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Permalink
https://escholarship.org/uc/item/23r690jk

Journal
PaleoBios, 35(0)

ISSN
0031-0298

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Publication Date
2018-01-12

Peer reviewed
ANDREW D. GENTRY AND JUN A. EBERSOLE (2018). The first report of *Toxochelys latiremis* Cope 1873 (Testudines: Panchelonioidea) from the early Campanian of Alabama, USA.

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

Citation: Gentry, A.D. and J.A. Ebersole. 2018. The first report of *Toxochelys latiremis* Cope 1873 (Testudines: Panchelonioidea) from the early Campanian of Alabama, USA. *PaleoBios*, 35. ucmp_paleobios_37558.
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 (Chelonioida). 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 chelonioids 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 chelonioid (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 chelonioids (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 chelonioid in North America (Nicholls and Russell 1990).

Based on the occurrence of fossil chelonioids 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 chelonioids 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 chelonioid 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 previously observed trends in North American chelonioid 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 chelonioids 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 site 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; KUVP, University of Kansas Museum of Natural History, Lawrence, USA; MSC, McWane Science Center, Birmingham, Alabama, USA; RMM, Red Mountain

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**Table 1.** List of chelonioid 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).

<table>
<thead>
<tr>
<th>Anderson River</th>
<th>Pembina Springs</th>
<th>Sharon Springs</th>
<th>Niobrara</th>
<th>Mooreville Chalk</th>
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<tbody>
<tr>
<td>--</td>
<td>Toxochelys</td>
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<td>Ctenochelys</td>
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<td>Porthochelys prionochoelys</td>
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<td>Peritresius</td>
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<td>Corsochelys</td>
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<td>Thinochelys</td>
</tr>
</tbody>
</table>
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 brachyrhinus CASE, 1898, p. 378.
Toxochelys serrifer CASE, 1898, p. 378.
Toxochelys 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
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

![Figure 2](https://example.com/image2.png) 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 asymetrica (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 Broten, 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 (KUVP 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 chelonioid sensu stricto taxa (i.e., Ctenochelys Zangerl, 1953; Prionochelys Zangerl, 1953). The sulcus of the broad dorsal 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 chelonioinds (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 chelonioid taxon current 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 Carrino 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
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 regions.
Table 2. Distribution of shell characteristics among 'toxochelyid'-grade taxa of the Mooreville Chalk. Index value of posterior peripherals calculated as (W / L) x 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).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Trait</th>
<th>Wider than long</th>
<th>As long as wide</th>
<th>Longer than wide</th>
<th>Longer than wide</th>
<th>As long as wide</th>
<th>Wider than long</th>
</tr>
</thead>
<tbody>
<tr>
<td>Width of vertebrals</td>
<td>RMM 5614 &amp; 5615</td>
<td>Wider than long</td>
<td>As long as wide</td>
<td>Longer than wide</td>
<td>Longer than wide</td>
<td>As long as wide</td>
<td>Wider than long</td>
</tr>
<tr>
<td>Neural crest w/epineurals</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td>Peripheral serrations</td>
<td>Absent</td>
<td>Weak/absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td>Width of posterior peripherals</td>
<td>Never exceeds length</td>
<td>Never exceeds length</td>
<td>Exceeds length</td>
<td>Never exceeds length</td>
<td>Never exceeds length</td>
<td>Never exceeds length</td>
<td>Never exceeds length</td>
</tr>
<tr>
<td>Peripherals 8–11 index value</td>
<td>60–75%</td>
<td>60–80%</td>
<td>85–110%</td>
<td>95–120%</td>
<td>60–70%</td>
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<td>80–90%</td>
</tr>
<tr>
<td>Carapacial fontanelles</td>
<td>Large</td>
<td>Small/absent</td>
<td>Absent</td>
<td>Large</td>
<td>Small</td>
<td>Moderate</td>
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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.

ACKNOWLEDGEMENTS

The authors would foremost like to thank James Parham for his many insightful discussions regarding the Late Cretaceous marine turtles of North America. Comments from Don Brinkman and one anonymous reviewer greatly improved the overall quality of the manuscript and figures. The project also benefited from the editorial comments provided by Diane M. Erwin. The authors also thank the following faculty at the University of Alabama at Birmingham for their support of this project as members of the doctoral research committee of ADG: Scott Brande, Stephen Watts, Ken Marion, and Thane Wibbels. Finally, we are grateful to Sandy M. Ebersole of the Geological Survey of Alabama in Tuscaloosa for providing the GIS shapefiles necessary to construct Fig. 1.

LITERATURE CITED


