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Research Article

A new species of extinct trionychid from the Early Oligocene (Orellan–Whitneyan NALMA) Brule Formation of North Dakota, USA

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Abstract

Softshell turtles (*Pan-Trionychidae*) have a particularly rich fossil record in North America, but only a few fragmentary remains have previously been reported from the Oligocene. A review of the literature suggests that *Trionyx punctiger* and *Trionyx leucopotamicus*, two taxa previously linked to the Oligocene, should be considered nomen dubia. We report well-preserved trionychid remains from the Early Oligocene (Orellan–Whitneyan) Brule Formation of southwestern North Dakota, including a complete cranium, mandible, and three partial shells that represent a new species of apalonine, *Rafetus lysoni*. The new species resembles other large-bodied apalonines from the Cenozoic of North America in skull morphology but differs notably in the poor development of carapacial and plastral callosities.

Keywords

morphological variation, taxonomy, Testudines, *Trionychidae*

Introduction

Softshell turtles (*Trionychidae*) are a diverse clade of reptiles with a rich fossil record across the globe, reaching back to the Early Cretaceous (Vitek and Joyce 2015; Georgalis and Joyce 2017). The shell of trionychids is decorated by a unique surface texture that allows confident identification of small fossil fragments in the field (Hutchison and Archibald 1986). Trionychids have a particularly rich fossil record in North America ranging from the Campanian to Eocene (Vitek and Joyce 2015), followed by a sudden hiatus, likely caused by regional drying (Hutchison 1992). Only a handful of fragmentary remains have been published so far from the Oligocene of the continent. In particular, Cope (1891) reported two fragments from what is plausibly the Early Oligocene (Orellan–Whitneyan North American Land Mammal Ages [NALMAs]) Brule Formation of North Dakota that serve as the basis of the taxon *Trionyx punctiger*, but as these fragments were never figured and now seem to be lost, this taxon is now considered to be a nomen dubium (Vitek and Joyce 2015). Many decades later, Arata and Jackson (1965) figured an indeterminate trionychid costal fragment from the Chickasawhay Formation of Wayne County, Mississippi. Hoganson and Lammers (1992) reported *Trionyx* to be present in the Brule Formation as well but listed and figured no remains. Hutchison (1996) referred shell fragments from the Brule Formation of North Dakota to *Apalone leucopotamica* (*Trionyx leucopotamicus* of Cope 1891), but these fragments remain unfigured to date as well. Incidentally, the holotype of *Trionyx leucopotamicus* from neighboring Saskatchewan, Canada, was originally believed to be Oligocene (Cope 1891; Hay 1908) and then late Eocene (Chadronian NALMA; Hutchison 1996; Vitek and Joyce 2015), but the type locality, Swift Current Creek, is actually middle

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Eocene in age (Uintan NALMA; Storer 1984; Perry et al. 2023), so all attributions of Oligocene trionychids to this taxon are somewhat dubious, especially as the type is not diagnostic (Vitek and Joyce 2015; also see Discussion below). Finally, Boyd and Welsh (2014) figured a minute trionychid shell fragment under the name *Apalone* from the Early Oligocene (Orellan NALMA) of Pennington County, South Dakota. The entire previously figured record of trionychids from the Oligocene of North America thus consists of two shell fragments, which insufficiently document the evolution of this clade during this key time interval.

The purpose of this contribution is to formally figure and describe a small collection of specimens collected from the Brule Formation of North Dakota over the course of the last decades, including a skull, a mandible, and three partial shells. The material collectively documents a new species, which we name herein *Rafetus lysoni* sp. nov.

Materials and methods

Geological settings

This study is based on five specimens housed at the AMNH and NDGS.

AMNH 12422: This near complete trionychid mandible was collected in 1951 by M. Skinner and L. Toohey from the "capping channel" at White Butte, Slope County, North Dakota. The capping rock at White Buttes was historically referred by some to the Arikaree Formation, which is Late Oligocene to Early Miocene (Arikareean NALMA) in age (Moore et al. 1959; Murphy et al. 1993). However, an unpublished microfossil fauna housed at NDGS indicates that this layer should be referred to the Brule Formation (W. Korth, pers. comm. 2025), which is regionally dated to span the Orellan and Whitneyan NALMAs, making it broadly Early Oligocene in age (Woodburne 2004; Korth et al. 2023).

NDGS 35: This partial anterior portion of a large carapace was collected from the lower sandstone interval (unit 4 of Murphy et al. 1993) at the base of Brule Formation outcrops at West Rainy Butte in Slope County, North Dakota. Few vertebrate fossils are reported from West Rainy Butte, but Prothero and Shubin (1989) proposed a Late Whitneyan "age" for at least a portion of the Brule Formation at this location based on the presence of the equid *Miohippus obliquidens*, but the stratigraphic interval that produced that specimen is unclear. We conclude that NDGS 35 is likely from a Whitneyan fauna, making it Early Oligocene in age.

NDGS 111, 112, and 551: These three shell specimens were all recovered from a single sublocality (NDGS L28) within the broader area referred to as Fitterer Ranch within Stark County, North Dakota (Skinner 1951). Recent biostratigraphic analyses conducted at Fitterer Ranch identified four stratigraphically segregated local faunae (Korth et al. 2023), ranging from a transitional Orellan/Whitneyan fauna from the lower portion of the Brule Formation (Fitterer Ranch Fauna A) to a Late Whitneyan fauna from the upper portion of the Brule Formation (Fitterer Ranch Fauna D). Locality NDGS L28 is part of the Early Whitneyan Fitterer Ranch Fauna B. These specimens were recovered from interbedded calcite cemented siltstones and mudstones. These beds were deposited stratigraphically above a discontinuous coarse sandstone, termed the "Fitterer Bed" by Murphy et al. (1993), that typically preserves stacked sets of foreset beds (Korth et al. 2019), indicating the presence of a large stream at this time that meandered through the local area. NDGS 111 consists of a nearly complete shell, NDGS 112 is a nearly complete skull (not including the mandible), and NDGS 551 is a partial carapace that is slightly larger than NDGS 111.

Visualization

All specimens (i.e., AMNH 12422 and NDGS 35, 111, 112, and 551) were documented using digital photography. The only available skull, NDGS 112, was additionally subjected to µCT scanning at the headquarters of North Star Imaging in Rogers, Minnesota, using a X5000 µCT scanner with a voltage of 150 kV and a current of 150 µA. The resulting 8-bit tiff stack of 2847 slides and effective voxel size of 43.8 µm were processed with the software Materialise Mimics v.24. Bone by bone semi-automatic segmentation was performed to obtain individual models of each bone. NDGS 111 was documented using a structured light portable scanner Artec Space Spider. The scans were acquired, processed and the model generated using Artec Studio 16 Professional. NDGS 35 and NDGS 551 were similarly documented using a structured light scanner Einscan-SP. The scans were acquired, processed, and the model generated using ExScan S version 3.1.2.0. The slice data, image stack, general cranium model, and individual bone models of NDGS 112 and the surface scan models of NDGS 35, 111, and 551 are available on Morphosource (https://www.morphosource.org/projects/000853209).

Institutional abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **NDGS**, North Dakota State Fossil Collection, North Dakota Geological Survey, Bismark, ND, USA; **USNM**, Smithsonian National Museum of Natural History, Washington DC, USA; **YPM**, Yale Peabody Museum, New Haven, CT, USA.

Systematic Paleontology

***Testudines* Batsch, 1788**
***Trionychidae* Bell, 1828**
***Apalonini* Kordikova, 1994**

***Rafetus lysoni* sp. nov.**
https://zoobank.org/1C94FB01-FDB4-49E0-B1B8-761CAFCF190D

Holotype. NDGS 112, a near complete skull (Figs 1–3).

Type locality. NDGS L28, a sublocality within the Fitterer Ranch area of Stark County, North Dakota, USA. Detailed geographic data available upon request from NDGS.

Type stratum. Brule Formation, White River Group, early Whitneyan NALMA, Oligocene.

Referred material. AMNH 12422, a mandible (Fig. 4); NDGS 35, the damaged anterior half of a large carapace (Fig. 5D, E); NDGS 111, a nearly complete shell (Fig. 5A, B); NDGS 551, a partial carapace (Fig. 5C). All referred specimens originate from the type stratum, but their stratigraphic placements within the Orellan to Whitneyan Brule Formation vary (see Geological Settings above).

Nomenclatural acts. This publication and its nomenclatural acts were registered at ZooBank prior to publication. The LSID of the publication is urn:lsid:zoobank.org:pub:95EE012C-04B5-459A-959A-B459C84A63D3 and that of the new species urn:lsid:zoobank.urn:lsid:zoobank.org:act:F17A908C-933A-47C7-917E-6779EE579B82.

Diagnosis. *Rafetus lysoni* sp. nov. can be diagnosed as a representative of *Trionychidae*, among others, by the presence of a reduced quadratojugal that does not contact the postorbital or maxilla, exclusion of the fused premaxillae from the apertura narium externa, a visual separation of the metaplastic bone from the remainders of the shell, the absence of peripherals, pygals, suprapygals, and shell scutes, and development of a boomerang-shaped entoplastron. *Rafetus lysoni* can most readily be differentiated from all other North American trionychids by the absence of a preneural in combination with large size (carapace disk length > 50 cm), mediolaterally narrow costal callosities, a greatly reduced nuchal callosity, a reduced count of medial hyo- and hypoplastral processes, two lateral hyoplastral processes, and a reduced hyo-hypoplastral callosity that barely covers their processes.

Etymology. The species epithets honors Tyler R. Lyson, eminent paleontologist, supreme collector of fossil turtles, trusted friend of the senior author, contributor of important fossils to the North Dakota State Fossil Collection, and, fittingly, a native of North Dakota.

Comments. For an extensive justification for the naming of a new taxon, please refer to the Discussion below.

Description. Skull (NDGS 112). ***Visualization*:** We provide labelled photographs and 3D renderings of NDGS 112 in standard anatomical views (Figs 1–3), but do not figure the rich inner anatomy of this specimen, as this would demand furnishing countless additional figures and because the complicated internal anatomy of turtles is best viewed by reference to the 3D models themselves. We thus urge the anatomically interested reader to download and study the models. The anatomy of trionychid turtles and a revised list of characters can be found in Girard and Joyce (2026).

***General*:** NDGS 112 is a notably complete skull (Figs 1–3). The presence of the premaxilla, a bone easily lost after death (Girard and Joyce 2026), suggests that this individual was likely buried fully intact. Minor cracks within the lateral wall of the brain case indicate that the skull was only lightly crushed dorsoventrally. A large, transverse crack is apparent, separating the skull into two halves. We suspect that this crack is the plane along which the skull split during collecting. The bones adjacent to this crack suffered some damage, in particular the left jugal, quadratojugal and squamosal, but this affects our anatomical interpretations only scarcely. The skull measures about 9 cm from the anterior tip of the snout to the basioccipital process and about 12 cm from the tip of the snout to the tip of the supraoccipital crest, which is comparable to large-sized extant *Apalone ferox* and *Rafetus euphraticus* (Girard and Joyce 2026).

***Prefrontal*:** The two prefrontals are well preserved, but minor damage is apparent to the narial region (Figs 1–3). The prefrontal is a midsized element that about equally roofs the narrow interorbital and short nasal region. Each element contacts its counterpart medially, the maxilla anteroventrally, the vomer medioventrally, and the frontal posterolaterally. As preserved, the dorsal margin of the external nares is laterally embayed, but damage to the anteromedial processes of both prefrontals suggests that this embayment was likely more pronounced originally. The prefrontals contribute to the orbit on both sides of the skull, but this contribution is greatly limited by processes formed by the maxilla and frontal along the orbit margin. Small foramina supraorbitale pierce both prefrontals just below their contribution to the orbit. As with most trionychids, the prefrontals jointly form a pointed median process that posteriorly limits the midline contact of the frontals. With the exception of its anterior tip, the midline contact of the prefrontal is fully underlain by the long anteromedial process of the frontal. This is best viewed in the associated 3D models. The prefrontal forms a broad descending process that splits ventrally into two branches. The medial branch contacts the vomer ventromedially and laterally frames the foramen fissura ethmoidalis. The ventrolateral branch contacts the maxilla ventrolaterally and anterolaterally frames the foramen orbito-nasale.

***Frontal*:** The frontals are preserved as two distinct elements (Figs 1–3). The dorsal exposure of the frontal is smaller than that of the prefrontal, but an elongate anteromedial process that extends into the narial cavity is hidden from dorsal view by the overlying prefrontals.

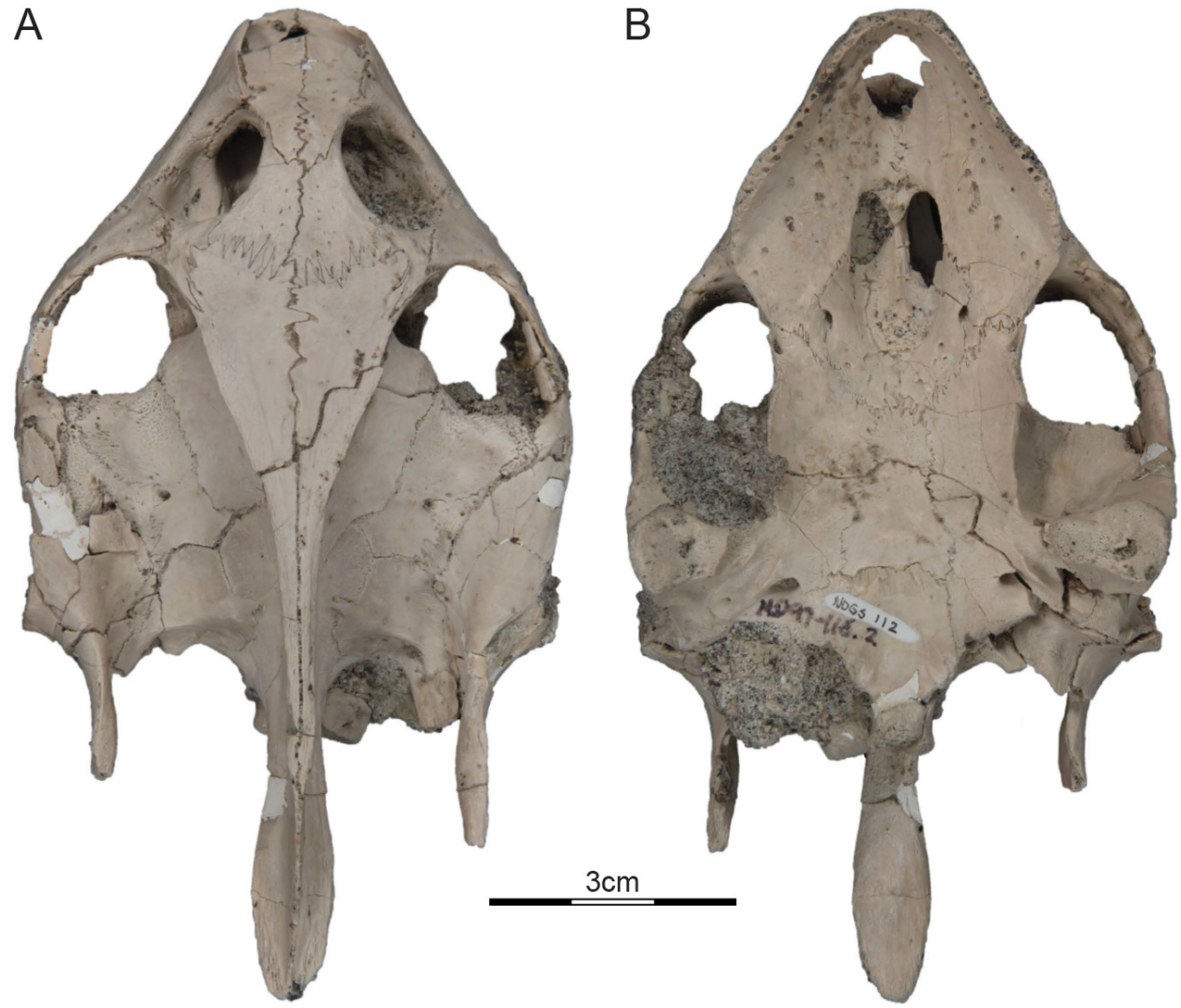

Figure 1. *Rafetus lysoni* sp. nov., NDGS 112, holotype cranium, Orellan/Whitneyan Brule Formation of North Dakota, USA. Photographs in (**A**) dorsal, and (**B**) ventral views.

The frontal contacts the prefrontal anteromedially, the postorbital posterolaterally, the parietal posteriorly, and its counterpart medially, and broadly contributes to the posteromedial margin of the orbit. The posterior contact with the parietal is strengthened by a dense, even comb of deep interdigitations. The frontal forms a process along the posterior margin of the orbit that stretches towards the jugals but is clearly separated on both sides of the skull from the jugal by a narrow contribution of the postorbital to the orbit. On the ventral side, the frontal forms a low crest that laterally defines a low sulcus olfactorius and is continuous anteriorly with the medial wall of the fissura ethmoidalis and posteriorly with the descending process of the parietal.

***Parietal*:** The parietals are well preserved with the exception of minor damage to the left descending process and a broad crack that runs diagonally across both elements (Figs 1–3). The dorsal plate of the parietal contacts the frontal anteriorly and the postorbital anterolaterally. Although a surficial contact is absent, the parietal forms a ventrolaterally curved process that runs below the postorbital to contact the jugal within the temporal fossa. The descending process ventrally contacts the palatine and epipterygoid anterior to the trigeminal foramen and laterally contacts the prootic and supraoccipital within the upper temporal fossa. The parietal dorsally roofs the cavum cranii, contributes to the anterolateral wall of the braincase, forms much of the processus trochlearis oticum, defines the anterior margin of the large trigeminal foramen, and posteriorly converges with its counterpart to cover the anterior portions of supraoccipital crest. The anterior contact with the frontal and postorbital are deeply interdigitated. Together with the postorbital, the parietal forms a low depression that is located posterior to the orbit within the dorsal skull roof. The descending process is anteriorly confluent with the low crista cranii and is laterally covered by the ascending process of the palatine. Further posteriorly, the descending process forms the thickened, anteromedial margin of the processes trochlearis oticum, which is developed as a thickened lip that overhangs the lower temporal fossa. The parietal broadly overlaps the prootic and supraoccipital laterally along

an oblique suture strengthened by numerous interdigitations not visible in external view. The transition from the dorsal skull surface to the upper temporal fossa is denoted by a distinct overhanging ridge. The cavum cranii does not appear inflated relative to other trionychids, such as *Plastomenus thomasii* (Evers et al. 2023), but a distinct, median depression anterior to the supraoccipital in the dorsal roof of the cavum cranii apparent in the 3D models is highly indicative for the former presence of a cartilaginous rider (*sensu* Werneburg et al. 2021).

***Postorbital*:** The postorbitals are fully intact on both sides of the skull (Figs 1–3). The postorbital is a notably small element that contacts the frontal anteromedially, the parietal posteromedially, and the jugal ventrally. All surrounding contacts are supported by fine interdigitations. The postorbital contributes minorly to the posterior rim of the orbit thus fully separating the frontal from the jugal. The postorbital similarly contributes minorly to the anterior rim of the upper temporal emargination, which hinders the parietal from contacting the jugal on the skull surface. Within the upper temporal fossa, the postorbital forms a curved ventrolateral process that reaches towards the anterior process of the quadratojugal but does not contact it (Fig. 3A). We find this unusual arrangement in the two CT scans available to us in *Rafetus euphraticus*, but only in one individual of *Apalone spinifera* in our sample of *Apalone* (see dataset of Girard and Joyce 2026). In the orbit, a ventral process of the jugal reaches toward the maxilla and reduces the contribution of the maxilla to the rim of the orbit, similar to *Rafetus euphraticus*. The postorbital contributes minorly to the septum orbito-temporale.

***Jugal*:** While the right jugal appears to be fully intact, the left jugal shows minor damage to its ascending and posterior processes (Figs 1–3). The jugal contacts the postorbital and parietal dorsally along its ascending process, the quadratojugal posteriorly along its posterior process, and the maxilla, palatine, and pterygoid ventrally along its base plate. The septum orbitotemporale is notably broad. The jugal forms a minor contribution to the orbit margin that narrowly separates the postorbital from the maxilla. The triangular medial process reaches medially to contact the palatine dorsally and the pterygoid ventrally and helps form the narrow posterior orbit wall. The broad, sheetlike posterior process forms a distinct ventrally oriented protuberance, likely for articulation with the temporal musculature, and broadly overlaps the quadratojugal from the side.

***Quadratojugal*:** The quadratojugals are preserved almost completely on both sides, but the morphology of the left one is distorted by a large crack (Figs 1–3). The quadratojugal is an elongate, distinctly triradiate element. The anterior process is fully preserved on the left side of the skull, but damaged on the right side. Its extent and shape can nonetheless be estimated by the outline of its articular scar on the inside of the jugal. In either case, the anterior process is an anteriorly thinning lamina of bone that is almost fully covered externally by the jugal. On the left side of the skull, the quadratojugal forms a fingerlike extension that nearly contacts the elongate posterior process of the postorbital. A clearer gap is apparent between these two bones on the right side of the skull. The quadratojugal is forked posteriorly to form two processes that broadly contact the quadrate posteriorly and frame the anterior margin of the cavum tympani. The narrow posteroventral process tapers to a point that extends towards the mandibular condyle but clearly does not reach it. The thick posterodorsal process is characterized by a rounded anterodorsal protrusion that laterally caps the trochlear process. Although the squamosals are damaged on both sides of the skull, articular scars suggest that the posterodorsal process was fully covered by the squamosals posterior to the anterodorsal protrusion. The quadratojugal and jugal jointly form a modest lower temporal emargination that is only interrupted by the ventral protuberance of the jugal.

***Squamosal*:** The right and left squamosal are both damaged but fully complement each other (Figs 1–3). As in all trionychids, the squamosal is a complex bone consisting of a cone shape anterior portion and an elongate posterior portion. The anterior portion broadly articulates with the opisthotic medially, the quadrate anteroventrally, and the quadratojugal anteriorly, forms the dorsal margin of the cavum tympani, and houses the voluminous, anteroposteriorly elongate antrum postoticum. The posterior portion contacts the opisthotic and quadrate behind the cavum tympani and forms tall and elongate squamosal horns that show a lateral concavity for the abductor musculature.

***Premaxilla*:** A single, median premaxilla is preserved (Figs 1, 2). It forms the anterior margin of the labial ridge and the anterior margin of the enlarged foramen intermaxillare, which is about 25% the length of the triturating surfaces. It is excluded from the ventral margin of the external nares by a median contact of the maxillae.

***Maxilla*:** The maxillae are massive elements that show no damage beyond minor cracks (Figs 1–3). The maxilla can be subdivided into a vertical plate that forms the lateral side of the snout and a horizontal plate that forms the triturating surface. The main body of the vertical process is about as high as the orbit in lateral view. Its triangular ascending process contacts the descending process of the prefrontal medially and forms the anterior margin of the orbit. Contact with the frontal is disrupted by a minor contribution of the prefrontal to the orbit. The vertical plate otherwise forms the ventral margin of the orbit, the lateral margin of the external nares, and has a broad and interfingered posterior contact with the jugal, a short anteromedial contact with the premaxilla and its counterpart, and displays a nasal pocket in the lateral wall of the nasal cavity. The distinct labial ridge is lightly convex in lateral view. Rows of neurovascular foramina are developed on the rim of the labial ridge itself and parallel to it on the external and internal side of the skull.

The horizontal plate of the maxilla forms lateral margins of the foramen intermaxillare and the internal

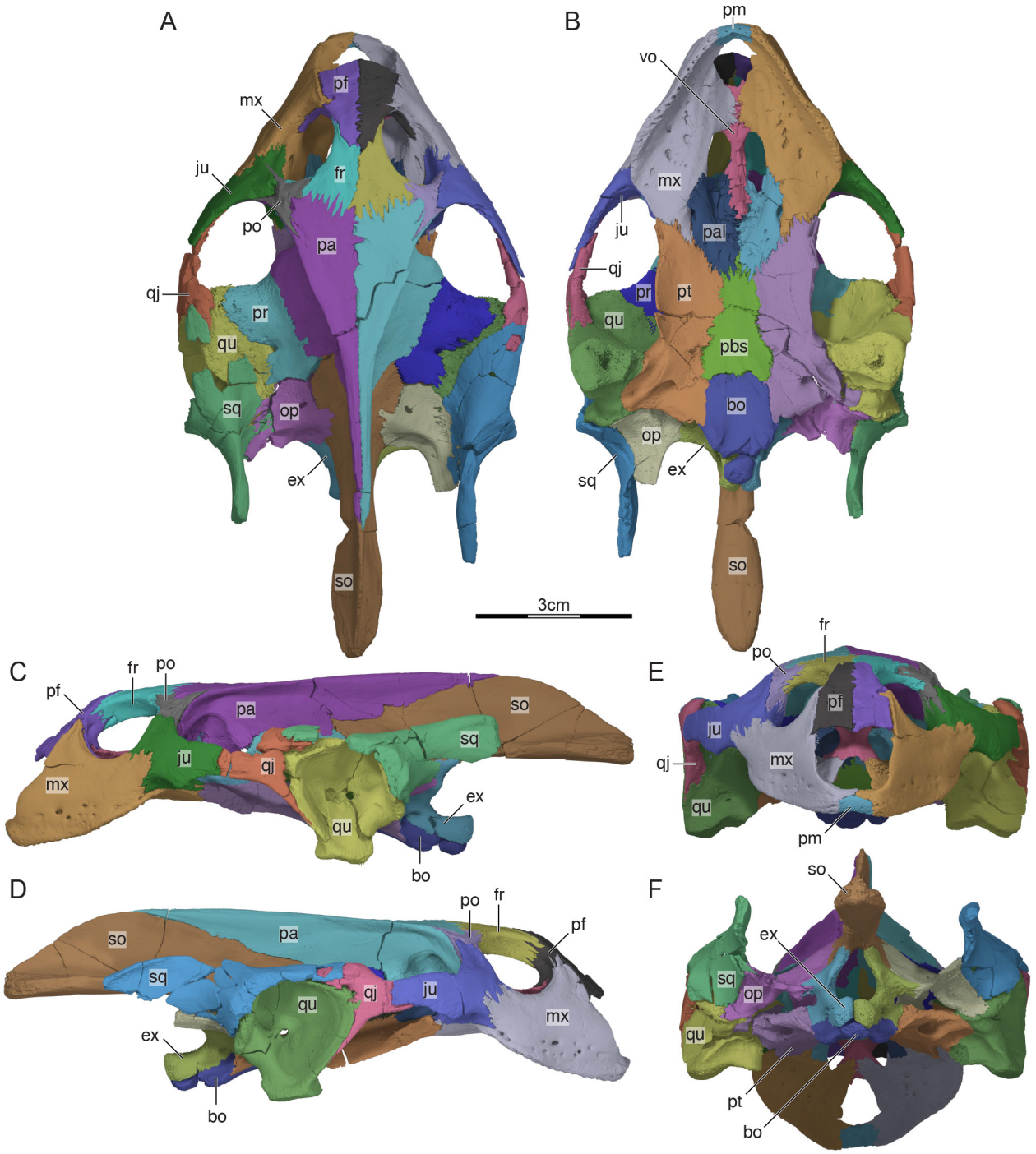

Figure 2. *Rafetus lysoni* sp. nov., NDGS 112, holotype cranium, Orellan/Whitneyan Brule Formation of North Dakota, USA. 3D rendered models in (**A**) dorsal, (**B**) ventral, (**C**) left latera, (**D**) right lateral, (**E**) anterior, and (**F**) posterior views. *Abbreviations*: bo, basioccipital; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pbs, parabasisphenoid; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

choanae, contacts the vomer laterally, the palatine posterolaterally, the pterygoid posteriorly, and the jugal posterodorsally. A small medial contact of the maxilla with its counterpart within the bony palate is present, but the bony palate itself (*sensu* Girard and Joyce 2026) is substantial at about 24% of the anteroposterior length of the triturating surfaces. This is longer than in all extant apalonines, but similar to Eocene representatives of the group, such as *"Trionyx" mira* (Hay, 1908), YPM 16104 ("*Trionyx" uintaensis* of Vitek 2011), and "*Trionyx" uintaensis* ("*Trionyx" tritor* of Hay, 1908). The maxilla forms the lateral border of the distinct foramen palatinum posterius but contributes neither to the canalis intrapalatinus nor the foramen palatinum anterius. The flat triturating surfaces are laterally defined by the sinuous labial ridge and the posterior third is about 190% the

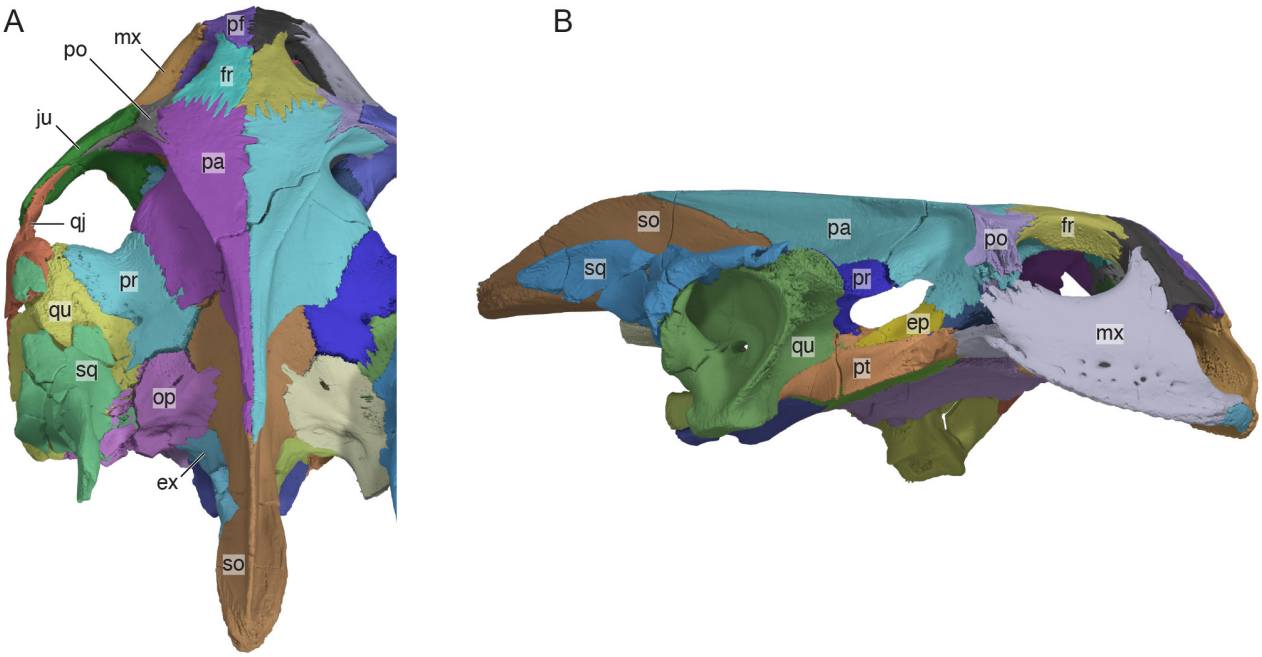

Figure 3. *Rafetus lysoni* sp. nov., NDGS 112, holotype cranium, Orellan/Whitneyan Brule Formation of North Dakota, USA. **A**. Oblique posteroventral view highlighting arrangement of bone in the postorbital bar. **B**. Oblique anterolateral view highlighting the trigeminal region. The right jugal and quadratojugal were removed for better view. *Abbreviations*: ep, epipterygoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pf, prefrontal; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal.

width of the anterior third. A palatal groove with parallel margins is present, but not distinct. The horizontal plate of the maxilla also floors the narial passage and parts of the orbit, two regions separated from one another by a low, rounded suborbital crest (*sensu* Evers et al. 2023) that is formed by the prefrontal, maxilla, and palatine. The supraalveolar canal, which runs within the maxilla for much of its length, is supplied by a relatively small foramen supramaxillare, located in the floor of the orbit, and a relatively large foramen supraalveolar, which is located anteriorly to the suborbital crest within the narial passage. The two foramina are identified as neurovascular entry points as they are associated with posteriorly oriented grooves.

***Vomer*:** The anterior part of the vomer is well-preserved, but its posterior processes is broken into several slightly displaced fragments and the posterior tip is likely missing altogether (Figs 1, 2). The vomer is a complex, anteroposteriorly elongate bone. Its anterior half forms an expanded ventral plate that floors the medial aspects of the narial passage and contacts the maxilla ventrolaterally. The ventral plate forms the posterior margin of the foramen intermaxillare and anteromedial margin of the internal nares and is partially hidden from ventral view by the irregular midline contact of the maxillae. The internal nares are located at about 50% of the anteroposterior length of the triturating surfaces. The fissura ethmoidalis is defined anteroventrally by paired ascending processes of the vomer and posterodorsally by the descending processes of the prefrontals. A distinct vomeral sulcus is apparent in the interorbital space. The posterior process of the vomer is damaged, as are the palatines, obscuring possible articulation scars between these bones. From what can be discerned, the posterior process is elongate, exhibits a low ventral ridge, expands posteriorly, and covers at least the anterior half, but certainly no more than the anterior two-thirds, of the midline suture between the palatines.

***Palatine*:** The palatines show crushing along the anteromedian contact, but are otherwise well preserved (Figs 1, 2). They consist of a horizontal plate that is domed to roof the narial canal and partially floors the cavum cranii and an ascending process that defined the most anterior portion of the braincase wall. The imprint of the narial passage ends posterior to the triturating surface, which is different from all modern apalonines, but similar to Eocene representatives, in particular *"Trionyx" mira* (Hay, 1908), YPM 16104 ("*Trionyx" uintaensis* of Vitek 2011), and "*Trionyx" uintaensis* ("*Trionyx" tritor* of Hay 1908). As a result, the proportion of the narial canal roofed by the palatine is unusually long as well. While the horizontal plate of the palatine contacts the vomer anteroventrally, the maxilla anterolaterally, the pterygoid posterolaterally, the parabasisphenoid posteriorly, and its counterpart medially, the ascending process forms a deeply interdigitated dorsal suture with the parietal and epipterygoid. A short dorsolateral contact with the medial process of the jugal is furthermore apparent just behind the orbit. The single, relatively large foramen palatinum posterius is located at the suture of the palatine with the maxilla just medial to the jugal contact. The lateral margin of the foramen palatinus posterius is formed by

the maxilla. A small contribution to this margin by the pterygoid is furthermore apparent on the right side. The intrapalatine canal and the foramen palatinum anterius, which is located lateral to the braincase wall, are fully formed by the palatine. Three small foramina palatinus accessorium puncture both palatines posteromedial to the foramen palatinum posterius. Those openings are arranged into a transverse row on the right side, but into a triangle on the left side. The palatines define the posterior margin of the narial canals, which are located at about 115% of the anteroposterior palatine length (see Girard and Joyce 2026).

***Quadrate*:** The quadrates are chipped and cracked on both sides of the skull, but their morphology can be appreciated nonetheless (Figs 1–3). The lateral part of the quadrate forms the rounded cavum tympani and the medial wall of the fully confluent antrum postoticum. The incisura columella auris is fully enclosed by the quadrate to form a canal. A low ridge connects the incisura columella auris to the margin of the cavum tympani. The quadrate contacts the quadratojugal anteriorly and is capped posterodorsally by the squamosal. The quadrate otherwise contacts the prootic anteromedially, the opisthotic posteromedially, and the pterygoid medioventrally. The quadrate minorly contributes to the processus trochlearis. Only an anteroposteriorly elongate sliver is visible in dorsal view, the rest being covered by the squamosal. The quadrate forms the lateral margin of the foramen stapedio-temporale, but the canal is only lightly incised into the quadrate on the left side of the skull and not at all on the right side. The lateral wall of the canalis cavernosus is apparent on the medial side of the quadrate. The mandibular condyles are low and unevenly divided anteroposteriorly into two facets that stand at an angle to one another. The medial facet is smaller than the lateral facet. Only moderate inflected ridges are apparent above the mandibular condyles and just below the entry point of the Eustachian tube.

***Epipterygoid*:** The right epipterygoid appears to be preserved intact (Fig. 3B). This element is an anteroposteriorly oriented, flat, triangular bone that tapers to a point posteriorly. It dorsally defines the ventral limit of the large trigeminal foramen, ventrally contacts the low crista pterygoidei of the pterygoid, contacts the parietal anterodorsally, and the palatine anteroventrally. Although only fragments of the left epipterygoid are preserved, articular scars suggest a morphology compatible with the right side.

***Pterygoid*:** The pterygoids are chipped and cracked on both sides of the skull, but their morphology can be fully appreciated nonetheless (Figs 1–3). The pterygoid is mostly a plate-like, horizontally oriented bone decorated ventrally by the low crista pterygoidei. On the ventral side of the skull the pterygoid contacts the maxilla and palatines anteromedially, the parabasisphenoid and basioccipital medially, and the quadrate laterally. Anterolaterally, the pterygoid contributes minorly to the triturating surfaces and forms a small, vertical process. The lateral margin of the pterygoid forms an outwardly bowed crest that ends near the quadrate process. A separate crest defines a distinct fossa above the mandibular condyle. On the dorsal side, the pterygoid contacts, from back to front, the exoccipital, the prootic, the epipterygoid, the parietal, the palatine, and the jugal. The pterygoid also forms a short contribution to the trigeminal foramen. The pterygoid broadly floors the cavum acustico-jugulare, the cavum labyrinthicum, and the recessus scalae tympani, but these three spaces are ventrally only poorly delineated from another by a low pterygoid ridge. The full length of the sulcus cavernosus is floored by the pterygoid. The large foramen posterius canalis carotici interni is fully located within the pterygoid and placed about at the level of basioccipital/parabasisphenoid contact. The canalis caroticus internus is oriented in an angle towards the midline of the skull. It is mostly surrounded with the pterygoid with minor contributions in the roof from the prootic. The foramen anterius canalis carotici lateralis is jointly formed by the pterygoid and parabasisphenoid and located below the base of the trabeculae of the parabasisphenoid. The canalis caroticus lateralis is anteriorly confluent with the sulcus cavernosus. The pterygoid ventrally defined the fenestra postotica, which is fully confluent with the foramen jugulare posterius. The two spaces are visually separated from one another by a minor ventral protrusion of the pterygoid.

***Prootic*:** The prootics show virtually no damage of note (Figs 1–3). The prootic is a larger bone that forms much of the elongate otic capsule and the dorsal and posterior walls of the particularly elongate trigeminal foramen. It contacts the parietal dorsomedially, the supraoccipital posteromedially, the opisthotic posteriorly, the quadrate laterally, the pterygoid ventrally, and the parabasisphenoid ventromedially. A contact with the epipterygoid is not apparent. The prootic contributes about half the length of the distinct processus trochlearis oticum, which broadly overhangs parts of the upper temporal fossa. The canalis stapedio-temporale, which extends anterodorsally from the cavum acustico-jugulare to the upper temporal fossa, is located between the prootic and the quadrate, but the majority of this canal is formed by the prootic. The ventral side of the right prootic shows a well-preserved fossa acustico-facialis with three nerve foramina: two foramina nervi acustici, which open into the cavum labyrinthicum, and a foramen nervi facialis. The nerve canal that leads laterally from the fossa acustico-facialis to the canalis cavernosus ventrally gives off a small sub-canal, which is formed by the prootic and pterygoid, that leads towards the canalis caroticus internus and that we interpret as the canalis pro ramo nervi vidiani. The geniculate ganglion is thus located within the prootic. A groove in the lateral wall of the canalis cavernosus that leads posteriorly from the facial nerve canal likely documents the passage of the hyomandibular nerve. While the prootic portion of the anterior semicircular canal is enclosed by the prootic, the prootic portion of the lateral semicircular canal is ventrally open. The prootic forms the anterior

margins of the fenestra ovalis and the hiatus acusticus, but both spaces remain open ventrally.

***Opisthotic*:** While the left opisthotic shows much damage, the right one is complete with notable exception of the posterior tip of the paroccipital process (Figs 1–3). The opisthotic contacts the prootic anteriorly along a vertical suture, the supraoccipital dorsomedially along a vertical suture supported by a sheet bone formed by the opisthotic that covers the supraoccipital, the exoccipital medially, the squamosal posterolaterally, and the quadrate anterolaterally along a deeply interdigitated suture. As in most trionychids, the processus interfenestralis is subdivided into a larger lateral and smaller medial subprocess, which together fully enclose the fenestra perilymphatica. The larger subprocess broadly contacts the pterygoid ventrally while the smaller subprocess, which is traversed at its base by the glossopharyngeal nerve, shows a short ventral contact with the basioccipital. The opisthotic roofs the recessus scalae tympani, the path of the stapedial foramen being impressed into its ventral surface. Similarly to the prootic, the opisthotic forms the posterior margins of the fenestra ovalis and the hiatus acusticus, but both spaces remain open ventrally. Furthermore, the opisthotic forms the anterior margin of the foramen jugulare anterius, which it fully encloses together with the exoccipital. The opisthotic portions of the posterior and lateral semicircular canals are fully enclosed. A ridge is present on the dorsal surface of the opisthotic, at the base of the processus paroccipitalis. An articular scar on the posterior process of the supraoccipital suggests that the paroccipital process inserts into the squamosal just before its posterior tip.

***Supraoccipital*:** The supraoccipital is well-preserved, even if affected by some cracking (Figs 1–3). The supraoccipital is an elongate bone that is medially capped by the parietals, anterolaterally contacts the prootic, posterolaterally the opisthotic, and ventrally the exoccipital. The supraoccipital roofs the cavum cranii, forms the dorsal margin of the foramen magnum, and produces an elongate supraoccipital crest that has a nuanced, T-shaped cross section and that extends posteriorly beyond the level of the equally elongate squamosal horns. The squamosal portion of the anterior semicircular canal is enclosed by bone, but not that of the posterior semicircular canal.

***Exoccipital*:** The exoccipitals are well-preserved with exception of a crack that runs through the condyle of the left element. The exoccipital is a small element that contacts the supraoccipital dorsally, the opisthotic anterolaterally, the pterygoids anteroventrally, the basioccipital ventrally, and its counterpart medially. The exoccipital forms the lateral and ventral margins of the foramen magnum and the posterior margins of the foramen jugulare anterius, which is fully enclosed by the exoccipital and opisthotic. Although the foramen jugulare posterius is confluent with the fenestra postotica, the exoccipital, opisthotic, and pterygoid helps define its medial extent by forming low processes. Three hypoglossal foramina can be identified in the models. The most posterior one is formed by the exoccipital only, the middle one by the exoccipital and basioccipital, and the small, anterior one by the basioccipital only. The exoccipital otherwise forms a third of the occipital condyle.

***Basioccipital*:** The unpaired basioccipital is preserved intact with exception of a chip missing from the base of the occipital condyle (Figs 1, 2). The elongate basioccipital contacts the exoccipital dorsally, the pterygoid laterally, the parabasisphenoid anteriorly, and the processus interfenestralis of the opisthotic anterodorsolaterally. The basioccipital forms the ventral third of the basioccipital condyle and a pair of small, but distinct, basioccipital tubercula. Of the three hypoglossal foramina, the basioccipital fully forms the small, anterior one and jointly encloses the middle one with help of the exoccipital. The outline of the recessus scalae tympani is impressed into the anterolateral margin of this bone.

***Parabasisphenoid*:** The parabasisphenoid is crossed by a transverse crack, but otherwise undamaged (Figs 1, 2). This unpaired bone contacts the palatines anteriorly, the pterygoids laterally, the basioccipital posteriorly, and the prootic anterodorsally. The ventral exposure, which is partially reduced by the neighboring bones, is flat, with exception of a nuanced, tubercular depression, which the parabasisphenoid forms together with the basioccipital. The posterior half of the parabasisphenoid forms the lightly depressed ventral flooring of the cavum cranii. Basis tuberculi basalis are not developed. The abducens nerve runs through a fully ossified canal that is only formed by the parabasisphenoid. While the posterior opening of this canal is located posterior to the clinoid processes in the floor of the cavum cranii, the anterior one is located near the anterior opening of the palatine canal, ventrolateral to the base of the clinoid process. The lateral wall of the internal carotid canal is formed by the parabasisphenoid. At the level of the sella turcica, the internal carotid splits into its equally sized branches. The cerebral branch forms a short canal that is fully located within the parabasisphenoid. The anterior openings are widely spaced. The lateral branch forms an equally short canal together with the pterygoid. As in most trionychids, the dorsum sellae is dorsoventrally low and overhangs a low but mediolaterally broad sella turcica. The sella turcica is laterally framed by widely spaced, elongate trabeculae, which are decorated at their base by spike-like clinoid processes.

***Stapes*:** The stapes are not preserved on either side of the skull.

Mandible (AMNH 12422). *General*: The mandible shows no signs of crushing and only very little damage, mostly missing chips along the labial margin of the triturating surfaces (Fig. 4). The postcoronoid bones are not fused and a splenial is not developed.

***Dentary*:** The two mandibular rami are fused to form a single element. The dentary contacts the coronoid posteriorly, the surangular posterolaterally, and the angular posteromedially (Fig. 4). The symphysis is relatively elongate, about 50% the anteroposterior length of the

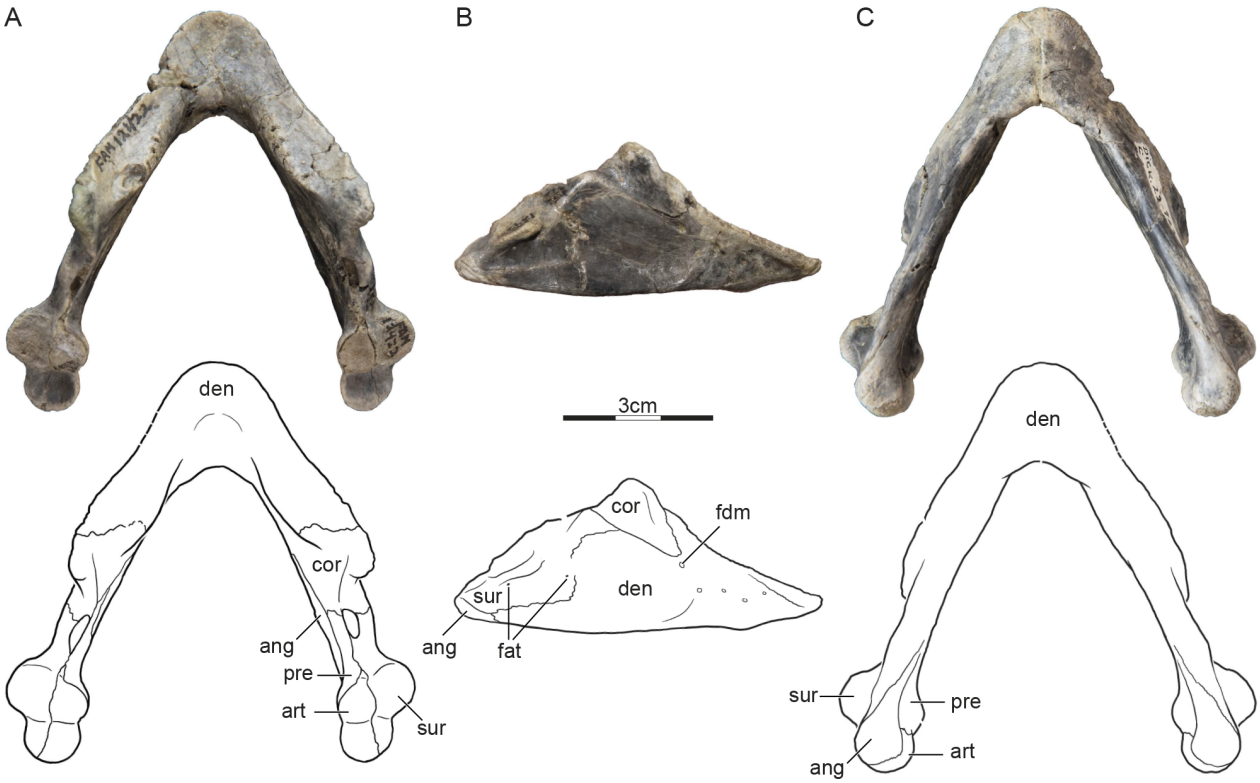

Figure 4. *Rafetus lysoni* sp. nov., AMNH 12422, mandible, Orellan/Whitneyan Brule Formation of North Dakota, USA. Photographs and interpretive line drawings in A) dorsal, B) right lateral, and C) ventral views. *Abbreviations*: ang, angular; art, articular; cor, coronoid; den, dentary; fat, foramen auriculotemporalis; fdm, foramen dentofaciale majus; pre, prearticular; sur, surangular.

triturating surfaces. The triturating surfaces, which are defined medially and laterally by indistinct lingual and labial ridge, respectively, are slightly expanded posteriorly to form a minor overhanging medial lip. The dentary lacks a median hook, accessory or symphyseal ridges, and dentofacial processes. As is typical for trionychids (Evers et al. 2023), the dentary forms a distinct ascending process that buttresses the tall coronoid process anteriorly. The dentary furthermore forms a tall sheet of bone that supports the coronoid process from posteriorly. The inconspicuous foramen dentofaciale majus is located near the anterior margin of the adductor fossa.

***Coronoid*:** The coronoid is a small, triangular bone that caps the tall coronoid process of the mandible (Fig. 4). The coronoid contacts the dentary anteriorly and ventrolaterally, the surangular posterolaterally, the prearticular posteromedially, and the angular medially. A distinct anteromedial process is developed that forms the expanded posterior portions of the triturating surfaces. The coronoid is the only bone to contribute to the coronoid process, which is dorsally rounded and lacks a posterior notch. A posteromedial process forming the medial wall of the fossa Meckelii is absent.

***Surangular*:** The surangular is a mostly vertically aligned sheet of bone that forms much of the posterolateral aspects of the mandible (Fig. 4). As an anterior surangular process is absent, its anterior contact with the dentary is only slightly sinuous. It otherwise has a short anterodorsal contact with the coronoid and broad contacts with the articular posteromedially and with the prearticular anteromedially. A contact with the prearticular anterior to the fossa Meckelii is absent. The lateral aspects of the surangular are pierced by two inconspicuous foramina auriculotemporalis. The surangular forms the greater portion of the medially expanded, concave articular surface relative to the articular, but the lesser portion of the short, but distinct retroarticular process.

***Angular*:** The angular is a spoon-shaped bone that caps the posteroventral aspects of the mandible (Fig. 4). The pointed anterior process fully separates the prearticular from contacting the dentary, while the expanded, posterior end cups the retroarticular process from below. The anterior process otherwise broadly contacts the coronoid dorsally.

***Prearticular*:** The prearticular is a vertically oriented bone that anteriorly contacts the coronoid, medially contacts the angular, and posteriorly contacts the articular (Fig. 4). The prearticular furthermore exhibits a broad lateral contact with the surangular posterior to the fossa Meckelii, which reduces the size of the latter. A contact with the dentary is absent. The prearticular forms a rounded posterior process that cups the anterior margins of the articular surface but does not directly contribute to it.

***Articular*:** The articular is a small, triangular bone that forms the lesser portion of the concave articular surfaces, but the greater portion of the short, but distinct, retroarticular process (Fig. 4). It contacts the prearticular

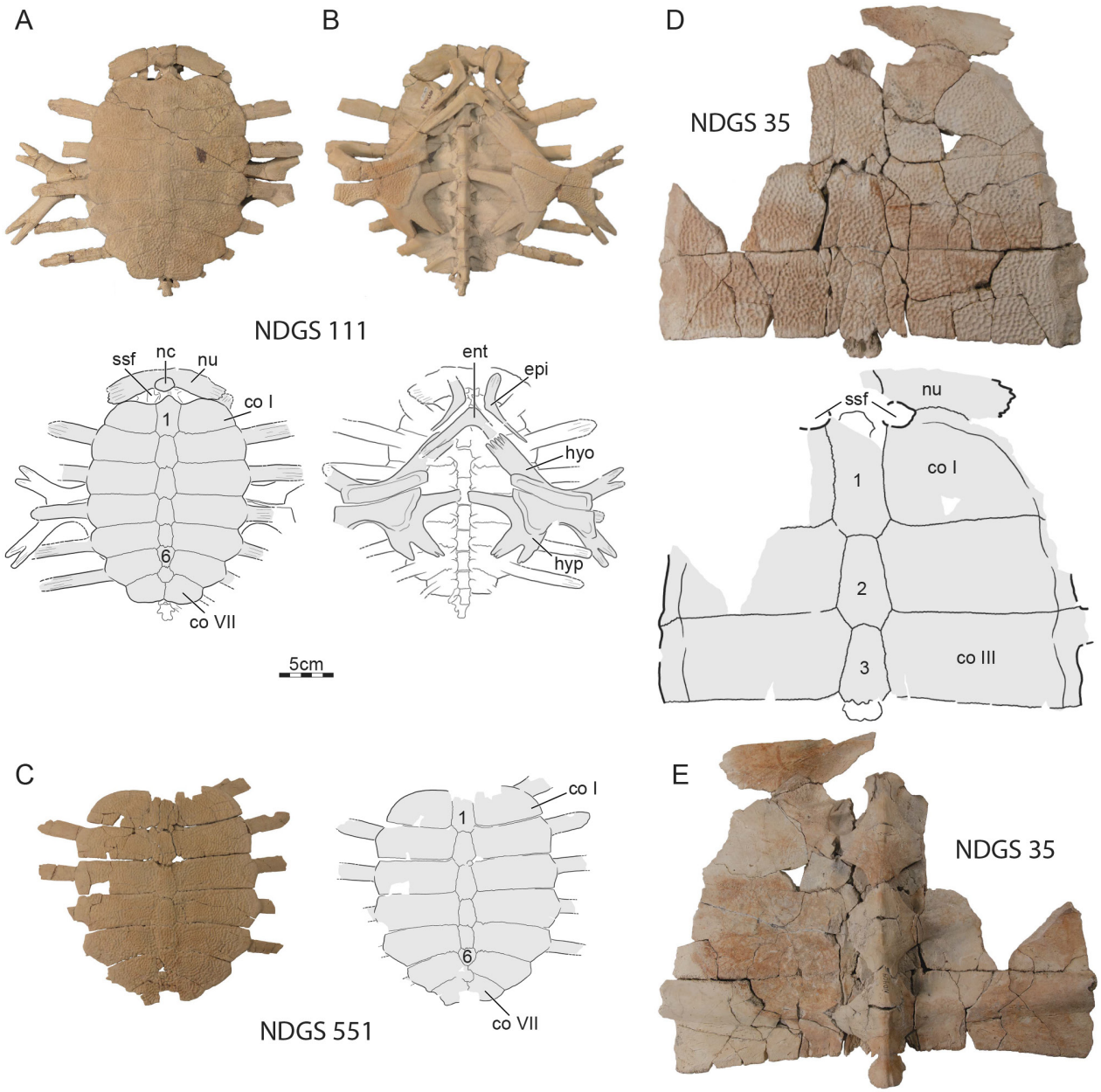

Figure 5. *Rafetus lysoni* sp. nov., shell material, Orellan/Whitneyan Brule Formation of North Dakota, USA. Photographs and interpretive line drawings of NDGS 111 in A) dorsal and B) ventral views, of NDGS 551 in C) dorsal view, and of NDGS 35 in D) dorsal, and E) ventral views. All specimens are to scale. *Abbreviations*: co, costal; ent, entoplastron; epi, epiplastron; hyo, hyoplastron; hyp, hypoplastron; nc, nuchal callosity; nu, nuchal; ssf, suprascapular fontanelle. Arabic numerals denote neurals and their position in the neural column.

anteromedially, the surangular laterally, and is cupped by the angular ventrally.

Shells (NDGS 35, 111, 551). ***General*****:** Three partial shells from the Brule Formation of North Dakota provide useful anatomical insights: NDGS 111, a near complete shell (Fig. 5A, B), NDGS 551, a partial carapace notably lacking the nuchal (Fig. 5C), and NDGS 35, the partial anterior half of a carapace (Fig. 5D). The most notable difference between these three specimens is their size. The carapace of NDGS 111 has a midline length of about 18.5 cm. NDGS 551 is incomplete, but we estimate its carapace length to have been about 24 cm by comparison to NDGS 111. As preserved, the midline length of NDGS 35 is about 26 cm, but we estimate it to have had a midline length of about 52 cm by comparison to NDGS 111. For simplicity, we will refer to these specimens as the small, medium, and large shells, respectively.

Carapace**:** The small and medium shells document that the carapacial disk consists of a nuchal, seven pairs of costals, and seven neurals (Fig. 5). A preneural is absent in both specimens. The surface texture pattern consists of an evenly distributed coarse netting. The recurved process of the nuchal forms a broad, but tightly packed comb, which we estimate to have been less than 45% of total carapace

width. A minute, round callosity is developed in the small specimen, but it lacks a posterior contact with the neural. True suprascapular fontanelles are thus not developed in this specimen. The nuchal is too poorly developed in the small specimen to allow the placement of the cervical joint to be assessed.

Only parts of the right half of the nuchal are preserved in the large specimen, but these document a highly unusual morphology among trionychids. The anterior portions of the lateral costiform processes are damaged, but what remains suggests that they form a tight comb that is located anterior to the costals. In extant trionychids, the nuchal only forms sutural contacts with the textured portions of the neurals and costals (Joyce 2025). The large specimen stands out by exhibiting a small textured patch near its midline, but a sutural contact with costal I is present nonetheless. The connection of the nuchal to the remainder of the carapacial shield is thus formed by deeper portions of the shell only. This appears to be unique among trionychids. Although the median portion of the nuchal and neural I are not preserved, the surrounding geometry suggests that a pair of true suprascapular fontanelles was developed, which, however, were not fully surrounded by textured bone.

The contiguous neural column of the small specimen consists of seven elements with a reversal as the fifth element (Fig. 5). A preneural is not developed. The neural column of the medium specimen differs by exhibiting a small, accessory midline contact of costal VI between neural VI and VII and by exhibiting an asymmetrical reversal spread over neurals IV and V. The large specimen confirms the absence of a regularly sized preneural. All shell specimens agree that the neurals are elongate elements.

The costals fan out evenly in all specimens (Fig. 5). The free rib ends are notably longer than the costals in the smallest specimen and somewhat shorter in the medium specimen. The free rib ends are damaged in the largest specimen, but can be speculated to have been relatively long, as the costal callosities are narrow. The lateral margins of the costals of the large specimen are damaged, but the intact portions show broad, untextured margins separated from the textured portions by a distinct step. As the deeper tissue is visibly distinct from the ribs, it is apparent that they represent metaplastically ossified dermis lacking surficial texturing (also see nuchal above).

***Plastron*:** NDGS 111 preserves a near complete plastron notably lacking xiphiplastra (Fig. 5B). The epiplastron possesses relatively elongate anterior processes that we estimate to have a length of about 50% of the slightly damaged lateral entoplastral processes. The spacing of the epiplastra is unclear, as both elements are displaced. Epiplastral callosities are not developed. The two broad lateral processes of the entoplastron converge upon each other at an angle of 90 degrees. A short, anterior plateau is developed between them at the anterior margin of the entoplastron. An entoplastral callosity is absent. The hyo- and hypoplastra jointly form a callosity, but are not fused to form a single element. The medial hyoplastral processes are composed of five tightly packed subprocesses. The hyo- and hypoplastra each form two lateral processes that converge upon one another at an angle of 70 degrees. The medial hypoplastral process is robust, ends bluntly, and is clearly separated from the posterior hypoplastral processes. The finely textured hyo-hypoplastral callosity covers much of the hyo- hypoplastral suture, contributes to the margins of the axillary and inguinal notches, but does not cover any of the processes.

Discussion

The validity of *Trionyx punctiger* and *Trionyx leucopotamicus*

Over the course of the last two centuries, countless fossil trionychid remains have been reported from North America that serve as the basis of more than 100 named species (Vitek and Joyce 2015; Valdes et al. 2017; Joyce et al. 2018 2019; Edgar et al. 2022; Jasinski et al. 2022; Lyson et al. 2021). The only name proposed to date for trionychid material possibly originating from the Oligocene of North Dakota is *Trionyx punctiger*, which was named as a sideline by Cope (1891) based on two fragments that he had previously reported (Cope 1883) from the "White River" of the Dakotas. As these elements cannot be identified in the Cope collections of the AMNH or USNM, they now appear to be lost (Vitek and Joyce 2015), including more detailed locality information that might have been associated with them. Hutchison (1996) stated that these fragments possibly originate from the Chadronian Chadron Formation of what is now Billings County, North Dakota. We agree with Hutchison (1996) that the material was collected in what is now North Dakota, as Cope (1883) wrote his letter from Sully Creek, a former town in what is now Billings County, North Dakota, but as White River deposits do not crop out in the direct vicinity of Sully Springs, we conclude that they might source from any of the many isolated late Eocene to Early Oligocene White River deposits known from nearby Billings, Dunn, Stark, or Slope counties. However, as Cope (1883) explicitly states that his fossils originate from the top of the section, we agree with Hutchison (1996) that it is plausible that they originate from what is now understood to be the Orellan–Whitneyan Brule Formation (see Geological Settings above), but as some outcrops do not reach the Brule Formation, we cannot be sure. According to Cope (1891), *Trionyx punctiger* can be diagnosed relative to his *Trionyx leucopotamicus*, a taxon based on a shell fragment the size of a thumb nail, by having less distinct sculpturing that reaches the sutural contacts of the costals but becomes less distinct towards their margins. These characteristics are utterly meaningless for diagnosing trionychids, given how much texture patterns vary interspecifically (Gardner and Russell 1994; Vitek and Joyce 2015). In conclusion, *Trionyx*

punctiger is based on two unfigured, now lost syntypes from the late Eocene to Early Oligocene of southwestern North Dakota diagnosed based on a character complex of no relevance to trionychid taxonomy. Thus, we agree with Vitek and Joyce (2015) that this taxon is a nomen dubium and that any referral of additional specimens is undesirable. Incidentally, this conclusion does not disrupt trionychid taxonomy, as *Trionyx punctiger* was consistently believed to be the invalid junior synonym of *Trionyx leucopotamicus* over the years (Hay 1908; Hummel 1932; Hutchison 1996).

The only other trionychid taxon based on material thought to be Oligocene at one point is the above-mentioned *Trionyx leucopotamicus* Cope, 1891. Cope (1891) named this species based on a small shell fragment (CMN 6323) that had been collected from the "White River" Swift Current Creek beds of Assiniboia, now southern Saskatchewan, which he believed to be Oligocene in age. Although *Trionyx leucopotamicus* should have been considered a nomen dubium by subsequent authors as it is based, once again, on undiagnostic remains, Hay (1908) assigned to it a reconstructed carapace (AMNH 6045) from the *Titanotherium* beds of the Hat Creek Basin of Nebraska, likely because he believed the material to originate from coeval White River deposits. Hat Creek is the primary river that drains much of northwestern Nebraska, so it is not possible to further constrict the origin of this specimen without further information. Hutchison (1996) concluded that Hay's (1908) complete hypodigm of *Trionyx leucopotamicus* is Chadronian (late Eocene) and assigned additional material from the Chadronian of South Dakota and the Orellan (Early Oligocene) of North Dakota, which was followed by Vitek and Joyce (2015). However, we here note that the Swift Current Creek fauna is long known to be Uintan (middle Eocene) in age (Storer 1984; Perry et al. 2023), so all attributions of Chadronian through Orellan trionychids to this taxon are somewhat dubious, especially as the holotype is undiagnostic. This taxonomic conundrum is typical for North American trionychids, as Hay (1908) regularly assigned specimens of some quality (i.e., AMNH 6045) to names based on undiagnostic remains. As Hay (1908) specimens quasi serve as the type of these taxa, Vitek and Joyce (2015) suggested that they should be designated as neotypes, which, however, demands writing a petition to International Commission of Zoological Nomenclature asking to make an exception to its rules. However, the International Commission of Zoological Nomenclature only rules in favor of petitions that resolve taxonomic instability by maintaining prevailing usage, which is characterized in Art. 23.9.1.2 (ICZN 1999) as usage found in "at least 25 works, published by at least 10 authors in the immediately preceding 50 years." We are thus doubtful that such a petition would even be considered, as *Trionyx leucopotamicus* is rarely discussed in the literature. We are thus left to conclude that *Trionyx leucopotamicus* should be viewed as a nomen dubium, as it is based on an undiagnostic trionychid shell fragment from the Uintan (middle Eocene) of Saskatchewan, and that the available Chadronian material might represent an unnamed trionychid species different from previously named trionychids from the Eocene and the new species we establish herein. Incidentally, AMNH 6045 is only a sub-ideal type for such a new species, as our personal observations suggest that much of its morphology is distorted by taphonomic damage and improper reconstruction.

Alpha taxonomy of Brule Formation trionychid material

As no valid species of trionychid has been named for material from the Oligocene of the entire North American continent, the quality material presented herein from the Orellan–Whitneyan Brule Formation of North Dakota almost by default represents a new taxon. We nonetheless summarize below why we believe our hypodigm to present a single species and briefly differentiate it from other valid species.

The five specimens described herein were collected from three different localities on different occasions but originate from a narrow geographical and temporal range, the Early Oligocene (Orellan–Whitneyan NALMAs) Brule Formation of Slope and Stark Counties, North Dakota. The holotype cranium (NDGS 112) and the referred mandible (AMNH 12422) agree by representing mid-sized animals with slightly expanded triturating surfaces and by displaying characteristics typical of wide-snouted species of Apalonini, in particular the development of large choanae, a large foramen intermaxillare, contribution of the vomer to the posterior margin of the foramen intermaxillare, the arrangement of the bones in the postorbital bar, a foramen jugulare posterius fully confluent with the fenestra postotica, presence of a moderate overhanging flange of the quadrate over the articular condyle, a moderately long mandibular symphysis lacking a ridge, and presence of weakly developed posteromedial flanges of the triturating surface. We are thus particularly confident that these two specimens represent the same species.

The postcranial material differs by representing three differently sized individuals. Although overlap is incomplete, all specimens agree in lacking a preneural and stand out by documenting narrow, neotenic costal callosities that only partially cover the ribs. The two smaller specimens (NDGS 111 and 551) furthermore agree by possessing a reversal towards the posterior of the column and, more notably, only seven pairs of costals. The large specimen (NDGS 35) additionally resembles the more complete small specimen (NDGS 111) by possessing a relatively narrow nuchal (ca. 45% of carapace width) with an unusually minute nuchal callosity. The apparent differences, in particular the stepped lateral margin of the costals and the sutural contact of the nuchal with costal I, resulting in the formation of paired suprascapular fontanelles, are consistent with ontogenetic changes (Joyce

2025). While the near complete reduction of the nuchal callosity is relatively unique among trionychids (also seen in some *Axestemys* spp.: Vitek 2012), the remaining characters listed above are broadly consistent with an apalonine identity (Joyce 2025).

In conclusion, the available material can all be assigned to the clade Apalonini and provides no evidence for the presence of more than one taxon. The sample thus plausibly documents an ontogenetic series of a large-sized species commencing with the two smaller shells, followed by the skull material, and, finally, the larger shell.

The new species differs from all named Neogene and extant species of *Apalone* by the presence of a highly reduced nuchal callosity, development of a small hyo-hypoplastral callosity that only partially covers the surrounding processes, relatively elongate anterior epiplastral processes, and two lateral hyoplastral processes (Valdes et al. 2017; Joyce 2025). The new species resembles *Rafetus euphraticus* and *Rafetus swinhoei* (Joyce 2025), but differs from *Rafetus bohemicus* (Chroust et al. 2023), by exhibiting two lateral hyoplastral processes. However, the new species differs distinctly from all currently recognized species of *Rafetus* (Chroust et al. 2023; Joyce 2025) by the presence of a highly reduced nuchal callosity.

Among named Eocene taxa, *Rafetus lysoni* sp. nov. most apparently contrasts *Axestemys* spp. (e.g., *A. byssinus*, *cerevisia*, and *ellipticus*) and *Plastomenus thomasii* (Cope, 1872) by lacking a preneural element (Hay 1908; Vitek 2012). *Rafetus lysoni* greatly differs from the Bridgerian "*Trionyx*" *scutumantiquum* Cope, 1873 ("*Trionyx*" *antiqua* of Vitek and Joyce 2015) by having a posteriorly recurved nuchal with a reduced nuchal callosity (not an anteriorly flat nuchal with broad nuchal callosity), narrow costal callosities with long free ribs ends, a reduced number of posteromedial hypoplastral process (not a dense fan of processes), and a reduced hyo-hypoplastral callosity that does not cover the processes (Hay 1908; Vitek and Joyce 2015). The new species furthermore differs greatly from the Bridgerian "*Trionyx*" *mira* (Hay 1908; Vitek and Joyce 2015) by being much larger, by having a much broader skull with more widely spaced orbits and expanded triturating surfaces, a reduced nuchal callosity, long free rib ends, and a reduced hyo-hypoplastral callosity, not an expanded one that fully covers the processes medially and protrudes deeply into the axillary notch. *Rafetus lysoni* similarly differs from the poorly known Uintan "*Trionyx*" *egregia* (Hay, 1908) (herein considered valid, contra Vitek and Joyce 2015) by its reduction of the nuchal and costal callosities (Hay 1908).

In contrast to all previously listed Eocene taxa, we note similarities between *Rafetus lysoni* sp. nov. and the Bridgerian "*Trionyx*" *uintaensis* (herein conceptualized to be restricted to material from the Bridger, contra Vitek and Joyce 2015) as the two possess two lateral hyoplastral processes, a reduced count of medial hyo- and hypoplastral processes, and a reduced hyo-hypoplastral callosity that only poorly covers the processes. The two taxa differ, nonetheless, in the starkly different development of the nuchal and costal callosities, which are poorly developed in *Rafetus lysoni*, but well developed in "*Trionyx*" *uintaensis* (Hay 1908; Zangerl 1944; Vitek and Joyce 2015).

Vitek (2011) described a skeleton from the Uintan (YPM PU16104) under the name "*Trionyx*" *uintaensis*, but we here disagree with the attribution of this specimen to this species, as it differs in age and in the development of a much better ossified plastron. Instead, this skeleton appears to represent a new, unnamed Uintan taxon. *Rafetus lysoni* sp. nov. resembles the skull of this unnamed taxon by exhibiting large foramen intermaxillare and choanae, vomer contributing to the posterior margin of the foramen intermaxillare, and foramen jugulare posterius fully conjoint with the fenestra postotica, but differs distinctly by possessing poorly ossified nuchal, costal, and hyo/hypoplastral callosities.

We thus conclude that the material from the Orellan–Whitneyan Brule Formation of North Dakota represents a novel morphotype that justifies assigning it to the new species *Rafetus lysoni.* It is unclear to us if this species can be extended to include Chadronian material, as most of those specimens lack basic description.

As trionychids show particularly high levels of homoplasy and polymorphism, it is difficult to evaluate the phylogenetic relationships of a species using key characteristics alone. The material described herein shows a series of apalonine characteristics, of which most have an uneven distribution across the apalonine tree. These include development of a curved lateral process of the postorbital that nearly contacts the anterior process of the quadratojugal within the upper temporal fossa (also present in *Rafetus euphraticus*, polymorphic in *Apalone spinifera*), development of a short bony palate with reduced intermaxillary contact and large intermaxillary foramen and palatal groove (present in all apalonines), location of the foramen alveolar superius anterior to the suborbital crest (also seen in *Apalone spinifera* and *Apalone mutica*), a short vomer with long contact between the palatines (present in *Apalone* spp.), absence of midline contact of pterygoids (also seen in *Apalone* spp.), absence of an underlap of the parabasisphenoid by the pterygoid (as seen in *Apalone ferox* and *Apalone mutica*), reduced costal callosities (as seen in *Apalone spinifera*), the plesiomorphic retention of two lateral hyoplastral processes (presence in *Rafetus* spp.), a reduced hyo-hypoplastral callosity (as seen in *Rafetus euphraticus*), and contribution of the hyo-hypoplastral callosity to the axillary notch (as seen in *Apalone* spp.). As the new species appears closest to *Rafetus*, we refer it to this genus to avoid the needless propagation of monotypic genus names. We will explore the phylogenetic position of *Rafetus lysoni* sp. nov. in an upcoming contribution focused on the evolutionary history of North American trionychids. If future work suggests that this species is more closely related to extant *Apalone* than extant *Rafetus*, we suggest referral to *Apalone* instead.

Paleoecology

Trionychids have a rich, but unevenly distributed fossil record across North America (Vitek and Joyce 2015). In a landmark paper, Hutchison (1992) documented a linear decline in aquatically adapted reptiles in the fossiliferous basins of the western interior, including trionychids, from the middle Eocene (Bridgerian) to early late Eocene (Uintan), followed by a strong decline between the late late Eocene (Chadronian) to Early Oligocene (Orellan). This does not document the global extinction of the effected taxa, but rather regional aridification (Hutchison 1992). Although extant trionychids inhabit a broad set of aquatic habitats across the globe (Ernst and Barbour 1989), we note that extant apalonines are mostly restricted to riverine habitats. The near absence of the group in Chadronian to Orellan deposits of the western interior as such perhaps signals the absence or scarcity of appropriate riverine habitats at that time. However, faunal and geological evidence at Fitterer Ranch indicates the local environment was wetter than contemporaneous deposits from elsewhere in the Great Plains region. Aqueous screen washing of rocks from the lower through middle portions of the Brule Formation at Fitterer Ranch produced a diverse lissamphibian fauna composed of fossorial (e.g., Scaphiopodidae), arboreal (e.g., Hylidae), and semiaquatic (e.g., Ranidae) taxa, indicative of a more mesic environment than typically recorded in Oligocene deposits within the Great Plains region (Driebergen 2019). Most of those fossils were recovered from sandstones deposited within incised stream channels at various stratigraphic positions within the lower to middle Brule Formation (Korth et al. 2023). Those sandstones indicate the presence of rivers or streams, or a series of rivers or streams, in the vicinity of the Fitterer Ranch locality at this time, providing support for the interpretation of a mesic environment at this site. Driebergen (2019) also identified a specimen of the caudatan *Siren dunni* (NDGS 2826), which indicates the presence of a year-round water source as extant sirenids are fully aquatic (Holman 2006). Finally, another locality at Fitterer Ranch (NDGS L4161) that is in a similar stratigraphic position as the one that produced the trionychid specimens (NDGS L28) produced a partial skeleton of an alligatorine (NDGS 22741), providing additional support for the presence of persistent water sources in southwestern North Dakota during the Whitneyan.

The environmental conditions recorded in the Brule Formation at White Butte and West Rainy Butte where AMNH 12422 and NDGS 35, respectively, were recovered have not been studied in as much detail as Fitterer Ranch. However, both of those specimens were recovered from sandstone deposits lithologically similar to those recorded at Fitterer Ranch, suggesting that persistent water sources (e.g., streams/rivers) were present at both locations and mesic environmental conditions were likely present in those areas. These unique environmental conditions in North Dakota during the Whitneyan allowed trionychids to thrive in this region despite their absence from contemporaneous faunae elsewhere in the Great Plains where more arid conditions persisted.

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Author contributions

LCG segmented skull. CAB and LCG 3D scanned specimens. WGJ created photographs and assembled figures. WGJ wrote primary draft of manuscript. All coauthors approved final draft.

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Data availability

All of the data that support the findings of this study are available in the main text.