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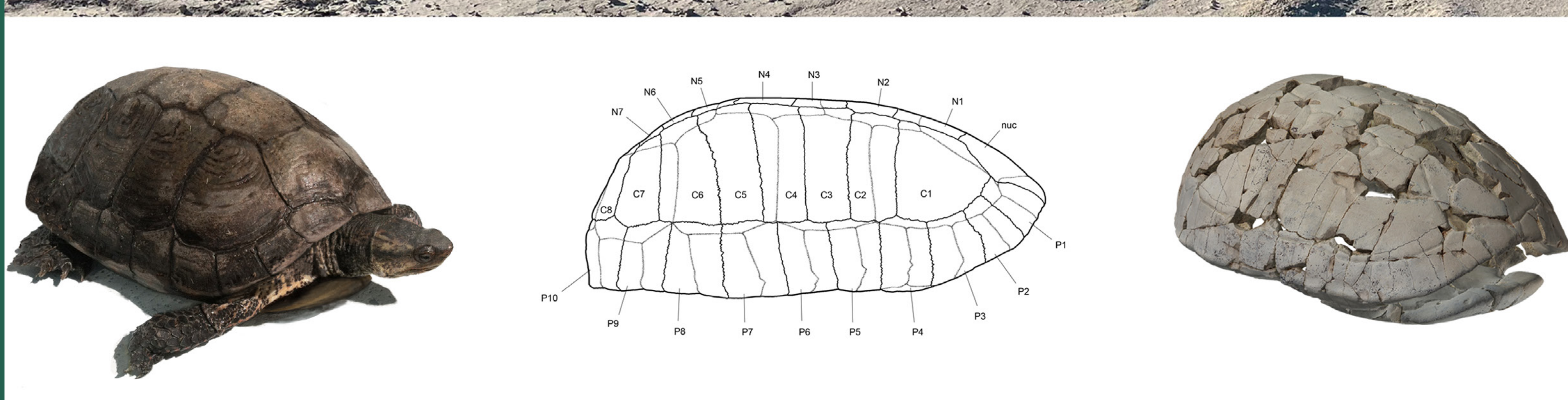

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Cover image: Badlands in Sioux County, Nebraska (top), type area of *Notapachemys oglala* (bottom) shown as reconstruction (left), line illustration (center), and photogrammetry model of holotype (right).

A NEW GEOEMYDID (TESTUDINES, AFF. RHINOCLEMMYDINAE) FROM THE UPPER EOCENE CHADRON FORMATION (WHITE RIVER GROUP) OF NORTHWESTERN NEBRASKA

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ABSTRACT

Notapachemys oglala, gen. et sp. nov., is described based on carapace and plastron fossils collected from upper Eocene (Chadronian NALMA, White River Group) exposures in northwestern Nebraska, U.S.A. It is recognized as having a thick, smooth, partly fused, acarinate, egg-shaped carapace with strong plastral hindlobe kinesis. Many of these traits are present in some ptychogastrine geoemydids, a group known from the early Eocene to late Miocene of Europe. However, other aspects of shell morphology such as a six-sided Neural 1, medial gular notch, lack of distal gular tubercles, absence of inguinal scutes, and elongate kinetic inguinal buttresses resemble semi-aquatic to semi-terrestrial species of the New World tropically distributed genus *Rhinoclemmys*. The new taxon is one of the oldest plausible stem rhinoclemmydine geoemydids that possesses a mosaic of ptychogastrine and rhinoclemmydine features, suggesting the possibility of a close but unresolved relationship between these two groups. A convoluted history of ptychogastrines and rhinoclemmydines in North America is further exemplified in the early Miocene of the Panama Canal Basin, where ptychogastrine fossils from the Las Cascadas Formation (~22–20 Ma) and the oldest *Rhinoclemmys* fossils from the Cucaracha Formation (~18–16 Ma) have been collected in a region where *Rhinoclemmys* still lives today.

Key words: White River, Nebraska, late Eocene, Chadronian, Geoemydidae, Rhinoclemmydinae, Ptychogastrini

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Bourque, J. R. 2021. A new geoemydid (Testudines, aff. Rhinoclemmydinae) from the upper Eocene Chadron Formation (White River Group) of northwestern Nebraska. Bulletin of the Florida Museum of Natural History 58(5):86–101.

INTRODUCTION

The Eocene-Oligocene transition is an interval of significant global climate change accompanied by faunal turnover (Prothero, 1994; Woodburn, 2004; Zachos et al., 2001). It marks the end of the Eocene Greenhouse World (late Chadronian) and onset of the Icehouse World in the Oligocene (early Orellan), with a notable decrease in marine and continental temperatures in the Orellan (Zachos et al., 2001; Zanazzi et al., 2007). Relatively little has been published regarding the non-testudinid semi- and fully aquatic freshwater turtles during this transition. Hutchison (1996) summarized the chelonians from this interval and noted seven aquatic/semi-aquatic turtle taxa that co-occurred in the Chadronian of the White River Group. Turtles previously reported from the Chadron include (after Hutchison, 1996): *Xenochelys formosa* Hay 1906, Anosteirinae, *Apalone leucopotamica* (Cope 1891), cf. *Echmatemys* sp., Ptychogastrini, *Pseudograptemys inornata* (Loomis 1904), and *Chrysemys antiqua* (Clark 1937). Only two of these (*A. leucopotamica* and '*C.*' *antiqua*) have been collected in the Orellan, and one, '*C.*' *antiqua* in the Whitneyan. Within this fauna, Hutchison (1996) reported the first occurrence of an undescribed ptychogastrine geoemydid (referred specimens: SDSM 10052, SDSM 11714, SDSM 28132, and SDSM 28133) with an akinetic plastral forelobe and kinetic plastral hindlobe. Ptychogastrines have a fossil record from the early Eocene to late Miocene of Europe (Hervet, 2006). Hervet (2006) presented phylogenetic hypotheses for ptychogastrine genera, but the relationship of ptychogastrines to other geoemydids is poorly understood. Referred specimens of Hutchison (1996) were not available for examination by JRB at the time of writing but are likely synonymous with a new taxon described herein.

Locality Background

Type and referred specimens described here were collected from White River Group Chadronian exposures around Twin Buttes on the Sand Creek Ranch, and adjacent areas in the Oglala National Grasslands, Sioux County, northwestern Nebraska from 2016 to 2021 (Figs. 1–2). The study area is just south of Toadstool Geological Park. Fossils have been collected in this region for well over 100 years (Loomis, 1904; O'Harra, 1920), and previously reported aquatic reptiles include some of oldest fossils of *Alligator prenasalis* from the Chadronian (Whiting and Hastings, 2015). Chadronian reptiles from directly around the Twin Buttes area are presented here and previously unreported. Fossils were found *in situ* amongst stratified bluish to blue-green and milk chocolate brown colored paleosols that occur stratigraphically below the UPW (Upper Purplish White Layer) that approximately demarcates the Eocene-Oligocene transition (LaGarry, 1998; Prothero and Emry, 2004). The blue-green paleosols in this region are easily recognized as Chadronian (O'Hara, 1920) because they produce late Eocene index taxa that do not occur in younger Orellan and Whitneyan sediments in the study area. Index taxa include titanotheres (Prothero and Emry, 2004), comprised of nearly complete *in situ* skeletons as well as isolated bones. All freshwater turtle fossils collected for this study were found in direct association or in the same stratigraphic horizons as titanothere fossils. Chadronian lizards, crocodilians, and freshwater turtles that co-occur with titanotheres in the Twin Buttes area include the large armored lizard *Helodermoides* sp., *Alligator* sp., *Xenochelys* sp. (small form), Kinosternidae gen. et sp. indet., '*Chrysemys*' *antiqua* (Emydidae), Anosteirinae, Trionychidae, Geoemydidae (Morphotype 1), and a aff. rhinoclemmydine geoemydid gen. et sp. nov. (semi-aquatic box turtle morphotype, described below). As is the case with titanotheres, these reptiles likewise disappear by the late Chadron and are not found in Orellan and Whitneyan deposits in the study area (pers. observ.). This differs from findings of Hutchison (1996) regarding post-Chadronian occurrences of *A. leucopotamica* and '*C.*' *antiqua*, as well as *Helodermoides* records in the Orellan (Sullivan and Holman, 1996), and may be the result of fewer Orellan–Whitneyan paleowetland deposits in the current study area. '*Chrysemys*' *antiqua* is the most common aquatic turtle collected in the region. The testudinid *Stylemys* is common in the Chadronian through Whitneyan, and *Oligopherus* is common in the Chadronian and Orellan. It is currently unclear how many testudinid species are involved spanning the Chadronian through Whitneyan in the study area.

MATERIAL AND METHODS

Virtual mesh models of UF 527000 and UF 527218 were produced using photogrammetry with a Canon EOS RP in the Division of Digital Imaging, Florida Museum of Natural History (FLMNH). Images used in figures were developed from the models. Mesh models are publicly available at https://www.morphosource.org using the following links: https://www.morphosource.org/concern/biological_specimens/000396342 and https://www.morphosource.org/concern/biological_specimens/000396355. MorphoSource Media IDs: UF 527000, carapace, images: 000396344; UF 527000, carapace, mesh: 000396347; UF 527000, plastron, images: 000396350; UF 527000, plastron, mesh: 000396350; UF 527218, plastron, images: 000396357; UF 527218, plastron, mesh: 000396360.

Materials Examined

Notapachemys oglala: UF 527000, UF 527218–UF 527223; *Bridgeremys pusilla*: UF 529329–UF 529331; Ptychogastrini gen. et sp. nov. (Las Cascadas Formation, Panama): UF 267054, UF 267127, UF 267136, UF 475212, UF 275421, UF 280152, UF 280422, UF 280569, UF 280570; *Rhinoclemmys annulata*: UF/H 99676; *Rhinoclemmys areolata*: UF/H 54199, UF/H 76922; *Rhinoclemmys funerea*: UF/H 137638, UF/H 152560; *Rhinoclemmys pulcherrima*: UF/H 41046 (Nicaragua), UF/H 52797 (Costa Rica), UF/H 55442 (Honduras), UF/H 55574 (Honduras), UF/H 76923 (Guatemala); *Rhinoclemmys rubida*: UF/H 51411, UF/H 54197, UF/H 54787, UF/H 54980. Numerous Old World geoemydid skeletal specimens currently housed in the Division of Herpetology, FLMNH, were used extensively for comparison during this study.

Institutional Abbreviations

SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota; **UF**, Division of Vertebrate Paleontology, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **UF/H**, Division of Herpetology, Florida Museum of Natural History, University of Florida, Gainesville, Florida.

Anatomical Abbreviations

Bones: **C**, costal; **ent**, entoplastron; **epi**, epiplastron; **hyo**, hyoplastron; **hyp**, hypoplastron; **N**, neural; **P**, peripheral; **xip**, xiphiplastron. Scutes: **abd**, abdominal; **anl**, anal; **ax**, axillary; **fem**, femoral; **gul**, gular; **hum**, humeral; **pec**, pectoral; **M**, marginal; **V**, vertebral. Other: **amd**, axillary musk duct; **axb**, axillary buttress; **axbs**, axillary buttress suture; **imd**, inguinal musk duct, **ingb**, inguinal buttress; **ingbs**, inguinal buttress suture; **ingr**, inguinal groove; **mgn**, medial gular notch.

SYSTEMATIC PALEONTOLOGY

Order TESTUDINES Batsch 1788
Family GEOEMYDIDAE Theobald 1868
Subfamily aff. RHINOCLEMMYDINAE Gray 1873

NOTAPACHEMYS OGLALA gen. et sp. nov.

Holotype.—UF 527000, nearly complete carapace and associated plastral forelobe (Figs. 3–6; Fig. 8). Collected by J. R. Bourque on 21 September, 2016.

Paratype.—UF 527218, nearly complete plastral hindlobe (Figs. 3 and 8). Collected by R. W. Portell and J. R. Bourque on 14 September, 2021.

Referred Specimens.—UF 527219, left portion of carapace (fused P6–8 and distal costals, a partial left hypo-xiphiplastron may be associated with specimen); UF 527220, right P4 and left P7 (probably associated); UF 527221, left P7 and right P11 (possibly associated); UF 527222, right partial xiphiplastron, proximal costal, partial left P1 (from same wash, possibly associated); UF 527223, left P11 (Fig. 7).

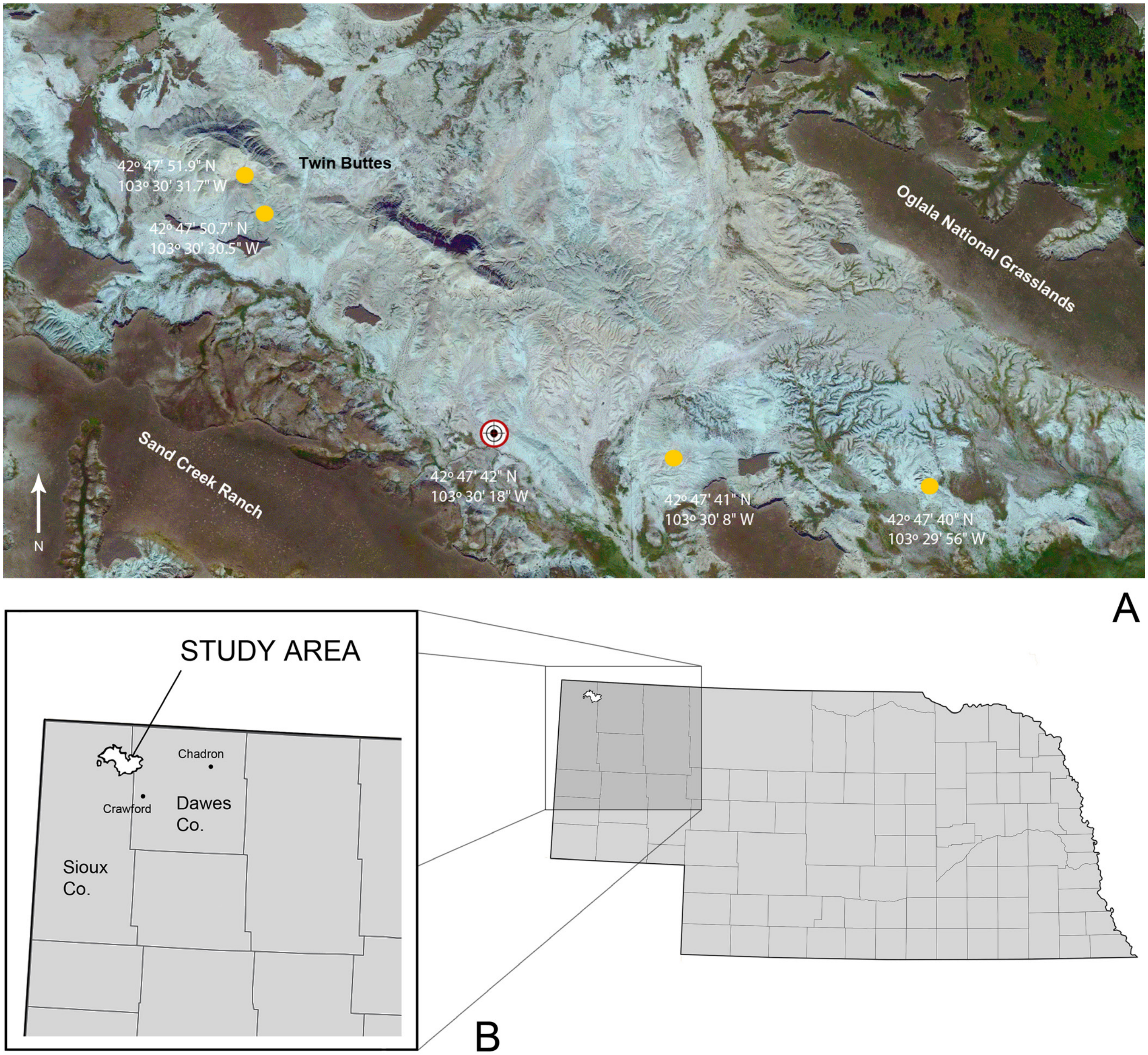

Figure 1. A) Satellite image of Twin Buttes area, Sioux County, Nebraska, the type locality of *Notapachemys oglala*. Holotype locality indicated by registration symbol. Paratype and referred specimen localities indicated by yellow dots. Image modified from Google Earth. Colors enhanced to better show blue-green Chadronian paleosols common in the study area that produce freshwater turtle fossils. B) County map of Nebraska, USA, with inset of study area in northwestern region.

Zoobank Nomenclatural Act.— Genus: urn:lsid:zoobank.org:act:F5639724-5694-4C7A-B34A-D2AE038C54A3. Species: urn:lsid:zoobank.org:act:48A12A5B-3785-4A40-9E7C-3E47437E6178.

Etymology.—Generic epithet is combination of Latin *notabilis* for 'remarkable', Greek *pachys* for 'thick', and *emys* for 'freshwater turtle'. Species epithet refers to the type area in and adjacent to the Oglala National Grasslands, which is named for a Lakotan community in the region.

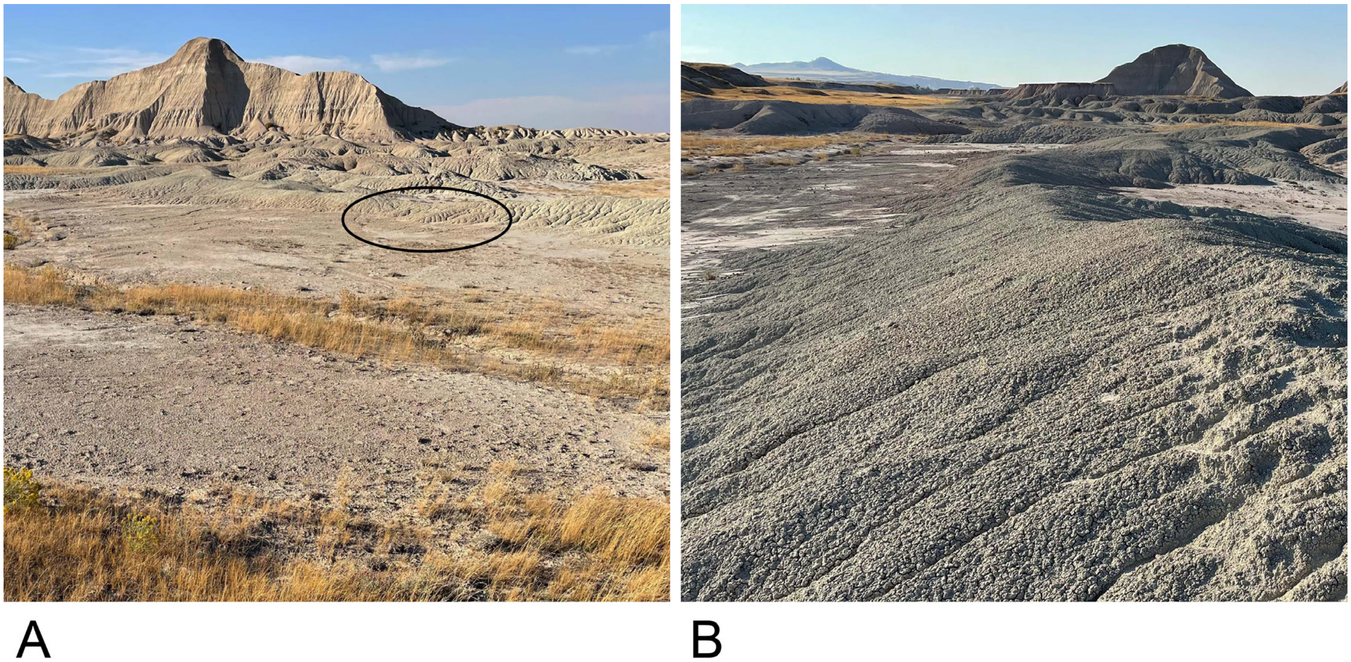

Figure 2. A) Type locality of *Notapachemys oglala* in September 2021, facing north. Oval indicates approximate collection spot of UF 527000, which was found at the base of the encircled low ridge. B) Type locality the same day facing northwest, illustrating the blue-green and brown Chadronian paleosols common in the area.

Type Localities.—(Figs. 1–2) Sioux County, Nebraska. Datum for all provided coordinates is WGS84. Holotype UF 527000: Sand Creek Ranch, Twin Buttes area, 42º 47’ 42” N, 103º 30’ 18” W. Found at base of low ridge situated just south by southwest of Twin Buttes (Figs. 1–2). Shell was weathering out and partially disarticulated, but partially buried *in situ* at contact between blue-green and bluish-brown paleosols. Paratype UF 527218: Twin Buttes Southeast, Oglala National Grasslands, 42º 47” 40’ N, 103º 29’ 56” W. Collected *in situ* amongst multiple titanothere skeletons from a blue-green paleosol layer. UF 527219: Sand Creek Ranch, Twin Buttes area, 42º 47” 50.7’ N, 103º 30’ 30.5” W; UF 527220: Sand Creek Ranch, Twin Buttes area, 42º 47” 51.9’ N, 103º 30’ 31.7” W; UF 527221: Twin Buttes Southeast, Oglala National Grasslands, 42º 47” 40’ N, 103º 29’ 56” W; UF 527222: Twin Buttes Southeast, Oglala National Grasslands, 42º 47” 41’ N, 103º 30’ 08” W; UF 527223: Dawes County, Nebraska, Oglala National Grasslands, 42º 48” 4’ N, 103º 27’ 45” W.

Occurrence.—Late Eocene, Chadronian NALMA, Chadron Formation, White River Group, ca. 35.5–33.8 Ma (Prothero and Emry, 2004).

Diagnosis.—The new taxon is diagnosed as a geoemydid in being a testudinoid with a short broad triangular cervical scute and presence of axillary and inguinal musk ducts, and in part as a rhinoclemmydine in having reduced to absent axillary scutes and no inguinal scutes (shared with some ptychogastrines). It is diagnosed as a new genus and species by the unique combination of the following: carapace thick and smooth (with some faint growth annuli); neurals acarinate; V1 broad, lateral sulci broadly overlap C1 and barely contact nuchal at widest point; N1 six-sided (shared with *Rhinoclemmys* at the exclusion of Ptychogastrini, *Echmatemys*, and *Bridgeremys pusilla*); anterior and posterior peripherals thick and flat dorsally (not flared) with marginals unnotched (giving carapace an egg-shaped appearance); bridge peripherals lack pronounced lateral keel dorsally; carapacial sutures fused (in adults); plastral bones fused except

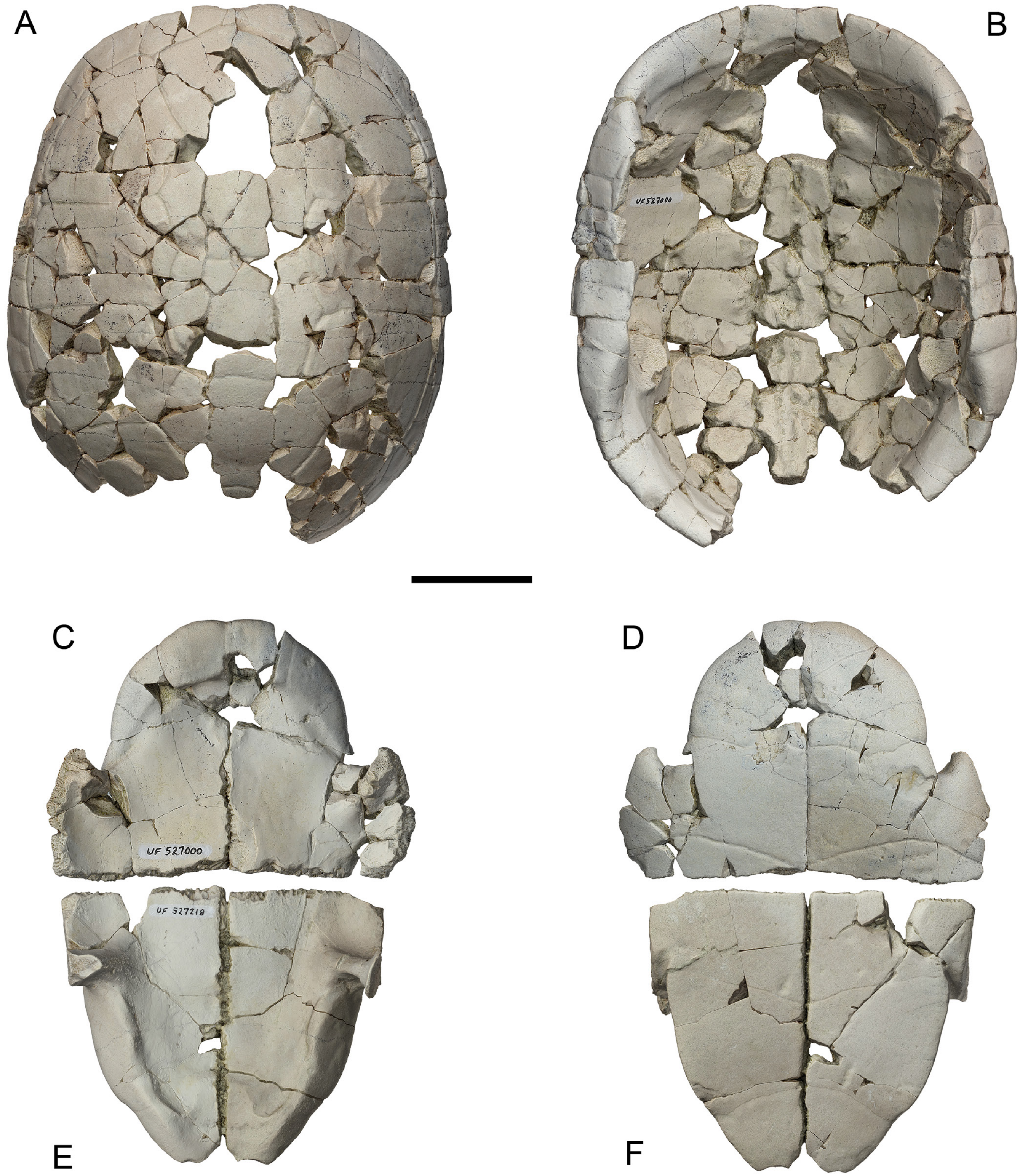

Figure 3. Type specimens of *Notapachemys oglala*. A–D) holotype UF 527000 and E–F) paratype UF 527218. Carapace in A) dorsal and B) ventral views. Plastral forelobe in C) dorsal and D) ventral views. Plastral hindlobe in E) dorsal and F) ventral views. Scale bar for A–D) equals 3 cm. E–F) rescaled to approximate size of C–D) to create composite plastron. Images produced using photogrammetry models.

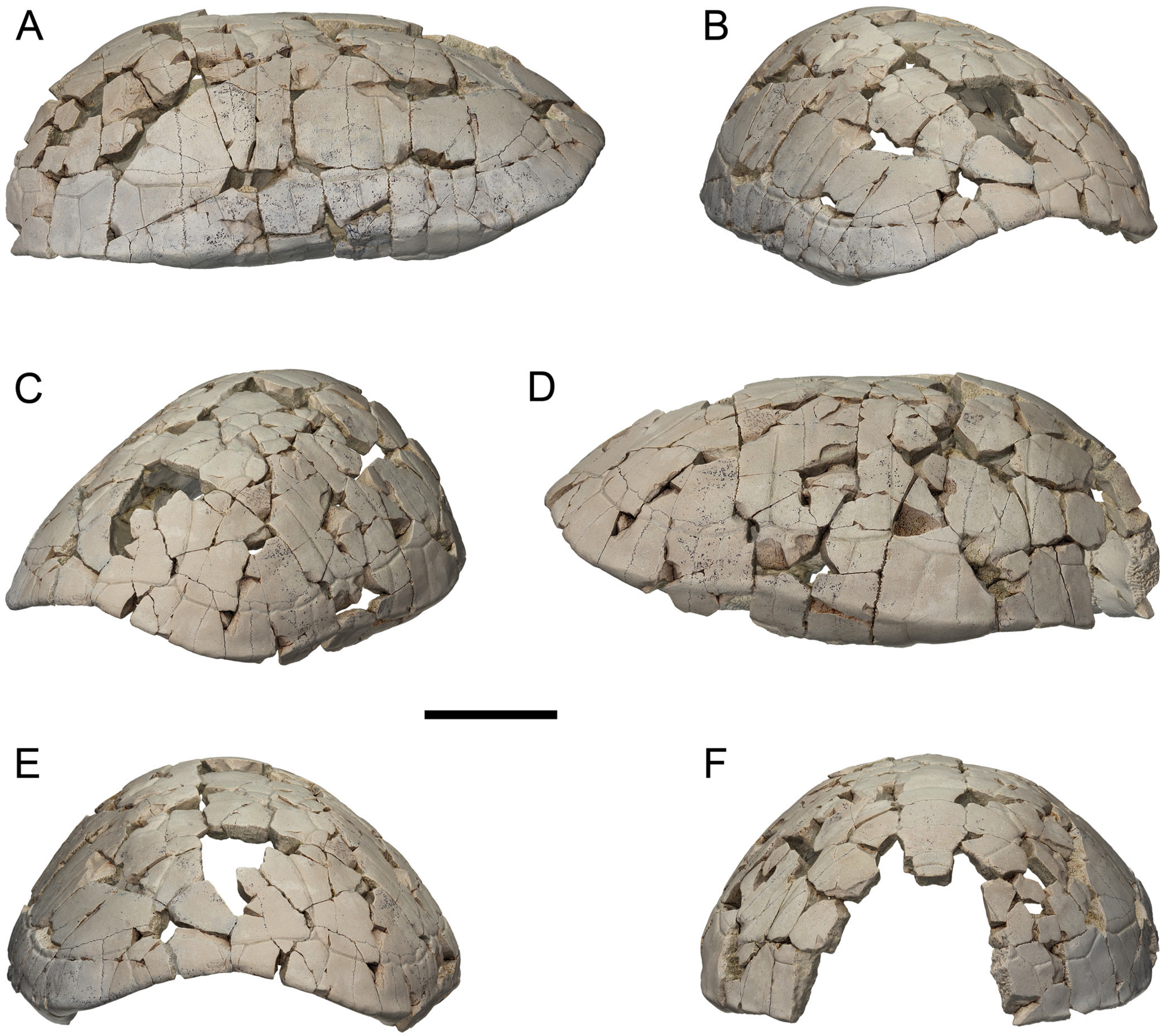

Figure 4. Carapace of UF 527000 in A) right lateral, B) right anterior, C) left anterior, D) left lateral, E) anterior, and F) posterior views. Images produced using photogrammetry model. Scale bar equals 3 cm.

transverse hyo-hypoplastral suture; medial hypo-xiphiplastral suture unfused; axillary buttresses suturally united to carapace; inguinal buttresses elongate and broadly L-shaped with ligamentous attachment to carapace, lack interdigitating sutural connection with carapace (shared with semi-aquatic species of *Rhinoclemmys*); gulars rounded anteriorly with moderate medial notch along anterior margin; pectoral-abdominal and abdominal-femoral sulci strongly curved posteriorly toward midline; distinct inguinal groove at base of inguinal buttress on ventrolateral hypoplastron.

DESCRIPTION AND COMPARISONS

Carapace.—The carapace of UF 527000 is nearly complete, missing N1, pygal, suprapygals, left and posterior portion of right C8, left P10, and P11 set. The general shape of the carapace is tall medioposteriorly and smooth with some faint

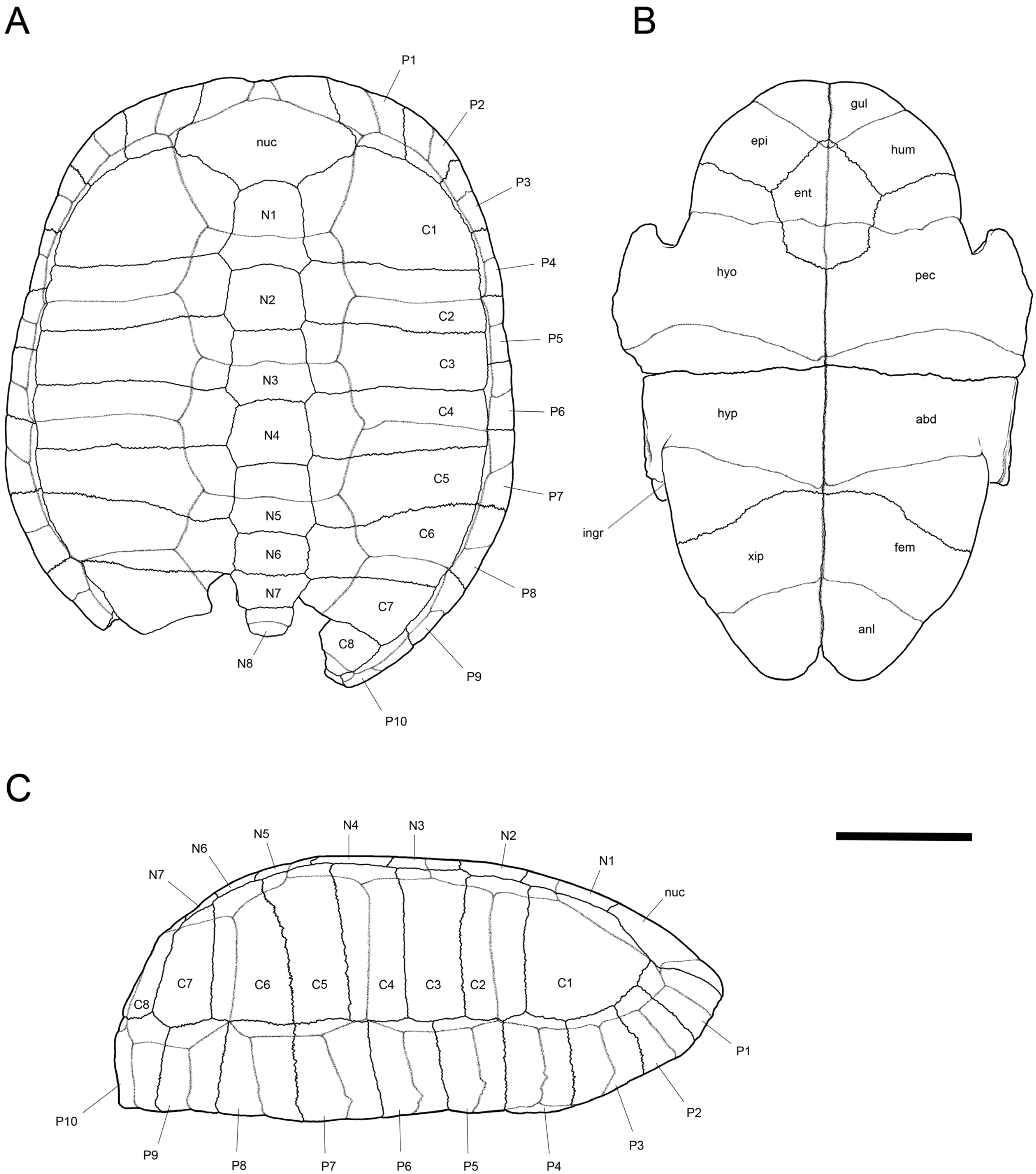

Figure 5. Carapace and plastron reconstruction of *Notapachemys oglala*. A) carapace in dorsal view. B) plastron in ventral view. C) carapace in right lateral view. See 'Anatomical Abbreviations' for labels. Scale bar equals 3 cm.

Figure 6. Articulated carapace and plastral forelobe of UF 527000 in oblique right anterolateral view. Image produced using photogrammetry model. Scale bar equals 3 cm.

growth annuli. The carapacial rim lacks inter-marginal notches. The nuchal lacks a substantial cervical notch. The neurals lack a mid-dorsal keel. The anterior and posterior peripherals are flat dorsally and not flared, and the bridge peripherals have only a faint lateral keel. These features give the carapace an egg-shaped appearance. The holotype of *Ptychogaster grundensis* Bachmeyer and Schaffer (1959) similarly lacks a distinct cervical notch, lacks a mid-dorsal keel, lacks a lateral peripheral keel, and has relatively non-flared posterior peripherals. *Rhinoclemmys* examined have flared posterior peripherals, faint to developed mid-dorsal keel, more pronounced lateral keel on the bridge peripherals, and a more distinct cervical notch.

The shell is that of an adult because all sutures are fully formed, many of which began to fuse in life. Fused sutures consist of N2–N4, N6–N8, left and right C2–C3, left C4–C7, and right C4–C6. UF 527000 is not maximum adult size for the species, evidenced by paratype UF 527218, which is slightly larger than UF 527000 (Table 1). Aged adults likely had a fully fused carapace and partially fused plastron similar to other box turtle morphotypes such as *Ptychogaster emydoides* Pomel (1847) and other members of the *Ptychogaster*/*Temnoclemmys* group (Bachmeyer and Schaffer, 1959; Schäfer, 2012; fig. 3), and extant *Terrapene*. The distal peripheral sutures that unite the carapace with the plastron likely remained unfused in adults.

V1 is broad and the lateral sulci are convex, like that of most *Rhinoclemmys*, *Bridgeremys pusilla*, and *Ptychogaster grundensis*. V1 through V4 are preserved and all are wider than long. N1 is missing, but the shape is discernable by the surrounding bones. It is six-sided which compares well with some *Rhinoclemmys*. Species of *Echmatemys* and *Bridgeremys pusilla* (Hay, 1908; Hutchison, 2006) have a simpler shaped ovoid four to five-sided N1. Ptychogastrines also have an ovoid N1, but this condition may be polymorphic in the middle Eocene taxon *Geiselemys ptychogastroides* (Hummel 1935). In UF 527000, N1–N8 are wider than long. N1–N5 are posteriorly symmetrically short-sided, N6 and N8 broadly rectangular, and N7 anteriorly symmetrically short-sided.

The carapace possesses axillary and inguinal musk ducts. The axillary musk duct is preserved on the left side only for UF 527000 and is located on the middle of P3 at the axillary buttress contact. The inguinal musk duct is visible on UF 527000 and referred specimens UF 527219–UF 527221 (Fig. 7). It is located on the posteromost P7, at the junction of the inguinal buttress and the M8 sulcus. The axillary bridge terminus is located on distalmost C1 and the bridge suture extends across P3 and anterior P4. The inguinal buttress terminus is located on C5–C6. The inguinal sutural facet is broad and extends across P7–P8. The axillary notches of the carapace are chipped, but the shell seems to lack axillary scutes, or if present they were very small in life. Inguinal scutes are absent. In UF 527000, there is a narrow area along the posterior bridge buttress (where the musk duct is located) that was an attachment area for skin or other connective tissue in life. By comparison, species of *Echmatemys*, *Bridgeremys pusilla*, and most extant Old World geoemydids have axillary and inguinal scutes. *Sacalia* has a similar condition to *Rhinoclemmys* in having small axillary scutes and no inguinal scutes.

Feature	UF 527000	UF 527218
CL (actual)	151	---
CL (total estimated)	155	---
CW (distorted)	123.52	---
FLL	72.3	---
FLW	102.62	---
NUCL	36.74	---
NUCW	43.95	---
N1L	21.88	---
N1W	22.44	---
N2L	16.62	---
N2W	20.22	---
N3L	17.88	---
N3W	21.86	---
N4L (approximate)	16.82	---
N4W (approximate)	20.59	---
N5L (approximate)	15.7	---
N5W	20.87	---
N6L	12.03	---
N6W	17.79	---
N7L	10.05	---
N7W	19.51	---
N8L	8.9	---
N8W	11.29	---
CERVL	8.16	---
CERVW	7.71	---
V1L (approximate)	40	---
V1W	46	---
V2L (approximate)	33	---
V2W	44.68	---
V3L	32.61	---
V3W (approximate)	45	---
V4L	33.56	---
V4W (approximate)	48	---
DGL	17.49	---
MGL	19.46	---
IHL	18.16	---
IPL	33.99	---
ENTL (approximate)	30.11	---
ENTW	27.5	---
HLL (midline)	---	87.08
HLL (total estimated)	---	95
HLW	---	107.97
CNW (approximate)	---	11.78
IABL	---	36.93
IFL	---	26.75
IAL	---	22.31

Table 1. Measurements (in mm) of UF 527000, holotype carapace and associated plastral forelobe, and UF 527218, plastral hindlobe. Abbreviations: CERVL, cervical scute length; CERVW, cervical scute width; CL, carapace length; CNW, caudal notch width; CW, carapace width; DGL, dorsal gular overlap length; ENTL, entoplastron length; ENTW, entoplastron width; FLL, plastral forelobe length; FLW, plastral forelobe width; HLL, plastral hindlobe length; HLW, plastral hindlobe width; IABL, interabdominal scute length; IAL, interanal scute length; IFL, interfemoral scute length; IHL, interhumeral scute length; IPL, interpectoral scute length; MGL, medial gular scute length; N_L, neural length; N_W, neural width; NUCL, nuchal length; NUCW, nuchal width; V_L, vertebral scute length; V_W, vertebral scute width.

Plastron.—The plastron of UF 527000 is missing the paired hypo- and xiphiplastra, however, a composite can be made using the paratype UF 527218, a plastral hindlobe (Figs. 3 and 5). The plastral forelobe is 46% carapace length. The gulars are thick, only slightly anteriorly prominent (Fig. 6), and rounded along the anterior margin with a slight medial gular notch (in dorsal-ventral aspect). The gular lacks a distal anteriorly projecting tubercle, which is present in most described species of ptychogastrines, i.e., 'ptychogasterid spikes' of Hervet (2004, 2006). A deep step is present along the posterodorsal gular margin that is shared with *Bridgeremys pusilla* and some ptychogastrines such as *Ptychogaster emydoides*. There is pathology on the right gular in the form of a puncture that may be a pre- or postmortem bite mark. There is moderate dorsal overlap of the gulars and humerals. The humerals, and pectorals broadly overlap the entoplastron in ventral aspect, and the gulars just contact the anterior of the entoplastron. There is a humeral-pectoral notch (or constriction) along the forelobe margin. The pectoral-abdominal sulcus is strongly curved medioposteriorly and nearly contacts the hyo-hypoplastral suture at the midline, similar to *Rhinoclemmys*. The abdominal-femoral sulcus is similarly oriented and nearly contacts the hypo-xiphiplastral suture.

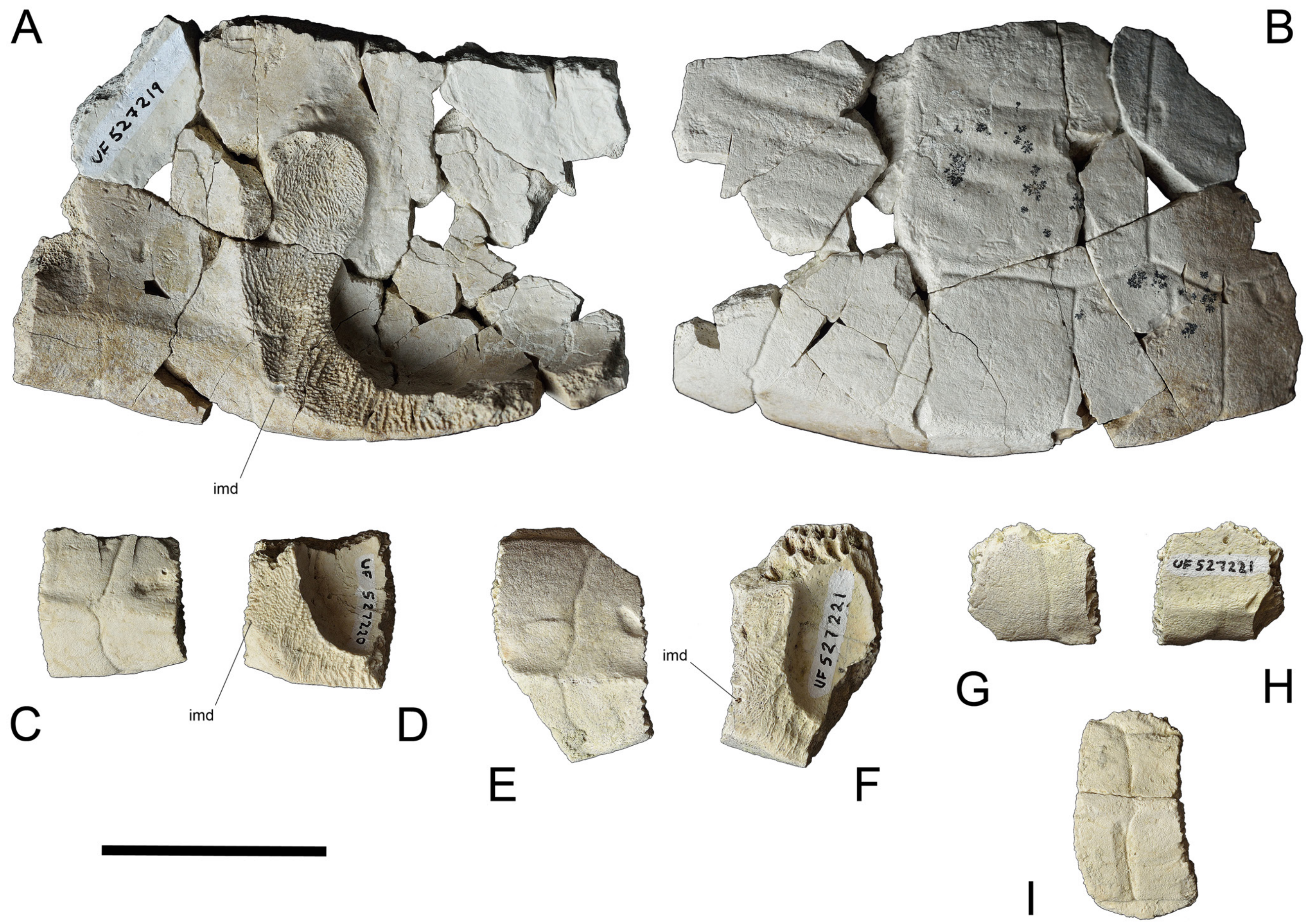

Figure 7. Referred specimens of *Notapachemys oglala*. A–B) UF 527219, partial left portion of fused carapace in A) ventral and B) dorsal views. C–D) UF 527220, left P7 in C) dorsal and D) ventral views. E–H) UF 527221, left P7 and right P11. E) left P7 in dorsal and F) ventral views. G) right P11 in dorsal and H) ventral views. I) UF 527220, right P4 in dorsal view. A), E), and F) illustrate broad flat kinetic sutural facet for articulation of the inguinal buttress and relative position of the inguinal musk duct. See 'Anatomical Abbreviations' for labels. Scale bar equals 3 cm.

The plastron exhibits partial sutural fusion. Sutures of the epi-, ento-, and hyoplastra are fused together, but the transverse hyo-hypoplastral suture is unfused. The medial hypo- and xiphiplastra sutures are also unfused. All unfused sutures have low relief sutural teeth and likely underwent passive kinesis along the hypoplastral midline, transverse hyo-hypoplastral junction, inguinal buttresses, and distal hyo-hypoplastral to marginal junction. The interhyoplastral suture appears to be only partly fused in UF 527000.

The axillary buttresses are suturally anchored to the carapace but possess relatively low relief sutural teeth and may have undergone some passive kinesis (Fig. 8). A similar connection is seen in extant *Rhinoclemmys areolata* (Fig. 9). The inguinal buttresses were significantly more mobile than the axillary buttresses. They are elongate, thick, and completely lack sutural teeth. In life these connected to the carapace via connective tissue, evidenced by low relief rugose texture along the articular facets of the buttress and carapace (Fig. 8). The distal end of the inguinal buttress is broad and flattened

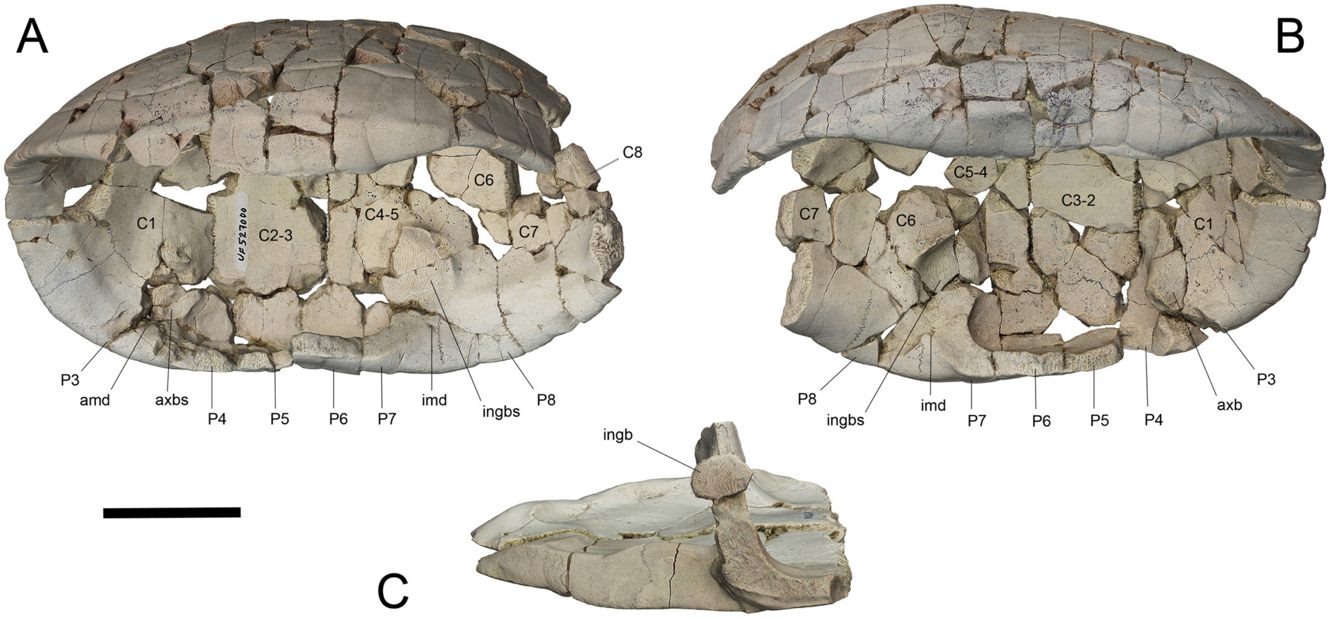

Figure 8. Plastral buttress articulations of *Notapachemys oglala*. Holotype UF 527000 in A) left ventrolateral view of right buttress articulations, and B) right ventrolateral view of left buttress articulations. C) plastral hindlobe UF 527218 in right dorsolateral view. The axillary buttresses suturally unite to the carapace and the inguinal buttresses were ligamentously attached in life, allowing for plastral hindlobe kinesis. See 'Anatomical Abbreviations' for labels. Images produced using photogrammetry models. Scale bar equals 3 cm.

distally where it articulated with a broad slightly concave facet on the inner carapace. Semi-aquatic rhinoclemmydines such as *Rhinoclemmys pulcherrima* and *Rhinoclemmys areolata* have similar inguinal buttress connections, while more aquatic species like *Rhinoclemmys funerea* and *Rhinoclemmys punctularia* have rigid suturally anchored axillary and inguinal buttresses. Inguinal buttresses of box turtle type ptychogastrines are far more reduced to almost absent (Hervet, 2006; pers. observ.).

A distinct inguinal groove is present at the base of the inguinal buttress on the ventral face of the hypoplastron (Fig. 5B) that is similar, but more anteriorly extensive than that of *Bridgeremys pusilla*. There is a deep ischiac depression on the dorsal xiphiplastron. The femoral and anal scutes have broad dorsal overlap and are tall and thick with a deep visceral step. There is a slight femoral-anal notch along the hindlobe margin. The posterior margin of the anal scute is chipped in the paratype but was likely bluntly pointed in life (Fig. 5). There is a small narrow caudal notch and it is currently unknown if notch size is sexually dimorphic.

DISCUSSION AND CONCLUSIONS

The shell morphology of *Notapachemys oglala* comprises a combination of characters present in the ptychogastrines, older north American Eocene geoemydids such as *Bridgeremys pusilla*, and New World rhinoclemmydine geoemydids like semi-aquatic and semi-terrestrial species of *Rhinoclemmys* (e.g., *R. pulcherrima* and *R. areolata*), the latter a genus that lives in the New World tropics of southern North America and northern South America today (Ernst and Barbour, 1989). *Bridgeremys pusilla* (Bridgerian to early Uintan, ~46–49 Ma) has been proposed as ancestral to *Rhinoclemmys* (Hutchison, 2006), and shares some traits with *Notapachemys* such as a wide V1,

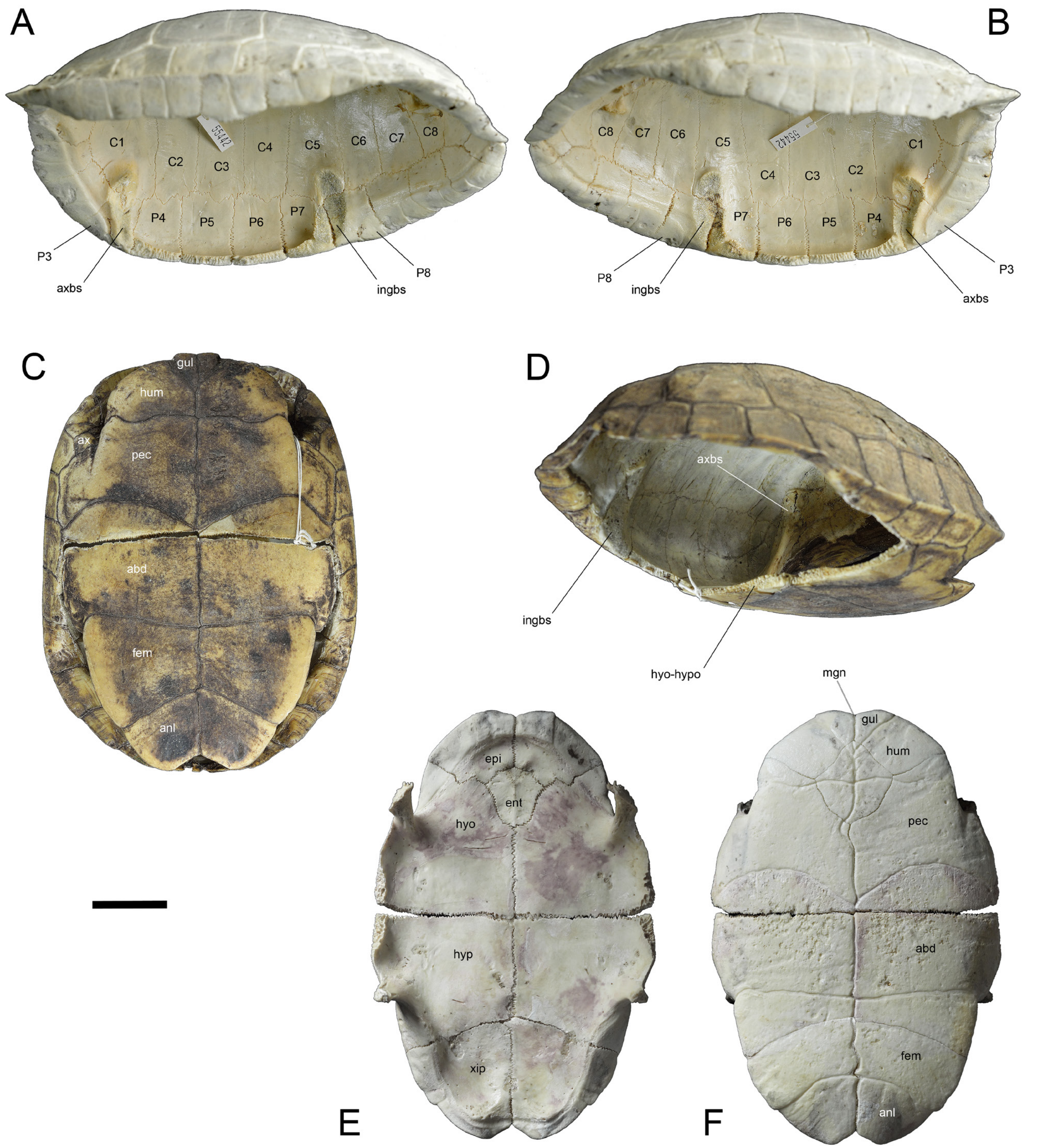

Figure 9. Plastral buttress articulations of some extant semi-aquatic/semi-terrestrial *Rhinoclemmys*. A–B) UF/H 55442, *Rhinoclemmys pulcherimma incisa* (Honduras) with kinetic to partially kinetic axillary and inguinal buttress articulations on the carapace. C–D) UF/H 76922, *Rhinoclemmys areolata* (Yucatan, Mexico) with suturally affixed axillary buttress and kinetic ligamentously attached inguinal buttress, similar to the condition of *Notapachemys oglala*. C) ventral view of plastron and D) right posteroventral view. E–F) plastron of *Rhinoclemmys pulcherimma manni* (Costa Rica), UF/H 52797 in E) dorsal and F) ventral views. See 'Anatomical Abbreviations' for labels. Scale bar equals 3 cm.

deep visceral gular step, and deep inguinal groove. Previously reported ptychogastrine fossils from the White River Group (Hutchison, 1992; 1996) are probably synonymous with *Notapachemys*, and there are similarities with some members of the Ptychogastrini (in particular the *Ptychogaster*/ *Temnoclemmys* group) such as a thick partly fused shell with strong plastral hindlobe kinesis, attributes typically seen in box turtle morphotypes. *Notapachemys* differs significantly from previously described ptychogastrines in having the combination of a six-sided N1, kinetic but more developed and elongate inguinal buttresses, medial gular notch, lack of distal gular tubercles, more posteromedially oriented pectoral-abdominal and posteromedially directed abdominal-femoral sulci, wider V1 to nuchal width, and deep ischiac depressions on the xiphiplastra.

There are undeniable morphological similarities between *Notapachemys oglala*, ptychogastrines, and rhinoclemmydines, either due to common ancestry or homoplasy. Temporally, a close relationship between the Rhinoclemmydinae and Ptychogastrini is conceivable, with the occurrence of the oldest ptychogastrine fossils from the early Eocene (Ypresian) of France (Hervet, 2006), the oldest proposed rhinoclemmydine ancestor *Bridgeremys pusilla* from the middle Eocene (Bridgerian to Uintan) of central North America (Hutchison, 2006; Adrian et al., 2021), and the first known occurrence of *N. oglala* from the late Eocene (Chadronian) of central North America. There is a unique regional and near temporal co-occurrence of the Ptychogastrini and Rhinoclemmydinae (two formerly disjunct turtle groups) in the early Miocene of the Panama Canal Basin. Well-preserved fossils of a new genus and species of ptychogastrine (to be described by JRB in a follow-up article; see Materials Examined) have been collected from the Las Cascadas Formation (Arikareean, ~22–20 Ma), indicating that this group had dispersed to southernmost North America by the early Miocene (Bourque et al., 2013; Rincon et al., 2012). Additionally, the oldest fossils of *Rhinoclemmys* are from the early Miocene of the Panama Canal Basin, from the slightly younger Cucaracha Formation (Hemingfordian, ~16–18 Ma) (Cadena et al., 2012; Rincon et al., 2012). These fossil records in the New World Tropics have potential significance when considered sequentially, and because the Panama Canal Basin is approximately centrally located within the geographic range of living *Rhinoclemmys* today (Ernst and Barbour, 1989).

Notapachemys oglala lived in the warm climate of the late Eocene and was likely regionally extirpated in central North America due to substantial cooling that occurred by the Oligocene (Zachos et al., 2001; Zanazzi et al., 2007). It is proposed here as being a semi-aquatic to semi-terrestrial turtle in having a thick, relatively high-domed, suturally fused carapace with non-flared posterior peripherals, in combination with plastral buttress attachments that most closely resemble extant semi-aquatic to semi-terrestrial geoemydids. Varying degrees of plastral kinesis were observed in multiple Old World and New World semi-aquatic/ semi-terrestrial geoemydid species examined for this study and kinesis has likely evolved numerous times within the family (Spinks et al., 2004). In addition to predator defense and limb mobility during terrestrial locomotion (e.g., climbing, walking, and running), hindlobe kinesis in semi-terrestrial/semi-aquatic species of *Rhinoclemmys* is in part an adaptation for oviposition, laying one to few very large sized eggs that are much wider than the posterior shell opening (Ernst and Barbour, 1989; pers. observ.).

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