A revised turtle assemblage from the Upper Cretaceous Menefee Formation (New Mexico, North America) with evolutionary and paleobiostratigraphic implications (#110982)

First submission

Guidance from your Editor

Please submit by **19 Jan 2025** for the benefit of the authors (and your token reward) .

Structure and Criteria
Please read the 'Structure and Criteria' page for guidance.

Custom checks
Make sure you include the custom checks shown below, in your review.

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

Files
Download and review all files from the materials page.

12 Figure file(s)
3 Table file(s)

Custom checks

Field study

- Have you checked the authors field study permits?
- Are the field study permits appropriate?

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- ✓ Original primary research within Scope of the journal.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ **Impact and novelty is not assessed.** Meaningful replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ All underlying data have been provided; they are robust, statistically sound, & controlled.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

A revised turtle assemblage from the Upper Cretaceous Menefee Formation (New Mexico, North America) with evolutionary and paleobiostratigraphic implications

Brent Adrian Corresp., 1 , **Heather F Smith** 1, 2 , **Andrew T. McDonald** 3

1 Arizona State University, Tempe, AZ, United States
2 Midwestern University, Glendale, AZ, United States
3 Western Science Center, Hemet, CA, United States

Corresponding Author: Brent Adrian
Email address: badrian@asu.edu

The middle Campanian Menefee Formation (Fm.) of the San Juan Basin of New Mexico is a relatively understudied terrestrial deposit in southern Laramidia preceding the fossil-rich upper Campanian Fruitland and Kirtland formations that have been studied for more than a century. Previous collection efforts have revealed diverse dinosaurian and crocodyliform fauna in the Menefee, including ankylosaurian, tyrannosaurid, hadrosaurid, ceratopsian, and neosuchian taxa. Nearly a decade has passed since the last description of the Menefee turtle fauna, and we present new material that provides insight into turtle evolution during the Campanian in the Colorado Plateau, with implications for Late Cretaceous turtle paleobiostratigraphy in Laramidia. Particularly, we extend the stratigraphic ranges of the baenids *Neurankylus baueri* and *Scabremys ornata* backwards from younger San Juan Basin strata, along with the nanhsiungchelyid *Basilemys*. Additional material increases Menefee representation of the relict helochelydrid *Naomichelys*, and the regionally prevalent derived baenids *Denazinemys* and *Thescelus*. Additionally, we report new pan-trionychian specimens, which provide insight into the persistence of *Adocus* and multiple trionychid and plastomenid species through the remainder of the Campanian in the San Juan Basin. A cluster analysis of turtle diversity across early-middle Campanian sites in Laramidia showed distributions consistent with latitudinal provinciality in some groups. For instance, derived baenids were restricted to latitudes south of southern Utah, along with marine taxa (bothremydids and protostegids) and pan-kinosternoids. Basin-scale endemism is also suggested by some baenid and trionychid distributions. Otherwise, the turtle fauna of the Menefee most closely resemble those of the similarly aged Wahweap Fm. in southern Utah, and the Aguja Fm. in the Big Bend area of Texas and Mexico to a lesser extent. The Menefee turtle assemblage is consistent with reconstructed paleoenvironments characteristic of the western shoreline of the Western

Interior Seaway. Recurrent cyclothems in these settings shaped the development of fluviodeltaic deposits that preserved distal components of large channels with surrounding floodplains and swamps, along with evidence of freshwater, brackish, and possibly shallow marine influence.

A revised turtle assemblage from the Upper Cretaceous Menefee Formation (New Mexico, North America) with evolutionary and paleobiostratigraphic implications

Brent Adrian[1], Heather F. Smith [1,2], Andrew T. McDonald [3]

[1] School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona, U.S.A.

[2] Department of Anatomy, Midwestern University, Glendale, Arizona, U.S.A.

[3] Western Science Center, Hemet, California, U.S.A.

Corresponding Author:
Brent Adrian[1]
900 S. Cady Mall, Tempe, Arizona, 85281, U.S.A.
Email address: badrian@asu.edu

Abstract

The middle Campanian Menefee Formation (Fm.) of the San Juan Basin of New Mexico is a relatively understudied terrestrial deposit in southern Laramidia preceding the fossil-rich upper Campanian Fruitland and Kirtland formations that have been studied for more than a century. Previous collection efforts have revealed diverse dinosaurian and crocodyliform fauna in the Menefee, including ankylosaurian, tyrannosaurid, hadrosaurid, ceratopsian, and neosuchian taxa. Nearly a decade has passed since the last description of the Menefee turtle fauna, and we present new material that provides insight into turtle evolution during the Campanian in the Colorado Plateau, with implications for Late Cretaceous turtle paleobiostratigraphy in Laramidia. Particularly, we extend the stratigraphic ranges of the baenids *Neurankylus baueri* and *Scabremys ornata* backwards from younger San Juan Basin strata, along with the nanhsiungchelyid *Basilemys*. Additional material increases Menefee representation of the relict helochelydrid *Naomichelys*, and the regionally prevalent derived baenids *Denazinemys* and *Thescelus*. Additionally, we report new pan-trionychian specimens, which provide insight into the persistence of *Adocus* and multiple trionychid and plastomenid species through the remainder of the Campanian in the San Juan Basin. A cluster analysis of turtle diversity across early-middle Campanian sites in Laramidia showed distributions consistent with latitudinal provinciality in some groups. For instance, derived baenids were restricted to latitudes south of southern Utah, along with marine taxa (bothremydids and protostegids) and pan-kinosternoids. Basin-scale endemism is also suggested by some baenid and trionychid distributions. Otherwise, the turtle fauna of the Menefee most closely resemble those of the similarly aged Wahweap Fm. in southern Utah, and the Aguja Fm. in the Big Bend area of Texas and Mexico to a lesser extent. The Menefee turtle assemblage is consistent with reconstructed paleoenvironments characteristic

of the western shoreline of the Western Interior Seaway. Recurrent cyclothems in these settings shaped the development of fluviodeltaic deposits that preserved distal components of large channels with surrounding floodplains and swamps, along with evidence of freshwater, brackish, and possibly shallow marine influence.

Introduction

Since 2011, yearly expeditions have been conducted to the Upper Cretaceous Menefee Formation (Fm.) in the San Juan Basin (SJB) of northwestern New Mexico (Beaumont, Dane & Sears, 1956; Miller, Carey & Thompson-Rizer, 1991) (Fig. 1). These efforts have involved researchers, students, and volunteers from various institutions, including the Western Science Center, Southwest Paleontological Society, and Zuni Dinosaur Institute for Geosciences. To this point, this fieldwork has resulted in the descriptions of the tyrannosaurid *Dynamoterror dynastes* McDonald, Wolfe & Dooley (2018), the ankylosaurian *Invictarx zephyri* McDonald & Wolfe (2018), and the brachylophosaurin hadrosaur *Ornatops incantatus* McDonald, Wolfe, Freedman Fowler & Gates (2021). *Menefeeceratops sealeyi* Dalman, Lucas, Jasinski, Lichtig & Dodson (2021) has also been described from the Menefee Fm. and could be the oldest member of the Centrosaurinae (Dalman et al., 2021). Remains of the giant alligatoroid *Deinosuchus* Holland (1909) represent one of the earliest occurrences in Laramidia and North America more broadly, demonstrating a stratigraphic range extension in the SJB (Mohler, McDonald & Wolfe, 2021).

Initial reports of turtles from the Menefee Fm. were mostly of fragmentary material from indeterminate baenids and trionychids across 13 localities (Hunt & Lucas, 1993). More recently, Lichtig & Lucas (2015) provided brief descriptions and two figures showing five Menefee turtle specimens. Remains are attributed to adocid (aff. *Adocus bossi* Gilmore (1919)), baenid (*Denazinemys* (Lucas & Sullivan, 2006) ~~and~~ indeterminate~~),~~ trionychid taxa, a single specimen of the helochelydrid *Naomichelys* Hay (1908), and a partial putative bothremydid shell (CHCU 81269). Perhaps the most comprehensive documentation of Upper Cretaceous turtles from the San Juan Basin was provided by Sullivan, Jasinski & Lucas (2013), focusing on the late Campanian (Kirtlandian) Fruitland and Kirtland formations. Additional studies focusing on these younger units include Sullivan et al. (1988), Lucas & Sullivan (2006), and Jasinski et al. (2018). The current study updates the taxonomic composition of the Menefee turtle assemblage, discusses stratigraphic range extensions for several taxa, and makes comparisons with stratigraphically correlative units to discuss paleobiogeographical patterns during the early to middle Campanian in Laramidia.

Geological setting

The Menefee Formation is part of the Mesaverde Group and is underlain by the regressive Point Lookout Sandstone and overlain by the transgressive Cliff House Sandstone (Collier, 1919; Sears, 1925; Dane, 1936; Sears, Hunt & Hendricks, 1941; Pike, 1947; Beaumont, Dane & Sears, 1956; Molenaar, 1983) (Fig. 1). The Menefee Fm. is divided into two formal members: the basal Cleary Coal Member (Beaumont, Dane & Sears, 1956) and the overlying Allison Member (originally the “Allison barren member” (Sears, 1925; Dane, 1936)). The nomenclature of the uppermost coal-bearing portion of the Menefee Fm. has been contentious, with some authors recognizing an unnamed upper coal member (e.g., Hayes & Zapp, 1955; Beaumont & Hoffman, 1992). Alternatively, Dane (1936) considered the uppermost coal-bearing strata to be part of the Allison Member. Miller (1984) and Miller, Carey & Thompson-Rizer (1991) agreed and proposed three informal subdivisions of the Allison Member, in ascending order: the Lower Beds, characterized by the lack of coal beds and calcareous concretions; the Juans Lake Beds, characterized by the presence of calcareous concretions; and the La Vida Beds, characterized by the absence of calcareous concretions and the presence of thin coal beds. The presence of calcareous concretions and lack of coal in the beds that produced the turtle fossils described here indicate that they pertain to the Juans Lake Beds (Miller, 1984; Miller, Carey & Thompson-Rizer, 1991). For further detailed description of the local geology of the study area, see Mohler, McDonald & Wolfe (2021).

The geochronological age of the Menefee Formation at different locations across its vast outcrop belt is difficult to determine due to the diachronous nature of its strata (Peterson & Kirk, 1977: fig. 2) and lack of an extensive sample of radioisotopic dates (Lucas et al., 2005). An age of 78.22 ± 0.26 Ma was derived from a bentonite layer near the top of the Menefee Fm. in the Gallina hogback in the northeastern San Juan Basin (Lucas et al., 2005). The ammonoid index fossil *Baculites perplexus* has been reported from the Cliff House Sandstone in Chaco Canyon in the vicinity of and on depositional strike from our study area (Siemers & King, 1974). In this area, the uppermost Menefee Fm. intertongues with and is overlain by the upper tongue (= Chacra Mesa tongue (Dane, 1936; Beaumont & Hoffman, 1992)) of the Cliff House Sandstone (Donselaar, 1989). Molenaar et al. (2002) showed an approximate age of between 78.5 Ma and 78.0 Ma for *B. perplexus*. Therefore, the turtles, crocodylomorphs, dinosaurs, and other fossils from our study area could be somewhat older than 78.0 Ma, but radioisotopic dating is necessary for greater accuracy and precision.

Materials & Methods

Fossil specimens were collected under permits NM11-005S, NM12-03S, NM16-11S, NM18-03S, and NM24-04S issued by the U.S. Bureau of Land Management (BLM) and are reposited at the Western Science Center in Hemet, California; Natural History Museum of Utah in Salt Lake City, Utah; and New Mexico Museum of Natural History & Science in Albuquerque, New

Mexico. The new turtle material described here was collected in the study area in San Juan County, New Mexico; exact locality data are on file at the BLM and the respective repositories. We apply the taxonomic scheme of turtles presented by Joyce (2007, 2017), and adhere to Phylocode guidelines unless otherwise indicated (e.g., Laurin, 2005; Joyce et al., 2021). Following Zangerl (1969), the two pairs of scales present on the anterior plastron are termed gular and intergular scales, where the intergulars are located anterior to the gular scales, and both sets of scales are anterior to the entoplastron.

To recognize patterns in the paleobiogeographic distribution of lower to middle Campanian turtle taxa along the eastern coast of Laramidia, we compiled faunal lists of turtle assemblages from geological units stratigraphically correlated with the Menefee Fm. using the regional stratigraphic correlations of Beveridge et al. (2022: fig. 9). Additional turtle assemblages were compared for the Aguja and Mesaverde formations in the Big Bend region of northern Mexico and Texas and northwestern Wyoming, respectively (see references in López-Conde et al., 2020; Wu et al., 2023). A hierarchical cluster analysis (paired group UPGMA using a Jaccard similarity index) was performed on the binary matrix of lower to middle Campanian turtle assemblages using PAST software (Hammer et al., 2001). Particular trionychid and plastomenid species were not included due to uncertainty of taxonomic consistency across the sampled sites. The Jaccard similarity index was selected because of its capabilities with binary data and strong performance in Mesozoic biogeographic studies (e.g., Schmachtenberg, 2008).

Institutional abbreviations

CHCU	Chaco Culture National Historical Park, Nageezi, New Mexico (collection housed at Hibben Center for Archaeological Research, University of New Mexico, Albuquerque, New Mexico)

NMMNH	New Mexico Museum of Natural History & Science, Albuquerque, New Mexico
PMU	Paleontologiska Museet, Uppsala, Sweden
ROM	Royal Ontario Museum, Toronto, Canada
UCMP	University of California Museum of Paleontology, Berkeley, California
UMNH	Natural History Museum of Utah, Salt Lake City, Utah
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C.
WSC	Western Science Center, Hemet, California

Results

Systematic Paleontology

Testudinata Klein, 1760

Baenidae Cope, 1882

Denazinemys Lucas and Sullivan, 2006

Denazinemys nodosa (Gilmore, 1916)

Fig. 2

Referred specimens: WSC 10769, posterior plastral lobe; WSC 10770, carapace fragment; NMMNH P-97386, right costal 1 fragment.

Description. WSC 10769 is the most intact specimen attributable to *Denazinemys nodosa* that we have collected, representing most of the posterior plastral lobe (Fig. 2A-B). It was broken unevenly from the rest of the plastron, and the lack of visible sutures in the specimen suggests the individual was developmentally mature (Fig. 2A). The right xiphiplastron is missing several pieces, especially posteriorly. A prominent ridge runs along the free margin on the ventral side, positioned almost a centimeter (cm) from the edge (Fig. 2A). The ridge likely represents the site of integumentary attachment and the body wall boundary. The shape of WSC 10769 is triangular and narrower posteriorly with a shallow anal notch that is slightly more developed than in the *D. nodosa* holotype (USNM 8345) (Sullivan, Jasinski & Lucas, 2013: fig. 20.2b). The preservation of any ventral sulcus pattern was disrupted by damage to the external cortex surrounding the midline, and the ventral surface is otherwise smooth and free of ornament (Fig. 2B). The typical extensive fusion known for baenids also obscures the pattern of sutures defining the posterior extent of the hypoplastron and the shape of the articulation with the xiphiplastra (Joyce et al., 2015). However, short segments of the femoral-anal sulci are intermittently intact in WSC 10769 and incised deeply, measuring almost a millimeter across. These segments suggest that the femoral-anal sulcus is straight rather than omega-shaped, which is the diagnostic shape for the sulcus in *Denazinemys* and also the derived group of baenids, Baenodda (Brinkman, 2003; Joyce & Lyson, 2015; Spicher et al., 2023). This would seem to undermine our referral of WSC 10769 to *Denazinemys*, except that the holotype USNM 8345 from the late Campanian Kirtland Fm. also has a nearly straight femoral-anal sulcus (Sullivan, Jasinski & Lucas, 2013: fig. 20.2b). This suggests that the shape of the sulcus is variable in *D. nodosa*, which should be reflected in future revisions of its diagnosis. The extent of variation and any temporal or geographic patterns for this trait are unknown due to low sample sizes, but could be investigated further as more material of this taxon is recovered.

The posterior lobe is wider at the level of the contact between the femoral-anal sulcus and the shell margins for WSC 10769 than for the holotype (Table 1). Similar to the holotype, the margins of the xiphiplastra at this contact are slightly indented in WSC 10769 (Fig. 2B). The lateral ends of the posterior plastral lobe occur near the contact between the abdominal-femoral sulcus and the shell margin at the base of the lobe, which is slightly wider in WSC 10769 compared to the holotype (Table 1; Fig. 2B). However, the length of the posterior plastral lobe, measured from the left terminus of the abdominal-femoral sulcus is almost the same between the two specimens.

WSC 10770 is an isolated carapacial fragment with a well-preserved example of the rounded, lumpy dorsal carapace texture of *D. nodosa* (Fig. 2C). The protrusions are distinguished from those of the nodosely-sculptured *Scabremys* (Sullivan, Jasinski & Lucas, 2013) by their generally rounded, ovoid, welt-like character. In contrast, the protrusions in *Scabremys* more closely resemble parasagittal rectilinear ridges that are more regular, antero-posteriorly oriented, and longer proportionally than in *Denazinemys* (Lucas & Sullivan, 2006; Sullivan, Jasinski & Lucas, 2013).

NMMNH P-97386 is a right costal 1 from a subadult *D. nodosa*, which is apparent due to lack of fusion with surrounding bony elements (Hutchison, 1984; Joyce & Lyson, 2015) (Fig. 2D-E). The dorsal surface is covered with the characteristic nodose texture of *D. nodosa*, and pustules vary in size and shape. Sulci are shallow and extend between pustules forming a cruciform pattern that divides the dorsal surface between the first two vertebral scales medially and the first two pleural scales on the lateral side (Fig. 2D). On the ventral side, the first thoracic rib is wide and low, crossing the surface transversely and terminating at an ovoid rib head (see Joyce, Schoch & Lyson, 2013) (Fig. 2E).

Neurankylus Lambe, 1902

Neurankylus baueri Gilmore, 1916

Fig. 3

Referred specimens: WSC 10612, partial articulated shell; CHCU 81269, partial plastron

Description. WSC 10612 is a partial articulated shell that includes approximately the anterior half of the carapace and most of the plastron. The anterior margin of the carapace is convex anteriorly, and the anterior marginal edge is rounded. WSC 10612 can be referred to *Neurankylus baueri* based on its large size and the arrangement of sulci on the ventral surface of the anterior plastral lobe (Fig. 3C-D). In particular, the gular scales are well-developed without meeting at the midline, and the intergular scales are U-shaped, contacting the humeral scales posteriorly (Larson et al., 2013; Sullivan, Jasinski & Lucas, 2013; Joyce & Lyson, 2015; Lichtig & Lucas, 2018). The bones of the shell are entirely fused and there are no discernable sutures, as is typical for baenids. The co-ossification of the shell, in addition to pervasive fracturing, limits the ability to discern some morphologies. However, the combination of bone and scale morphologies described above is consistent with those known for *N. baueri* (see summary of *Neurankylus* in Joyce & Lyson, 2015). Preserved sulci typically have rough edges, reaching 2.4 millimeters (mm) wide and ~1 mm deep. They define the extent of marginal scales 1-2, vertebral scale 1, the medial side of marginal scale 3, the vertebral-pleural sulci on the left side, the right lateral edge and posterolateral corner of the cervical scale, and the right pleural-marginal sulcus, including the posterolateral corner of pleural scale 1 (on costal 2) (Fig. 3A-B). Costals 1-4 are preserved on the left side, along with costals 1-2 on the right. The cervical scale is single, undivided, rectangular, and wider than long. The vertebral scales are also wider than long. Vertebral scale 1 contacts the cervical scale, marginal scales 1 and 2, and pleural scale 1. Marginal scale 2 contacts marginal scales 1 and 3, pleural scale 1, and vertebral scale 1. The surfaces of the carapace and plastron are nearly smooth, consistent with previous descriptions (e.g., Larson et al., 2013; Joyce & Lyson, 2015). Table S1 provides additional measurements for some discernable bones and scales.

Similar to the carapace, the plastron is heavily fractured and missing most of the posterior lobe (Fig. 3C-D). The anterior plastral lobe is wider than long and rounded anteriorly. In addition to the arrangement of gular/intergular scales described above, most of the humeral, pectoral, and femoral scales are at least partially preserved, along with left inframarginal scales 1-3, and partial marginals along the ventral bridge on the left side. Based on comparison with the reconstruction of *N. baueri* by Gilmore (1916), the length of the carapace of WSC 10612 is estimated to be 584 mm, exceeding the diagnostic threshold of 500 mm for *Neurankylus* spp. (Joyce and Lyson, 2015). The number of possible linear measurements for WSC 10612 was limited due to complete shell fusion and extensive fracturing. However, these distances are broadly similar to those of the holotype (Fig. 4; Table S1). WSC 10612 slightly exceeds the holotype specimen, USNM 8344, in the length of the cervical and first vertebral scales in the carapace and the midline contact lengths of pectoral and abdominal scales (Sullivan, Jasinski & Lucas, 2013; Lichtig & Lucas, 2018) (Fig. 4). USNM 8344 has a somewhat (~20%) wider second vertebral scale and longer midline contact of the humeral scales, but its plastron differs more substantially, with an anterior plastral lobe that is ~52% longer and ~31% wider (Fig. 4). Proportional differences could be due to dimorphism, but probably not ontogeny due to overall size similarity. USNM 8344 is also younger (Hunter Wash Mbr. of the Kirtland Fm.), so morphological differences could reflect changes in plastral dimensions over time (Lichtig & Lucas, 2018).

CHCU 81269 is a partial plastron of a turtle that was recovered from Chaco Culture National Historical Park in 2007. Santucci et al. (2015) briefly mentioned the specimen as a pelomedusid pleurodiran (side-necked turtle), while Lichtig & Lucas (2015) provided a morphological assessment and referred it to the bothremydid taxon *Elochelys* cf. *E. perfecta* based primarily on purported similarities in the posterior plastral lobe sulci. The ventral surface of the posterior plastral lobe is the only portion of CHCU 81269 with a discernable pattern of sulci (Fig. 5A, C). The posterior plastral lobe is a fused, thick plate of bone that is missing its posterior rim (Fig. 5C). Shell fusion and lack of sutures are unknown among the numerous pleurodirantaxa (including bothremydids) surveyed by Gaffney, Tong & Meylan (2006), though it is a key trait of baenids (Hutchison, 1984; Joyce & Lyson, 2015). Additional fusion is also apparent in a previously unidentified fragment (Lichtig & Lucas, 2015: fig. 9D), which is identified here as a sequence of fused neurals, also consistent with the pattern observed in Baenidae (see examples in Smith et al., 2017). Critically, the dorsal surface of the posterior plastral lobe also lacks any evidence of articular scars associated with pelvic (ischial and pubic) articulations, which are commonly-recognized synapomorphies for Pleurodira that would have been evident and diagnostic for bothremydids (Gaffney, Tong & Meylan, 2006; Mayerl et al., 2017: fig. 1) (Fig. 5B). The pattern of sulci on the posterior plastral lobe of CHCU 81269 is generally similar to the published pholidoses of *Elochelys perfecta* (Nopcsa, 1931; Gaffney, Tong & Meylan, 2006: fig. 270C-D). However, it is also similar to that of *Neurankylus baueri* in both sulcus arrangement and posterior plastral lobe shape (Sullivan, Jasinski & Lucas, 2013: fig. 20.6a-b) (Fig. 5C), which are well documented in specimens from the San Juan Basin (Lichtig & Lucas 2016, 2018). CHCU 81269 also lacks a prominent anal notch and we were unable to confirm a small mesoplastron such as those of bothremydids (Gaffney, Tong & Meylan, 2006; Pérez-García et al., 2017). Also, the locations of sulci in the bridge region were consistent with the anterior inframarginal scales of baenids (Gaffney, Tong & Meylan, 2006; Joyce & Lyson, 2015). The length and width of the posterior plastral lobe (11 and 14.5 cm, respectively) of CHCU 81269 are somewhat smaller than the *N. baueri* holotype (USNM 8344), but larger than the reconstructed plastron of *E. perfecta* (Gaffney, Tong & Meylan, 2006; Sullivan, Jasinski & Lucas, 2013). The lack of shell texture noted for CHCU 81269 is also more consistent with *N. baueri* than for pleurodires, which typically have a variant of a characteristic "pelomedusoid" pattern (see Gaffney, Tong & Meylan, 2006). In summary, the traits that favor an identification of *Neurankylus baueri* for CHCU 81269 rather than *Elochelys* cf. *E. perfecta* include: extensive shell fusion and a lack of discerable sutures; absent pelvic articular structures on the dorsal surface of the xiphiplastron; missing small, laterally located mesoplastra; bridge sulci consistent with baenid inframarginal scale pattern; anal notch lacking; and the absence of a typical vermiform pelomedusoid shell texture. Based on these characteristics and the lack of parsimony incumbent with referral to an extra-continental bothremydid taxon, we refer CHCU 81269 to *N. baueri*.

Scabremys Sullivan, Jasinski & Lucas, 2013

Scabremys ornata (Gilmore, 1935)

Fig. 6

Referred specimen: UMNH VP 28352, nearly complete articulated shell.

Description. UMNH VP 28352 is a partial, articulated shell with a complete plastron and a partial carapace that is preserved in its entire length (Fig. 6). As in the *N. baueri* specimen described above, the shell is filled in by dark gray mudstone and dark brown sideritic concretion, entirely co-ossified with no discernable sutures, and is badly fractured. The shell is referrable to *Scabremys ornata* and differs from the coeval and similar *Denazinemys nodosa* (see Lucas &

Sullivan, 2006). Unlike *D. nodosa,* the carapace of UMNH VP 28352 is oval, with the widest point midway along the carapace (Sullivan, Jasinski & Lucas, 2013: fig. 20.3). The shell sculpture of *S. ornata* is nodose and similar to *D. nodosa*, but is composed of raised, longitudinal ridges what are somewhat regular in length and alignment along the entire carapacial midline, with narrow grooves between them (Sullivan, Jasinski & Lucas, 2013). The sculptural morphology of UMNH VP 28352 is consistent with *S. ornata* (Fig. 6C, D). In comparison, the sculpture of *D. nodosa* is more rounded, irregular, and not ridge-like (see below). The ridges of *S. ornata* are concentrated on the first four vertebral scales and the medial sides of the costals, but are more laterally extensive in *D. nodosa* (Sullivan, Jasinski & Lucas, 2013: figs. 20.3a, 20.2a). Unlike *D. nodosa*, the first vertebral scale of UMNH VP 28352 is hexagonal and widest anteriorly (Sullivan, Jasinski & Lucas, 2013; Joyce & Lyson, 2015). Intergular scales are absent and the gular scales are not divided, which is the diagnostic arrangement for *S. ornata* (Sullivan, Jasinski & Lucas, 2013) (Fig. 6A, B). A few intermittent sulci are preserved on the carapace of UMNH VP 28352, indicating the posterior and lateral edges of vertebral scale 1, the right lateral edge of vertebral scale 2, the contact between pleural scales 1 and 2 on the right side, as well as edges of an anterior (cf. third) marginal scale on the right side (Fig. 6D).

The posterior edge of the carapace and part of the right margin are preserved and have rounded edges in cross section. The posteriormost edge of the carapace is flat and transitions on the right side to a postero-laterally facing, slightly concave segment of the margin (Fig. 6C, D). Unlike *Denazinemys*, the posterior edge of the carapace extends beyond the plastron (Sullivan, Jasinski & Lucas, 2013). Vertebral scale 5 reaches the rounded posterior carapace margin in both species (Lucas & Sullivan, 2006; Sullivan, Jasinski & Lucas, 2013). The distinctive ridged surface texture of *S. ornata* is preserved on the right anterior side of the dorsal carapace and near the midline (Fig. 6C). Otherwise, the shell surface is nearly smooth, with texture formed by short, fine wrinkles.

Sulci on the ventral side of the anterior plastral lobe of UMNH VP 28352 define the contact between the gular, humeral, and pectoral scales (Fig 6A-B). The gular-humeral and humeral-pectoral sulci are mostly straight and approximately perpendicular to the midline. The anterior plastral lobe is wider than long, broadly convex anteriorly, and extends slightly past the anteriormost margin of the carapace. The posterior plastral lobe is approximately the same size as the anterior lobe and is also rounded, but it has a flat posteriormost margin with no anal notch (Fig. 6A-B). The shape of the posterior plastral lobe of UMNH VP 28352 is more evenly rounded than that of *Denazinemys*, and there is no indentation of the margin at the ends of the femoral-anal sulcus (Fig. 2B). The general shapes and proportions of the plastral lobes are similar between *Scabremys* and *Denazinemys*, but there are distinct differences between the scalation of these areas. Similar to the anterior sulci, the femoral-anal sulcus of UMNH VP 28352 is mostly straight and perpendicular to the midline (Fig. 6A, B). This pattern differs from *Denazinemys* specimens recovered in the Menefee Fm. (e.g., WSC 10769), in which those sulci are oriented posterolaterally (Fig. 2B). The anal scales are substantially shorter than wide (Lucas & Sullivan, 2006; Sullivan, Jasinski & Lucas, 2013). Large portions of the lateral carapace are missing, but sulci partially define the edges of probably the first three inframarginal scales on the right. The lateral portions of the shell are missing posterior to approximately peripheral 5 on the left and posterior to peripheral 6 on the right (Fig. 6C, D). The straight plastral length of UMNH VP 28352 is 39 cm, and the carapace measures 43 cm along the midline.

Thescelus Hay, 1908

Thescelus cf. *rapiens* Hay 1908

Fig. 7

Referred specimen: NMMNH P-97384, right half of anterior plastral lobe and associated partial nuchal.

Description: NMMNH P-97384 is an isolated right half of an anterior plastral lobe. It is recognized as a sexually mature baenid based on the fusion of bones (Fig. 7). The ventral surface lacks regular surface texture, but has low, uneven topography and some small, shallow pits (Fig. 7A). This differs from the finely crenulated, pleurosternid-like texture known for *Thescelus insiliens* (Joyce & Lyson, 2015). The sulci on the ventral surface are relatively wide with poorly-defined edges, and the lobe margin is indented where it meets them (Fig. 7A). NMMNH P-97384 is recognized as a derived baenid (Baenodda), unlike *N. baueri*, based on substantial midline contact of the gular scales and reduction of the intergular scales (Brinkman 2003b; Joyce & Lyson, 2015). The presence of gular scales differentiates NMMNH P-97384 from *Scabremys*, and they are more reduced than in *Denazinemys* (Sullivan, Jasinski & Lucas, 2013). The anterior plastral lobe is rounded, unlike *N. baueri*, lacks the nodose texture of *Scabremys* and *Denazinemys*, and is smaller than the other sympatric baenid taxa. On the dorsal side of the lobe, there is a rough patch of bone along the medial edge where the entoplastron is fused with surrounding elements, and there is a beveled free margin that is wider anteriorly and indicates an integumentary transition from keratin to skin. The anterior plastral lobe proportions and sulci of NMMNH P-97384 most resemble *T. rapiens* (PMU.R22) (Sullivan, Jasinski & Lucas, 2013: fig. 20.8c-d). Sullivan, Jasinski & Lucas, (2013) recognized *T. hemispherica* Gilmore 1935 from the Hunter Wash Mbr. of the Kirtland Fm. and noted the difficulty in distinguishing *T. hemispherica* from *T. rapiens*. However, Joyce & Lyson (2015) considered the former taxon a *nomen dubium* and retained the latter as valid. Our tentative taxonomic referral to

T. cf. *rapiens* reflects a degree of uncertainty pending more Menefee material and potential taxonomic clarity within the genus in future.

NMMNH P-97384 also includes an associated portion of a nuchal that cannot be confidently attributed to a side (Fig. 7C-D). It is a marginal component of the carapace with a rounded edge and a superficially damaged ventral side. Two sulci on the dorsal surface diverge toward the margin, and are conspicuously large, measuring approximately two millimeters in depth and width (Fig. 7C). The sulci separate the triangular first marginal scale from the cervical and second marginal scales. This is the only part of the carapace margin of *T. rapiens* (Sullivan, Jasinski & Lucas, 2013: fig. 20.8c) where marginal scales are triangular and small.

Helochelydridae Chkhikvadze, 1970 sensu Joyce et al., 2021

Naomichelys Hay, 1908

Naomichelys sp.

Fig. 8A-D

Referred specimens: WSC 10884, partial nuchal; WSC 10885, hypoplastron fragment.

Description. WSC 10884 is a fragment of an element from the periphery of the carapace that is likely anterior due to its obtuse edge. The specimen can be readily identified by the isolated columnar projections that adorn the dorsal surface, which are diagnostic of the broadly distributed North American helochelydrid genus *Naomichelys* (Joyce, Sterli & Chapman, 2014; Joyce, 2017) (Fig. 8A). A different specimen of *Naomichelys* from the Menefee Formation was described by Lichtig & Lucas (2015). WSC 10884 is likely a central portion of the nuchal based on its rounded cross-section, which is thickest in association with a concave margin near the midline of the nuchal or at buttresses of the plastron (Joyce, Sterli & Chapman, 2014; Herzog, 2019). WSC 10884 is missing sulci or ridges that would occur at buttresses (Joyce, Sterli & Chapman, 2014: fig. 8). As with other (especially Late Cretaceous) occurrences (e.g., Adrian et al., 2019, 2023a; Herzog, 2019), material from this genus is not diagnosable to its type species, *Naomichelys speciosa* Hay 1908, as it is implausible that one species could achieve such widespread temporal and geographic distribution (see Joyce, Sterli & Chapman, 2014).

WSC 10885 is an isolated hypoplastron fragment that likely belonged to the right posterior (inguinal) buttress (see Joyce, Sterli & Chapman, 2014: fig. 8.2). The element is irregularly rhomboidal and all edges are broken except the longest, which is relatively thick and rounded (Fig. 8C-D). The thick portion is part of the thickened edge that lines the edge of the buttress opposite the posterior plastral lobe on the dorsal surface. The second longest edge preserves the constricted end of the thick, round edge posteriorly, and portions of costiform processes project from the lateral edge of the element (Fig. 8C-D). These processes were attachment sites for ligamentous tissue that partially formed the bridge in *Naomichelys*, similar to *Aragochersis lignitesta* (Pérez-García et al., 2020; Lawver & Garner, 2023).

Testudines Batsch, 1788

Pan-Trionychia Joyce, Parham & Gauthier, 2004 sensu Joyce et al., 2021

Adocidae Cope, 1870

Adocus Cope, 1868

Adocus sp.

Fig. 8E-H

Referred specimens: WSC 10763, a sixth left costal; WSC 10765, a (cf. fifth) neural.

Description. WSC 10763 is a sixth left costal representing *Adocus* sp. It is referred by diamond-shaped pits arranged in rows, and by the marginal-pleural sulcus occurring significantly medial to the costal-peripheral suture (Hay, 1908; Gilmore, 1919; Meylan & Gaffney, 1989; Sullivan, Jasinski & Lucas, 2013). Texture is concentrated at 4-5 pits per mm, similar to *Adocus kirtlandius* Gilmore (1919) from the Kirtland and Fruitland formations (Sullivan, Jasinski & Lucas, 2013). The sixth costal likely articulated medially with the sixth and last neural (Gilmore, 1919). Sulci on the dorsal surface divide marginal scales 8-9 laterally, pleural scales 3-4 in the middle, and vertebral scale 4 medially (Fig. 8C). The ventral surface of the costal is mostly flat and smooth, exhibiting minimal relief of the embedded rib; however, the reduced rib head is typical of *Adocus* (Meylan & Gaffney, 1989). A small protrusion of the rib end beyond the costal is preserved laterally, however its sutural lateral edge indicates peripheral articulation, differentiating the specimen from Trionychidae (Vitek & Joyce, 2015). The maximum width of WSC 10763 is intermediate in size between that of *A. kirtlandius* and *A. bossi* Gilmore (1919) from younger Campanian units in the San Juan Basin (Table 2).

WSC 10765 is an unassociated hexagonal neural that can be attributed to *Adocus* sp. based on a patch of faint surface texture on the anterior end of the dorsal side (Fig. 8~~E, F~~). Though worn, the pits are consistent in size with better preserved *Adocus* specimens from the Menefee and aligned in regular rows unlike those of trionychids (Sullivan, Jasinski & Lucas, 2013; Vitek & Joyce, 2015). The neural is broken near a faintly distinguishable sulcus that crosses the dorsal surface on its distal half, just posterior to a transverse crack on the left side (Fig. 8~~E~~) (Meylan & Gaffney, 1989). The dimensions of the neural and location of the transverse sulcus suggest the specimen is the fifth in the neural series (Gilmore, 1919; Sullivan, Jasinski & Lucas, 2013: fig.

20.10). The ventral surface has remnants of the bases of vertebral articulations along the midline, with one large midline scar and two thinner flanking ridges (Fig. 8~~F~~). The margins of WSC 10765 comprise dense, finely-grooved sutures typical of *Adocus* (Hay, 1908; Gilmore, 1919). The length of the fifth neural is considerably greater than that of *A. kirtlandius*, but only slightly exceeds that of *A. bossi* (Table 2).

Nanhsiungchelyidae Yeh, 1966

Basilemys Hay, 1902

Basilemys sp.

Fig. 8I

Referred specimen: WSC 10883, peripheral fragments.

Description. Remains of *Basilemys* (WSC 10883) were discovered for the first time in the Menefee Fm. in the field season of 2023. The fragments clearly belong to the peripheral ring, where deep pitting occurs on both the dorsal and ventral sides of the broadly rounded peripherals, a diagnostic feature of the genus (Brinkman & Nicholls, 1993; Mallon & Brinkman, 2018). The bones are clearly distinct from *Adocus* in the size and coarseness of the pits, and cannot belong to a trionychid because they represent peripherals and have a more regular surface sculpture with higher relief. The ornamentation of WSC 10883 is similar in arrangement to that of *Adocus*, but the pits are substantially larger, deeper, and have distinct points that project from the junctions of ridges between pits (Fig. 8I). The ornate surface sculpture of *Basilemys* has also been described as triangular tubercles separated by pits (Brinkman & Nicholls, 1993).

Pan-Trionychidae Joyce, Parham & Gauthier, 2004 sensu Joyce et al., 2021

Plastomenidae Hay, 1902 sensu Joyce et al., 2021*Helopanoplia* Hay, 1908

Helopanoplia sp.

Fig. 9A-B

Referred specimen: WSC 10767, an edge fragment of a second costal; UMNH VP 36786, an indeterminate costal edge fragment.

Description. A pan-trionychid, *Helopanoplia* (Hay, 1908), is recognized in the Menefee only from costal fragments and is less abundant than "*Trionyx*" *robustus* (see below). Its pit morphology is distinctly intermediate in size (1.7–4.4 mm diameter) between *"Trionyx"* sp. 'large' and "*Trionyx" robustus* (Fig. 10C). Its recessed areas are less pit-like and flatter than the other Menefee trionychid forms. The ridges between these recessed areas are thin, form polygonal rather than ovoid shapes, and are not rounded. Additionally, the costal free margin is bounded by an upturned ridge approximately 0.75 cm wide on WSC 10767~~.~~ (Fig. 9A). WSC 10767 preserves the upturned rim of the carapacial "shoulder" that is associated with the second costals in *Helopanoplia*, and UMNH VP 36786 displays the lateral margin that is characteristic of most other costals (see Joyce & Lyson, 2017: 9) (Fig. 9B).

WSC 10767 and UMNH VP 36786 share similarities with *Helopanoplia* specimens UCMP 194095 and UCMP 194260 from the Kaiparow~~ti~~s Fm., primarily in the distinctive dorsal carapace sculpture where pits are subequal in size and the border between them is formed by a sharp ridge varying in height (Hutchison, Knell & Brinkman, 2013: 311; fig. 13.14 a-b). There is also a distinctly upturned lip along the free edge that lacks pits in both Menefee specimens, similar to that of the blunt shoulder formed by costals II on the carapace of *Helopanoplia* (Joyce & Lyson, 2017: fig. 4A).

Plastomenidae indet.

Fig. 9C-D

Referred specimens: NMMNH P-97383 and NMMNH P-97389, shell fragments

Description. NMMNH P-97383 and NMMNH P-97389 are small shell fragments of pan-trionychid turtles, which can be identified based on their characteristic pitted dorsal textures (Fig. 9). NMMNH P-97383 is approximately triangular, and one edge is curved while the others are straighter (Fig. 9C). NMMNH P-97389 is irregular in shape and has a more poorly preserved dorsal surface (Fig. 9D). They can be distinguished from the trionychid morphotypes described below by the combination of very small (~1 mm diameter) pits and a very thin (~3 mm) shell. The trionychid form with the smallest pits (“*Trionyx*” *robustus*) differs by having a considerably thicker shell (also recognized by Joyce, Lyson & Sertich, 2018). In addition to finely pitted texture, NMMNH P-97383 also has a faint ridge crossing its surface, similar to those of the plastomenid *Gilmoremys gettyspherensis* Joyce, Lyson & Sertich (2018) (Plastomeninae indet. of Sullivan, Jasinski & Lucas, 2013). However, the paucity of recovered material for this smallest pan-trionychid constrains our referral to a particular plastomenid species (see phylogenetic hypothesis of Girard et al., 2024).

Trionychidae Bell, 1828 sensu Joyce et al., 2021

Trionychinae Lydekker, 1889 sensu Joyce et al., 2021

“*Trionyx*” sensu Vitek & Joyce, 2015

“Trionyx” sp. ‘large’

Fig. 10A~~,~~ B

Referred specimen: WSC 10768, a right first costal.

Description. The largest pan-trionychid known from the Menefee is recognized by fragments that often have free costal edges with a border that lacks pitting (Fig. 10A, B). Its surface ornamentation is distinct from the smaller forms (see below) and is distinguished by relatively large circular to irregular ovoid pits (2.5–4.5 mm diameter) (Fig. 10A, B). The pits are separated by relatively wide ridges that are low and rounded. WSC 10768 represents a nearly complete first right costal and is the most complete specimen of this taxon known from the Menefee. In most of the superficial layers of pitting on the dorsal side, the most exterior cortical layers are broken away, leaving remnants with variably intact pitted surfaces (Fig. 10A, B). Broken edges of fragments from this taxon frequently display the distinctive laminar "plywood-like" internal microstructure of trionychids without the need for magnification (Scheyer et al., 2007; Lichtig & Lucas, 2015; Vitek & Joyce, 2015). Apart from the free margin, sutured edges of the costal are better preserved on the ventral side (Fig. 10B). The shapes of the edges can indicate the shapes of adjacent bones. For instance, the two distinct concavities on the medial side of WSC 10768 suggest two distinct bones (e.g., neurals or preneurals) medial to the first costal, a feature associated with the legacy taxon *Aspideretoides* (Fig. 10B) (Gardner, Russell & Brinkman, 1995). The anterior border of the costal suggests that the nuchal was considerably wider than long. The ventral surface also preserves the first rib, which is directed anteriorly toward the nuchal, and its broad, flat head occupies the medial end of the costal (Fig. 10B). WSC 10768 shares similar traits to an unnamed species of *Aspideretoides* (*"Trionyx"* sensu Vitek & Joyce, 2015) described from the Kaiparowits Fm. (UCMP 194124), which is referred based on its aforementioned neural area subdivision (Hutchison, Knell & Brinkman, 2013: 313; fig. 13.14c). UCMP 194124 is differentiated from *Axestemys splendida* Vitek (2012) by the anterior curve of the first costal as opposed to its straight lateral extension, and WSC 10768 shares this difference (Hutchison, Knell & Brinkman, 2013). Dorsal surface sculpture is also similar between UCMP 194124 and WSC 10768 in its even, pitted distribution across the shell, with reduced pit size near the edge of the shell (Fig. 10A). The borders between pits are often wide with rounded or flat tops (Hutchison, Knell & Brinkman, 2013: fig. 13.14c).

"Trionyx" robustus (Gilmore, 1919)

Fig. 10C~~,~~ D

Referred specimen: WSC 10766, right partial posterior carapace.

Description. A form attributed to *"Trionyx" robustus* has the smaller pits of the two trionychine taxa recognized here from the Menefee Fm. and is best represented by WSC 10766, a portion of the right posterior carapace (Fig. 10C, D). Unlike the other forms, the pits are rounded and closely arranged, extending almost completely to the free costal margins. Most pits are similar in size, arranged in rows, and range in diameter from 0.7–1.5 mm. However, they sometimes coalesce and are somewhat amorphous, typically becoming fainter toward the center of the carapace (Fig. 10C, D). On its ventral side, a posterior rib diverges slightly posteriorly from the anterior sutural edge and reaches the free margin, where its end is broken and missing (Fig. 10D). WSC 10766 is consistent with a nearly complete carapace of "*T.*" *robustus* from the Fruitland Fm. (PMU.R30; Sullivan, Jasinski & Lucas, 2013: fig. 20.15d) in size and morphology. Based on its similarity in size with that specimen, WSC 10766 likely belonged to an individual around 23 cm in carapace length.

Quantitative results

The revised turtle assemblage from the Menefee Fm. is summarized in Figure 11 and discussed in detail below. Results from the cluster analysis show substantial variation in composition and diversity among the lower-middle Campanian stratigraphic units sampled (Fig. 12). Of these sites, species diversity is highest in the Aguja Fm. and generally higher in southern Laramidian units (Fig. 12B). The most broadly distributed taxa are the helochelydrid *Naomichelys* and pan-trionychian immigrants from Asia (i.e., *Adocus*, *Basilemys*, Trionychidae spp.). The nanhsiungchelyid *Basilemys* is the only turtle known ubiquitously across the included stratigraphic units. Chelydridae are known from the Mesaverde Fm. northward (Varricchio & Horner, 1993; Brandvold, Brandvold & Sweeney, 1996; Peng, Russell & Brinkman, 2001; DeMar & Breithaupt, 2006, 2008; Cullen et al., 2016) (Fig. 12). Kinosternoids (usually cf. *Hoplochelys*) are reported from Campanian strata in Mexico, and the stem kinosternid *Yelmochelys rosarioae* Brinkman, Aguillon-Martinez, Hutchison & Brown (2016) was tentatively identified from the Aguja Fm. and younger strata (Sankey, Lucas & Sullivan, 2006; López-Conde, Chavarría-Arellano & Montellano-Ballesteros, 2020). Derived baenids are not known north of Utah during the early-middle Campanian. The Wahweap and Menefee formations each had the baenids *Neurankylus* and *Denazinemys* (Fig. 12). *Adocus, Thescelus*, and *Scabremys* are known from the Menefee but have not been reported from the Wahweap, while *Arvinachelys* and *Compsemys* are known from the Wahweap but not the Menefee. The derived baenids *Arvinachelys* and *Scabremys* are also known from higher in the stratigraphic sections of the Kaiparowits Plateau and the San Juan Basin, respectively (Hutchison, Knell & Brinkman, 2013; Sullivan, Jasinski & Lucas, 2013; Holroyd & Hutchison, 2016). Fully marine bothremydids were constrained to the Aguja Fm. in the early-middle Campanian, and the protostegid *Terlinguachelys fischbecki* Lehman & Tomlinson (2004) is known from the same unit.

Discussion

Menefee Formation turtle assemblage composition

Previous studies reported a turtle assemblage from the Menefee Fm. that was broadly similar (e.g., adocid, trionychid, baenid, and bothremydid taxa) to those of the well-known upper Campanian Fruitland and Kirtland formations, but less diverse and seemingly more primitive (e.g., Lichtig & Lucas, 2015). The assemblage we report from the Menefee Fm. confirms the work of previous studies, apart from the ostensible presence of bothremydids, while also increasing the known local diversity of turtle species, primarily by retrograding the stratigraphic ranges of *Neurankylus*, *Scabremys*, *Basilemys*, and *Thescelus* (Fig. 11). This increases the number of baenids, including stem and derived forms, to four and brings the Menefee Fm. more in line with correlative mid-Campanian units elsewhere in Laramidia (Fig. 12). The revised turtle assemblage from the Menefee Fm. exceeds the diversity known from the Ne-nah-ne-zad Mbr. of the Fruitland Fm. due to the presence of *Naomichelys* (Sullivan, Jasinski & Lucas, 2013; Lichtig & Lucas, 2015) (Fig. 11). Compared to the Hunter Wash Mbr. of the Kirtland Fm., the Menefee turtle assemblage is missing *Boremys grandis*, *Compsemys*, and a representative of Bothremydidae (Sullivan, Jasinski & Lucas, 2013). The ubiquity of *Basilemys* during the middle Campanian in Laramidia contrasts with a patchier distribution for *Adocus*, which has not been reported from the Two Medicine or Wahweap formations (Varricchio & Horner, 1993; Holroyd & Hutchison, 2016). The persistent endemic helochelydrid *Naomichelys* is represented in New Mexico by only three shell fragments including the two described above; the rarity of the genus in New Mexico suggests it was relatively scarce on the Menefee paleolandscape, or at least in the paleoenvironments represented (i.e., fluviodeltaic and floodplain deposits) (Lichtig & Lucas, 2015). *Naomichelys* is known primarily from fragments (Joyce, 2017), and it is not known in the San Juan Basin after the Menefee Fm. (Lichtig & Lucas, 2015). The Menefee specimens were discovered near the top (WSC 10885) and bottom (WSC 10884) of the stratigraphic range included in our study area, making it likely that *Naomichelys* persisted to the top of the Allison Member, at least locally. Its final occurrences in Laramidia are from the late Campanian of Mexico (Reynoso, 2006; López-Conde et al., 2018). The surface sculpture and marginal and nuchal morphologies of two of the trionychid forms recognized in the Menefee Fm. strongly resemble those that are characteristic of the genus *Aspideretoides* Gardner, Russell & Brinkman 1995. For instance, the medial edge of the first costal of "*Trionyx*" sp. 'large' (WSC 10768) suggests the presence of a preneural and a nuchal that is approximately four times wider than long (Fig. 9A~~,~~ B). The presence of a preneural is considered primitive for trionychids (Gaffney, 1979; Meylan, 1984, 1987). *Aspideretoides* (*"Trionyx"*) is also known from the Campanian of Central Asia (Vitek & Danilov, 2010), which has been interpreted as evidence of multiple trionychid dispersal events to North America from Asia. However, problems persist with the diagnostic characters for the genus (Hutchison, 2000; Vitek & Joyce, 2015). It is plausible that future discoveries will provide enough diagnostic material to increase taxonomic resolution for the trionychid taxa that inhabited southern Laramidia in the middle Cretaceous.

The recognition of *Helopanoplia* in the Menefee Fm. represents an early occurrence of the genus, which is otherwise reported from the Campanian only in the Kaiparowits and Aguja formations, where the deposits are dated to the middle to late Campanian (Sankey, Lucas & Sullivan, 2006; Gasaway & Sankey, 2007; Hutchison, Knell & Brinkman, 2013). This early occurrence suggests a southern Laramidian origin for the genus if the attributions are accurate, and the potential presence of two sympatric plastomenids in the Menefee Fm. matches the diversity of trionychid species. The size distributions of sympatric soft-shelled species also suggest possible niche separation if the current approximate size estimations are correct. Further trionychid discoveries in the Menefee could make this a testable line of inquiry. The pan-trionychids included in the current study are not taxonomically separated for the purposes of the cluster analysis due to taxonomic uncertainty in the group across sampled stratigraphic units.

Increased taxonomic confidence may be possible for *Adocus* in its specific representation through the stratigraphic section, though systematic problems with the genus remain (see Danilov et al., 2013). However, regional comparisons among specimens may elucidate variation in anterior plastral lobe morphologies, which suggests that two species of *Adocus* are present in the Kaiparowits Fm., similar to the upper Campanian portion of the San Juan Basin (Gilmore, 1919; Hutchison, Knell & Brinkman, 2013; Sullivan, Jasinski & Lucas, 2013).

Stratigraphic range extensions

The specimens reported here allow us to confidently extend the stratigraphic ranges of several turtle species to the Menefee Fm. from higher in the San Juan Basin stratigraphic section (Fig. 11). The first is the stem baenid *Neurankylus baueri*, which is known from the younger Kirtland Fm., but not the intervening Fruitland Fm. (Sullivan, Jasinski & Lucas, 2013). The same stratigraphic revision is applied to the derived baenids *Scabremys ornata* and *Thescelus*, which are known from the upper Campanian Kirtland Fm. (Sullivan, Jasinski & Lucas, 2013). The stratigraphic range of *Basilemys* in the San Juan Basin is also extended back to the Menefee Fm. (Fig. 11). *Basilemys gaffneyi* Sullivan, Jasinski & Lucas (2013) is known from the upper Fruitland and lower Kirtland formations, while the occurrences from the Menefee and Aguja formations predate the earliest named species of *Basilemys* (*B. variolosa* Cope 1876) from the

Judith River Fm. in central Montana (Langston, 1956; Sullivan, Jasinski & Lucas, 2013; Mallon & Brinkman, 2018; López-Conde, Chavarría-Arellano & Montellano-Ballesteros, 2020). Consistent with previous studies, the trionychid/plastomenid record in the Menefee Fm. is currently rich in variation and apparently speciose, although most material is fragmentary and isolated, confounding attribution (Lichtig & Lucas, 2015). However, we have presented material representing two taxa each belonging to plastomenid and trionychid forms (Vitek, 2012; Vitek & Joyce, 2015; Girard et al., 2024). The consistent recovery of plastomenid turtles from large sandstone channel deposits demonstrates a preference for riverine conditions (Lyson, Petermann & Miller, 2021; Girard et al., 2024). The diversity of pan-trionychids in the Menefee Fm., along with their size range, suggests that local freshwater hydrological regimes manifested in a variety types, representing both higher and lower energy environments.

Revised turtle paleobiostratigraphy

Results from the cluster analysis reveal patterns in the diversity and distribution of turtles in Laramidia during the early-middle Campanian, though the sample is not comprehensive and is subject to typical constraints associated with the fossil record (e.g., low sample sizes, taxonomic uncertainty, poor dating; see Maidment et al., 2021) (Fig. 12). First, *Naomichelys* has a broad distribution among the sampled sites, and the Menefee Fm. is noteworthy in producing the only three fragments from the taxon that have been reported in New Mexico (Joyce et al., 2011; Lichtig & Lucas, 2015). Also, the broad pattern of early-middle Campanian baenid distribution is consistent with a low latitude origin for the derived group of baenids (Baenodda), which first appeared in the Cenomanian in Appalachia (*Gehennachelys maini* Adrian, Smith & Noto, 2023) and Turonian of Laramidia (*Edowa zuniensis* Adrian, Smith, Kelley & Wolfe, 2023) (Joyce & Lyson, 2015). In particular, the stratigraphic extension of *Scabremys* to the Menefee Fm., combined with its presence in the Aguja Fm., demonstrates a broader geographical and temporal range than previously appreciated (Tomlinson, 1997; López-Conde et al., 2019; López-Conde, Chavarría-Arellano & Montellano-Ballesteros, 2020), similar to the spatiotemporal distribution of *Denazinemys* and *Thescelus*. The cluster analysis shows a distinct trend of higher turtle diversity at lower latitudes (Fig. 12B). *Basilemys* and Pan-trionychidae were ubiquitously present in the sampled stratigraphic units, and *Naomichelys* and *Adocus* were the next most widely distributed clades across latitudes. Prior to the late Campanian, derived baenids (e.g., *Arvinachelys*, *Denazinemys*, *Scabremys*, *Thescelus*) only occurred in the Wahweap Fm. and southwards (Holroyd & Hutchison, 2016), and kinosternoids were restricted to Gulfian latitudes ~~at~~ the Aguja Fm (Brinkman, et al., 2016; Holroyd & Hutchison, 2016; López-Conde, Chavarría-Arellano & Montellano-Ballesteros, 2020). No sampled taxa were found exclusively in northern latitudes, consistent with previous difficulties in defining a distinctly northern turtle fauna (Holroyd et al., 2015).

The revised taxonomic identity of CHCU 81269 from a bothremydid to the baenid *N. baueri* has biogeographical significance. First, it simplifies our understanding of North American bothremydid distribution during the Campanian by constraining it to the Aguja Fm. prior to the late Campanian. It also suggests that there was a hiatus of the pleurodiran clade in the Western Interior between their earliest known invasion into Laurasia during the Cenomanian (Joyce, Lyson & Kirkland, 2016; Pérez-García et al., 2017; Adrian et al., 2021) and *Chedighaii hutchisoni* in the upper Campanian Kirtland Fm. (Gaffney, Tong & Meylan, 2006; Sullivan, Jasinski & Lucas, 2013). This species is known only from a skull, and questions remain about its phylogenetic relationship with *Bothremys* (see Gaffney, Tong & Meylan, 2006) (Fig. 11). The recognition made here of *Neurankylus baueri* in the Menefee Fm. constitutes the earliest occurrence of the species (Joyce & Lyson, 2015; Holroyd and Hutchison, 2016). This pattern was previously overlooked due to the original misidentification of CHCU 81269 as a bothremydid (Lichtig & Lucas, 2015).

Our comparison of *N. baueri* shell dimensions confirms similarity of Menefee specimen WSC 10612 with the younger holotype, and also supports the hypothesis of Joyce & Lyson (2015) that anterior lobe dimensions are highly variable in baenids (Fig. 4). Plastral lobe dimensions have also been used to differentiate between palatobaenines, eubaenines, and *Neurankylus* spp. (Adrian et al., 2023b).

Numerous previous studies have also reported patterns suggesting a distinct southern Laramidian turtle assemblage (Tomlinson, 1997; Hutchison et al., 1998; Rodriguez-de la Rosa & Cevallos-Ferriz, 1998; Brinkman, 2003b; Brinkman & Rodriguez-de la Rosa, 2006; Sankey, Lucas & Sullivan, 2006). For baenids in particular, Joyce & Lyson (2015) recognized *Boremys pulchra* Lambe 1906, *Neurankylus eximius* Lambe 1902, and *Plesiobaena antiqua* Lambe 1902 as northern taxa, and six southern taxa: *Arvinachelys goldeni* Lively 2015, *Boremys grandis* Gilmore 1935, *D. nodosa*, *N. baueri*, *S. ornata*, and *T. rapiens*. Though various hypotheses of provinciality and endemism have been vigorously debated, large scale distribution patterns are not broadly consistent in timing or extent across faunal groups, and a clear consensus has not been established regarding the latitudinal ranges of purported provinces within the Western Interior Basin (WIB) (Lucas et al., 2016; Maidment et al., 2021). However, refined geochronology of Campanian continental strata in the WIB has revealed temporal overlap among the richest dinosaur-bearing intervals in the Dinosaur Park Fm. of Alberta, the Judith River and Two Medicine formations of Montana, and the Kaiparowits Fm. of Utah (Ramezani et al., 2022). Given the expanse and complexity of geological and climatic change that is included in the history of the WIB, perhaps a single explanatory model is unreasonable to expect, and may be impossible given the inherent uncertainty and complexity that exists in the fossil record. Rather, constraining the temporal, spatial, and taxonomic parameters may focus on the responses of particular biotas across group-specific spatio-temporal parameters. This approach is particularly relevant for San Juan Basin turtles because of uncertainty surrounding the timing of the Laramide tectonism in north-central New Mexico, which is believed to have started around 75-70 Ma. The lack of precise temporal data makes it challenging to pinpoint when this tectonic event first began (Thacker et al., 2023). The turtle distributional patterns and stratigraphic range extensions described here demonstrate that turtle assemblages in the San Juan Basin show broad compositional continuity from the Allison Member of the Menefee Fm. through the Kirtland Fm. The likely presence of multiple trionychid taxa in the Menefee that resemble younger taxa suggests endemism in the group prior to the upper Campanian (Fig. 11). Overall, the revised Menefee assemblage presented here increases the known diversity of turtles in the middle Campanian of the San Juan Basin, aligning it more closely with younger strata, particularly the Fruitland Fm. and Hunter Wash Mbr. of the Kirtland Fm. (Fig. 11) (Sullivan, Jasinski & Lucas, 2013). Future collection efforts in the Menefee may further reduce the faunal differences in the sequence, which currently involve the taxa *Boremys grandis*, Kinosternoidea, and any marine taxa (bothremydids or chelonioids).

Conclusions

The Menefee Fm. turtle discoveries reported here update our understanding of San Juan Basin turtle fauna in the temporal interval preceding the rich deposits of the later Campanian. Compared to the last published inventory of the Menefee Fm. turtle assemblage (Lichtig & Lucas, 2015), we demonstrate a stratigraphic range extension of approximately three million years in the San Juan Basin stratigraphic sequence for *Neurankylus baueri*, *Scabremys*, *Thescelus, Basilemys*, and Plastomenidae (Fig. 11). These additions to the Menefee turtle fauna increase its similarity with the younger Fruitland and Kirtland formations and stratigraphically correlative units, especially in southern Laramidia (e.g., Wahweap and Aguja formations) (Fig. 12). Two Menefee trionychids are referred to trionychine taxa that are similar to species that have been assigned to the genus *Aspideretoides* (or "*Trionyx*"), and two more are referred to plastomenid taxa (Hutchison, Knell & Brinkman, 2013). The occurrence of one of these, *Helopanoplia,* is early and it also occurs later in the Campanian at the Kaiparowits and Aguja formations. Its presence in the Menefee Fm., along with "*Trionyx*" sp. 'large', suggests a particular similarity with pan-trionychid taxa described from the Kaiparowits Fm. (Hutchison, Knell & Brinkman, 2013). The relatively small indeterminate plastomenid could represent *Gilmoremys gettyspherensis* (Joyce, Lyson & Sertich, 2018) or a related form, but more material is needed to confirm. *Adocus* specimens from the Menefee are generally larger than *A. kirtlandius* (Sullivan, Jasinski & Lucas, 2013), but more material is required to make specific attributions. We describe two fragments of the helochelydrid *Naomichelys*, which constitute the second and third specimens known from the Menefee Fm. and New Mexico more broadly (Lichtig & Lucas, 2015). This suggests local and regional rarity of the genus, which is relatively close in time to its final occurrences in Laramidia, in Mexico during the late Campanian (Reynoso, 2006; López-Conde et al., 2018). The current study increases the diversity of baenids known from the Menefee Fm., including the stem species *N. baueri* and three derived forms that are regionally distributed: *Denazinemys*, *Scabremys*, and *Thescelus* (Fig. 11). We reassign CHCU 81269 to *N. baueri*, and have seen no evidence for the presence of a bothremydid in the Menefee Fm. Though the fossil material described here improves our understanding of the turtles of the Menefee Fm., the unit requires a considerable amount of additional work given its temporal and geographic span, apparent biodiversity, general lack of lateral stratigraphic continuity, and sparse geochronological record (Lucas et al., 2005).

Acknowledgements

Fieldwork permits were issued by the U.S. Bureau of Land Management (NM11-005S, NM12-03S, NM16-11S, NM18-03S and NM24-04S). The authors would like to thank the large number of volunteers who have worked in Menefee Fm. field efforts since 2011, especially those from the Southwest Paleontological Society. Staff and volunteers at the Western Science Center have also contributed substantially to fieldwork and skillful preparation of numerous Menefee fossils. Among these, special appreciation goes to Lab Manager Leya Collins and volunteer Joe Reavis. A great deal of work, expertise, and assistance was also provided by the Zuni Dinosaur Institute for Geosciences. We thank staff at the Natural History Museum of Utah, especially Carrie Levitt-Bussian, for access to collections and arranging loan of specimens to Western Science Center, and we thank volunteer preparators Paul Boyle and Lewis “Hook” Ershler for their work on UMNH VP 28352. We express thanks to the National Park Service and Chaco Culture National Historical Park for access and permission to study CHCU 81269 under permit CHCU-2023-SCI-0008. In particular, Claire Kittell, Denise Robertson, Lori Stephens and Cynthia Wiley are appreciated for facilitating access to the specimen.

References

Adrian B, Smith HF, Kelley K, and Wolfe DG. 2023a. A new baenid, *Edowa zuniensis* gen. et sp. nov., and other fossil turtles from the Upper Cretaceous Moreno Hill Formation (Turonian), New Mexico, USA. *Cretaceous Research* 144:105422. 10.1016/j.cretres.2022.105422

Adrian B, Smith HF, and Noto CR. 2023b. A revision of "*Trinitichelys*" *maini* (Testudinata: Baenidae) and additional material of its new genus from the Lewisville Formation (Woodbine Group, Cenomanian), Texas, USA. *Palaeontologia Electronica* 26:1-43. 10.26879/1266

Adrian B, Smith HF, Noto CR, and Grossman A. 2021. An early bothremydid from the Arlington Archosaur Site of Texas. *Scientific Reports* 11(9555):1-14. 10.1038/s41598-021-88905-1

Adrian B, Smith HF, Noto CR, and Grossman A. 2019. A new baenid, "*Trinitichelys*" *maini* sp. nov., and other fossil turtles from the Upper Cretaceous Arlington Archosaur Site (Woodbine Formation, Cenomanian), Texas, USA. *Palaeontologia Electronica* 22.3.81:1-29. /10.26879/1001

Batsch AJGC. 1788. *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen. Erster Theil. Allgemeine Geschichte der Natur; besondre der Säugthiere, Vögel, Amphibien und Fische*. Jena: Akademische Buchhandlung.

Beaumont EC, and Hoffman GK. 1992. Interrelationships between the Upper Coal Member of the Menefee Formation, the La Ventana Tongue, and the Lewis Shale in the southeastern San Juan Basin, New Mexico. In: Lucas SG, Kues BS, Williamson TE, and Hunt AP, eds. *San Juan Basin IV*: New Mexico Geological Society, 207-216.

Beaumont EC, Dante C, and Sears JD. 1956. Revised Nomenclature of Mesaverde Group in San Juan Basin, New Mexico. *AAPG Bulletin* 40:2149-2162.

Bell T. 1828. *Characters of the order, families, and genera of the Testudinata*: W. Phillips.

Beveridge TL, Roberts EM, Ramezani J, Titus AL, Eaton JG, Irmis RB, and Sertich JJ. 2022. Refined geochronology and revised stratigraphic nomenclature of the Upper Cretaceous Wahweap Formation, Utah, USA and the age of early Campanian vertebrates from southern Laramidia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 591:110876.

Blakey RC. 2014. Paleogeography and paleotectonics of the Western Interior Seaway, Jurassic-Cretaceous of North America. *Search and Discovery* 30392:1-17.

Brandvold M, Brandvold J, and Sweeney F. 1996. Taphonomy of the Jones' site, Two Medicine Formation (Campanian) of north-central Montana with evidence of theropod feeding techniques based on bioturbation. *Journal of Vertebrate Paleontology* 16:23A.

Brinkman DB. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. *Canadian Journal of Earth Sciences* 40:557-571. 10.1139/E02-080

Brinkman D, and Nicholls EL. 1993. New specimen of *Basilemys praeclara* Hay and its bearing on the relationships of the Nanhsiungchelyidae (Reptilia: Testudines). *Journal of Paleontology* 67:1027-1031.

Brinkman D, and De La Rosa RR. 2006. Nonmarine turtles from the Cerro del Pueblo Formation (Campanian), Coahuila State, Mexico. *New Mexico Museum of Natural History and Science Bulletin* 35:229-234.

Brinkman DB, Aguillon-Martinez MC, Hutchison JH, and Brown CM. 2016. *Yelmochelys rosarioae* gen. et sp. nov., a stem kinosternid (Testudines; Kinosternidae) from the Late Cretaceous of Coahuila, Mexico. *Paleobios* 33:1-20.

Chkhikvadze V. 1970. Classification of the subclass Testudinata. *Nauchnaya Sessiya Instituta Paleobiologii, Tezisy Dokladov* 14:7-8.

Cobban W. 1962. *Baculites* from the lower part of the Pierre Shale and equivalent rocks in the Western Interior. *Journal of Paleontology*:704-718.

Collier AJ. 1919. Contributions to economic geology, 1918, Part II, Mineral fuels--Coal south of Mancos, Montezuma County, Colorado. Bulletin 691-K:293-310

Cope ED. 1882. Contributions to the History of the Vertebrata of the Lower Eocene of Wyoming and New Mexico, Made during 1881. *Proceedings of the American Philosophical Society* 20:139-197.

Cope ED. 1876. Descriptions of some vertebrate remains from the Fort Union Beds of Montana. *Proceedings of the Academy of Natural Sciences of Philadelphia* 28:248-261.

Cope ED. 1870. Observations on the Reptilia of the Triassic formations of the Atlantic regions of the Unites States. *Proceedings of the American Philosophical Society* 11:442-446.

Cope ED. 1868. On some Cretaceous Reptilia. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1868:233-242.

Cullen TM, Fanti F, Capobianco C, Ryan MJ, and Evans DC. 2016. A vertebrate microsite from a marine-terrestrial transition in the Foremost Formation (Campanian) of Alberta, Canada, and the use of faunal assemblage data as a paleoenvironmental indicator. *Palaeogeography, Palaeoclimatology, Palaeoecology* 444:101-114.

Dalman SG, Lucas SG, Jasinski SE, Lichtig AJ, and Dodson P. 2021. The oldest centrosaurine: a new ceratopsid dinosaur (Dinosauria: Ceratopsidae) from the Allison Member of the Menefee Formation (Upper Cretaceous, early Campanian), northwestern New Mexico, USA. *PalZ* 95:291-335.

Dane CH. 1936. Geology and fuel resources of the southern part of the San Juan Basin New Mexico. Washington: Government Printing Office.

Danilov IC, Syromyatnikova EV, Skutschas PP, Kodrul TM, and Jin J. 2013. The first 'true' *Adocus* (Testudines, Adocidae) from the Paleogene of Asia. *Journal of Vertebrate Paleontology* 33:1071-1080. 10.1080/02724634.2013.768254.

DeMar DGJ, and Breithaupt BH. 2008. Terrestrial and aquatic vertebrate paleocommunities of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn basins, Wyoming, USA. In: Sankey JT, and Baszio S, eds. *Vertebrate Microfossil Assemblages: Their role in Paleoecology and Paleobiogeography*. Bloomington, Indiana: Indiana University Press, 78-103.

DeMar DGJ, and Breithaupt BH. 2006. The nonmammalian vertebrate microfossil assemblages of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn basins, Wyoming. *New Mexico Museum of Natural History and Science Bulletin* 35.

Donselaar M. 1989. The Cliff House Sandstone, San Juan Basin, New Mexico; model for the stacking of" transgressive" barrier complexes. *Journal of Sedimentary Research* 59:13-27.

Eaton, Jeffrey G. 1990. Stratigraphic revision of Campanian (Upper Cretaceous) rocks in the Henry Basin, Utah. *The Mountain Geologist* 27:27-38.

Fowler DW. 2017. Revised geochronology, correlation, and dinosaur stratigraphic ranges of the Santonian-Maastrichtian (Late Cretaceous) formations of the Western Interior of North America. *PLoS ONE* 12:e0188426. 10.1371/journal.pone.0188426

Gaffney ES. 1979. Description of a large trionychid shell from the Eocene Bridger Formation of Wyoming. *Contributions to Geology, University of Wyoming* 17:53-57.

Gaffney ES, Tong H, and Meylan PA. 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History* 300:1-318. https://doi.org/10.1206/0003-0090(2006)300[1:EOTSTT]2.0.CO;2

Gardner JD, Russell AP, and Brinkman DB. 1995. Systematics and taxonomy of soft-shelled turtles (Family Trionychidae) from the Judith River Group (Mid-Campanian) of North America. *Canadian Journal of Earth Sciences* 32:631-643.

Gasaway S, and Sankey J. 2007. Paleoecology of a *Chasmosaurus mariscalensis* bonebed, Late Cretaceous (late Campanian), Big Bend National Park, Texas. *Journal of Vertebrate Paleontology* 27(3): 79A

Gilmore CW. 1935. On the Reptilia of the Kirtland Formation of New Mexico, with descriptions of new species of fossil turtles. *Proceedings of the United States National Museum* 83:159-188.

Gilmore CW. 1919. Reptilian faunas of the Torrejon, Puerco, and underlying Upper Cretaceous formation of San Juan County, New Mexico. *US Geological Survey Professional Paper* 119:1-117.

Gilmore CW. 1916. Contributions to the geology and paleontology of San Juan County, New Mexico. 2. Vertebrate faunas of the Ojo Alamo, Kirtland, and Fruitland formations. *United States Geological Survey Professional Paper* 98:279-308.

Girard LC, Erickson JM, Lyson TR, Hoganson JW, and Joyce WG. 2024. The cranial and postcranial morphology of *Hutchemys rememdium* and its impact on the phylogenetic relationships of Plastomenidae (Testudinata, Trionychidae). *Swiss Journal of Palaeontology* 143:1-36.

Hammer O, Harper DAT, and Ryan PD. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4:1-9.

Hay OP. 1908. *The Fossil Turtles of North America*. Washington D.C.: Carnegie Institute of Washington.

Hay OP. 1902. Bibliography and Catalogue of the Fossil Vertebrata of North America. *Bulletin of the United States Geological Survey* 179:868.

Hay OP. 1899. On the nomenclature of certain American fossil vertebrates. *American Geologist* 24:345-349.

Hayes PT, and Zapp AD. 1955. Geology and fuel resources of the Upper Cretaceous rocks of the Barker Dome-Fruitland area, San Juan County, New Mexico. *US Geological Survey Oil and Gas Investigation Map* OM-144, 1:62,500.

Haynes D, Vogel J, and Wyant D. 1972. Geology, structure, and uranium deposits of the Cortez quadrangle. *Colorado and Utah: US Geological Survey Miscellaneous Geologic Investigations Map* 1:629.

Herzog LL. 2019. Morphological characteristics and variability of helochelydrid turtles in North America: Evidence for a new species. M.S. Thesis, North Carolina State University.

Holland WJ. 1909. *Deinosuchus hatcheri*, a new genus and species of crocodile from the Judith River beds of Montana. *Annals of the Carnegie Museum* 6:281-294.

Holroyd PA, and Hutchison HJ. 2016. Fauna and setting of the *Adelolophus hutchisoni* type locality in the Upper Cretaceous (Campanian) Wahweap Formation of Utah. *Paleobios* 33:1-9.

Holroyd PA, Hutchison HJ, Nicholson DB, and Goodwin MB. 2015. Network analysis demonstrates southern provinciality in Campanian North American turtles. *Society of Vertebrate Paleontology, Programs with Abstracts*:145.

Hunt AP, and Lucas SG. 1993. Cretaceous vertebrates of New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 2:77-91.

Hutchison JH. 2000. Diversity of Cretaceous turtle faunas of Eastern Asia and their contribution to the turtle faunas of North America. *Paleontological Society of Korea Special Publication* 4:27-38.

Hutchison JH. 1984. Determinate growth in the Baenidae (Testudines): Taxonomic, ecologic, and stratigraphic significance. *Journal of Vertebrate Paleontology* 3:148-151.

Hutchison JH, Knell MJ, and Brinkman DB. 2013. Turtles from the Kaiparowits Formation, Utah. In: Titus AL, and Loewen MA, eds. *At the top of the Grand Staircase: the Late Cretaceous of Southern Utah*. Bloomington, IN: Indiana University Press, 295-318.

Hutchison J, Eaton J, Holroyd P, Goodwin M, Hill L, and Koselak J. 1998. Larger vertebrates of the Kaiparowits Formation (Campanian) in the Grand Staircase-Escalante National Monument and adjacent areas. Learning from the Land Grand Staircase-Escalante National Monument Science Symposium Proceedings US Department of the Interior, Bureau of Land Management, Washington DC. p 391-398.

Jasinski SE, Sullivan RM, Lichtig AJ, Lucas SG, and Dodson P. 2018. Baenid (Baenidae: Testudines) lower jaws from the Late Cretaceous and Paleocene of the San Juan Basin, New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 79:311-318.

Joyce WG. 2017. A review of the fossil record of basal Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 58:65-113.

Joyce WG. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 48:1-102.

Joyce WG, and Lyson TR. 2017. The shell morphology of the latest Cretaceous (Maastrichtian) trionychid turtle *Helopanoplia distincta*. *PeerJ* 5:e4169. DOI 10.7717/peerj.4169

Joyce WG, and Lyson TR. 2015. A review of the fossil record of turtles of the clade Baenidae. *Bulletin of the Peabody Museum of Natural History* 56:147-183.

Joyce WG, Anquetin J, Cadena E-A, Claude J, Danilov IC, Evers SW, Ferreira GS, Gentry AD, Georgialis G, Lyson TR, Pérez-García A, Rabi M, Sterli J, Vitek NS, and Parham JF. 2021. A nomenclature for fossil and living turtles using phylogenetically defined clade names. *Swiss Journal of Palaeontology* 140:1-45.

Joyce WG, Lyson TR, and Sertich JJ. 2018. A new species of trionychid turtle from the Upper Cretaceous (Campanian) Fruitland Formation of New Mexico, USA. *Journal of Paleontology* 92:1107-1114.

Joyce WG, Lyson TR, and Kirkland JI. 2016. An early bothremydid (Testudines, Pleurodira) from the Late Cretaceous (Cenomanian) of Utah, North America. *PeerJ* 4:1-22.

Joyce WG, Sterli J, and Chapman SD. 2014. The skeletal morphology of the solemydid turtle *Naomichelys speciosa* from the Early Cretaceous of Texas. *Journal of Paleontology* 88:1257-1287.

Joyce WG, Schoch RR, and Lyson TR. 2013. The girdles of the oldest fossil turtle, Proterochersis robusta, and the age of the turtle crown. *BMC Evolutionary Biology* 13:1-9.

Joyce WG, Chapman SD, Moody RTJ, and Walker CA. 2011. The skull of the solemydid turtle *Helochelydra nopscai* from the Early Cretaceous of the Isle of Wight (UK) and a review of Solemydidae. *Special Papers in Palaeontology* 86:75-97.

Joyce WG, Parham JF, and Gauthier JA. 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.

Klein I. 1760. Klassification und kurze Geschichte der Vierfüßigen Thiere.(translation by FD Behn) Jonas Schmidt. *Lübeck (381 pp)*.

Lambe LM. 1906. *Boremys*, a new chelonian genus from the Cretaceous of Alberta. *Ottawa Naturalist* 19:232-234.

Lambe LM. 1902. New genera and species from the Belly River Series (mid-Cretaceous). *Contributions to Canadian Paleontology* 3:25-81.

Langston W. 1956. The shell of *Basilemys variolosa* (Cope). *Bulletin of the National Museum of Canada* 147:155-163.

Larson DW, Longrich NR, Evans DC, and Ryan MJ. 2013. A new species of *Neurankylus* from the Milk River Formation (Cretaceous: Santonian) of Alberta, Canada, and a revision of the type species *N. eximius*. In: Brinkman DB, Holroyd PA, and Gardner JD, eds. *Morphology and evolution of turtles*. Dordrecht: Springer Science+Business Media, 389-405.

Laurin M, de Queiroz K, Cantino P, Cellinese N, and Olmstead R. 2005. The PhyloCode, type, ranks, and monophyly: a response to Pickett. *Cladistics* 21:605-607.

Lawver DR, and Garner BA. 2023. Skeletal variation of the stem turtle *Naomichelys speciosa* (Testudinata: Helochelydridae): insights from a new specimen from the Lower Cretaceous Cloverly Formation of Montana. *Cretaceous Research* 149:105551.

Lehman TM, and Wick SL. 2010. *Chupacabrachelys complexus*, n. gen. n. sp. (Testudines: Bothremydidae), ~~f~~from the Aguja Formation (Campanian) of West Texas. *Journal of Vertebrate Paleontology* 30:1709-1725.

Lehman TM, and Tomlinson SL. 2004. *Terlinguachelys fischbecki*, a new genus and species of sea turtle (Chelonioidea: Protostegidae) from the Upper Cretaceous of Texas. *Journal of Paleontology* 78:1163-1178.

Lehman TM, Wick SL, Macon CC, Wagner JR, Waggoner KJ, Brink AA, and Shiller TA. 2024. Stratigraphy and depositional history of the Aguja Formation (Upper Cretaceous, Campanian) of West Texas, southwestern USA. *Geosphere* 1:1-55.

Lehman TM, Wick SL, Brink AA, and Shiller II TA. 2019. Stratigraphy and vertebrate fauna of the lower shale member of the Aguja Formation (lower Campanian) in West Texas. *Cretaceous Research* 99:291-314.

Lichtig AJ, and Lucas SG. 2018. *Neurankylus*, a Cretaceous-Paleocene baenid turtle from North America. *New Mexico Museum of Natural History and Science Bulletin* 79:323-361.

Lichtig AJ, and Lucas SG. 2016. A new species of *Neurankylus* (Testudines: Baenidae) from the Upper Cretaceous Crevasse Canyon Formation, southern New Mexico, USA. *New Mexico Museum of Natural History and Science Bulletin* 74:117-119.

Lichtig AJ, and Lucas SG. 2015. Cretaceous turtles of New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 67:129-137.

Lively JR. 2015. A new species of baenid turtle from the Kaiparowits Formation (Upper Cretaceous, Campanian) of southern Utah. *Journal of Vertebrate Paleontology* 35:1-16.

López-Conde OA, Chavarría-Arellano, and Montellano-Ballesteros M. 2020. Nonmarine turtles from the Aguja Formation (Late Cretaceous, Campanian) of Chihuahua, Mexico. *Journal of South American Earth Sciences* 102:1-10.

López-Conde OA, Chavarría-Arellano ML, Montellano-Ballesteros M, and Hernandez-Rivera R. 2019. El primer registro del baénido ~~*Scabremys*~~ sp. para el Cretácico Tardió (Campaniano) de la Formación Aguja, Chihuahua. *Convención Geológica Nacional* 1:~~1-~~18.

López-Conde OA, Sterli J, Chavarría-Arellano ML, Brinkman DB, and Montellano-Ballesteros M. 2018. Turtles from the Late Cretaceous (Campanian) of El Gallo Formation, Baja California, Mexico. *Journal of South American Earth Sciences* 88:693-699.

Lucas SG, and Sullivan RM. 2006. *Denazinemys*, a new name for some Late Cretaceous turtles from the Upper Cretaceous of the San Juan Basin, New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 35:223-228.

Lucas SG, Sullivan RM, Lichtig AJ, Dalman SG, and Jasin~~k~~ski SE. 2016. Late Cretaceous dinosaur biogeography and endemism in the Western Interior Basin, North America: a critical re-evaluation. *New Mexico Museum of Natural History and Science Bulletin* 71:194-213.

Lucas SG, Spielmann JA, Braman DR, Brister BS, Peters L, and McIntosh WC. 2005. Age of the Cretaceous Menefee Formation, Gallina Hogback, Rio Arriba County, New Mexico. In: Lucas SG, Lueth VW, and Owen DE, eds. *Geology of the Chama Basin*: New Mexico Geological Society, 231-235.

Lydekker R. 1889. Catalogue of the fossil Reptilia and Amphibia in the British Museum, Part III. The Order Chelonia. *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History)*. London: British Museum (Natural History), 1-239.

Lyson TR, Petermann H, and Miller IM. 2021. A new plastomenid trionychid turtle, *Plastomenus joycei*, sp. nov., from the earliest Paleocene (Danian) Denver Formation of south-central Colorado, USA. Journal of Vertebrate Paleontology 41:e1913600.

Maidment SC, Dean CD, Mansergh RI, and Butler RJ. 2021. Deep-time biodiversity patterns and the dinosaurian fossil record of the Late Cretaceous Western Interior, North America. *Proceedings of the Royal Society B* 288:20210692.

Mallon JC, and Brinkman DB. 2018. *Basilemys morrinensis*, a new species of nanhsiungchelyid turtle from the ~~Horse~~ Canyon Formation (Upper Cretaceous) of Alberta, Canada. *Journal of Vertebrate Paleontology*:1-11.

Mayerl CJ, Pruett JE, Summerlin MN, Rivera ARV, and Blob RW. 2017. Hindlimb muscle function in turtles: is novel skeletal design correlated with novel muscle function. *Journal of Experimental Biology* 220:2554-2562.

McDonald AT, Wolfe DG, Freedman Fowler EA, and Gates TA. 2021. A new brachylophosaurin (Dinosauria: Hadrosauridae) from the Upper Cretaceous Menefee Formation of New Mexico. *PeerJ* 9:e11084.

McDonald AT, and Wolfe DG. 2018. A new nodosaurid ankylosaur (Dinosauria: Thyreophora) from the Upper Cretaceous Menefee Formation of New Mexico. *PeerJ* 6:e5435.

McDonald AT, Wolfe DG, and Dooley Jr AC. 2018. A new tyrannosaurid (Dinosauria: Theropoda) from the Upper Cretaceous Menefee Formation of New Mexico. *PeerJ* 6:e5749.

Meylan PA. 1987. The phylogenetic relationships of soft-shelled turtles (family Trionychidae). *Bulletin of the American Museum of Natural History* 186:1-101.

Meylan PA. 1984. Evolutionary relationships of recent trionychid turtles: evidence from shell morphology. *Studia Geologica Salmanticensia* especial 1:169-188.

Meylan PA, and Gaffney ES. 1989. The Skeletal Morphology of the Cretaceous Cryptodiran Turtle, *Adocus*, and the Relationships of the Trionychoidea. *American Museum Novitiates* 2941:1-60.

Miller RL. 1984. Subdivisions of the Menefee formation and cliff house sandstone (Upper Cretaceous) in southwest San Juan basin, New Mexico. *US Geological Survey Bulletin*:A29-A53.

Miller RL, Carey MA, and Thompson-Rizer C. 1991. Geology of the La Vida Mission Quadrangle, San Juan and McKinley Counties, New Mexico. *US Geological Survey Bulletin* 1940.

Molenaar CM. 1983. Major depositional cycles and regional correlations of Upper Cretaceous rocks, southern Colorado Plateau and adjacent areas. In: Reynolds MW, and Dolly ED, eds. *Mesozoic paleogeography of the west-central United States*. Denver: Rocky Mountain Symposium 2, The Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists, 201-223.

Molenaar CM, Cobban WA, Merewether EA, Pillmore CL, Wolfe DG, and Holbrook JM. 2002. Regional stratigraphic cross sections of Cretaceous rocks from east-central Arizona to the Oklahoma panhandle. *USGS Miscellaneous Field Studies Map* MF-2382.

Nopsca BF. 1931. Sur des nouveaux restes de Tortues du Danien du Midi de la France. *Bulletin de la Societe Geologique de France* 1:223-236.

Pecha ME, Gehrels GE, Karlstrom KE, Dickinson WR, Donahue MS, Gonzales DA, and Blum MD. 2018. Provenance of Cretaceous through Eocene strata of the Four Corners region: Insights from detrital zircons in the San Juan Basin, New Mexico and Colorado. *Geosphere* 14:785-811.

Peng J, Russell AP, and Brinkman DB. 2001. Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman Formations of the Judith River Group (Campanian) of southeastern Alberta: An illustrated guide. *Provincial Museum of Alberta Natural History Occasional Paper* 25:1-54.

Pérez-García A, Espílez E, Mampel L, and Alcalá L. 2020. A new basal turtle represented by the two most complete skeletons of Helochelydridae in Europe. *Cretaceous Research* 107:104291.

Pérez-García A, Antunes MT, Barroso-Barcenilla F, Callapez PM, Segura M, Soares AF, and Torices A. 2017. A bothremydid from the middle Cenomanian of Portugal identified as one of the oldest pleurodiran turtles in Laurasia. *Cretaceous Research* 78:61-70.

Peterson F, Kirk AR. 1977. Correlation of the Cretaceous rocks in the San Juan Basin, Black Mesa, Kaiparowits and Henry Basins, southern Colorado Plateau. *New Mexico Geological Society 28th Annual Fall Field Conference Guidebook*: 167-178.

Pike WS. 1947. *Intertonguing marine and nonmarine Upper Cretaceous deposits of New Mexico, Arizona, and southwestern Colorado*: Geological Society of America Memoir 24:1-102.

Ramezani J, Beveridge TL, Rogers RR, Eberth DA, and Roberts EM. 2022. Calibrating the zenith of dinosaur diversity in the Campanian of the Western Interior Basin by CA-ID-TIMS U–Pb geochronology. *Scientific Reports* 12:16026.

Reynoso V-H. 2006. Research on fossil amphibians and reptiles in Mexico, from 1869 to early 2004 (including marine forms but excluding pterosaurs, dinosaurs, and obviously, birds). In: Vega ~~Fea~~, ed. *Studies on Mexican Paleontology*: Springer, 209-231.

Rosa RAR-DL, and Cevallos-Ferriz SR. 1998. Vertebrates of the El Pelillal locality (Campanian, Cerro del Pueblo Formation), southeastern Coahuila, Mexico. *Journal of Vertebrate Paleontology* 18:751-764.

Rowe T, Cifelli RL, Lehman TM, and Weil A. 1992. The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos Texas. *Journal of Vertebrate Paleontology* 12:472-493.

Sankey JT. 2005. Late Cretaceous vertebrate paleoecology Big Bend National Park, Texas. Dinosaur Park Symposium Short Papers, Abstracts, and Program, September. p 24-25.

Sankey JT, Lucas S, and Sullivan R. 2006. Turtles of the upper Aguja Formation (late Campanian), Big Bend National Park, Texas. *New Mexico Museum of Natural History and Science Bulletin* 35:235-243.

Santucci VL, Tweet J, Bustos D, Von Haden J, and Varela P. 2015. Vertebrate paleontological resources from National Park Service areas in New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 64:1-9.

Schmachtenberg WF. 2008. Resolution and limitations of faunal similarity indices of biogeographic data for testing predicted paleogeographic reconstructions and estimating intercontinental distances: a test case of modern and Cretaceous bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology* 265:255-261.

Scholle PA. 2003. Geologic Map of New Mexico, 1:500,000. New Mexico Bureau of Geology and Mineral Resources.

Sears JD. 1925. *Geology and coal resources of the Gallup-Zuni basin, New Mexico*: US Government Printing Office.

Sears JD, Hunt CB, Hendricks TA. 1941. Transgressive and regressive Cretaceous deposits in southern San Juan Basin, New Mexico. *U.S. Geological Survey Professional Paper* 193-F: 101-119.

Scheyer TM, Sander PM, Joyce WG, Böhme W, and Witzel U. 2007. A plywood structure in the shell of fossil and living soft-shelled turtles (Trionychidae) and its evolutionary implications. *Organisms, Diversity & Evolution* 7:136-144.

Siemers CT, and King NR. 1974. Macroinvertebrate paleoecology of a transgressive marine sandstone, Cliff House Sandstone (Upper Cretaceous), Chaco Canyon, northwestern New Mexico. *Ghost Ranch (Central Northern NM) Guidebook of the New Mexico Geological Society* 25:267-271.

Smith HF, Hutchison HJ, Townsend BKE, Adrian B, and Jager D. 2017. Morphological variation, phylogenetic relationships, and geographic distribution of the Baenidae (Testudines), based on new specimens from the Uinta Formation (Uinta Basin), Utah (USA). *PLoS ONE* 12:1-40.

Spicher GE, Sertich JJW, Girard LC, Joyce WG, Lyson TR, and Rollot Y. 2023. A description of a *Denazinemys nodosa* specimen (Testudinata, Baenidae) from the Late Cretaceous Kaiparowits Formation of southern Utah. *Fossil Record* 26:151-170.

Sullivan RM, and Lucas SG. 2006. The Kirtlandian ~~L~~and-vertebrate "~~A~~ge"—Faunal composition, temporal position and biostratigraphic correlation in the nonmarine Upper Cretaceous of Western North America *New Mexico Museum of Natural History and Science Bulletin* 35:7-29.

Sullivan RM, and Lucas SG. 2003. The Kirtlandian, a new land-vertebrate “age” for the Late Cretaceous of western North America. *New Mexico Geological Society Guidebook* 54:369-377.

Sullivan RM, Jasinski SE, and Lucas SG. 2013. Re-Assessment of Late Campanian (Kirtlandian) turtles from the Upper Cretaceous Fruitland and Kirtland ~~F~~ormations, San Juan Basin, New Mexico. In: Brinkman DB, Gardner JD, and Holroyd PA, eds. *Morphology and ~~e~~volution of ~~t~~urtles*. Dordrecht: Springer Science & Business Media, 337-386.

Sullivan RM, Lucas SG, Hunt AP, and Fritts TH. 1988. Color pattern in the selmacryptodiran turtle *Neurankylus* from the Early Paleocene (Puercan) of the San Juan Basin, New Mexico. *Contributions in Science* 401:1-9.

Thacker JO, Karlstrom KE, Kelley SA, Crow RS, and Kendall JJ. 2023. Late Cretaceous time-transgressive onset of Laramide arch exhumation and basin subsidence across northern Arizona–New Mexico, USA, and the role of a dehydrating Farallon flat slab. *GSA Bulletin* 135:389-406.

Tomlinson SL. 1997. Late Cretaceous and Early Tertiary turtles from the Big Bend Region, Brewster County, Texas. Texas Tech University.

Varricchio DJ, and Horner JR. 1993. Hadrosaurid and lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of Montana: taphonomic and biologic implications. *Canadian Journal of Earth Sciences* 30:997-1006.

Vitek NS. 2012. Giant fossil soft-shelled turtles of North America. *Palaeontologia Electronica* 15:1-43.

Vitek NS, and Joyce WG. 2015. A review of the fossil record of New World turtles of the clade *Pan-Trionychidae*. *Bulletin of the Peabody Museum of Natural History* 56:185-244.

Vitek NS, and Danilov IC. 2010. New Material and a Reassessment of Soft-Shelled Turtles (Trionychidae) from the Late Cretaceous of Middle Asia and Kazakhstan. *Journal of Vertebrate Paleontology* 30:383-393.

Wu KY, Heuck J, Varriale FJ, and Farke A. 2023. A baenid turtle shell from the Mesaverde Formation (Campanian, Late Cretaceous) of Park County, Wyoming, USA. *Peer Community Journal* 3:1-10.

Yeh H-K. 1966. A new Cretaceous turtle of Nanhsiung, northern Kwangtung. *Vertebrate PalAsiatica* 10:191-200.

Zangerl R. 1969. The turtle shell. In: Gans C, ed. *Biology of the Reptilia*. New York: Academic Press, 311-339.

Tables and figures

Table 1. Dimensions of the posterior plastral lobe and sulci (in cm) from the *Denazinemys nodosa* holotype USNM 8345, WSC 10769, a line drawing of the *Scabremys ornata* holotype USNM 13229 by Gilmore (1935) (reproduced by Sullivan, Jasinski & Lucas, 2013: fig. 20.3b-c), and UMNH VP 28352.

Table 2. Comparative measurements of Menefee *Adocus* specimens with measurements (in cm) from taxa described by Gilmore (1919).

Figure 1. Index map of New Mexico and surrounding areas. Green outline indicates boundary of San Juan Basin and the Menefee Formation is shaded blue (Collier, 1919; Haynes, Vogel & Wyant, 1972; Scholle, 2003). Figure created using Google Earth Pro (Image Landsat/Copernicus) and Adobe Illustrator v.28.4.1. Scale = 100 kilometers.

Figure 2. *Denazinemys nodosa* posterior plastral lobe (WSC 10769) in A) dorsal, and B) ventral views; C) dorsal surface of carapace fragment (WSC 10770) showing characteristic welt-like sculpture; D) dorsal and E) ventral sides of costal 1 (NMMNH P-97386). Note different scale for C-E (each 3 cm); solid blue lines indicate sulci and dashed blue line shows location of fused sutures. Abbreviations: AFs= abdominal-femoral sulcus; FAs= femoral-anal sulcus; Pl= pleural scale; Ve= vertebral scale.

Figure 3. Shell of *Neurankylus baueri* (WSC 10612) in: dorsal A) photograph and B) line drawing; ventral view C) photograph and D) line drawing. Abbreviations: Ab=abdominal scale, Ce=cervical scale, Gu=gular scale, Hu=humeral scale, Ig=intergular scale, Im=inframarginal scale, Ma=marginal scale, Pe=pectoral scale, Pl=pleural scale, Ve=vertebral scale. Blue lines indicate sulci; arrow points in anterior ("A") direction; scale = 5 cm.

Figure 4**.** Comparison of linear shell measurements (except carapace length, which is estimated) between *Neurankylus baueri* specimen WSC 10612 and the holotype (USNM 8344), using measurements from the text of Gilmore (1916). Abbreviations: Abd= abdominal scale, Antlobe L= anterior plastral lobe length, Antlobe W= anterior plastral lobe width, Ce= cervical scale, Gul= gular scale, Hum= humeral scale, L= maximum length; ML= midline length; Pec= Pectoral scale; VE= vertebral scale, W= maximum width.

Figure 5. CHCU 81269, a partial plastron of *Neuranklyus baueri*, previously attributed to the bothremydid *Elochelys* cf. *E. perfecta* (Lichtig & Lucas, 2015): A) ventral view, B) dorsal view, C) pholidosis of posterior plastral lobe, with sulci indicated in gray. Dotted line indicates reconstructed edge. Scale = 3 cm.

Figure 6. Shell of *Scabremys* (UMNH VP 28352) in: ventral A) photograph and B) line drawing; dorsal view C) photograph and D) line drawing. Abbreviations: An=anal scale, Gu=gular scale, Fe= femoral scale, Hu=humeral scale, Im=inframarginal scale, Ma=marginal scale, Pe=pectoral scale, Pl=pleural scale, Ve=vertebral scale. Blue lines indicate sulci; arrow points in anterior ("A") direction; scale = 5 cm.

Figure 7. Right half of the anterior plastral lobe of *Thescelus* cf. *rapiens* (NMMNH P-97384) in A) ventral and B) dorsal views, and an associated partial nuchal showing sulci that define the

borders of the first marginal scale in C) dorsal and D) ventral views. Abbreviations: Ex= extragular scale; Gu= gular scale; Hu= humeral scale. Blue lines indicate sulci; scale = 3 cm.

Figure 8. *Naomichelys* sp. partial nuchal (WSC 10884) in: A) dorsal, and B) ventral views~~.~~ and unassociated hypoplastron fragment (WSC 10885) in C) ventral, and D) dorsal views *Adocus* sp. left costal 6 (WSC 10763) in: E) dorsal, and F) ventral views; neural cf. 5 (WSC 10765) in: G) dorsal, and H) ventral views. I) *Basilemys* sp. (WSC 10883) indeterminate peripherals. Scale = 3 cm.

Figure 9. Carapace fragments of *Helopanoplia*: WSC 10767, costal edge fragment (A), and UMNH VP 36786 (B), a marginal costal fragment; Plastomenidae indet. shell fragments (C) NMMNH P-97383and (D) NMMNH P-97389. Note different scales between the top (3 cm) and bottom (1 cm) row.

Figure 10. Material representing two distinct trionychine forms in the Menefee Fm.: right first costal of *"Trionyx"* sp. 'large' (WSC 10768) in: A) dorsal, and B) ventral views;; right posterior carapace of "*Trionyx" robustus* (WSC 10766) in: C) dorsal and D) ventral views.

Figure 11. Revised biostratigraphic distribution of turtle taxa in a simplified stratigraphic column of Campanian units in the San Juan Basin. Blue bars indicate stratigraphic intervals added or extended in the current study to the species inventory provided in Sullivan, Jasinski & Lucas, (2013: 360, fig. 20.18). Geological data sourced from Miller (1984), Miller, Carey & Thompson-Rizer (1991), Lucas et al. (2005), Sullivan & Lucas (2006), Fowler (2017), Pecha et al. (2018), and Ramezani et al. (2022). Turtle occurrence data sourced from Lucas, Hunt & Sullivan (2006), Sullivan, Jasinski & Lucas (2013), Lichtig & Lucas (2015, 2018), and Joyce, Lyson & Sertich (2018).

Figure 12. Paleobiogeographical distribution of turtle taxa along the western shoreline of the Western Interior Seaway during the early-middle Campanian. A) Paleogeography of the Western Interior during the middle Campanian (Blakey, 2014); B) two-way hierarchical clustering of stratigraphic units and taxa. Published sources of turtle assemblages include: Aguja Fm. (Rowe et al., 1992; Lehman & Tomlinson, 2004; Sankey, 2005; Sankey, Lucas & Sullivan, 2006; Gasaway & Sankey, 2007; Lehman & Wick, 2010; Lehman et al., 2019, 2024; López-Conde et al., 2019; López-Conde, Chavarría-Arellano & Montellano-Ballesteros, 2020); Foremost Fm. (Peng, Russell & Brinkman, 2001; Cullen et al., 2016); Masuk Fm. (Eaton, 1990); Mesaverde Fm. (DeMar & Breithaupt, 2006, 2008; Wu et al., 2023); Two Medicine Fm. (Varricchio & Horner, 1993; Brandvold, Brandvold & Sweeney, 1996); Wahweap Fm. (Holroyd & Hutchison, 2016).

Figure 1

Index map of New Mexico and surrounding areas.

Green outline indicates boundary of San Juan Basin and the Menefee Formation is shaded blue (Collier, 1919; Haynes, Vogel & Wyant, 1972; Scholle, 2003). Figure created using Google Earth Pro (Image Landsat/Copernicus) and Adobe Illustrator v.28.4.1. Scale = 100 kilometers.

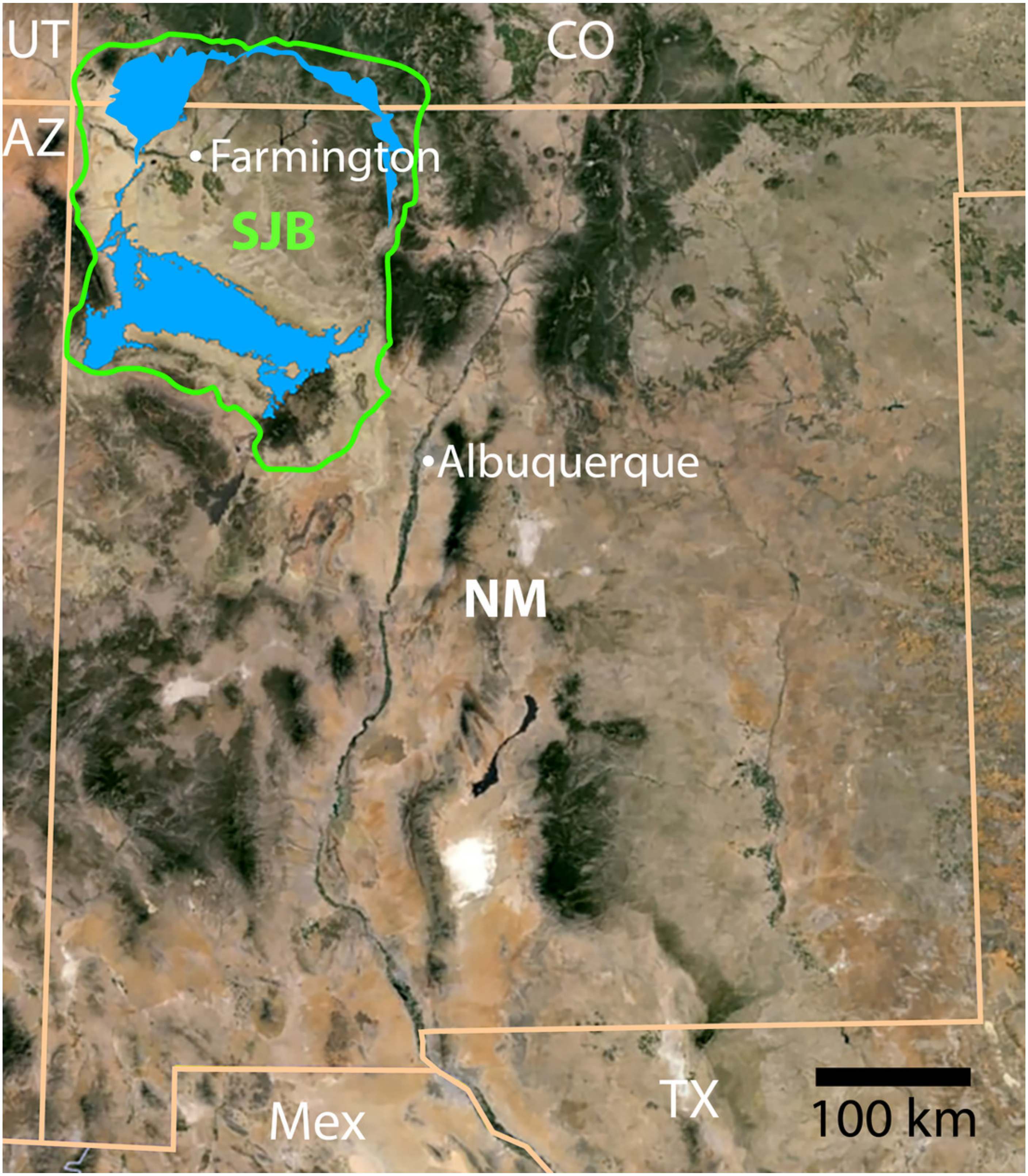
UT
CO
AZ
Farmington
SJB
Albuquerque
NM
TX
Mex
100 km

Figure 2

Denazinemys nodosa posterior plastral lobe (WSC 10769).

A) Dorsal, and B) ventral views; C) dorsal surface of carapace fragment (WSC 10770) showing characteristic welt-like sculpture; D) dorsal and E) ventral sides of costal 1 (NMMNH P-97386). Note different scale for C-E (each 3 cm); solid blue lines indicate sulci and dashed blue line shows location of fused sutures. Abbreviations: AFs= abdominal-femoral sulcus; FAs= femoral-anal sulcus; Pl= pleural scale; Ve= vertebral scale.

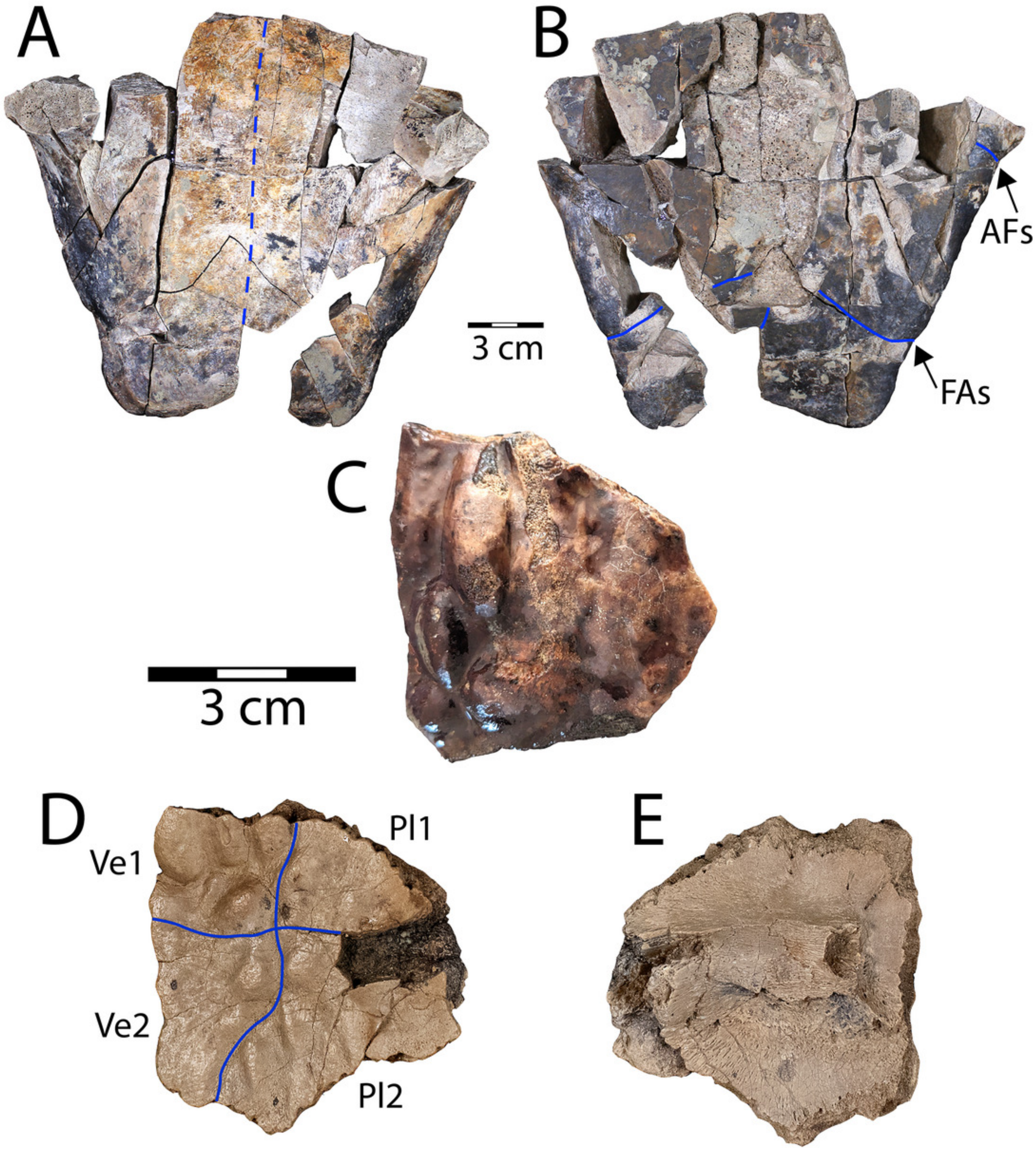
A
B
AFs
FAs
3 cm
C
3 cm
D
Ve1
Pl1
Ve2
Pl2
E

Figure 3

Shell of *Neurankylus baueri* (WSC 10612).

Dorsal A) photograph and B) line drawing; ventral view C) photograph and D) line drawing. Abbreviations: Ab=abdominal scale, Ce=cervical scale, Gu=gular scale, Hu=humeral scale, Ig=intergular scale, Im=inframarginal scale, Ma=marginal scale, Pe=pectoral scale, Pl=pleural scale, Ve=vertebral scale. Blue lines indicate sulci; arrow points in anterior ("A") direction; scale = 5 cm.

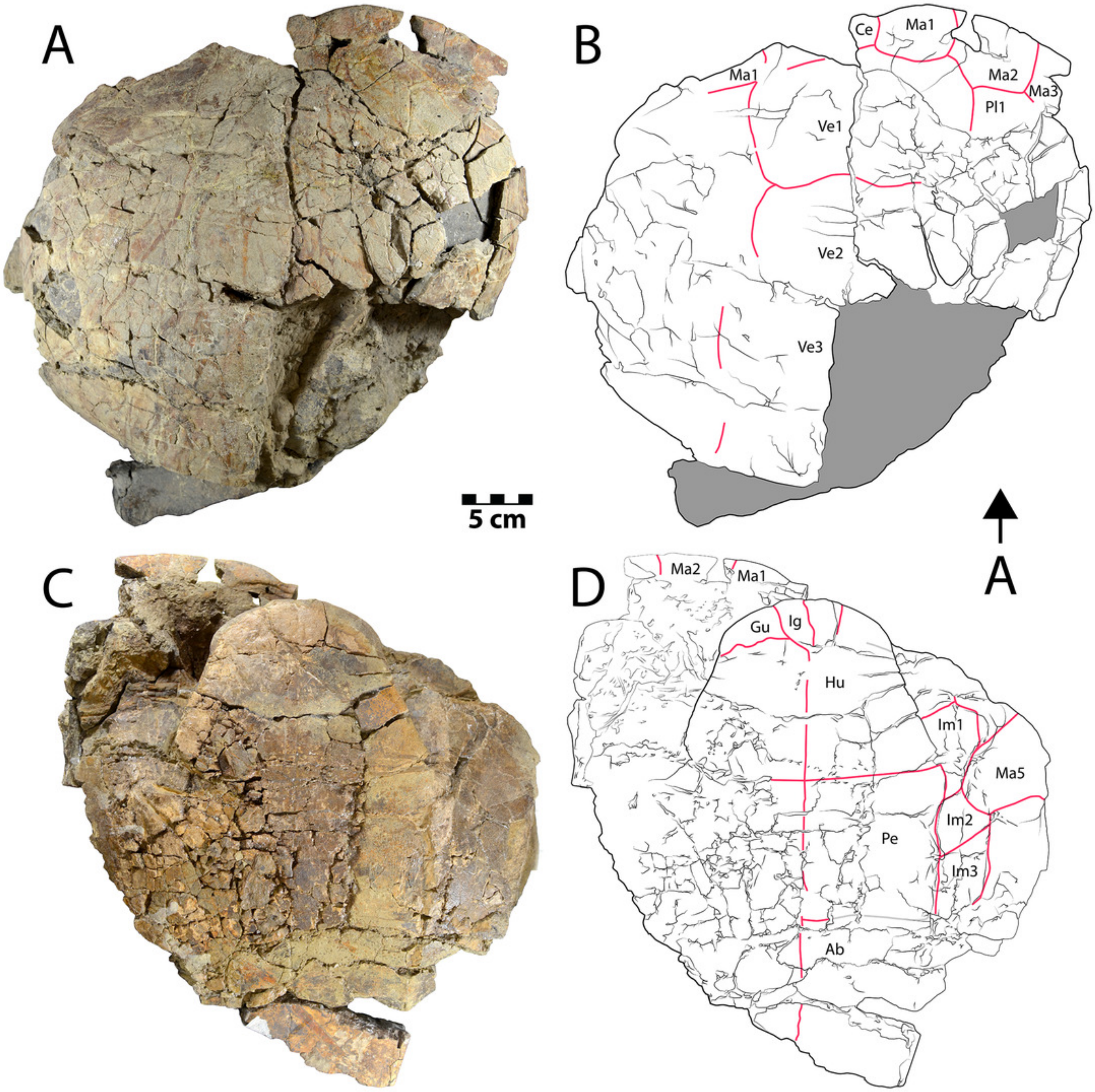
A
B
Ce
Ma1
Ma1
Ma2
Ma3
Pl1
Ve1
Ve2
Ve3
5 cm
A
C
D
Ma2
Ma1
Gu
Ig
Hu
Im1
Ma5
Im2
Pe
Im3
Ab

Figure 4

Comparison of linear shell measurements (except carapace length, which is estimated) between *Neurankylus baueri* specimen WSC 10612 and the holotype (USNM 8344).

Abbreviations: Abd= abdominal scale, Antlobe L= anterior plastral lobe length, Antlobe W= anterior plastral lobe width, Ce= cervical scale, Gul= gular scale, Hum= humeral scale, L= maximum length; ML= midline length; Pec= Pectoral scale; VE= vertebral scale, W= maximum width.

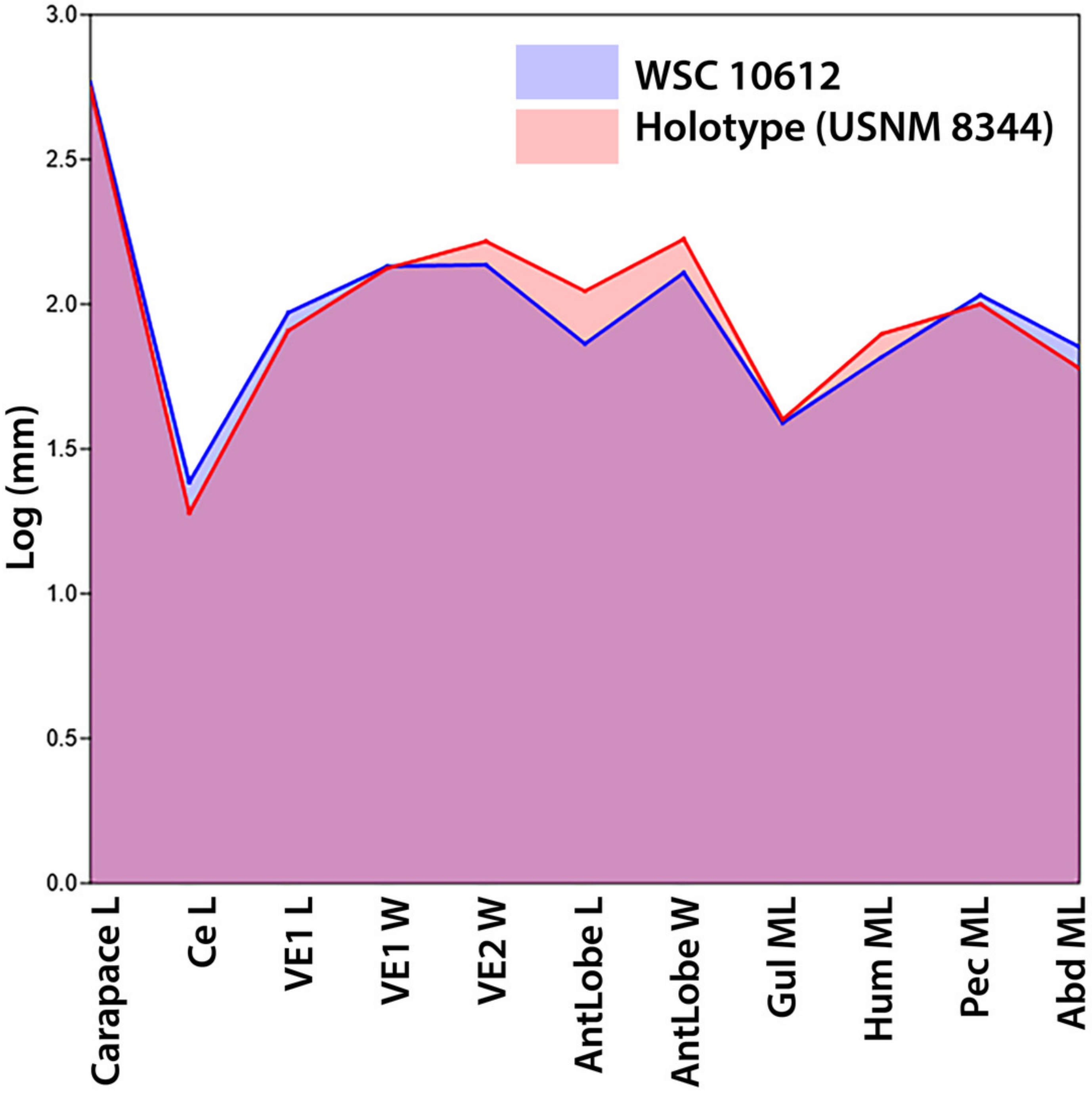
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Log (mm)
WSC 10612
Holotype (USNM 8344)
Carapace L
Ce L
VE1 L
VE1 W
VE2 W
AntLobe L
AntLobe W
Gul ML
Hum ML
Pec ML
Abd ML

Figure 5

CHCU 81269, a partial plastron of *Neuranklyus baueri*, previously attributed to the bothremydid *Elochelys* cf. *E*. *perfecta* (Lichtig & Lucas, 2015).

A) Ventral view, B) dorsal view, C) pholidosis of posterior plastral lobe, with sulci indicated in gray. Dotted line indicates reconstructed edge. Scale = 3 cm.

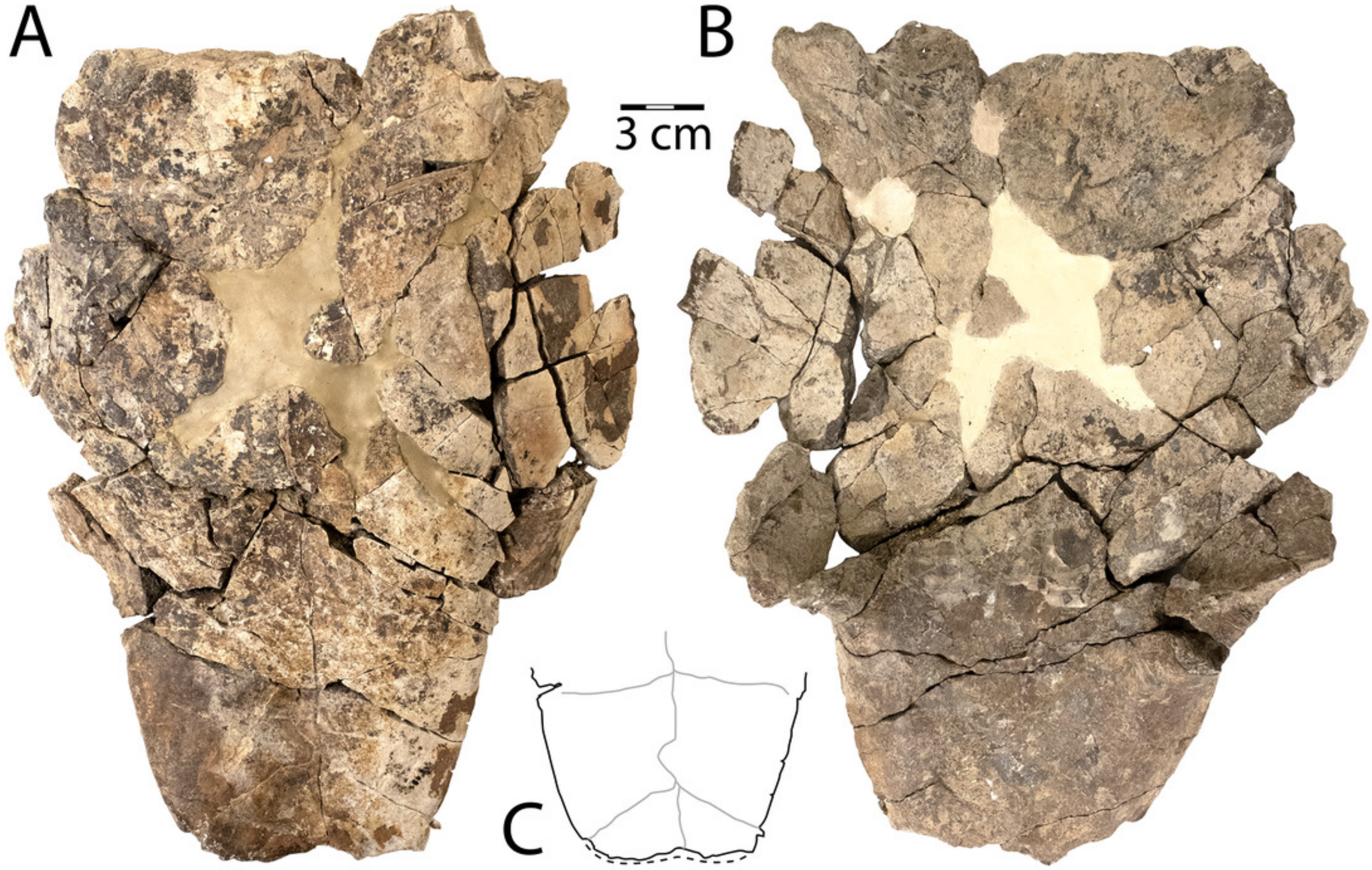

Figure 6

Shell of *Scabremys* sp. (UMNH VP 28352).

Ventral A) photograph and B) line drawing; dorsal view C) photograph and D) line drawing. Abbreviations: An=anal scale, Gu=gular scale, Fe= femoral scale, Hu=humeral scale, Im=inframarginal scale, Ma=marginal scale, Pe=pectoral scale, Pl=pleural scale, Ve=vertebral scale. Blue lines indicate sulci; arrow points in anterior (“A”) direction; scale = 5 cm.

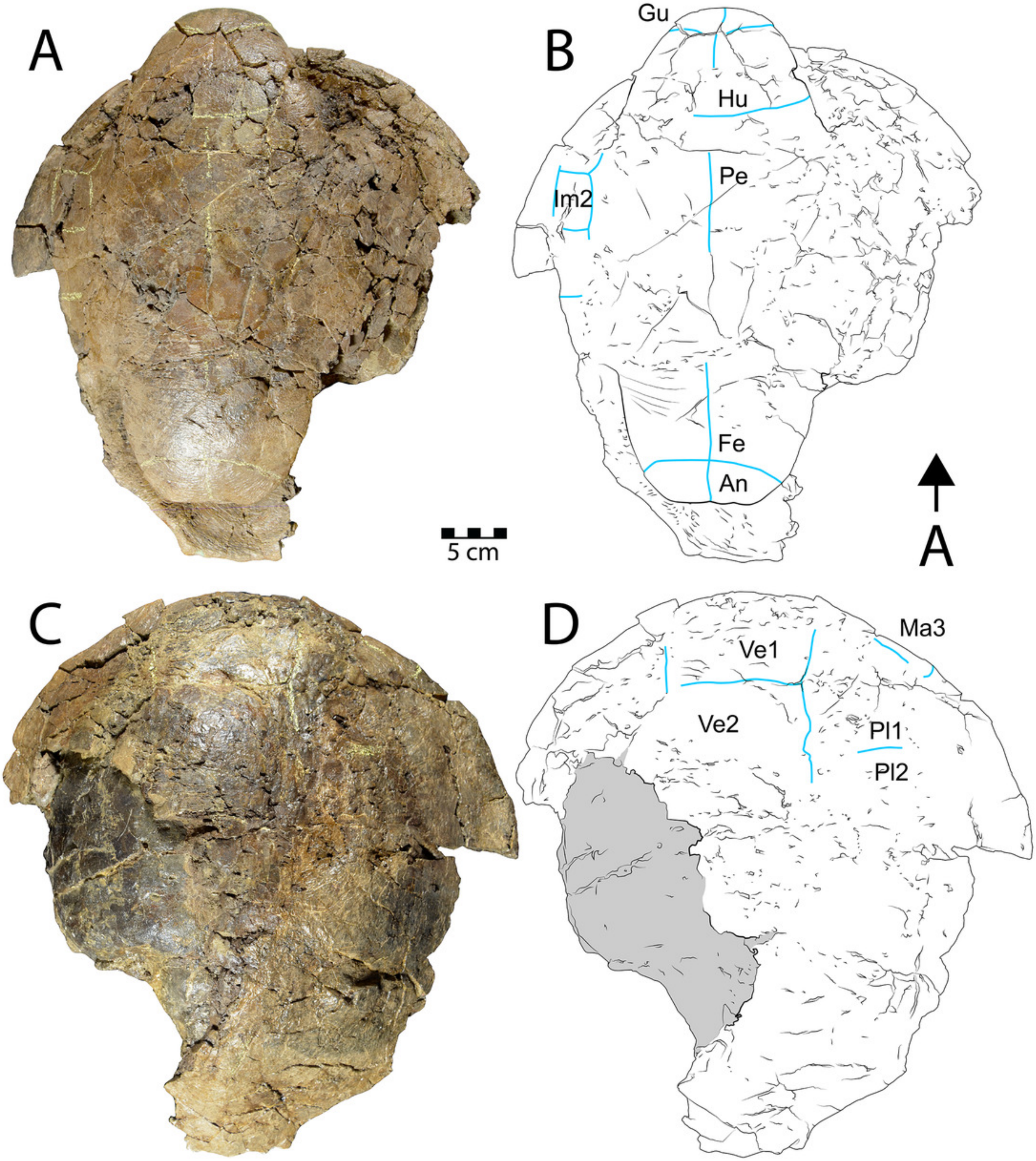
A
B
Gu
Hu
Pe
Im2
Fe
An
5 cm
A
C
D
Ve1
Ma3
Ve2
Pl1
Pl2

Figure 7

Right half of the anterior plastral lobe of *Thescelus* cf. *rapiens* (NMMNH P-97384).

A) Ventral and B) dorsal views, and an associated partial nuchal showing sulci that define the borders of the first marginal scale in C) dorsal and D) ventral views. Abbreviations: Ex= extragular scale; Gu= gular scale; Hu= humeral scale. Blue lines indicate sulci; scale = 3 cm.

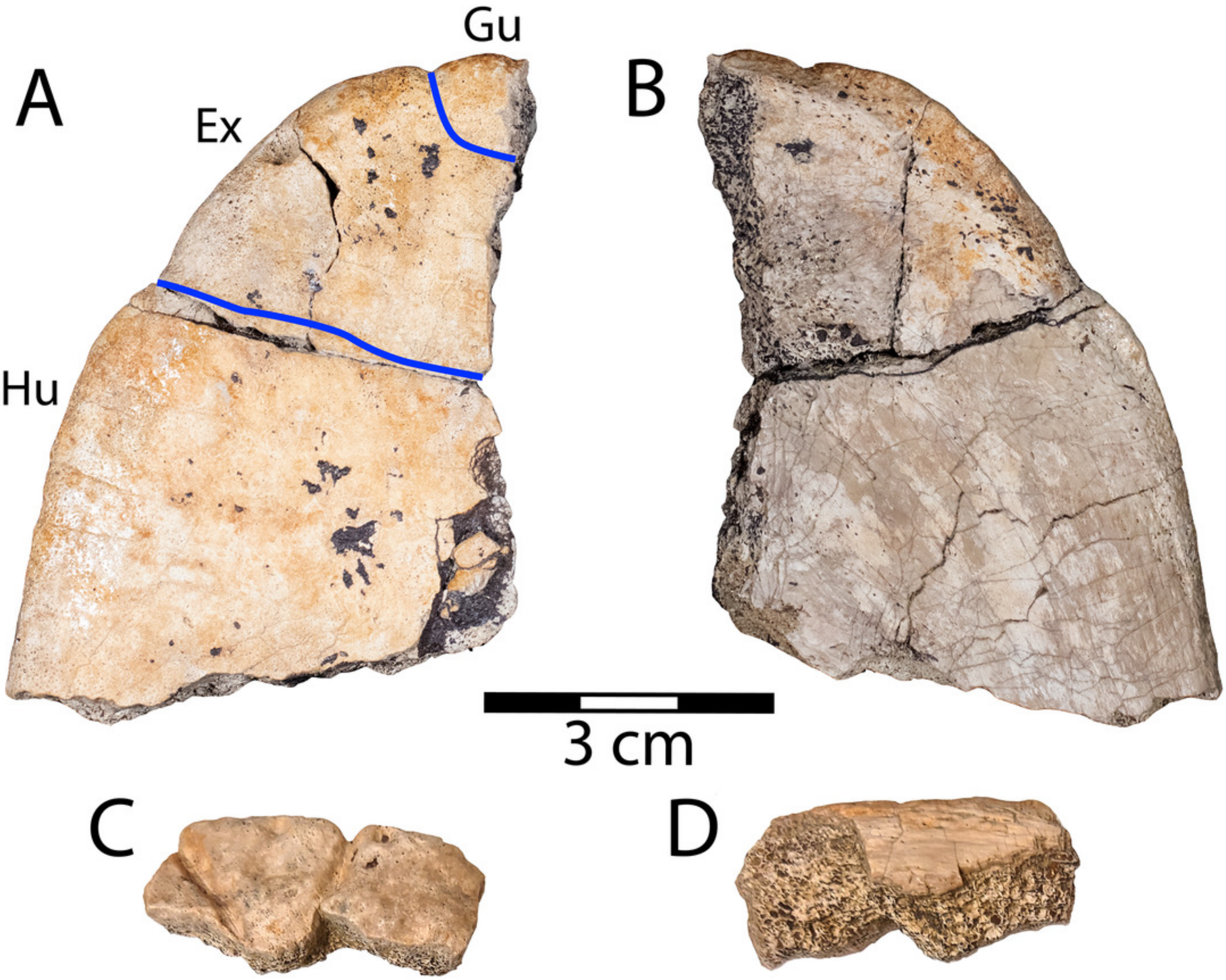

Figure 8

Naomichelys sp. partial nuchal (WSC 10884).

A) Dorsal, and B) ventral views and unassociated hypoplastron fragment (WSC 10885) in C) ventral, and D) dorsal views *Adocus* sp. left costal 6 (WSC 10763) in: E) dorsal, and F) ventral views; neural cf. 5 (WSC 10765) in: G) dorsal, and H) ventral views. I) *Basilemys* sp. (WSC 10883) indeterminate peripherals. Scale = 3 cm.

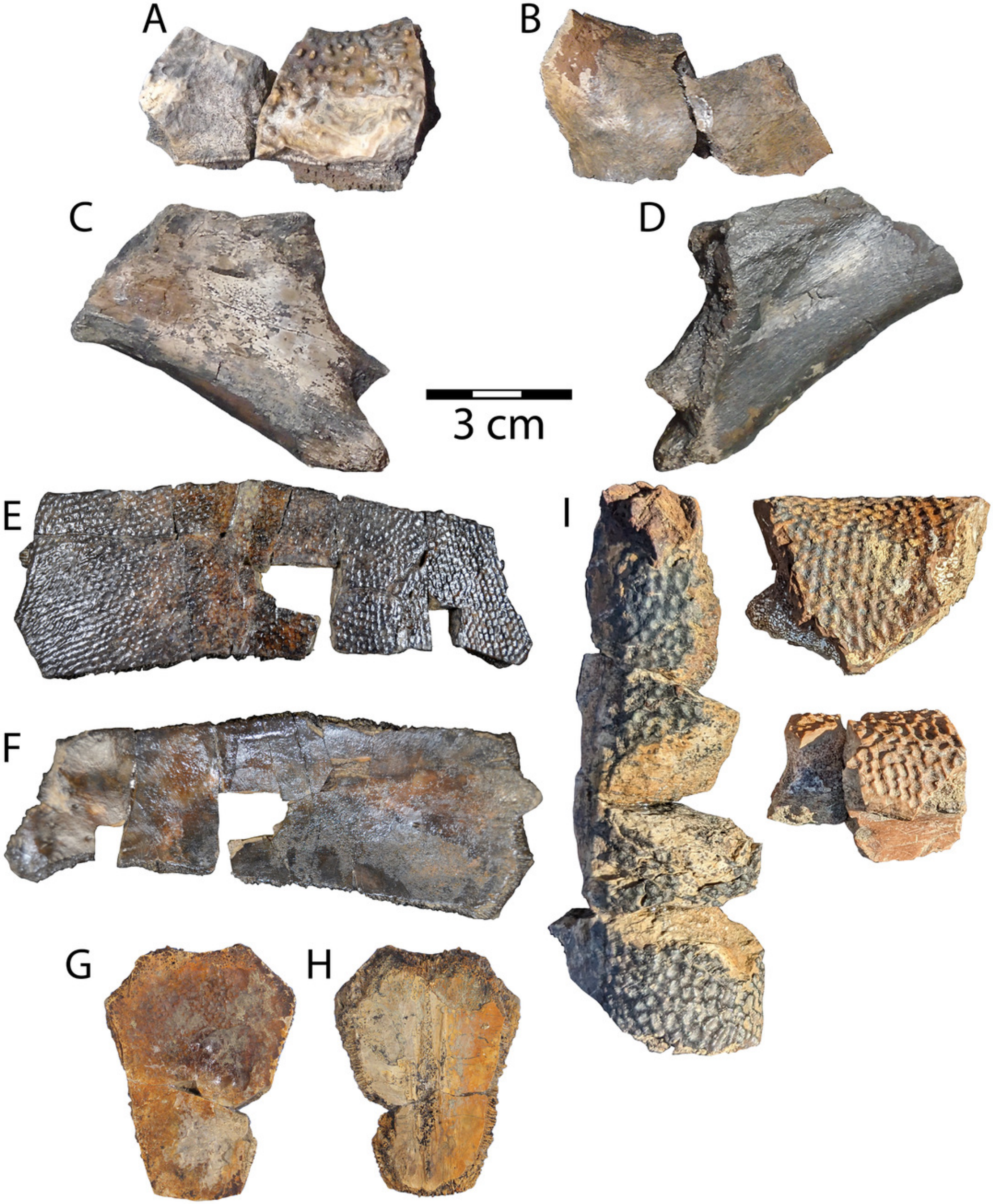
A
B
C
D
3 cm
E
F
G
H
I

Figure 9

Carapace fragments of *Helopanoplia* sp. (WSC 10767).

Costal edge fragment (A), and UMNH VP 36786 (B), a marginal costal fragment; Plastomenidae indet. shell fragments (C) NMMNH P-97383and (D) NMMNH P-97389. Note different scales between the top (3 cm) and bottom (1 cm) row.

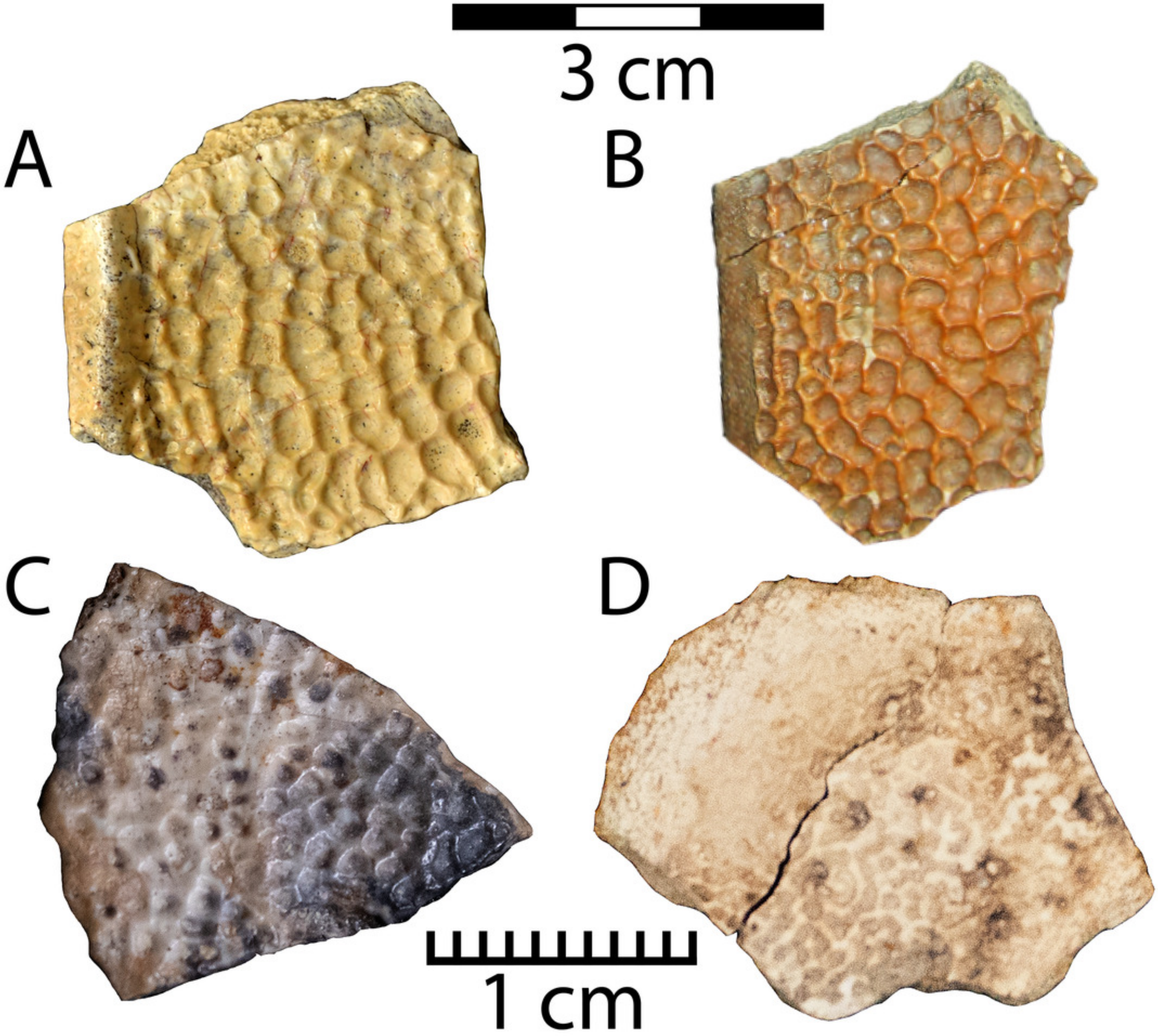

Figure 10

Material representing two distinct trionychine forms in the Menefee Fm.

Right first costal of *“Trionyx”* sp. ‘large’ (WSC 10768) in: A) dorsal, and B) ventral views; right posterior carapace of “*Trionyx*” *robustus* (WSC 10766) in: C) dorsal and D) ventral views.

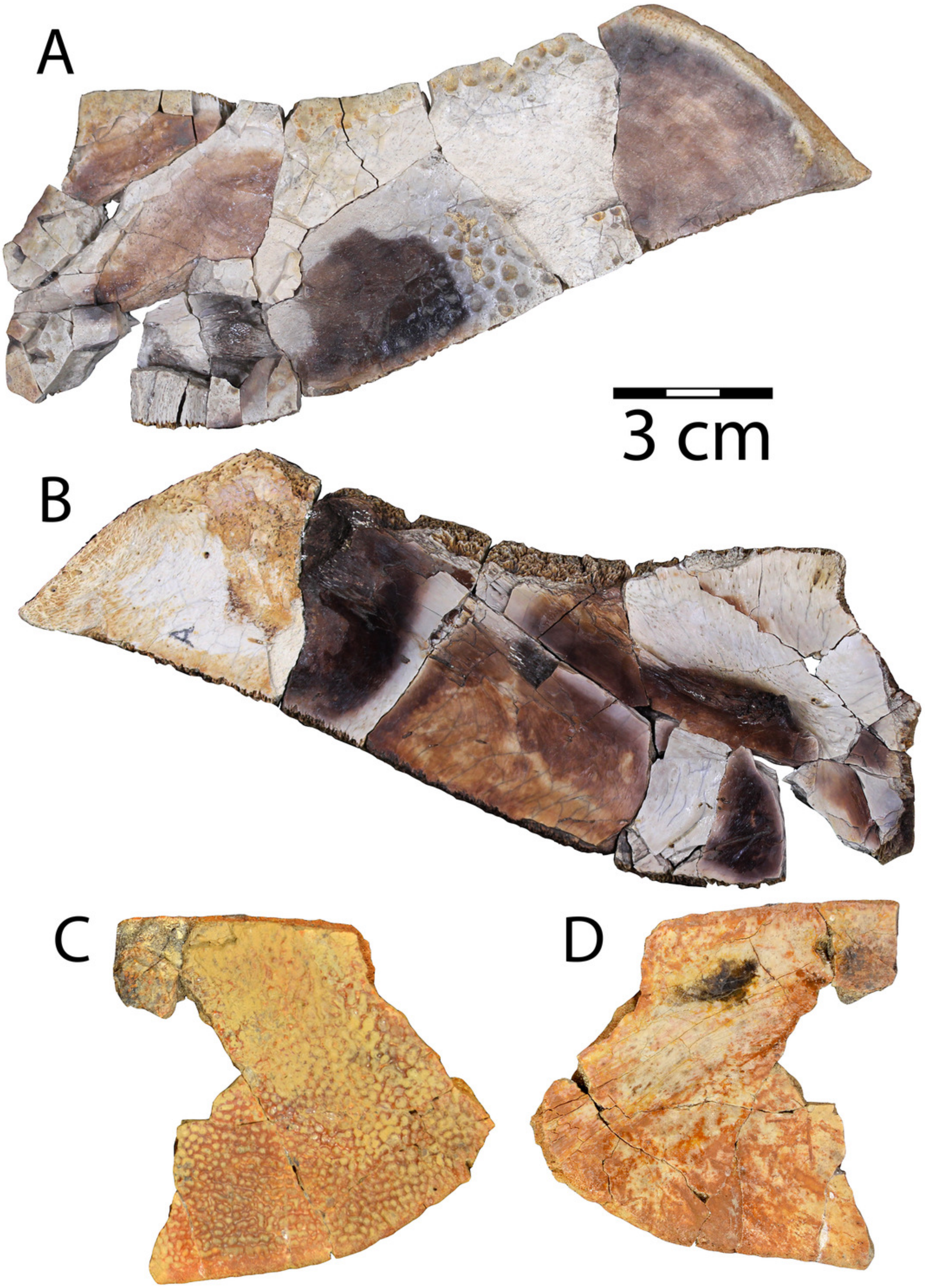
A
3 cm
B
C
D

Figure 11

Revised biostratigraphic distribution of turtle taxa in a simplified stratigraphic column of Campanian units in the San Juan Basin.

Blue bars indicate stratigraphic intervals added or extended in the current study to the species inventory provided in Sullivan, Jasinski & Lucas, (2013: 360, fig. 20.18). Geological data sourced from Miller (1984), Miller, Carey & Thompson-Rizer (1991), Lucas et al. (2005), Sullivan & Lucas (2006), Fowler (2017), Pecha et al. (2018), and Ramezani et al. (2022). Turtle occurrence data sourced from Lucas, Hunt & Sullivan (2006), Sullivan, Jasinski & Lucas (2013), Lichtig & Lucas (2015, 2018), and Joyce, Lyson & Sertich (2018) .

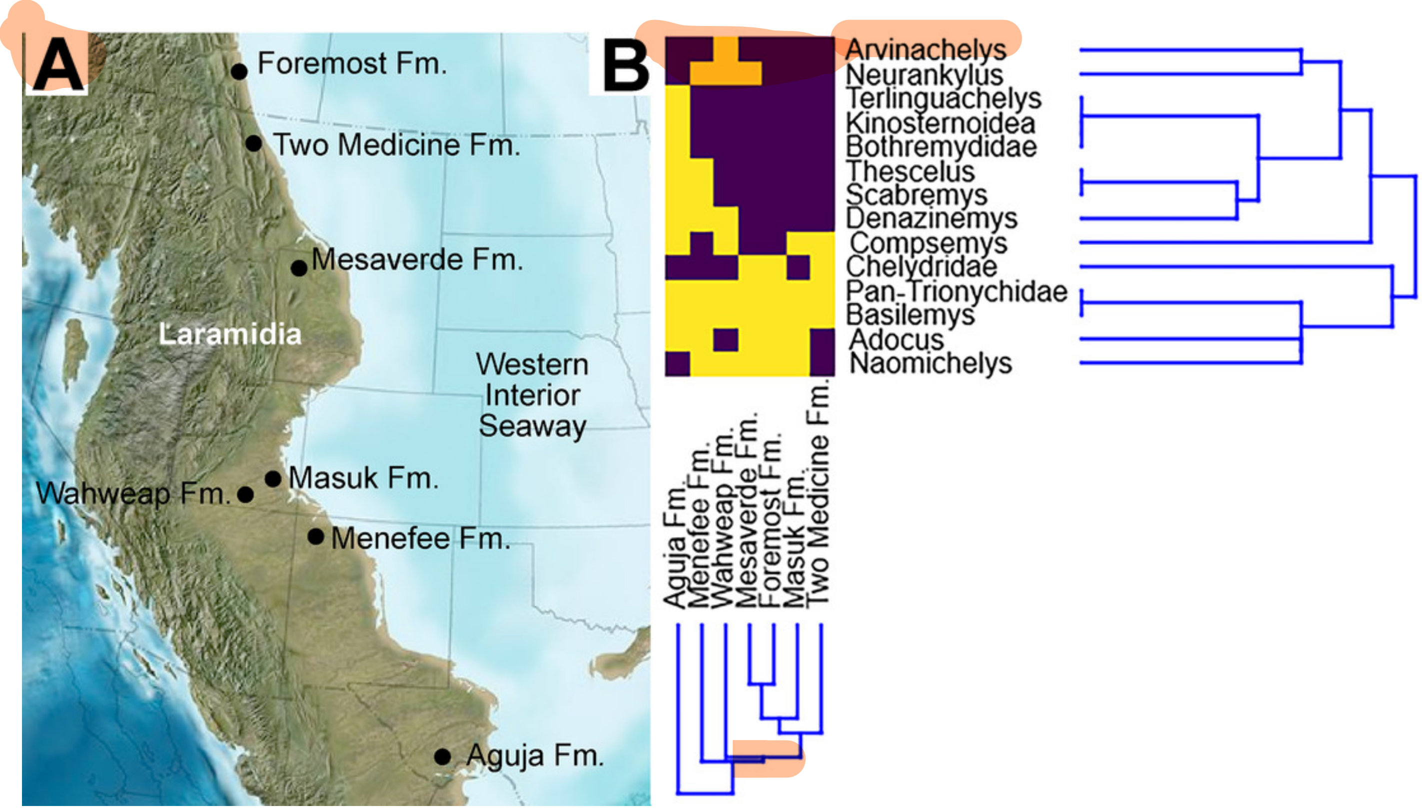

Figure 12

Paleobiogeographical distribution of turtle taxa along the western shoreline of the Western Interior Seaway during the early-middle Campanian.

A) Paleogeography of the Western Interior during the middle Campanian (Blakey, 2014); B) two-way hierarchical clustering of stratigraphic units and taxa. Published sources of turtle assemblages include: Aguja Fm. (Rowe et al., 1992; Lehman & Tomlinson, 2004; Sankey, 2005; Sankey, Lucas & Sullivan, 2006; Gasaway & Sankey, 2007; Lehman & Wick, 2010; Lehman et al., 2019, 2024; López-Conde et al., 2019; López-Conde, Chavarría-Arellano & Montellano-Ballesteros, 2020); Foremost Fm. (Peng, Russell & Brinkman, 2001; Cullen et al., 2016); Masuk Fm. (Eaton, 1990); Mesaverde Fm. (DeMar & Breithaupt, 2006, 2008; Wu et al., 2023); Two Medicine Fm. (Varricchio & Horner, 1993; Brandvold, Brandvold & Sweeney, 1996); Wahweap Fm. (Holroyd & Hutchison, 2016).

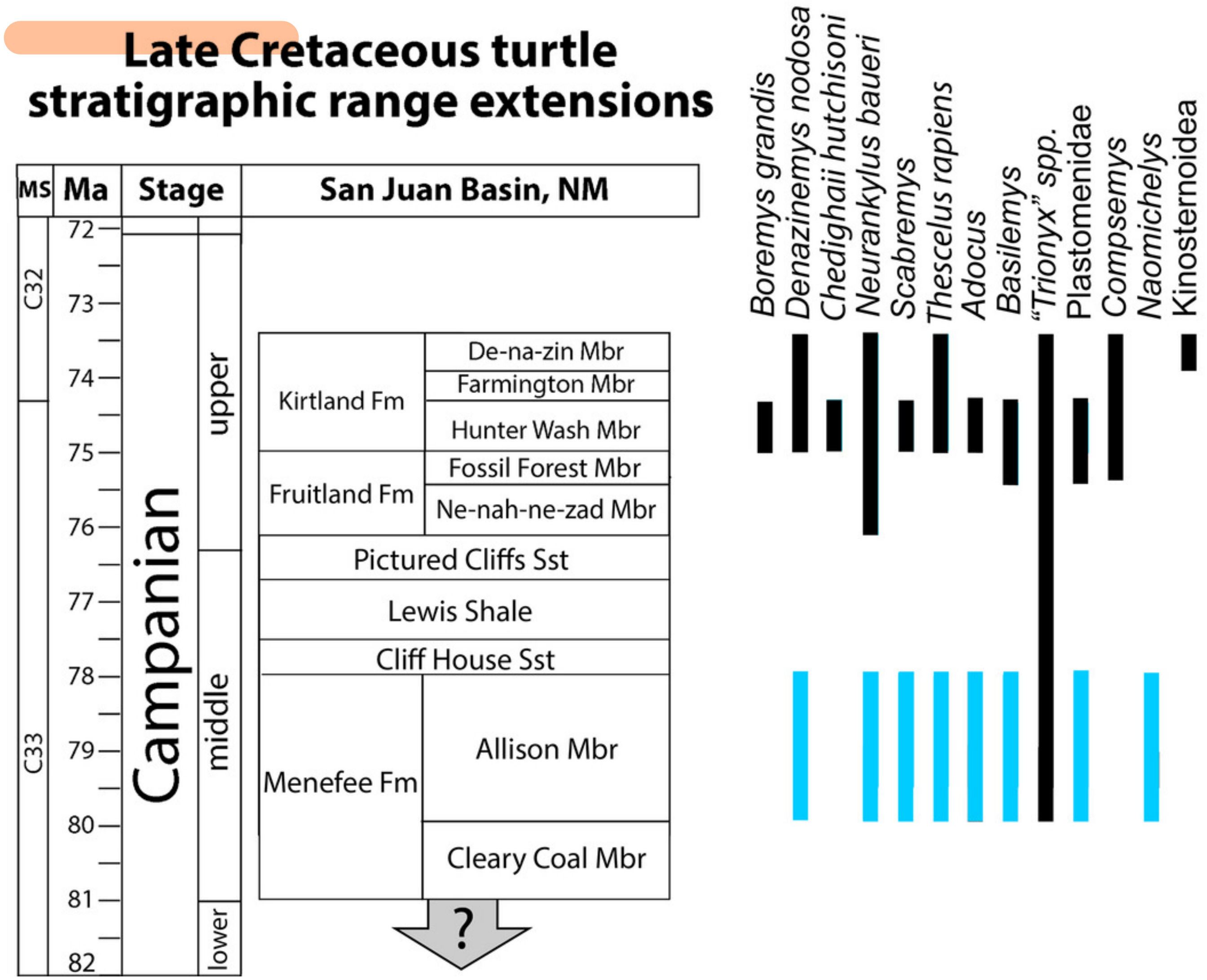
Late Cretaceous turtle
stratigraphic range extensions
MS
Ma
Stage
San Juan Basin, NM
C32
C33
72
73
74
75
76
77
78
79
80
81
82
Campanian
upper
middle
lower
Kirtland Fm
De-na-zin Mbr
Farmington Mbr
Hunter Wash Mbr
Fruitland Fm
Fossil Forest Mbr
Ne-nah-ne-zad Mbr
Pictured Cliffs Sst
Lewis Shale
Cliff House Sst
Menefee Fm
Allison Mbr
Cleary Coal Mbr
?
Boremys grandis
Denazinemys nodosa
Chedighaii hutchisoni
Neurankylus baueri
Scabremys
Thescelus rapiens
Adocus
Basilemys
“Trionyx” spp.
Plastomenidae
Compsemys
Naomichelys
Kinosternoidea

Table 1(on next page)

Dimensions of the posterior plastral lobe and sulci (in cm).

Measurements from the *Denazinemys nodosa* holotype USNM 8345, WSC 10769, a line drawing of the *Scabremys ornata* holotype USNM 13229 by Gilmore (1935) (reproduced by Sullivan, Jasinski & Lucas, 2013: fig. 20.3b-c), and UMNH VP 28352.

Specimen	**Abdominal-femoral sulcus width**	**Femoral-anal sulcus width**	**Posterior plastral lobe length**	**Straight carapace length**	**Straight plastral length**
D. nodosa holotype (USNM 8345)	14.3	10.1	10.5	—	—
WSC 10769 (*Denazinemys* posterior plastral lobe)	18.2	12.1	10.6	—	—
Scabremys holotype (USNM 13229) line drawing (Gilmore, 1935)	15.4	10.5	11.5	42.5	38.6
UMNH VP 28352, nearly complete articulated *Scabremys* shell	16.0	10.7	9.9	43.0	39.0

Table 2 (on next page)

Comparative measurements of Menefee *Adocus* specimens.

Measurements (in cm) from taxa described by Gilmore (1919).

Taxon	Specimen	Neural 5 length	Costal 6 width
Adocus sp. (this study)	WSC 10763 and 10765	5.3	10.7
Adocus kirtlandius	USNM 8593	3.4	9.3
Adocus bossi	USNM 8613	5.1	14.4

Measurement	WSC 10612	USNM 8344
Cervical scale		
Length	24.3	19.0
Width	*37.8	14.0
Vertebral 1 scale		
Length	93.6	81.0
Width	135.3	133.0
Vertebral 2 scale		
Length	*80.3	106.0
Width	136.8	165.0
Inframarginal 1 scale		
Length	66.0	
Width	60.6	
Carapace thickness at middle of costal 1, left side	19.0	
Anterior carapace sulcus width	2.4	
Anterior plastral lobe		
Length	73.0	111.0
Width	128.5	168.0
Posterior plastral lobe		
Length		122.0
Width	*75.0	185.0

Commented [SEJ1]: Provide further information, probably as a caption above the table, to what this is as the file may not be directly connected with the main text file. I would also include the title and authors of the paper to make sure they are clearly connected. Also clearly identify the taxa for the specimens, and that 8344 is the holotype.

Plastral scale midline contacts		
Gular	38.9	40.0
Humeral	65.7	79.0
Pectoral	107.7	100.0
Abdominal	71.2	60.0