 are referred to *T. latiremis* based on the only currently recognized post-cranial diagnosis for the species which was provided by Nicholls (1988).

The *T. latiremis* specimens identified in the present study indicate that this species of panchelonioid had a

range that nearly covered the extent of the WIS and occupied marine habitats from present day Canada to the U.S. Gulf Coast (Fig. 6). In contrast, seemingly less pelagically specialized species such as *Toxochelys moorevillensis* and *Ctenochelys acris* were restricted to the southernmost

Table 2. Distribution of shell characteristics among ‘toxocheleid’-grade taxa of the Mooreville Chalk. Index value of posterior peripherals calculated as $(W / L) \times 100$. Carapacial fontanelle character states are defined as follows: **Small** – fontanelles do not exceed 25% of the width of the adjacent costal plates. **Moderate** – width of fontanelles is 25-50% of the width of the adjacent costal plates. **Large** – fontanelles whose width is greater than 50% of the width of the adjacent costal plates. Taxonomy follows [Hirayama \(1997\)](#).

Trait	RMM 5614 & 5615	<i>Toxocheilus latiremis</i>	<i>Toxocheilus moorevillensis</i>	<i>Thinochelys lapisossea</i>	<i>Ctenochelys stenoporus</i>	<i>Ctenochelys acris</i>	<i>Prionocheilus matutina</i>
Width of vertebrals		Wider than long	As long as wide	Longer than wide	Longer than wide	As long as wide	Wider than long
Nuchal embayment	Deep	Deep	Shallow/absent	Absent	Deep	Deep	Deep
Neural crest w/epineurals	Absent	Absent	Absent	Absent	Present	Present	Present
Peripheral serrations	Absent	Weak/absent	Absent	Absent	Present	Present	Present
Width of posterior peripherals	Never exceeds length	Never exceeds length	Exceeds length	Exceeds length	Never exceeds length	Never exceeds length	Never exceeds length
Peripherals 8–11 index value	60-75%	60-80%	85-110%	95-120%	60-70%	65-95%	80-90%
Carapacial fontanelles		Large	Small/absent	Absent	Large	Small	Moderate

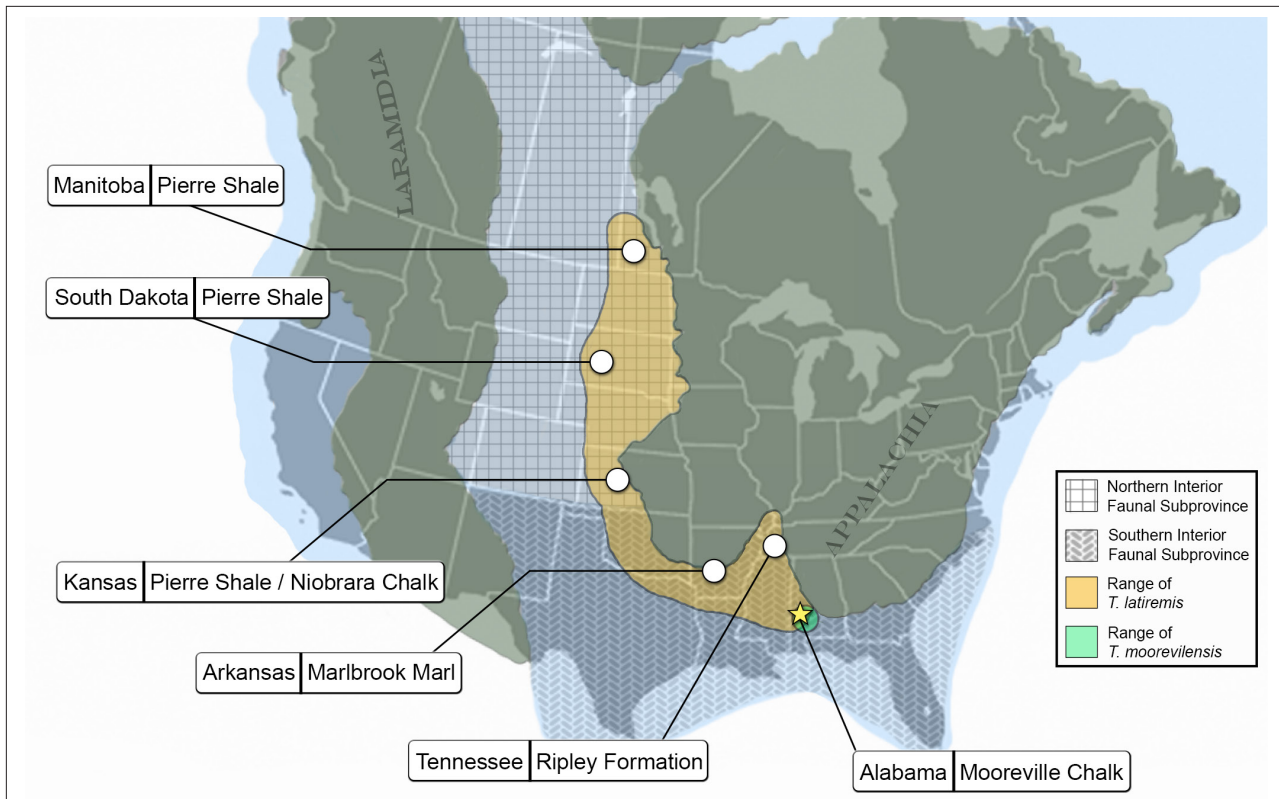


Figure 6. Map of North America showing the reported occurrence and biogeographic ranges of *Toxocheilus*. Cited specimen information is as follows: **Alabama**—RMM 5614, RMM 5615, *this study*. **Arkansas**—FMNH P27047, [Schmidt \(1944\)](#). **Kansas**—AMNH 2362, [Cope \(1873\)](#); YPM 3602, AMNH 5118, [Zangerl \(1953\)](#). **Manitoba**—ROM 25863, [Nicholls \(1988\)](#). **South Dakota**—AMNH 6080, [Hay \(1905\)](#). **Tennessee**—UT K20, [Collins \(1951\)](#). Extent of the northern and southern faunal subprovinces *sensu* [Nicholls and Russell \(1990\)](#).

portion of the WIS within the ME. Previous authors have postulated that the regional endemism of certain Cretaceous species of North American fossil chelonioids was not a result of their 'functional primitiveness' (Hirayama 1997, p. 238). However, newly described material belonging to the forms endemic to the ME show that these species were clearly not well adapted to an open-ocean ecology and were likely near-shore or neritic species incapable of penetrating the deeper waters of the central and northern WIS (Gentry 2016).

According to Nicholls and Russell (1990), the distribution patterns of North American Late Cretaceous marine tetrapods indicate the presence of two distinct faunal subprovinces within the WIS. The fossil occurrence of certain chelonioid taxa during the early Campanian makes marine adapted turtles a rare exception to these biogeographical subdivisions with at least one chelonioid species, *T. latiremis*, ranging from the northern portion of the NIFS to the southern extent of the SIFS (Fig. 6). The identification of *T. latiremis* remains from the Mooreville Chalk of Alabama currently represents the southernmost occurrence of this species and expands its geographic range to the southeastern-most areas of the Late Cretaceous ME. The discovery of *T. latiremis* fossils in what has been described as the SIFS increases the diversity of fossil turtles in this region and further supports the historically observed biogeographical patterns for fossil marine adapted turtles in the WIS during the Late Cretaceous (Nicholls and Russell 1990). In addition, this occurrence supports the existence of a broad overlap between the northern and southern subprovinces especially with regard to marine turtles. The similarities between the WIS and the ME marine turtle faunas, coupled with the high degree of marine turtle endemism unique to the southern portions of the ME, suggest that the ME may have been an endemic center for Late Cretaceous marine adapted turtles.

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