Smith et al. *Swiss Journal of Palaeontology* (2025) 144:23
https://doi.org/10.1186/s13358-025-00363-8

Swiss Journal of Palaeontology

RESEARCH

Open Access

A novel marine turtle (Pan-Chelonioidea: Ctenochelyidae) from the Maastrichtian Neylandville Marl Formation of north central Texas, U.S.A

Heather F. Smith[1,2*], Brent Adrian[2] and Patrick Kline[3]

Abstract

The marine turtle family Ctenochelyidae was a Late Cretaceous North American radiation of Pan-Chelonioidea, broadly distributed along the coastlines of the Atlantic Coastal Plain and Mississippi Embayment. Here, we describe a large, mostly articulated carapace representing a novel species of the ctenochelyid genus *Asmodochelys* from the Maastrichtian Neylandville Marl Formation in north central Texas. The specimen is diagnosed as a ctenochelyid by its large cordiform carapace with a broad nuchal embayment, prominent neural keel with epineural ossifications, and costoperipheral fontanelles. It has a unique combination of characters: large size (~ 120 cm); epineurals dorsal to N1/2, N3/4, N5/6, and N7/8; robust articulation between costal 1 and peripherals 1–2; lack of postnuchal fontanelles; pronounced anterior horn-like projection of peripheral 1; weakly scalloped posterior peripherals. Maximum parsimony phylogenetic analyses were conducted in TNT v1.6, and in the resulting majority-rule consensus trees, the specimen was positioned at the base of Ctenochelyidae in an unresolved polytomy with *Asmodochelys parhami* and the unresolved clade of (*Peritresius ornatus* + *Prionochelys matutina* + *Ctenochelys acris* + *Ctenochelys stenoporus*). The Neylandville Marl lies within the faunal zone of the marine oyster *Exogyra cancellata*, providing a particular marine ecological context that extends from Mexico to New Jersey. The new species extends the stratigraphic range of *Asmodochelys* into the Maastrichtian of the Gulfian Series, and geographically further west of the Mississippi Embayment to north-central Texas. It is one of the latest surviving members of the Ctenochelyidae persisting into the Maastrichtian, a time of global climatic cooling when other major Campanian marine turtle lineages, such as protostegids and *Toxochelys*-like early stem-chelonioids faced extinction.

Keywords Pan-Chelonioidea, Testudines, Sea turtle, Late Cretaceous, Phylogeny, Evolution, Morphology, Taxonomy

Handling editor: Yann Rollot.

This article is part of the Special Issue Proceedings of the Symposium on Turtle Evolution.

*Correspondence:
Heather F. Smith
hsmith@midwestern.edu
Full list of author information is available at the end of the article

Introduction

The largest crown clade of marine turtles, Chelonioidea (sensu Joyce et al., 2004, 2021), is globally distributed and currently comprises a total of seven species including six from the crown clade of extant hard-shelled marine turtles (Cheloniidae) and leatherback marine turtles (Dermochelyidae), whose single extant form is *Dermochelys coriacea* (TTWG, 2017). Pan-Chelonioidea has a substantial fossil record spanning more than 90 million years, making it the oldest living marine tetrapod lineage (Gentry et al., 2019; Pyenson et al., 2014). The question regarding which lineages of the diverse marine turtle fossil record are attributable to the superfamily Pan-Chelonioidea is not fully resolved (Cadena & Parham, 2015; Evers & Benson, 2019; Joyce et al., 2021). However, it confidently includes some genera recovered from the Late Cretaceous of North America that may have had worldwide distributions, such as *Desmatochelys* (Cadena & Parham, 2015), *Leyvachelys* (Cadena, 2015), and *Euclastes* (Parham & Pyenson, 2010).

Chelonioids form a secondarily marine-adapted group (Bardet et al., 2014; Benson et al., 2013; Evers & Benson, 2019; Hirayama, 1998; Motani, 2009; Motani & Vermeij, 2021) and unlike many other Cretaceous reptiles, survived the Cretaceous-Paleogene mass extinction (see Hutchison & Archibald, 1986; Benson et al., 2010; Parham & Pyenson, 2010; Evers & Benson, 2019; Menon et al., 2024). The understanding of the rich fossil record of Late Cretaceous sea turtles has been confounded due to poorly justified taxonomic decisions and incomplete, fragmentary preservation, with some important exceptions (e.g., *Nichollsemys baieri* Brinkman et al., 2006; Menon et al., 2024). These factors have led to phylogenetic uncertainty and obfuscated character evolution at the base of Chelonioidea.

Menon et al. (2024, this volume) provide a thorough summary of the evolution of marine turtles during the Cretaceous, and placed the Ctenochelyidae within the stem-chelonioids. Ctenochelyidae is phylogenetically defined as originating from the most recent common ancestor of *Ctenochelys* (formerly *Toxochelys*) *stenoporus, Prionochelys matutina,* and *Peritresius* (formerly *Chelone*) *ornatus,* and most recently *Asmodochelys parhami* Gentry et al., 2019, along with their congenerics *Ctenochelys acris*, *Prionochelys nauta,* and *Peritresius martini* (Gentry, 2017, 2018; Gentry et al., 2018). Other genera (i.e., *Euclastes* and *Pacifichelys*) have been hypothesized as belonging to the stem of Cheloniidae, a possible sister group to Ctenochelyidae (Gentry, 2018; Kear & Lee, 2006; Lapparent de Broin et al., 2014; Lynch & Parham, 2003; Parham, 2005; Parham & Pyenson, 2010). Divergence time estimates from recent phylogenetic studies based on molecular sequence data and fossil calibrations suggest that the chelonioid crown group originated between the early Campanian and Eocene, with some disagreement regarding finer time scales (Joyce et al., 2013; Near et al., 2005; Pereira et al., 2017; Thomson et al., 2021). Thus, the fossil record can be grossly aligned with molecular divergence estimates, and the discovery of additional well-preserved fossils from this interval will enable better phylogenetic resolution within Chelonioidea.

The current study describes a novel marine turtle species from the Maastrichtian of north-central Texas. HNSMWS-2018.1 is a nearly complete carapace that was discovered eroding from the north bank of the South Sulphur River in Hunt County, Texas. This specimen is the first vertebrate to be formally described from the Neylandville Formation, but its numerous invertebrate taxa were well described by Stephenson (1941). A phylogenetic analysis of HNSMWS-2018.1 was performed to determine placement within the most recent evolutionary and paleobiogeographic hypotheses of Late Cretaceous marine turtles, and its morphology is assessed for insights into its paleoecology.

Geological setting

The marine Neylandville Formation forms a narrow band of outcrops that are overlain by the Nacatoch Sandstone, and lying atop the Marlbrook Marl Formation in the uppermost Taylor Group (Fig. 1) (Patterson, 1983; Stephenson, 1941). Together, Neylandville and Nacatoch deposits are equivalent to the combined Demopolis-Ripley sequence of the eastern Gulf region (Monroe, 1947). The lower 300 or 400 feet of the basal Navarro Group, which includes the Neylandville Fm., comprises gray calcareous shale-bearing clays or marls that weather to light gray, forming an irregular topography (Barnes et al., 1992). Neylandville deposits are best known for bearing a distinctively robust invertebrate fauna (102 named species), and the most significant species (*Exogyra cancellata* Stephenson, 1914 and *Anomia tellinoides* Morton, 1833) are known from several localities near Cooper and Greenville in Texas (Stephenson, 1941: Table 1). These species are restricted to the *Exogyra cancellata* ammonite subzone (basal *E. costata* zone) that traversed the Atlantic and Gulf Coastal Plains from New Jersey to Kaufman County, Texas, and is further recognized at Ciudad del Maiz in San Luis Potosi, Mexico, approximately 440 miles south of Eagle Pass, Texas (see first figures of Stephenson, 1933, 1941). This subzone is also preserved in southwestern Arkansas as part of the upper Marlbrook Marl Fm., which excluding the upper half of the "Saratoga" chalk member, forms the upper several meters of the Marlbrook (Stephenson, 1933, 1941). The boundary between the Neylandville Fm. and underlying Marlbrook

Marl Fm. occurs near the Campanian–Maastrichtian transition (Barnes et al., 1992). Neylandville Fm. is thus early Maastrichtian in age (younger than approximately 70.6 Ma) and correlated with the middle and upper parts of the Pierre shale and equivalents in the Western Interior (Stephenson, 1941). This is indicated by the common occurrence of invertebrates including *Ostrea plumosa*, *Placenticeras meeki*, *Baculites claviformis*, *Exogyra costata*, as well as several analogous species known by different names at the interior sites. The *Exogyra cancellata* subzone is also equivalent to upper Campanian and lower Maastrichtian deposits in the European stratigraphic section (Stephenson, 1933). Excluding stratigraphically long-ranging invertebrate taxa, at least 33 of the Neylandville species described by Stephenson (1941) ranged upward into the overlying Nacatoch sand, and only five or six ranged downward into the Taylor Group, suggesting a greater affinity with the younger geological units.

Institutional abbreviations

ALMNH, Alabama Museum of Natural History, Tuscaloosa, Alabama, U.S.A; **AMNH**, American Museum of Natural History, New York, New York, U.S.A;**FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A; **HNSMWS**, Heard Natural Science Museum and Wildlife Sanctuary, McKinney, Texas, U.S.A; **MMNS**, Mississippi Museum of Natural Science, Jackson, Mississippi, U.S.A; **MSC**, McWane Science Center, Birmingham, Alabama, U.S.A; **NJSM**, New Jersey State Museum, Trenton, New Jersey, U.S.A; **RMM** former Red Mountain Museum, Birmingham, Alabama, U.S.A. (collections now at MSC); **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

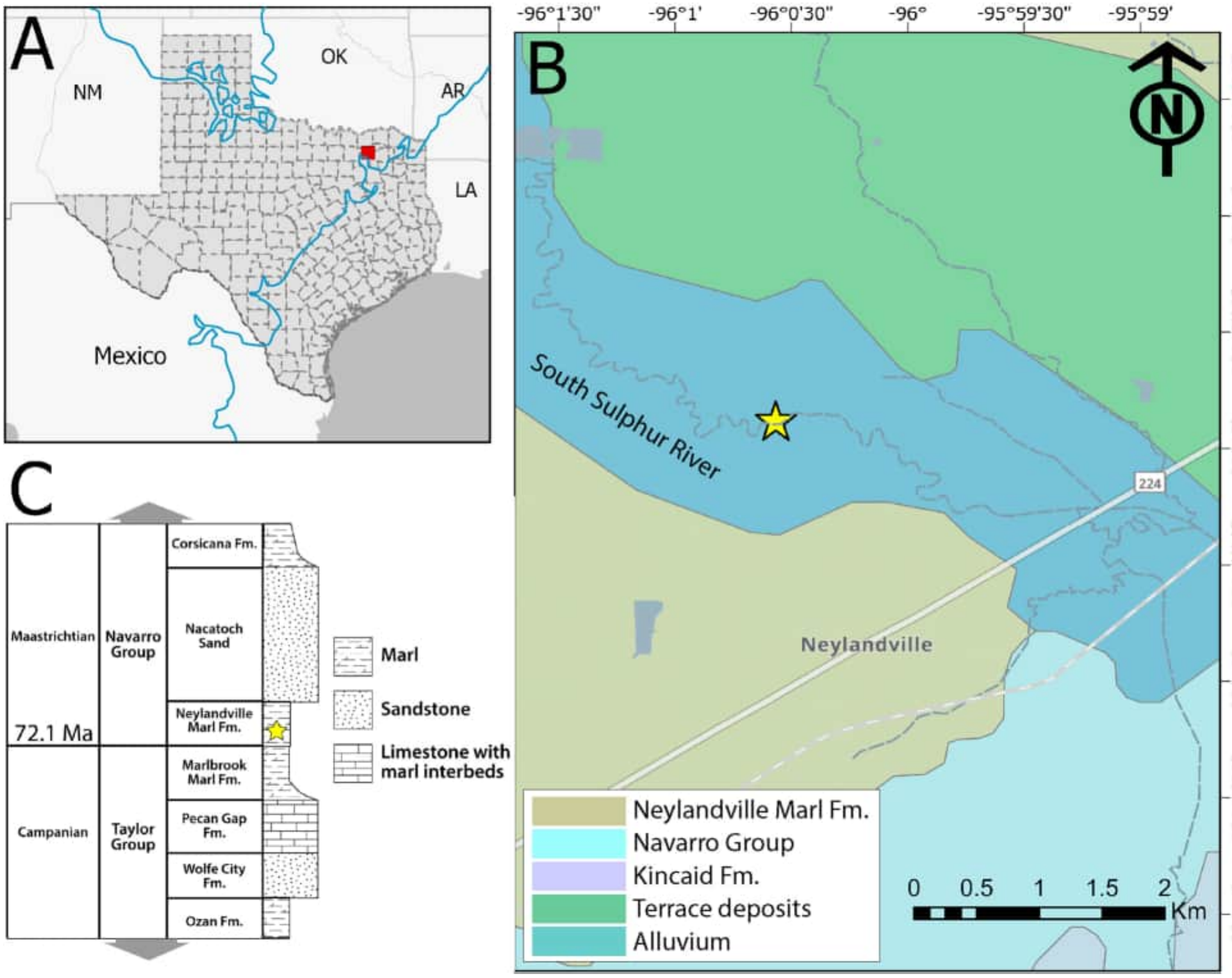

Fig. 1 Index map showing: **A** Geographic location of type locality in north central Texas, U.S.A.; **B** Stratigraphic map of South Sulphur River showing geographic locations of Neylandville Marl Formation and nearby deposits; **C** Stratigraphic column. Red square in part A indicates Hunt County, Texas, the county of specimen recovery. Blue lines in part A indicate the paleoshoreline which was reconstructed based on Blakey (2014). Yellow stars indicate the location of *Asmodochelys leviathan* sp. nov. holotype specimen HNSMWS-2018.1. Figure created with ArcGISPro 3.4 and Adobe Illustrator 29.3.1. Data sources: Esri, TomTom, Garmin, FAO, NOAA, USGS. Part C after Jacobs et al. (2013)

Table 1 Provenance data for ctenochelyid taxa compared in this study, including Age, specimen numbers, species, location, and reference

Age	Taxa	Specimens	Formation (state)	References
Maastrichtian	*Peritresius ornatus*	ALMNH 5497 MMNS 4003 MMNS 4546 MMNS 4547 MMNS 5533 MMNS 5710	Prairie Bluff Chalk (AL, MS)	Gentry et al., 2018: table 1
	Peritresius ornatus	NJSM 11051	Lower Redbank Marl, New Egypt Fm. (NJ)	Baird, 1964
Campanian	*Peritresius martini*	ALMNH 6191	Ripley Fm. (AL, MS)	Gentry et al., 2018: table 1
	Peritresius ornatus	ALMNH 8988 MSC 5741 MMNS 5102 MMNS 5876 MMNS 5274 MMNS 7521 MMNS 8632.4	Ripley Fm. (AL, MS)	Gentry et al., 2018: table 1
	Asmodochelys parhami	MMNS 3958	'Muldrow' Mbr., Demopolis Chalk (AL, MS)	Gentry et al., 2019
	Asmodochelys parhami	MSC 35984	Bluffport Marl Mbr., Demopolis Chalk (AL)	Gentry et al., 2019
	Peritresius ornatus	ALMNH 5887	Bluffport Marl Mbr., Demopolis Chalk (AL)	Gentry et al., 2018: table 1
	Peritresius ornatus	ALMNH 3900 ALMNH 6256	Demopolis Chalk (AL, MS)	Gentry et al., 2018: table 1
	Ctenochelys acris	FMNH P27354 MSC 35085 RMM 3050 RMM 6157	Mooreville Chalk (AL)	Zangerl, 1953: 242; Gentry, 2017
	Peritresius ornatus	ALMNH 3780	Mooreville Chalk (AL)	Zangerl, 1953: 242; Gentry et al., 2018: table 1
	Prionochelys matutina	MSC 1719 MSC 1915 MSC 2045 MSC 2610 MSC 2720 MSC 3036 MSC 3140 MSC 3500 MSC 5626 MSC 6086 MSC 38604 MSC 39013 MSC 39030	Mooreville Chalk (AL)	Gentry, 2018
Santonian	*Prionochelys matutina*	MSC 2250	Tombigbee Sand Mbr., Eutaw Fm. (AL)	Gentry, 2018
Coniacian-Campanian	*Ctenochelys stenoporus*	AMNH 6137	Niobrara Chalk (KS)	Baird, 1964

Methods and materials

The specimen was carefully removed from the riverbed along with a large portion of mudstone matrix that holds the carapace together, Mechanical reinforcement was added during preparation to further reinforce its structure. This benefitted the preservation of the dorsal side of the carapace but unfortunately precludes examination of the ventral side. The specimen was photographed using a Nikon D5100 digital camera, and figures were created using Adobe Illustrator and Photoshop 2025. Fine sutures were located visually and traced with ultraviolet (UV) ink, and then photographed while illuminated under UV light. Measurements were taken to the nearest millimeter using Mitutoyo digital calipers. A 3D model of the carapace of HNSMWS-2018.1 was produced using photogrammetry on a Google Pixel 8 phone using the WIDAR-3D Scan & Edit app (WOGO Inc.; Tullos, 2024). The model is available on MorphoSource at the following link: https://doi.org/10.17602/M2/M699482.

Phylogenetic analysis

The HNSMWS-2018.1 specimen was scored for the full character sets from: (1) Menon et al. (2024) resulting in a matrix of 356 characters and 98 taxa (Supplementary File S1); (2) Gentry et al. (2019), resulting in a matrix of 347 characters and 89 taxa (Supplementary File S2). Both data matrices were employed because while the Menon et al. character matrix is more recent, it contains fewer ctenochelyid species (n = 2 vs n = 5 in Gentry), and it was therefore predicted to be useful for inferring whether HNSMWS-2018.1 fell within the Ctenochelyidae but not for resolving relationships within the clade. A maximum parsimony phylogenetic analysis was conducted in Tree Analysis using New Technology (TNT) v1.6 (Goloboff & Morales, 2023), involving a traditional heuristic search with a tree bisection reconnection (TBR) swapping algorithm consisting of 1000 Wagner tree replicates. For the Menon et al. (2024) analysis, the following characters were treated as ordered: 7, 14, 18, 21, 34, 61, 65, 67, 74, 76, 79, 90, 93, 94, 103, 107, 117, 123, 130, 131, 138, 142, 145, 147, 205, 210, 217, 248, 253, 281, 292, 305, 325, 339, 340, 344. For the Gentry et al. (2019) analysis, these characters were treated as ordered: 7, 18, 58, 67, 74, 76, 77, 78, 79, 93, 94, 98, 103, 130, 145, 147, 157, 206, 218, 254, 293, 306, 327, 341, 342, 346. Following Gentry et al. (2019) and contra Menon et al. (2024), we coded *Ctenochelys* and *Peritresius martini* as lacking a continuous keel on the costals (Menon character 190, Gentry character 188; state 0). Menon et al. pruned from their tree the rogue taxon *Corsochelys haliniches* Zangerl, (1960). As this species falls outside the clade of primary interest in the present study, we predicted that it would be unlikely to affect the position of HNSMWS-2018.1. Nevertheless, we ran the analysis twice with and without *Corsochelys haliniches.* Character optimization was performed to identify unambiguous synapomorphies.

Systematic paleontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Chelonioidea Baur, 1893

Ctenochelyidae Karl, Biermann, and Tichy, 2012 (sensu Gentry, 2018).

Genus *Asmodochelys* Gentry, Ebersole, and Kiernan, 2019

Asmodochelys leviathan sp. nov.

http://Urn:lsid:zoobank.org:act: 2D516704-9587-454D-A1D8-990A6A2C6827

Figures 2, 3, 4, 5.

Etymology: The species epithet refers to the concept of Leviathan, based in pre-biblical Middle Eastern mythology, in particular a sea monster named Lotan that was defeated by the god Baal. Over time, the term has become more broadly used to refer to any gigantic, powerful entity or large sea monster.

Holotype: HNSMWS-2018.1, a nearly complete carapace, including nuchal, neurals 1–8, suprapygal 1, pygal, costals 1–8, an isolated section of left peripherals 8–10, an isolated partial left portion of the anterior plastron with likely partial epiplastron and hyoplastron, partial right ?pubis.

Type locality and horizon: North shore of South Sulphur River, Hunt County, Texas; Neylandville Formation; lower Navarro Group. Exact locality data is on file with Heard Natural Science Museum and Wildlife Sanctuary (HNSMWS) in McKinney, Texas.

Diagnosis

Asmodochelys leviathan sp. nov. is a large-bodied Cretaceous pan-chelonioid that can be diagnosed as a member of Ctenochelyidae based on a prominent single neural keel, the presence of epineural ossifications, and a cordiform carapace (Baird, 1964; Gentry, 2017, 2018; Gentry et al., 2018, 2019). It can be referred to *Asmodochelys* based on its thick shell and deep nuchal embayment; lack of nuchal fontanelles (unlike other ctenochelyids; Baird, 1964); horn-like protuberances from the anterodorsal margins of the first peripherals; first epineural positioned at N1/2; relatively short, narrow, and minimally scalloped posterior peripherals (Gentry et al., 2019).

Asmodochelys leviathan sp. nov. has the following unique combination of traits: broad thick nuchal with deep nuchal embayment including the first peripherals; well-developed anteriorly projecting protuberances on pe1; robust articulations between costal 1 and both peripherals 1 and 2 resulting in costoperipheral fontanelles that begin at costal 3; lack of postnuchal fontanelles; absent preneural; 8 neurals; epineural ossifications at N1/2, N3/4, N5/6, and N7/8; thin, narrow, weakly scalloped posterior peripherals. Its carapace is highly domed, and the anterior carapace is substantially deeper than other ctenochelyid species, most similar to *Asmodochelys parhami* (Gentry et al., 2019). In contrast to all other known ctenochelyids (*Ctenochelys*, *Peritresius, Prionochelys*, and *Asmodochelys parhami)* only *Asmodochelys leviathan* sp. nov. has a robust articulation among the nuchal and first two anterior peripherals, with no evidence of costoperipheral fontanelles in this area (Baird, 1964; Gentry, 2017, 2018; Gentry et al., 2018, 2019; Matzke, 2007).

Asmodochelys leviathan sp. nov. differs from its congeneric *Asmodochelys parhami* in its extensive contact between costal 1 and the first two peripherals. This arrangement results in free peripherals that are associated with costoperipheral fontanelles beginning at costal 3 in *Asmodochelys leviathan* sp. nov., whereas in *Asmodochelys parhami*, these fontanelles extend along the entire length of the carapace, contacting the nuchal, pygal, and all intervening costals. *Asmodochelys leviathan* sp. nov. has 8 neurals compared to the putative ?9 neurals in *Asmodochelys parhami*. The positions of the epineurals also differ, falling at N1/2, N3/4, N5/6, and N7/8 in *Asmodochelys leviathan* sp. nov., and at N1/2, N2/3, N4/5, and N6/7 in *Asmodochelys parhami* (Table 2). Posterior peripherals are narrow and weakly scalloped in both species compared to other ctenochelyids, but the condition is amplified in *Asmodochelys parhami*, which has even narrower and less scalloped peripherals (Table 3).

Comparative diagnosis

The carapace of HNSMWS-2018.1 is comparable in size (~ 120 cm) with *Ctenochelys acris* and *Asmodochelys parhami,* but larger than size estimates (~ 80 cm) for *Prionochelys nauta* and *Ctenochelys stenoporus, Peritresius martini* (90 cm), and *Peritresius ornatus* (75 cm) (Baird, 1964; Gentry, 2018; Gentry et al., 2018, 2019; Hirayama, 1997). *Asmodochelys leviathan* sp. nov. has a highly domed carapace, which is also diagnostic for *Peritresius*, but is otherwise not well known for other ctenochelyid species (Gentry et al., 2018). Its shell sculpturing is smooth as in most ctenochelyid taxa and differs from the distinct vermiculate texture of *Peritresius ornatus* (Baird, 1964; Gentry et al., 2018: Fig. 7).

The anterior margin of the carapace flares more widely than in *Asmodochelys parhami*, and the curvature of the nuchal embayment is more open anteriorly, with longer and more protruding anterior points of the first peripherals (Gentry et al., 2019). The nuchal embayment of the *Asmodochelys leviathan* sp. nov. is broad as in *Allopleuron hoffmani* Felder, 1980, and comprises the nuchal and first peripherals, similar to *Asmodochelys parhami, Allopleuron hoffmani* (Mulder, 2003), and *"Allopleuron" insularis* Weems, 1988, but distinct from *Ctenochelys* spp. and *Prionochelys matutina*, in which only the nuchal contributes to the embayment (Gentry, 2017, 2018; Matzke, 2007; Zangerl, 1953). These horn-like protuberances are pronounced as in *"Allopleuron" insularis*, and are more developed than in *Asmodochelys parhami,* but are not present in *Ctenochelys, Prionochelys* and *Peritresius* (Baird, 1964; Gentry, 2017, 2018; Gentry

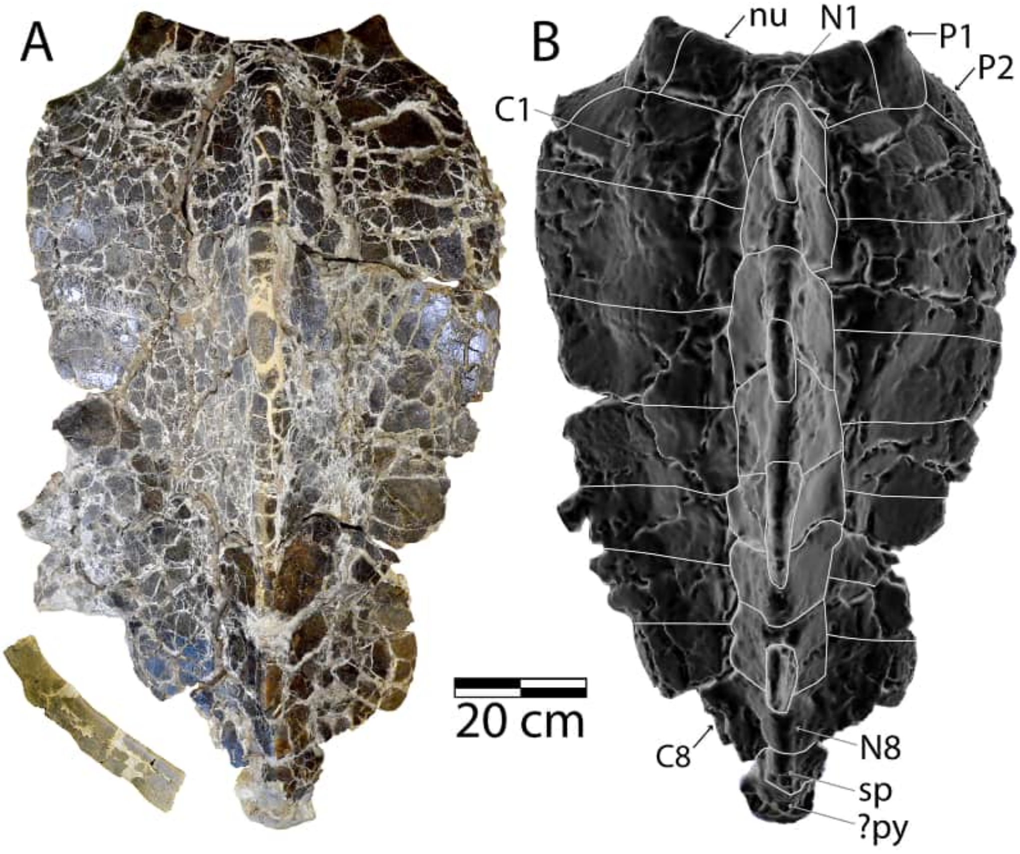

Fig. 2 HNSMWS-2018.1, holotype of *Asmodochelys leviathan* sp. nov., articulated carapace in: **A** dorsal photograph and **B** digital model. C: costal, N: neural, nu: nuchal, P: peripheral, py: pygal, sp: suprapygal

et al., 2018, 2019). Nuchal fontanelles are absent in both *Asmodochelys* species, but are present in all other ctenochelyid genera, including *Ctenochelys, Prionochelys,* and *Peritresius* (Gentry, 2017, 2018; Gentry et al., 2018, 2019; Matzke, 2007; Zangerl, 1953).

Asmodochelys leviathan sp. nov. lacks a preneural, consistent with *Asmodochelys parhami* and *Peritresius ornatus* (Baird, 1964; Gentry et al., 2018, 2019), while preneurals are present in *Ctenochelys* spp. and *Prionochelys* spp. (Gentry, 2017, 2018; Matzke, 2007; Zangerl, 1953). A prominent midline neural keel is present, as in other Ctenochelyidae and many Protostegidae such as *Allopleuron hoffmani*, *Archelon ischyros*, and *Calcarichelys gemma* (Hooks, 1998; Mulder, 2003; Wieland, 1909), and the presence of epineurals characterizes *Asmodochelys leviathan* sp. nov. and all other Ctenochelyidae, and differentiates them from Protostegidae, *Toxochelys* Cope, 1873, and *Thinochelys* Zangerl, 1953. The neurals of *Asmodochelys leviathan* sp. nov. are generally equilateral, although sometimes slightly longer than wide as in *Asmodochelys parhami* and *Peritresius ornatus*; however, neurals are generally longer than wide in *Ctenochelys* spp. and *Prionochelys* spp. (Gentry, 2017, 2018; Matzke, 2007; Zangerl, 1953). *Asmodochelys leviathan* sp. nov. and *Asmodochelys parhami* each have an epineural that is dorsal to the contact between the first two neurals, which is absent in *Ctenochelys*, *Prionochelys* and *Peritresius* (Gentry et al., 2019) (Table 3).

Asmodochelys leviathan sp. nov. has posterior peripherals that are considerably narrower than long. Both *Asmodochelys* spp. and *Peritresius* spp. differ from *Prionochelys* spp. and *Ctenochelys* spp. by having narrower posterior peripherals resulting in lower posterior peripheral indices ([W/L]*100) (Gentry et al., 2019) (Table 3). Posterior peripherals are slightly scalloped in *Asmodochelys leviathan* sp. nov., as in *Asmodochelys parhami*, moderately scalloped in *Ctenochelys* spp. and *Peritresius* spp., and highly scalloped in *Prionochelys* spp. (Table 3).

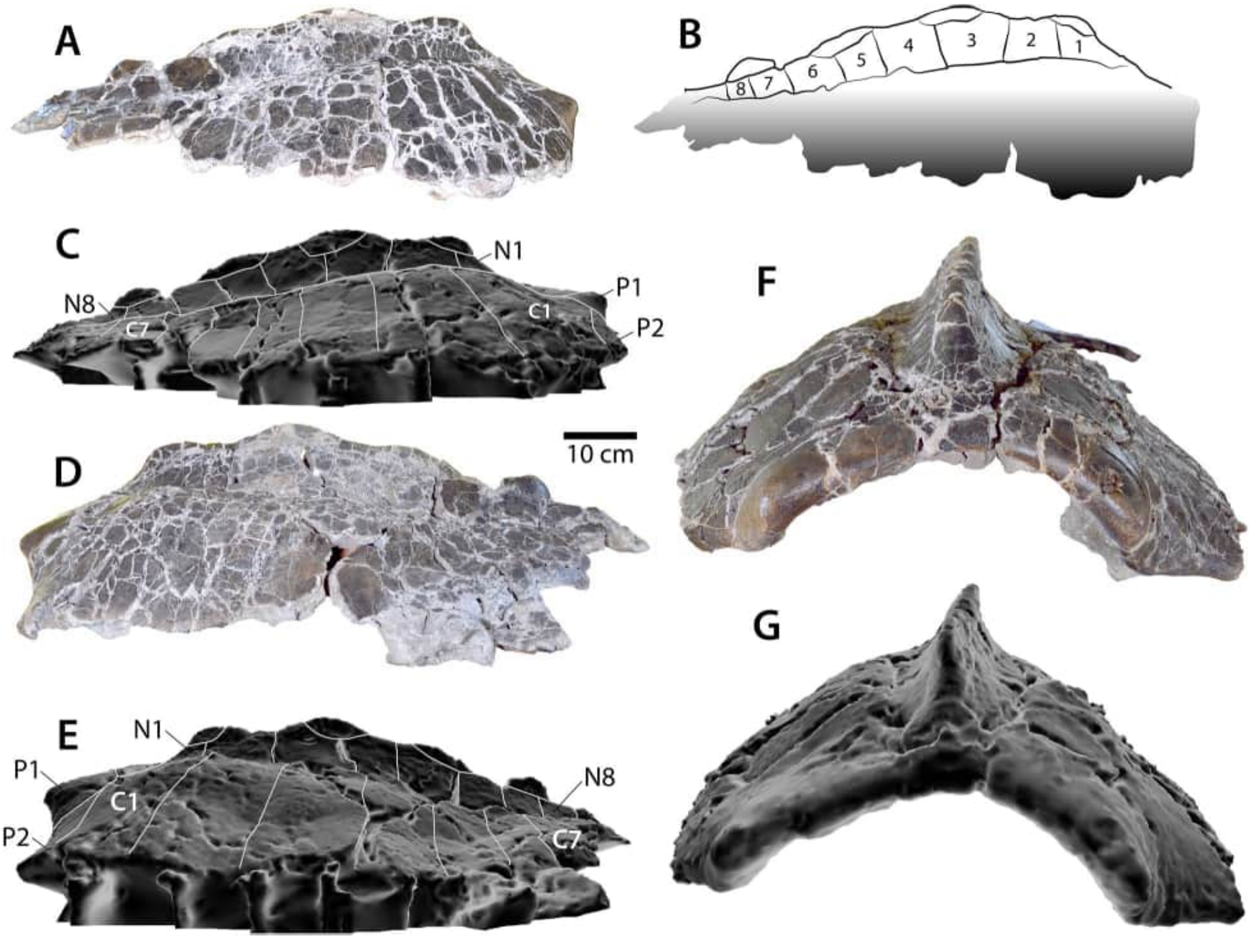

Fig. 3 HNSMWS-2018.1, holotype of *Asmodochelys leviathan* sp. nov., articulated carapace in: **A** right lateral photograph, **B** lateral line drawing, **C** right lateral digital model, **D** left lateral photograph, **E** left lateral digital model, **F** anterior photograph, and **G** anterior digital model. C: costal, N: neural, P: peripheral. Scale = 10 cm and applies to photographs, with similar scale for digital models

While very little beyond the carapace is preserved in HNSMWS-2018.1, it shares with all other ctenochelyid taxa epiplastra that are elongate in shape, a character also shared with many other pan-chelonioids but that differs from the laterally expanded, wing-like shape of epiplastra in protostegids (e.g., Hirayama & Tong, 2006; Cadena & Combita-Romero, 2023).

Description

The holotype specimen HNSMWS-2018.1 is large in size, robust, and cordiform in shape with a straight antero-posterior length of 117 cm (Fig. 2). Its relatively tall dome is well preserved with an estimated width (excluding peripherals) of approximately 71 cm (Fig. 3). Overall, the carapace is preserved such that its complete costal width is mostly retained, with rounded lateral edges and broken ribs marking the medial edges of fontanelles beginning in the posterior half of the third costals (Fig. 2B). The superficial dorsal surface of the carapace preserves its smooth, textureless surface in many small patches (Fig. 2A). Sutures are formed by fine, meandering seams without superficial relief and in many places are indistinguishable from modifications due to extensive fracturing. Sulci are narrow, shallow, and only defined on the dorsal surface of the posterior peripherals between bony articulations.

The nuchal embayment of HNSMWS-2018.1 is striking in its broad anterior curvature (Fig. 2). It is formed by the nuchal and first peripherals, and its medio-lateral diameter is 41.5 cm. The nuchal is approximately trapezoidal in shape when viewed dorsally, and it contacts the first costals, peripherals, and neural. The nuchal has a posterior concavity at the midline that accommodates the anterior edge of neural 1. The first peripherals have robust, antero-laterally directed horn-like projections, and the thickness of the anterior carapace rim at these points is approximately 5 cm. There is no evidence of fontanelles (including postnuchal) in the entire anterior portion of the carapace, and the articulations between bony elements are robust (Figs. 2, 3). HNSMWS-2018.1 has a single tall keel projecting dorsally along its neural row (Fig. 3). The keel is warped slightly to the left at its posterior end, likely due to diagenetic effects. There are eight neurals, which have antero-posterior diameters that reach or exceed their mediolateral widths, and are shortest at the anterior and posterior ends (Figs. 2B, 3B). There are four long, narrow epineural bones articulated atop the junction between some adjacent neurals forming distinct

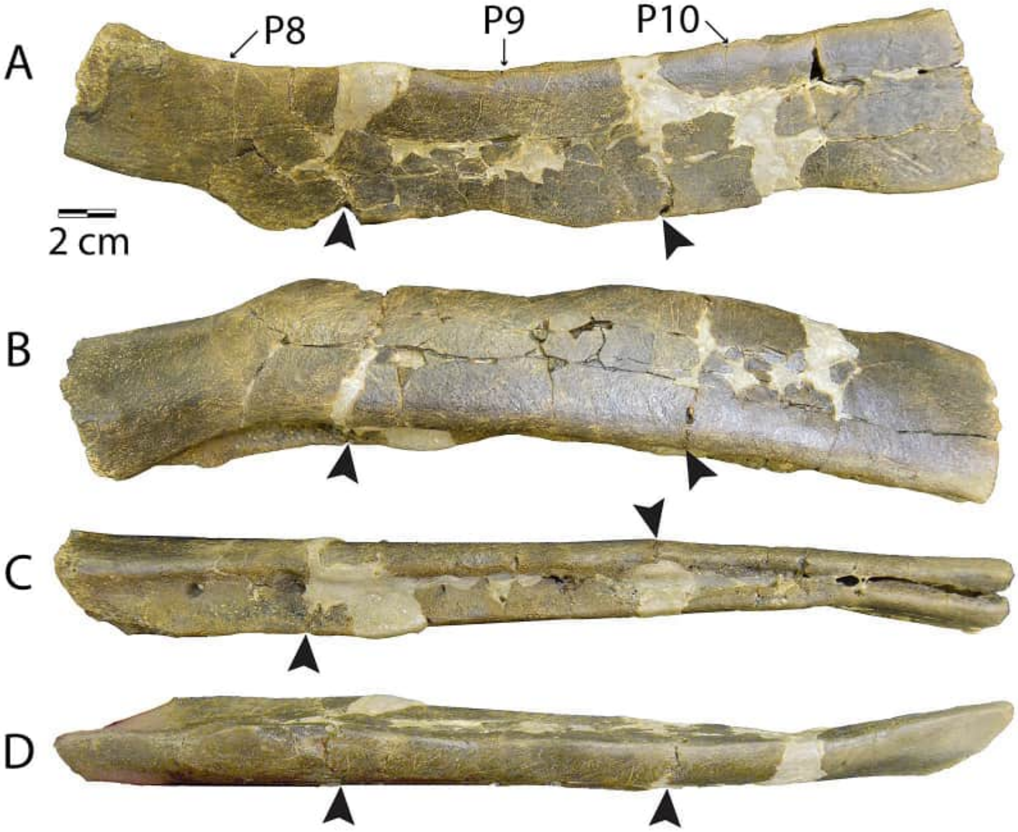

Fig. 4 Isolated peripheral sequence (8–10) from the left side of HNSMWS-2018.1, *Asmodochelys leviathan* sp. nov. in: **A** dorsal, **B** ventral, **C** medial, and **D** lateral views. The anterior direction is to the left in all views. Black arrowheads indicate sutures

peaks, or elevations of the keel. Elevations occur between neural pairs 1–2, 3–4, 5–6, and 7–8 (Figs. 2, 3). The anterior three elevations have rounded, gently sloping peaks in lateral view with a steeper inclination on the anterior side of the first peak. The posteriormost elevation is separated from the anterior peaks by a relatively low saddle, and has somewhat steeper slopes than its counterparts. The posterior two epineurals articulate mostly with their respective anterior neurals. The posterior end of the axial skeleton is damaged and not complete, though at least two midline bones are present posterior to neural 8, the first of which is interpreted as suprapygal 1. This bone forms a less quadrangular and more triangular than the neurals, and is also narrower mediolaterally. It is flanked laterally by the eighth costals, which are truncated leaving only their medial ends. Another bone is present posteriorly that is smaller and more quadrangular without its dorsal portion, most likely representing the pygal, although the possibility that it may be a second suprapygal cannot be entirely excluded. The posteriormost extent of the carapace is rounded, suggesting its natural end. The incomplete condition of the posterior carapace allows us to identify at least one suprapygal with confidence (Figs. 2B). However, discerning the exact arrangement of posterior carapace bones will require additional fossil material.

HNSMWS-2018.1 preserves the first two anterior peripherals on each side and also an isolated segment of three posterior peripherals from the left side that likely represent the eighth through tenth elements (Figs. 2A, 4). The first peripherals are located lateral to the nuchal and form the distinctive horn-like projections that laterally constrain the prominent nuchal embayment (Figs. 2, 3). They also contact the first costal posteriorly and the second peripherals postero-laterally. The second peripherals articulate along their entire lengths with the lateral edges of the first costal, and there is no evidence of fontanelles in the area. The posterior peripherals are weakly scalloped and widest in their posterior halves, with a slightly upturned lateral margin (Fig. 4). Interperipheral sutures are slightly posteriorly oriented, and the cross-sectional shape of the peripherals becomes more acute posteriorly. A well-developed medially-facing channel extends along the posterior peripherals and becomes dorsoventrally taller toward the posterior end. There is a small articular pit in the center of the channel near the longitudinal midpoint of each posterior peripheral, which likely joined the lateral end of ribs that extended from the costals (Fig, 4C). Overall, costals are well preserved in HNSMWS-2018.1 and most project in a straight manner laterally from the neurals (Figs. 2B, 3C, 3E). The antero-posterior diameter of the first two pairs of costals are similar and consistent mediolaterally. The diameters of the costals posterior to these are smaller and decrease gradually toward the posterior shell. The lateral edge of the costals is rounded without bony articulation beginning at costal 3, indicating that costoperipheral fontanelles begin at this point and continue posteriorly.

Only a small portion of the plastron of HNSMWS-2018.1 is adhered by matrix to the ventral side of costal 5 on the left side. The preserved plastral elements are tentatively identified here as portions of the epiplastron and hyoplastron (Fig. 5A). They are clearly displaced from their original positions. The preserved epiplastral

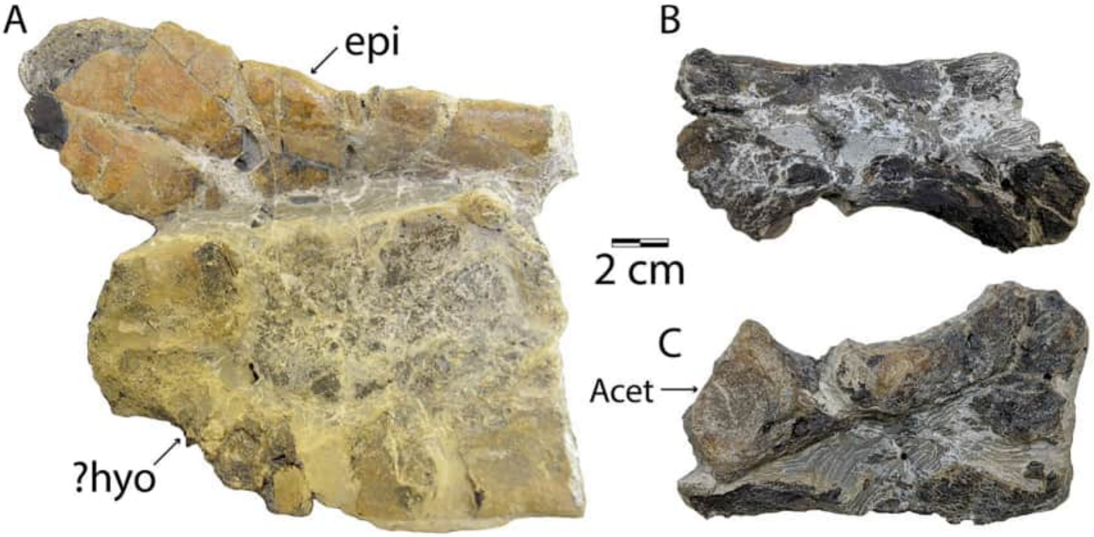

Fig. 5 **A** Epiplastral and ?hyoplastral pieces of HNSMWS-2018.1, *Asmodochelys leviathan* sp. nov. in ventral view. Right ?pubis in: **B** internal pelvic and **C** external pelvic views. Acet: acetabulum; epi: epiplastron; ?hyo: likely partial hyoplastron

Table 2 Positions of the epithecal ossifications in *Asmodochelys leviathan* sp. nov. and comparative ctenochelyid species

Taxon	N1-2	N2-3	N3-4	N4-5	N5-6	N6-7	N7-8	N8-sp1	sp1-sp2
Asmodochelys leviathan sp. nov.	▨		▨		▨		▨		
Asmodochelys parhami	▨	▨		▨		▨			
Ctenochelys acris		▨		▨		▨			
Ctenochelys stenoporus		▨		▨		▨			▨
Peritresius ornatus			▨		▨		▨		
Prionochelys matutina		▨		▨		▨			▨
Prionochelys nauta		▨			▨			▨	▨

Shaded boxes indicate locations of epithecals. N: neural, sp: suprapygal. Neural series in *Asmodochelys parhami* based on composite of two specimens

section is elongate, plank-like and curved slightly away from the other element, which overlaps it ventrally. The latter portion has a curved edge adjoining the epiplastron, but is otherwise too poorly preserved to interpret confidently. The epiplastral portion is 21.9 cm long and 7.7 cm at its widest point, while the other (hyoplastral?) portion is 18.1 cm in its longest dimension (presumably the mediolateral width), and 11.9 cm orthogonally.

A single element of non-shell postcranial material is associated with HNSMWS-2018.1. We interpret this piece as a pelvic element, likely the right pubis. It is flat and roughly rhomboidal, and its surface is significantly abraded (Figs. 5B, 5C). It preserves the pubic contribution to the acetabulum, and its articular surface is ovoid and concave. Proximal to the acetabulum, the bone constricts into a stout neck. The cranial border of the pubis is concave and contains a rounded tuberosity, while the caudal border is straight. The pubis expands medially towards the pubic symphysis, as the bone flattens and becomes thinner (Figs. 5B, 5C).

Phylogenetic results

Phylogenetic topology

The phylogenetic analysis using the Menon et al. (2024) data matrix resulted in 40 minimum length trees of 1687 steps (Fig. 6A). In the Majority Rule consensus tree (55%), *Asmodochelys leviathan* sp. nov. was positioned as the sister taxon to *Ctenochelys*. The pair was positioned at the base of the clade that contained crown Chelonioidea + the other non-Protostegid and non-'Toxochelyinae' sensu Zangerl (1953) Pan-Chelonioids. This analysis confirmed the position of *Asmodochelys leviathan* sp. nov. within Ctenochelyidae. The second iteration pruning *Cordochelys haliniches* from the tree did not result in a different position of *Asmodochelys leviathan* sp. nov. or otherwise alter the topology of the tree.

The phylogenetic analysis using the Gentry et al. (2019) data matrix resulted in 355 minimum length trees of 1564 steps (Fig. 6B). In the Majority Rule consensus tree (54%), *Asmodochelys leviathan* sp. nov. was positioned in an unresolved polytomy with *Asmodochelys parhami* and the unresolved clade of (*Peritresius ornatus* + *Prionochelys matutina* + *Ctenochelys acris* + *Ctenochelys stenoporus*). The lack of resolution within the clade may stem from the comparative incompleteness of HNSMWS-2018.1 resulting in a large number of missing character states.

Character optimization

In the Menon et al. (2024) dataset, *Asmodochelys leviathan* sp. nov. and *Ctenochelys* spp. were differentiated by three characters: (1) absent post-nuchal fontanelles in *Asmodochelys leviathan* sp. nov. (ch. 200, state 0); (2) absent fontanelle between first costal and anterior margin of carapace in *Asmodochelys leviathan* sp. nov. (ch. 214, state 0); 3) shape of posterior costals (ch. 215), which are roughly square (state 1) in *Asmodochelys leviathan* sp. nov. and much wider mediolaterally than long (state 0) in *Ctenochelys* spp.

The other purported ctenochelyid in the Menon et al. analysis, *Peritresius martini,* had no autapomorphic characters and was positioned outside Ctenochelyidae as the sister to *Cabindachelys landanensis*. It was differentiated from the latter by a single character, lacking a continuous keel on the costals (ch. 190, state 0). *Peritresius martini* differed from *Asmodochelys leviathan* sp. nov. and *Ctenochelys* spp. in having a unique position of rib-free peripherals (ch. 217, state 2). It also differed from *Ctenochelys* spp. in having vertebral 3–4 sulcus positioned on neural 6

Table 3 Diagnostic characters in *Asmodochelys leviathan* sp. nov. compared to other ctenochelyid species

	***Asmodochelys leviathan* sp. nov**	***Asmodochelys parhami***	***Ctenochelys acris***	***Ctenochelys stenoporus***	***Prionochelys matutina***	***Prionochelys nauta***	***Peritresius martini***	***Peritresius ornatus***
Reference	This study	Gentry et al. (2019)	Gentry (2017); Zangerl (1953)	Matzke (2007); Zangerl (1953)	Gentry et al. (2018); Zangerl (1953)	Gentry et al. (2018); Zangerl (1953)	Gentry et al. (2018)	Baird (1964)
Carapace length	117 cm	~ 100–150 cm	120 cm	?	90–100 cm	80 cm	90 cm	75 cm
Carapace shape	Cordiform	Cordiform	Cordiform	Ovoid	Cordiform	Cordiform	Ovoid	Cordiform
Shell sculpturing	Relatively smooth	Relatively smooth	Relatively smooth	Relatively smooth	Relatively smooth	Relatively smooth	Relatively smooth	Pronounced vermiculate sculpturing
Epineurals	Present	Present	Present	Present	Present	Present	Present	Present
Postnuchal fontanelle	Absent	Absent	Present	Present	Present	Present	?	Present
Carapacial fontanelles	Reduced: Only co-pe	Reduced: Only co-pe	Small	Large	Moderate	Large	Moderate	Large
Nuchal embayment	Deep, incl P1	Deep, 1/2 P1	Moderate, only nuchal	Moderate, only nuchal	Deep, mostly nuchal	Deep, incl P1	?	Moderate, mostly nuchal
Co1 artic P1?	Present	Absent	Absent	Absent	Absent	?	?	Absent
Preneural	Absent	?	Variable	Variable	Present	Present	?	Absent
Number of neurals	8	9?	8	8	8	8	?	7?
Neural width	Most slightly wider than long	Most wider than long	Longer than wide	Mostly longer than wide	Longer than wide	Mostly longer than wide	?	Slightly wider than long
Width of vertebrals	?	?	As long as wide	Longer than wide	Wider than long	?	?	Longer than wide
Suprapygals	1 +	2	2	2	2	1?	2	2
Peripheral scalloping	Slight	Slight	Highly	Moderate	Highly	Moderate	Moderate	Moderate
Posterior peripheral index	Thin, narrow: 53.3%	Thin narrow: 36.7%	Wider: 66.7%	Wider: 64.4%	Wider: 77.0%	Wider: 73.1%	Thin, narrow: 49.2%	Thin, narrow: 39.7%

(ch. 230, state 0), well developed central processes on its cervical vertebrae (ch. 297, state 1) and two pairs of inframarginal scales (ch. 279, state 1), although *Asmodochelys leviathan* sp. nov. was unscorable for these characters.

For the Gentry et al. (2019) matrix, character optimization revealed that *Asmodochelys leviathan* sp. nov. differs from other Ctenochelyids except *Asmodochelys parhami* in: absent posteromedial nuchal fontanelles (ch. 198, state 0). Ctenochelyidae shares one autapomorphic character state to the exclusion of all other clades: present epineurals (ch 203, state 1). They also share numerous other synapomorphic and plesiomorphic states. *Peritresius ornatus* differs from *Asmodochelys leviathan* sp. nov. and all other ctenochelyids in having shell sculpturing that shows development of striations, vermiculations, striations, or pitting (ch. 190, state 1). *Asmodochelys parhami* differs from other ctenochelyids in: peripheral gutter absent or only anteriorly developed (ch. 204, state 0), although *Asmodochelys leviathan* sp. nov. could not be definitively scored for this character.

Peritresius martini had no autapomorphic characters and was positioned outside Ctenochelyidae as the sister to *Allopleuron hoffmani* from which it was differentiated by a single character, presence of plastral scutes (ch. 257, state 0). *Peritresius martini* differs from other ctenochelyids in having strong hyo-hypoplastral serrations (ch. 237, state 1), and from *Peritresius ornatus* in having minimal shell sculpturing (ch. 190, state 0).

Discussion

Ctenochelyid phylogenetic structure

The results from both phylogenetic analyses place *Asmodochelys leviathan* sp. nov. within Ctenochelyidae, and the latter clade as the sister group to the clade of stem + crown Chelonioidea (Fig. 6). This finding supports interpretations by previous studies that ctenochelyids are more closely related to crown Chelonioidea than protostegids, 'Toxochelyinae' sensu Zangerl (1953), or most other Late Cretaceous marine turtle taxa (e.g., Gentry, 2018; Gentry et al., 2018, 2019; Menon et al., 2024). While this study identified *Asmodochelys* spp. as falling just outside the clade of the rest of the Ctenochelyidae, the specific phylogenetic relationships among *Ctenochelys* spp., *Prionochelys* spp., and *Peritresius ornatus* were not further resolved. Although it has been hypothesized that *Ctenochelys* and *Peritresius* may be sister taxa (e.g., Baird, 1964; Gentry et al., 2018), phylogenetic analyses that also include *Prionochelys* tend to result in an unresolved polytomy among the three (e.g., Gentry et al., 2019; Hirayama, 1997), as in this study. The evolutionary relationship between the two species of *Asmodochelys* is not fully understood, but endemic speciation is common

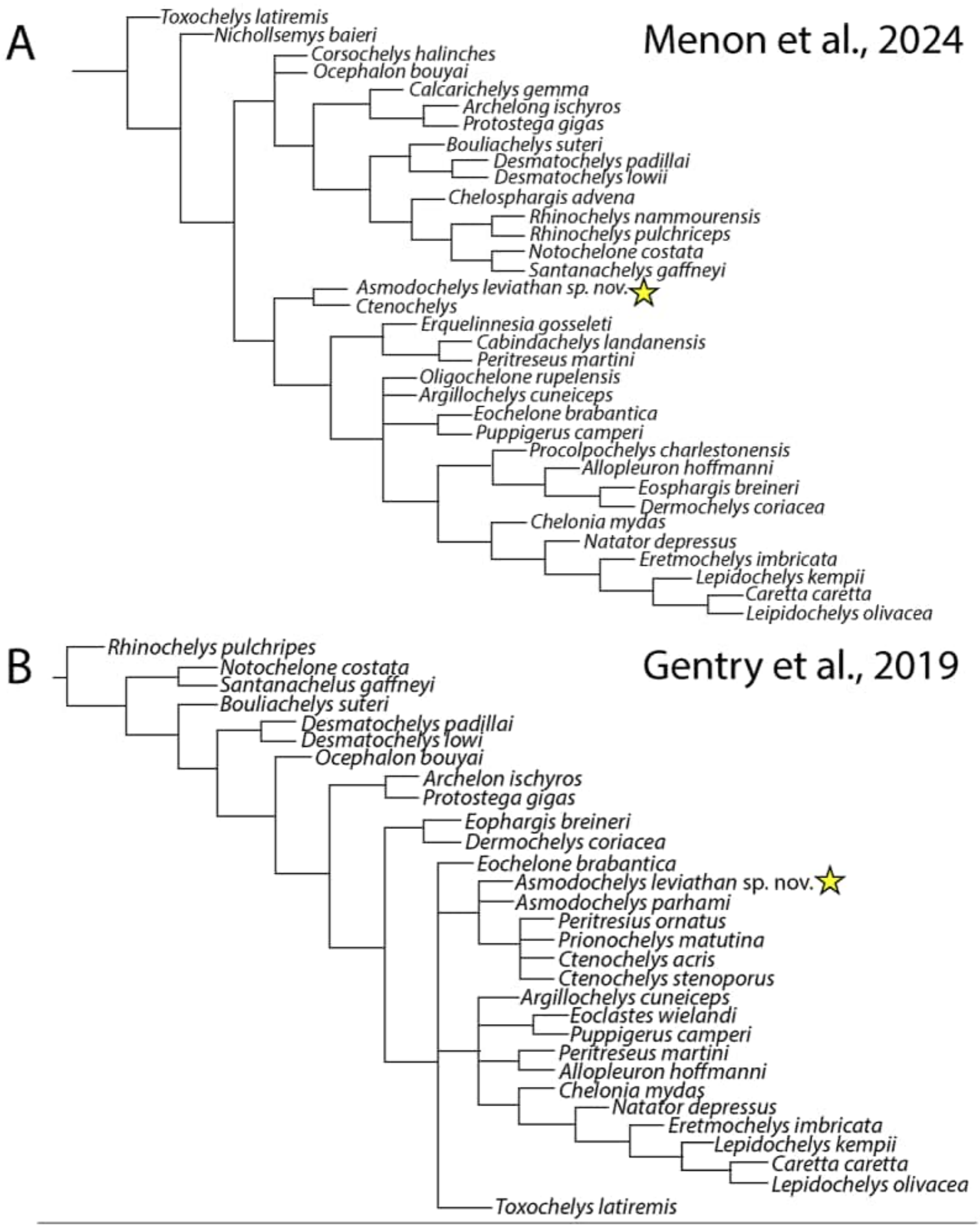

Fig. 6 Phylogenetic tree illustrating the phylogenetic position of *Asmodochelys leviathan* sp. nov. (yellow star) within Pan-Chelonioidea, based on matrices of: **A** Menon et al. (2024), and **B** Gentry et al. (2019)

among Cretaceous chelonioids sensu stricto (Gentry et al., 2018; Hirayama, 1997).

Interestingly, *Peritresius martini* was not recovered as a member of the ctenochelyid clade in either phylogenetic analysis of the study. This finding could result from a lack of proper resolution stemming from missing information. As the taxon is comparatively poorly sampled and known only from a limited number of isolated elements, it could only be coded for 55/347 characters (15.8%) in the Gentry et al. (2019) dataset and 81/356 (22.8%) in the Menon et al. (2024) matrix. In their analysis, Gentry and colleagues (2019) coded *Peritresius martini* as having the diagnostic ctenochelyid neural keel (ch. 189, state 1) and epineurals (ch. 203, state 1). However, as the original description of *Peritresius martini* did not include any neural material (Gentry et al., 2018) and we are not aware of any subsequent formal attributions to the hypodigm, it is unclear how *Peritresius martini* was coded for these characters. We also did not observe any specific characters linking *Peritresius martini* with *Peritresius ornatus*, a finding which is consistent with Gentry et al. (2018) who noted that they failed to recover any unambiguous synapomorphies connecting the two taxa. The phylogenetic position of *Peritresius martini* in both analyses, in conjunction with the relative incompleteness of the holotype and lack of clear synapomorphies shared with *Peritresius ornatus* indicate that its purported position within *Peritresius,* and even Ctenochelyidae, is not well supported.

Morphological variation within Ctenochelyidae

Ctenochelyids share a clear suite of synapomorphic traits including a prominent neural keel, epineural ossifications, and a generally cordiform carapace. While epineurals have been reported in other marine turtle taxa, such as *Archelon ischyros* Wieland, 1896 (Wieland, 1909), an absent suture in coronal view of YPM 294 suggests that the neural ridges in this species may not represent separate epineural bones. Epineural configuration in ctenochelyids, however, is consistent and unites the clade.

The most apparent morphological differences among the ctenochelyid genera occur in the degree of anterior carapace ossification, extent and configuration of the nuchal embayment, number and composition of midline carapacial elements, and posterior peripheral width and scalloping (Table 3). Anteriorly, ctenochelyid taxa fall along a continuum of carapacial ossification versus reduction by fontanelles. *Peritresius ornatus* and *Ctenochelys* spp. exhibit large postnuchal fontanelles and extensive costoperipheral fontanelles anterior to the first costal with no contact between it and the anterior peripherals (Baird, 1964; Zangerl, 1953). In contrast, *Prionochelys nauta* exhibits moderately sized postnuchal fontanelles and smaller costo-peripheral fontanelles anterior to the first costal. *Asmodochelys parhami* lacks postnuchal fontanelles, but still displays a costoperipheral fontanelle anterior to costal 1. *Asmodochelys leviathan* sp. nov. is the most anteriorly ossified species, entirely lacking both postnuchal fontanelles and a costoperipheral fontanelle anterior to costal 1.

Similarly, the ctenochelyid genera form a morphological continuum regarding the nuchal embayment. The embayment in *Ctenochelys* spp. is moderate but composed primarily of the nuchal; whereas, the first peripherals also contribute slightly to the embayment of *Peritresius ornatus* and *Prionochelys* spp. (Baird, 1964; Gentry, 2017; Matzke, 2007; Zangerl, 1953). The two *Asmodochelys* species are united by a deep, broad nuchal embayment that includes a significant contribution from first peripherals possessing anterior hornlike projections that extend the embayment anteriorly. Some characters of the nuchal region, including a broad nuchal embayment that includes the first peripherals and anteriorly projecting nuchal “horns” are also found in some penecontemporaneous protostegids, such as *Allopleuron hoffmani, “Allopleuron” insularis, Archelon ischyros*, and *Calcarichelys gemma* (Felder, 1980; Hooks, 1998; Mulder, 2003; Weems, 1988). In addition to being broad and anteriorly projecting, the nuchal of *Asmodochelys leviathan* sp. nov. is exceptionally thick with a pronounced dorsoventral arch, resulting in an anterior shell that is remarkably robust. The wide nuchal embayment suggests a large head that could have been well-protected by the robust nuchal region. This morphology may parallel the condition in modern sea turtles such as *Caretta caretta* or *Dermochelys coriacea* although its anterior embayment in the nuchal region is composed of anterior osteoderm armor rather than a robust nuchal bone.

Regarding the midline carapacial elements, preneurals are present in *Ctenochelys* spp. and *Prionochelys* spp. although they vary intraspecifically (Gentry, 2017, 2018; Zangerl, 1953), although they are absent in *Peritresius ornatus* and both *Asmodochelys* spp. (Baird, 1964; Gentry et al., 2019). The neural series of most ctenochelyids comprises eight neurals. In contrast, *Asmodochelys parhami* is uniquely described as having nine neurals (Gentry et al., 2019). However, since the neural series of *Asmodochelys parhami* is based on two different individuals, the estimation of the number of neurals present should be interpreted with caution. Baird (1964) described *Peritresius ornatus* as possessing seven neurals and two suprapygals based on his interpretation that there was insufficient space for two full-sized neurals posterior to the sixth. However, he acknowledged the possibility that the seventh and eighth neurals were present but reduced to the typical length of a single neural.

Most ctenochelyids are described as having two suprapygals and a pygal posterior to the neural row. *Prionochelys* spp. were initially interpreted as having nine neurals followed by either one or no suprapygals (Zangerl, 1953). However, subsequent studies have revealed the presence of eight neurals (N) and two suprapygals (spy) in at least *Prionochelys matutina* (Gentry, 2018). Thus, it is possible that the 9N + 1spy arrangement interpreted by Zangerl for *Prionochelys nauta* is in fact an 8N + 2spy arrangement. In that case, all previously described ctenochelyids would be characterized by two suprapygals. Though we acknowledge some uncertainty in the suprapygal region of *Asmodochelys leviathan* sp. nov. due to the incomplete nature of HNSMWS-2018.1, we can only report that there are at least two bony elements posterior to the eighth neural. We tentatively interpret these bones as a single suprapygal and a pygal. The second element in this postneural series is broader than the first and is posteriorly convex, unlike the narrow, posteriorly flattened suprapygal 2 of most other ctenochelyids. However, since the posterior margin of the HNSMWS-2018.1 carapace is damaged and incomplete, it is also possible that the pygal is missing entirely from the specimen, and instead two suprapygals are preserved. In fact, as most other ctenochelyids are described as having two suprapygals, it is entirely conceivable that the same arrangement also occurs in *Asmodochelys leviathan* sp. nov.

Finally, the posterior peripheral region differs among ctenochelyid taxa in its mediolateral width and extent of scalloping (Table 3). *Ctenochelys* spp. and *Prionochelys* spp. typically have wider posterior peripherals with more pronounced scalloping (Gentry, 2017, 2018; Zangerl, 1953). In contrast, the posterior peripherals of *Asmodochelys* spp. and *Peritresius* spp. are narrower (Gentry et al., 2019), as evidenced by a lower peripheral index (Table 3). Scalloping in this region is moderate in *Peritresius* spp., and slight in *Asmodochelys* spp.

Stratigraphic and geographic chelonioid distribution

Asmodochelys leviathan sp. nov. extends the stratigraphic range of *Asmodochelys* into Maastrichtian deposits, and also expands the known geographic range of the genus westward into Gulfian units southwest of the Mississippi Embayment (Gentry et al., 2019). The only other definitively known Maastrichtian ctenochelyid is *Peritresius ornatus* from the Prairie Bluff Chalk in Alabama and Mississippi and the lower Redbank Marl of the New Egypt Fm. in New Jersey (Baird, 1964; Gentry et al., 2018). However, an additional putative ctenochelyid candidate was recently described from the Maastrichtian type area of the Netherlands (Heere et al., 2023). There is disagreement regarding the timing of the closure of the Western Interior Seaway during the Maastrichtian (see Schwarzhans & Stringer, 2020). However, otolith assemblages from teleost fishes have indicated that there was a fundamental difference between fish faunas of the late Maastrichtian Kemp Clay in Texas and Maastrichtian deposits in Mississippi (i.e., early Maastrichtian Ripley Fm. and late Maastrichtian Owl Creek Fm.) (Schwarzhans & Stringer, 2020). This contrast was likely due to substantial environmental differences, including generally turbid and muddy ecosystems in the Kemp Clay versus clearer water conditions at the Mississippi Maastrichtian locations (especially the Ripley Fm.). Additionally, the ingress of cold water into the Gulf of Mexico through the WIS differentiated the Maastrichtian aquatic environments in present day Texas from those of Mississippi, which had warmer subtropical temperatures. These paleoenvironmental differences are reflected in the fish assemblages of these locations, termed WIS (referring to the seaway) for the Texas community and Appalachian for the community that included the Mississippi Embayment and Atlantic shorelines (Schwarzhans & Stringer, 2020). The WIS and Appalachian teleost fish communities have a percentage similarity measurement of less than 10% (Schwarzhans & Stringer, 2020). The division between these Maastrichtian fish communities is consistent with the paleogeographic distribution of ctenochelyids during this interval, suggesting that *Peritresius ornatus* was sympatric with the Appalachian fish community and *Asmodochelys leviathan* sp. nov. with the WIS fish assemblage. The close geographic proximity of Neylandville Fm. and Kemp Clay outcrops along the South Sulphur River supports the association of the former unit with the WIS fish community. From a global perspective, long term marine environmental changes during the latest Cretaceous included ocean water chemistry variation and sea level regression (Ikejiri et al., 2020). There is strong oxygen isotopic evidence that ocean temperatures fell during this interval, which (along with other factors) has been linked to a reduction of mosasaur species and may have also contributed to a decrease in the diversity of chelonioid turtles (Hirayama, 1997; Polcyn et al., 2014; Puckett, 2005; Pyenson et al., 2014; Weems, 1988).

Paleoecology

The invertebrate faunal composition of the *Exogyra cancellata* zone indicates that its sediments were deposited in relatively shallow water, but the absence of cross bedding in these strata indicates that they settled in water that was too deep for disturbance by waves and currents, probably at a depth between 27.5–183 m (Stephenson, 1933). As mentioned above, *Asmodochelys leviathan* sp. nov. is the first turtle described from the Neylandville Fm. Sympatric vertebrate material is scarce and mostly comprises teeth representing a diversity of mosasaurid genera including *Prognathodon*, *Plioplatecarpus*, *Mosasaurus*, and possibly *Tylosaurus* (Jiménez-Huidobro & Caldwell, 2016; Lindgren et al., 2011; Thurmond, 1969). The composition of the Neylandville mosasaur assemblage reflects the increasing global dominance of mosasaurine species (e.g., *Mosasaurus*, *Prognathodon*) over the other major groups of mosasaurs (i.e., Tylosaurinae and Plioplatecarpinae). The generic diversity of the latter subfamilies was limited during the Maastrichtian, perhaps due to lack of dental adaptation (see Konishi et al., 2014). Evidence of mosasaur predation on turtles is well documented in the fossil record (e.g., Konishi et al., 2014; Shimada et al., 2002), and some of the mosasaurs of the Neylandville Fm. were likely large enough to predate even large marine turtles such as *Asmodochelys* spp.

Fishes from the Neylandville Fm. in Texas are not well known, with only myliobatiform (cownose ray) teeth reported from Kaufman County in Texas (Meyer, 1974). However, a substantially more diverse fish assemblage (25 spp.) has been documented from younger strata in the late Maastrichtian Kemp Clay, which is also exposed along the South Sulphur River in Texas (Schwarzhans & Stringer, 2020). The Kemp Clay preserves mud-bottomed paleoenvironments, which accounts for its diversity of anguilliform fishes. Kemp Clay deposits have been interpreted as estuarine with some freshwater influence, but the presence of rudists, ammonites, and benthic foraminifera (e.g., eels) indicates a fully marine environment (Case & Cappetta, 1997; Stephenson, 1938). Sharks have not been reported from the Neylandville Fm, but evidence of attacks on large marine turtles have been documented in the Late Cretaceous Mooreville Chalk of Alabama (Shimada & Hooks, 2004).

Conclusions

A novel Cretaceous marine turtle, *Asmodochelys leviathan* sp. nov., is described from the Maastrichtian Neylandville Formation in north-central Texas. The discovery of a novel species of *Asmodochelys* expands the diversity of Ctenochelyidae, and the preservation of the type specimen allows for a thorough morphological account of articulated carapace morphology, which is rare in the group. The species is described based on a well-preserved carapace, which displays many of the diagnostic characteristics consistent with Ctenochelyidae, including a large body size, prominent midline neural keel, epineural ossifications, and costoperipheral fontanelles. The new species differs from congeneric *Asmodochelys parhami* in having 8 neurals with epineurals positioned at N1/2, N3/4, N5/6, and N7/8, as well as a robust articulation between costal 1 and the first two peripherals resulting in an absent anterior costoperipheral fontanelle in the area. *Asmodochelys leviathan* sp. nov. extends the stratigraphic range of the genus into the Maastrichtian of the Gulfian Series (Hill, 1901), and geographically further west of the Mississippi Embayment to north-central Texas (Gentry et al., 2019). It is one of the latest surviving members of the Ctenochelyidae along with *Peritresius ornatus*, and it helps fill a gap in the basal pan-chelonioid record by providing data from Late Cretaceous Gulfian deposits following the closure of the Western Interior Seaway.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-025-00363-8.

Supplementary material 1.

Supplementary material 2.

Acknowledgements

The authors would like to gratefully acknowledge staff and volunteer preparators at the Heard Natural Science Museum and Wildlife Sanctuary (HNSMWS), especially Darlene Sumerfelt, Margie Kline, Deborah Canterbury, Jim Dulian, Karleen Hoffmann, Mittie McDonald, Susan Smith, Patti Tuck, and Fletcher Wise. We thank A. Mac Glaess for donating the specimen to HNSMWS. We also thank the organizers of the 2024 Turtle Evolution Symposium, Walter Joyce, Serjoscha Evers, and Yann Rollot, and reviewers Juliette Menon and Andrew Gentry for insightful comments that improved the manuscript.

Author contributions

HFS, BA, and PK collected data. HFS and BA conducted formal analyses. HFS and BA wrote the main manuscript text. BA prepared all figures. All authors reviewed the manuscript.

Funding

Not applicable.

Availability of data and materials

The 3D model of HNSMWS-2018.1 is available on MorphoSource at the following link: https://doi.org/10.17602/M2/M699482. All other data are included within this manuscript or as supplementary materials.

Declarations

Ethics and consent to participate declarations

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

[1]Department of Anatomy, Midwestern University, 19555 N. 59th Ave., Glendale, AZ 85308, USA. [2]School of Human Evolution and Social Change, Arizona State University, P.O. Box 872402, Tempe, AZ 85282, USA. [3]Perot Museum of Nature and Science, 2201 N Field St, Dallas, TX 75201, USA.

Received: 4 February 2025 Accepted: 19 March 2025

References

Baird, D. (1964). A fossil sea-turtle from New Jersey. *New Jersey State Museum Investigations, 1*, 3–26.

Bardet, N., Falconnet, J., Fischer, V., Houssaye, A., Jouve, S., Suberbiola, X. P., Pérez-García, A., Rage, J.-C., & Vincent, P. (2014). Mesozoic marine reptile palaeobiogeography in response to drifting plates. *Gondwana Research, 26*, 869–887.

Barnes, V. E., Hartmann, B., & Scranton, D. F. (1992). *Geologic map of Texas*. University of Texas at Austin.

Batsch, A. (1788) Versuch einer Anleitung, zur Kenntniû und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena, 528.

Baur, G. (1893). Notes on the classification of Cryptodira. *American Naturalist, 27*, 672–675.

Benson, R. B., Butler, R. J., Lindgren, J., & Smith, A. S. (2010). Mesozoic marine tetrapod diversity: Mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proceedings of the Royal Society b: Biological Sciences, 277*, 829–834.

Benson, R.-B.-J., MacLeod, N., Archibald, J.-D., & Levin, P. (2013). Marine reptiles. In N. MacLeod, J.-D. Archibald, & P. Levin (Eds.) *Grzimek's animal life encyclopedia, extinction* (pp. 267–279). Farmington Hills, Michigan: Gale Cengage Learning.

Blakey, R. C. (2014). Paleogeography and paleotectonics of the Western Interior Seaway, Jurassic-Cretaceous of NorthAmerica. *Search and Discovery, 30392*, 1–17.

Brinkman, D., Hart, M., Jamniczky, H., & Colbert, M. (2006). *Nichollsemys baieri* gen. et sp. nov., a primitive chelonioid turtle from the late Campanian of North America. *Paludicola, 5*, 111–124.

Cadena, E. A., & Combita-Romero, D. A. (2023). The onset of large size in Cretaceous marine turtles (Protostegidae) evidenced by new fossil remains from the Valanginian of Colombia. *Zoological Journal of the Linnean Society, 202*, zlad053.

Cadena, E. A., & Parham, J. F. (2015). Oldest known marine turtle? A new protostegid from the Lower Cretaceous of Colombia. *PaleoBios, 32*, 1–42.

Case, G., & Cappetta, H. (1997). A new Selachian fauna from the late Maastrichtian of Texas (Upper Cretaceous/Navarroan; Kemp formation). *Münchner Geowissenschaftliche Abhandlungen A, 34*, 131–189.

Cope, E. D. (1868). On some Cretaceous Reptilia. *Proceedings of the Academy of Natural Sciences of Philadelphia, 1868*, 233–242.

Cope, E. D. (1873). *Sixth annual report of the United States geological survey of the Territories, embracing portions of Montana, Idaho, Wyoming, and Utah : being a report of progress of the explorations for the year 1872*. Washington Government Printing Office.

Evers, S. W., & Benson, R. B. (2019). A new phylogenetic hypothesis of turtles with implications for the timing and number of evolutionary transitions to marine lifestyles in the group. *Palaeontology, 62*, 93–134.

Felder, P. J. (1980). Resten van fossiele Zeeschildpadden gevonden in het Krijt van Limburg (Deel I). *Natuurhistorisch Maandblad*, *69*, 78–85, 100–104, 117–124.

Garman, S. (1880). On certain species of Chelonioidae. *Bulletin of the Museum of Comparative Zoology Harvard, 6*, 123–126.

Gentry, A. D. (2017). New material of the Late Cretaceous marine turtle Ctenochelys acris Zangerl, 1953 and a phylogenetic reassessment of the 'toxochelyid'-grade taxa. *Journal of Systematic Palaeontology, 15*(8), 675–696.

Gentry, A. D. (2018). *Prionochelys matutina* Zangerl, 1953 (Testudines: Pan-Cheloniidae) from the Late Cretaceous of the United States and the evolution of epithecal ossifications in marine turtles. *PeerJ, 6*, e5876.

Gentry, A. D., Ebersole, J. A., & Kiernan, C. R. (2019). *Asmodochelys parhami*, a new fossil marine turtle from the Campanian Demopolis Chalk and the stratigraphic congruence of competing marine turtle phylogenies. *Royal Society Open Science, 6*, 191950.

Gentry, A. D., Parham, J. F., Ehret, D. J., & Ebersole, J. A. (2018). A new species of *Peritresius* Leidy, 1856 (Testudines: Pan-Cheloniidae) from the Late Cretaceous (Campanian) of Alabama, USA, and the occurrence of the genus within the Mississippi Embayment of North America. *PLoS ONE, 13*, e0195651.

Goloboff, P. A., & Morales, M. E. (2023). TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics, 39*(2), 144–153.

Hay, O. P. (1908). *The fossil turtles of North America*. Carnegie Institute of Washington.

Heere, J. A., Wallaard, J. J. W., Mulder, E. W. A., Ponstein, J., & Schulp, A. S. (2023). The first report of Chelonioidea cf. *Ctenochelys* from the late Cretaceous of the Maastrichtian type area. *Netherlands Journal of Geosciences, 102*, e6.

Hill, R. T. (1901). Geography and geology of the Black and Grand Prairies, Texas. *U.S. Geological Survey Annual Report, 7*, 1–666.

Hirayama, R. (1997). Distribution and diversity of Cretaceous chelonioids. In J. M. Callaway & E. M. Nicholls (Eds.), *Ancient Marine Reptiles* (pp. 225–241). Academic Press.

Hirayama, R. (1998). Oldest known sea turtle. *Nature, 392*, 705–708.

Hooks, G. E., III. (1998). Systematic revision of the Protostegidae, with a redescription of *Calcarichelys gemma* Zangerl, 1953. *Journal of Vertebrate Paleontology, 18*, 85–98.

Hutchison, H. J., & Archibald, D. J. (1986). Diversity of turtles across the Cretaceous/Tertiary Boundary in northeastern Montana. *Palaeogeography, Palaeoclimatology, Palaeoecology, 55*, 1–22.

Ikejiri, T., Lu, Y., & Zhang, B. (2020). Two-step extinction of Late Cretaceous marine vertebrates in northern Gulf of Mexico prolonged biodiversity loss prior to the Chicxulub impact. *Scientific Reports, 10*, 4169.

Jacobs, L.L., Polcyn, M.J., Winkler, D., Myers, T.S., Kennedy, J.G., Wagner, J.B. (2013). Late Cretaceous strata and vertebrate fossils of North Texas. In B.B. Hunt & E.J. Catlos (Eds.) *GSA Field Guide 30. Late Cretaceous to Quaternary Strata and Fossils of Texas: Field Excursions Celebrating 125 Years of GSA and Texas Geology, GSA South-Central Section Meeting, Austin, Texas, April 2013* (pp. 1–13). Austin, Texas: Geological Society of America

Jiménez-Huidobro, P., & Caldwell, M. W. (2016). Reassessment and reassignment of the early Maastrichtian mosasaur *Hainosaurus bernardi* Dollo, 1885, to Tylosaurus Marsh, 1872. *Journal of Vertebrate Paleontology, 36*, e1096275.

Joyce, W. G., Anquetin, J., Cadena, E.-A., Claude, J., Danilov, I. C., Evers, S. W., Ferreira, G. S., Gentry, A. D., Georgialis, G., Lyson, T. R., Pérez-García, A., Rabi, M., Sterli, J., Vitek, N. S., & Parham, J. F. (2021). A nomenclature for fossil and living turtles using phylogenetically defined clade names. *Swiss Journal of Palaeontology, 140*, 1–45.

Joyce, W. G., Parham, J. F., & Gauthier, J. A. (2004). Developing a protocol for the conversion of rank-based taxon names to phylogenetically define clade names, as exemplified by turtles. *Journal of Paleontology, 78*, 989–1013.

Joyce, W. G., Parham, J. F., Lyson, T. L., Warnock, R. C. M., & Donoghue, P. C. J. (2013). A divergence dating analysis of turtles using fossil calibrations: An example of best practices. *Journal of Paleontology, 87*, 612–634.

Karl, H.-V., Biermann, S., & Tichy, G. (2012). The oldest true sea turtle of the world, *Oertelia gigantea* (Oertel, 1914) n. gen. from the Aptian of Kastendamm near Hanover, Germany). *Studia Palaeocheloniologica, 4*, 107–128.

Kear, B. P., & Lee, M. S. Y. (2006). A primitive protostegid from Australia and early sea turtle evolution. *Biology Letters, 2*, 116–119.

Konishi, T., Newbrey, M. G., & Caldwell, M. W. (2014). A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the Bearpaw Formation, western Canada, and the first stomach contents for the genus. *Journal of Vertebrate Paleontology, 34*, 802–819.

Lapparent de Broin, F., Bardet, N., Amaghzaz, M., & Meslouh, S. (2014). A strange new chelonioid turtle from the Latest Cretaceous Phosphates of Morocco. *Comptes Rendus Palevol, 13*, 87–95.

Lindgren, J., Polcyn, M. J., & Young, B. A. (2011). Landlubbers to leviathans: Evolution of swimming in mosasaurine mosasaurs. *Paleobiology, 37*, 445–469.

Lynch, S., & Parham, J. (2003). The first report of hard-shelled sea turtles (*Cheloniidae sensu lato*) from the Miocene of California, including a new species (*Euclastes hutchisoni*) with unusually plesiomorphic characters. *PaleoBios, 23*(3), 21–35.

Matzke, A. T. (2007). An almost complete juvenile specimen of the ctenochelyid turtle *Ctenochelys stenopus* (Hay 1904) from the Upper Cretaceous Niobrara Formation of Kansas. *Palaeontology, 50*, 669–691.

Menon, J. C., Brinkman, D. B., Hermanson, G., Joyce, W. G., & Evers, S. W. (2024). New insights into the early morphological evolution of sea turtles by re-investigation of *Nichollsemys baieri*, a three-dimensionally preserved fossil stem chelonioid from the Campanian of Alberta, *Swiss Journal of Palaeontology,* Canada. *143*, 27.

Meyer, R.L. (1974). *Late Cretaceous elasmobranchs from the Mississippi and east Texas embayments of the Gulf Coastal Plain*. Ph.D. Thesis, Southern Methodist University.

Monroe, W. H. (1947). Stratigraphy of outcropping Cretaceous beds of southeastern states. *American Association of Petroleum Geologists Bulletin, 31*, 1817–1824.

Morton, S. (1833). Synopsis of the organic remains of the ferruginous sand formation of the United States. *American Journal of Science, 1*, 128–132.

Motani, R. (2009). The evolution of marine reptiles. *Evolution: Education and Outreach, 2*, 224–235.

Motani, R., & Vermeij, G. J. (2021). Ecophysiological steps of marine adaptation in extant and extinct non-avian tetrapods. *Biological Reviews, 96*, 1769–1798.

Mulder, E. W. A. (2003). Comparative osteology, palaeoecology and systematics of the Late Cretaceous turtle *Allopleuron hofmanni* (Gray 1831) from the Maastrichtian type area. *Pubicaties Van Het Natuurhistorisch Genootschap in Limburg, 1*, 23–92.

Near, T. J., Bolnick, D. I., & Wainwright, P. C. (2005). Fossil calibrations and molecular divergence in centrarchid fishes (Teleostei: Centrarchidae). *Evolution, 59*, 1768–1782.

Parham, J. F. (2005). A reassessment of the referral of sea turtle skulls to the genus *Osteopygis* (Late Cretaceous, New Jersey, USA). *Journal of Vertebrate Paleontology, 25*, 71–77.

Parham, J. F., Otero, R. A., & Suárez, M. E. (2014). A sea turtle skull from the Cretaceous of Chile with comments on the taxonomy and biogeography of *Euclastes* (formerly *Osteopygis*). *Cretaceous Research, 49*, 181–189.

Parham, J. F., & Pyenson, N. D. (2010). New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. *Journal of Paleontology, 84*, 231–247.

Patterson, J. E. (1983). Exploration potential and variations in shelf plume sandstones, Navarro Group (Maestrichtian), East Central Texas. *American Association of Petroleum Geologists Bulletin, 68*(4), 515.

Pereira, A. G., Sterli, J., Moreira, F. R. R., & Schrago, C. G. (2017). Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. *Molecular Phylogenetics and Evolution, 113*, 59–66.

Polcyn, M. J., Jacobs, L. L., Araújo, R., Schulp, A. S., & Mateus, O. (2014). Physical drivers of mosasaur evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology, 400*, 17–27.

Puckett, T. M. (2005). Santonian-Maastrichtian planktonic foraminiferal and ostracode biostratigraphy of the northern Gulf Coastal Plain, USA. *Stratigraphy, 2*, 117–146.

Pyenson, N. D., Kelley, N. P., & Parham, J. F. (2014). Marine tetrapod macroevolution: Physical and biological drivers on 250 Ma of invasions and evolution in ocean ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology, 400*, 1–8.

Schwarzhans, W., & Stringer, G. L. (2020). Fish otoliths from the late Maastrichtian Kemp Clay (Texas, USA) and the early Danian Clayton Formation (Arkansas, USA) and an assessment of extinction and survival of teleost lineages across the K-Pg boundary based on otoliths. *Rivista Italiana di Paleontologia e Stratigrafia, 126*, 395–446.

Shimada, K., Everhart, M., & Hooks, G. (2002). Ichthyodectid fish and protostegid turtle bitten by the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*. *Journal of Vertebrate Paleontology, 22*, 106A.

Shimada, K., & Hooks, G. (2004). Shark-bitten protostegid turtles from the Upper Cretaceous Mooreville Chalk, Alabama. *Journal of Paleontology, 78*, 205–210.

Stephenson, L.W. (1914). Cretaceous deposits of the eastern Gulf region and species of *Exogyra* from the eastern Gulf region and the Carolinas. Geological Professional Survey Paper 81. US Government Printing Office.

Stephenson, L. W. (1933). The zone of *Exogyra cancellata* traced twenty-five hundred miles. *American Association of Petroleum Geologists Bulletin, 17*, 1351–1361.

Stephenson, L.W. (1938). A new Upper Cretaceous rudistid from the Kemp Clay of Texas. Geological Professional Survey Paper 193-A. US Government Printing Office.

Stephenson, L. W. (1941). *The larger invertebrate fossils of the Navarro Group of Texas*. The University of Texas Publication.

Thomson, R. C., Spinks, P. Q., & Shaffer, H. B. (2021). A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. *Proceedings of the National Academy of Sciences USA, 118*(7), e2012215118.

Thurmond, J. T. (1969). Notes on mosasaurs from Texas. *Texas Journal of Science, 21*, 69–79.

Tong, H., Hirayama, R., Makhoul, E., & Escuillié, F. (2006). *Rhinochelys* (Chelonioidea: Protostegidae) from the Late Cretaceous (Cenomanian) of Nammoura, Lebanon. *Atti della Società Italiana di Scienze Naturali e Del Museo Civico di Storia Naturale di Milano, 147*(1), 113–138.

[TTWG] Turtle Taxonomy Working Group [Rhodin, A.G.J. Iverson, J.B., Bour, Fritz, U., Georges, A., Shaffer, H.B., & van Dijk, P.P.]. (2017). *Turtles of the world: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status, 8th ed*. Chelonian Research Foundation.

Tullos, N. A. (2024). Comparison of the WIDAR application with a manual photogrammetry method of creating 3D models of cadaveric hearts. *Medical Science Educator, 34*, 1261–1262.

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., & Brown, K. M. (2017). More-complete remains of *Procolpochelys charlestonensis* (Oligocene, South Carolina), an occurrence of *Euclastes* (upper Eocene, South Carolina), and their bearing on Cenozoic pancheloniid sea turtle distribution and phylogeny. *Journal of Paleontology, 91*, 1228–1243.

Wieland, G. R. (1896). *Archelon ischyros*: A new gigantic cryptodire testudinate from the Fort Pierre Cretaceous of South Dakota. *American Journal of Science, S4–2*(12), 399–412.

Wieland, G. R. (1909). Revision of the Protostegidae. *American Journal of Science, 27*, 101–130.

Wood, R. C., Johnson-Gove, J., Gaffney, E. S., & Maley, K. F. (1996). Evolution and phylogeny of leatherback turtles (Dermochelyidae), with descriptions of new fossil taxa. *Chelonian Conservation and Biology, 2*, 266–286.

Zangerl, R. (1953). The vertebrate fauna of the Selma Formation of Alabama. Part IV. The turtles of the family Toxochelyidae. *Fieldiana, Geology Memoirs, 3*, 137–277.

Zangerl, R. (1960). The vertebrate fauna of the Selma Formation of Alabama. Part V. An advanced cheloniid sea turtle.Fieldiana, *Geology Memoirs, 3*, 279–312.

Publisher's Note