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Tyler R. Lyson, Holger Petermann & Ian M. Miller

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A NEW PLASTOMENID TRIONYCHID TURTLE, *PLASTOMENUS JOYCEI*, SP. NOV., FROM THE EARLIEST PALEOCENE (DANIAN) DENVER FORMATION OF SOUTH-CENTRAL COLORADO, U.S.A.

TYLER R. LYSON, * HOLGER PETERMANN,  and IAN M. MILLER 

Department of Earth Sciences, Denver Museum of Nature & Science, 2001 Colorado Boulevard, Denver, Colorado 80205, U.S.A., tyler.lyson@dmns.org

ABSTRACT—North American soft-shelled turtles, including trionychines and plastomenids, are incredibly abundant in latest Cretaceous through earliest Paleocene sediments. Here we describe a new species of plastomenid turtle, *Plastomenus joycei*, based on a nearly complete early Danian skeleton from the Denver Formation in the Denver Basin, Colorado. *Plastomenus joycei* is differentiated from all other plastomenid turtles based on the presence of large eighth costals that are much longer than wide, sinusoidal raised ridges on the carapace, flat posterior edge of the carapace, spike-like epiplastra that lack callosities, a broad entoplastron that lacks a callosity, hyoplastra with two lateral processes, presence of metaplastically ossified hyoplastral shoulders (i.e., anteriorly protruding lappets), and a broad midline contact between the hypo- and xiphoplastra. *Plastomenus joycei* broadly resembles the Cretaceous *Gilmoremys* spp. and the Eocene *Plastomenus thomasi* and exhibits intermediate morphology between the two, most notably in the degree of ossification of the plastron. The increase in plastral ossification, as well as a decrease in overall size and an increase in the doming of the shell, co-occurs with the Cretaceous–Paleogene mass extinction and these morphological changes may be in response to an increase in mammalian predators during the early Paleogene. *Plastomenus joycei* is most commonly found in riverine sandstone sediments and is hypothesized to be a riverine turtle.

<http://zoobank.org/urn:lsid:zoobank.org:pub:F4FE56A9-3E63-4BF0-A5CB-0CF0F9B6B045>

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Upper Cretaceous and Lower Paleogene rocks are broadly exposed in the Northern Great Plains of North America and have yielded a diverse assemblage of fossil freshwater turtles. These assemblages document turtle diversity across the Cretaceous/Paleogene (K/Pg) boundary and suggest widespread survival of freshwater turtles across this mass extinction event (Hutchison and Archibald, 1986; Bryant, 1989; Archibald and Bryant, 1990; Holroyd and Hutchison, 2002; Lyson and Joyce, 2009a, 2009b, 2010, 2011; Knauss et al., 2011; Lyson et al., 2011, 2016, 2019a; Holroyd et al., 2014; Joyce et al., 2019). These assemblages are typically dominated in both diversity and sheer numbers by baenid and trionychid turtles (Holroyd and Hutchison, 2002; Hutchison and Holroyd, 2003; Sullivan et al., 2013; Holroyd et al., 2014; Lyson et al., 2019a). Fossil trionychid turtles are easily distinguished from other types of turtles by their pitted, metaplastic ossification found on the shell and numerous North American fossil taxa have been named, often based on fragmentary scraps of shell (Vitek and Joyce, 2015). There are two large subgroups of trionychid turtles in the latest Cretaceous and earliest Paleocene of North America—trionychines and plastomenids. Plastomenid turtles are endemic to North

America and are typified by having a plastron that is better ossified compared with that in trionychine soft-shelled turtles (Joyce et al., 2009; Hutchison, 2009; Vitek and Joyce, 2015).

The last decade has seen a flurry of activity in describing new specimens, naming new taxa, and exploring the broader evolutionary relationships of plastomenid turtles with that of other extant and extinct trionychids (Joyce et al., 2009, 2018; Hutchison, 2009; Joyce and Lyson, 2010, 2011, 2017). Herein, we describe a new taxon of early Danian plastomenid turtle, *Plastomenus joycei*, sp. nov., based on a nearly complete skeleton, as well as additional referred material, from the Denver Formation in the Denver Basin, Colorado of North America. In addition, we explore the phylogenetic relationship of plastomenid turtles.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **DMNH**, Denver Museum of Nature & Science, Denver, Colorado, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **USNM**, Smithsonian National Museum of Natural History, Washington, D. C., U.S.A.

Anatomical Abbreviations—**cav**, caudal vertebra; **ce**, cervical vertebra; **co**, costal; **den**, dentary; **epi**, epiplastron; **ent**, entoplastron; **fe**, femur; **fi**, fibula; **hyo**, hyoplastron; **hypo**, hypoplastron; **hu**, humerus; **is**, ischium; **xi**, xiphoplastron.

GEOLOGICAL SETTING

The type *Plastomenus joycei* specimen and all referred specimens are from the Denver Basin, Colorado (Fig. 1). The holotype,

*Corresponding author

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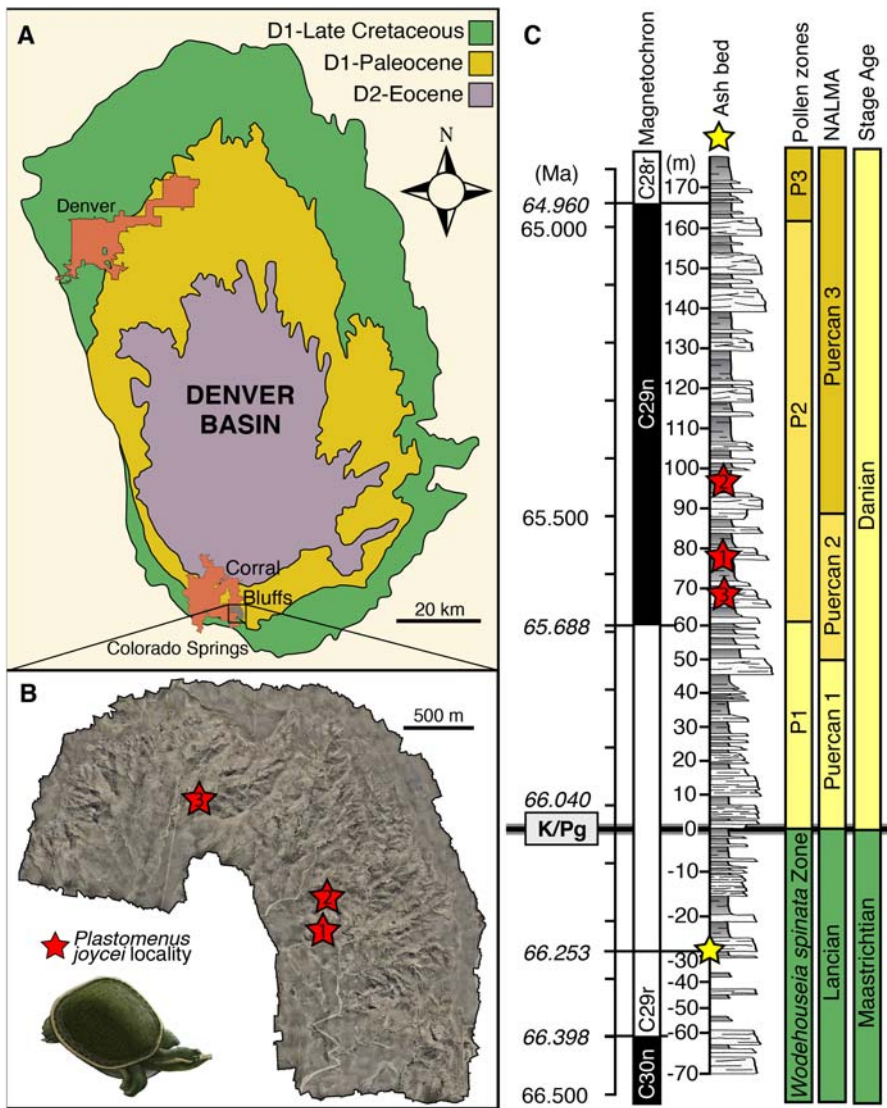


FIGURE 1. Geographic, magnetostratigraphic, and biostratigraphic placement of localities at which specimens of *Plastomenus joycei* occur. **A**, Map of the Denver Basin showing the location of the Corral Bluffs study area (highlighted by box and enlarged in part **B**) in the southwestern region of the basin. **B**, High-resolution photogrammetry model of the eastern portion of the Corral Bluffs study area that produced specimens of *P. joycei* (red stars): 1, DMNH EPV.95454/DMNH Loc. 6517; 2, DMNH EPV.130989/DMNH Loc. 8432; 3, DMNH EPV.134085/DMNH Loc. 7317 (Table 1). **C**, Magnetostratigraphic, lithostratigraphic, and biostratigraphic log showing stratigraphic placement of localities at which *P. joycei* (red stars) occur. Stratigraphy is tied to the Geomagnetic Polarity Time Scale (GPTS 2012; Gradstein et al., 2012; Ogg, 2012) using remnant magnetization of the rocks in the Corral Bluffs study area, two CA-ID-TIMS U-Pb-dated volcanic ash beds (yellow star; they are at the same stratigraphic level), and the palynologically defined K/Pg boundary (italicized dates) (Fuentes et al., 2019; Lyson et al., 2019b). The composite lithostratigraphic log is dominated by intercalated mudstone and sandstone, reflecting a variety of fluvial facies (Lyson et al., 2019b). Pollen interval zones are defined by diversification of *Momipites* spp. (fossil juglandaceous pollen) (Nichols and Fleming, 2002) and placement of North American Land Mammal Ages (NALMA) follows Lyson et al. (2019b) as defined by Lofgren et al. (2004). **Abbreviations:** **Ma**, million years ago; **K/Pg**, Cretaceous–Paleogene boundary.

as well as two of the three referred specimens, are from localities located in El Paso County in south-central Colorado, east of Colorado Springs, in an area referred to as the Corral Bluffs study area (Fig. 1); the third referred specimen was found as float in Arapahoe County, Colorado, in similarly aged sediments. The Corral Bluffs study area is located in the Denver Basin—an Upper Cretaceous to Eocene depocenter that formed during the Laramide orogeny (Raynolds and Johnson, 2003; Fig. 1). The Corral Bluffs section occurs within the D1 sequence of the Denver Formation (Raynolds, 1997, 2002), which is latest Cretaceous to early Paleocene in age (ca. 68–64 Ma). Initial biostratigraphic work at Corral Bluffs indicated that the fossiliferous cliff-forming outcrops were earliest Paleocene in age (Brown, 1943; Raynolds, 2002; Eberle, 2003; Johnson et al., 2003), but more recent biostratigraphic work recognized the North American Land Mammal Ages (NALMA) Lancian through Puercan (Pu) III (Lyson et al., 2019b). Recent chronostratigraphic work in the Corral Bluffs study area identified magnetochrons 30n through 28r, with the majority of the fossil-producing outcrop occurring within magnetochron 29n (Hicks et al., 2003; Fuentes et al., 2019). Dinosaur fragments are abundant in the flats

below the Corral Bluffs cliff-forming outcrops and a palynologically defined Cretaceous/Paleogene (K/Pg) boundary was identified in the low-lying dry washes near the base of the cliffs (Fuentes et al., 2019).

The chronostratigraphic framework of the Corral Bluffs study area provided by Fuentes et al. (2019) provides the basis for the age model for the fossiliferous outcrops and allows each fossil locality to be precisely dated (Lyson et al., 2019b). The interpolated ages for three paleomagnetic chron boundaries (C30n/C29r, C29r/C29n, and C29n/C28r), the K/Pg boundary, and one chemical abrasion isotope dilution thermal ionization mass spectrometry (CA-ID-TIMS) $^{206}\text{Pb}/^{238}\text{U}$ date are used to determine average sedimentation rates between each dated horizon (Fuentes et al., 2019; Lyson et al., 2019b). We use the Geomagnetic Polarity Time Scale (Gradstein et al., 2012; Ogg, 2012), but also provide ages using a second age model for the Corral Bluffs study area that uses ages calculated from the K/Pg boundary and magnetochron boundaries from the eastern portion of the Denver Basin (Clyde et al., 2016) (Table 1). For the GPTS 2012 age model: C29n/C28r is 64.958 Ma, C29r/C29n is 65.688 Ma, the K/Pg boundary is 66.04 Ma, and C30n/C29r is 66.398

TABLE 1. Stratigraphic placement, age of locality using two age models, elements preserved, and depositional environment for each specimen of *Plastomenus joycei* recovered from the Corral Bluffs study area.

DMNH Specimen#/ locality#	Stratigraphic position (m) relative to K/Pg	Age model GPTS (2012) (Ma)	Age model Clyde (et al. 2016) (Ma)	Element	Lithology	Depositional environment
EPV.130989/Loc. 8432	95.50	65.445	65.500	Hyo/hyoplastron, costals	Sandstone	River channel
EPV.95454/ Loc. 6517	86.69	65.506	65.576	Skeleton	Sandstone	River channel
EPV.134085/ Loc. 7317	68.74	65.630	65.731	Carapace fragments	?	?

Ma. For the Clyde et al. (2016) age model: C29n/C28r is 64.893 Ma \pm 0.056 my, C29r/C29n is 65.806 Ma \pm 0.048 my, the K/Pg boundary is 66.021 Ma \pm 0.024 my, and C30n/C29r is 66.436 Ma \pm 0.039. All *P. joycei* specimens were found within magnetochron 29n. See Table 1 for stratigraphic placement, age of locality for both age models, elements preserved, and depositional environment for each specimen of *P. joycei* recovered from the Corral Bluffs study area.

The early Paleocene mammals *Carsiptychus coarctatus* (Cope, 1883) and *Ectoconus ditrigonus* (Cope, 1884), representative of the Pu II NALMA (Lofgren et al., 2004), have been recovered nearby the holotype locality, as well as nearby both referred specimens from the Corral Bluff study area (Lyson et al., 2019b; Fig. 1). In addition, all *P. joycei* specimens were found within the *Momipites wyomingensis*–*Kurtzipites trispissatus* Interval Zone (P2) (Nichols and Fleming, 2002; Lyson et al., 2019b) (Fig. 1).

Lithologies at Corral Bluffs are predominantly mudstones and sandstones (Lyson et al., 2019b; Fig. 1). Five dominant facies are recognized in the Corral Bluffs study area: (1) coarse thick-bedded sandstone interpreted as river/stream complexes; (2) intercalated thin-bedded coarse sandstone and mudstone interpreted as crevasse splay; (3) massive mudstone interpreted as a floodplain; (4) thin-bedded siltstone and claystone interpreted as localized ponded water; and (5) banded siltstone and claystone with minor thin-bedded fine sandstone interpreted as more widespread ponded water or wetlands (Lyson et al., 2019b). Fossil turtles and mammals are preferentially found in certain facies (Lyson et al., 2019b). The holotype specimen (DMNH EPV.95454) and referred specimen (DMNH EPV.130989) were both found in a coarse-grained, thick-bedded sandstone interpreted as river/stream complexes. The second referred specimen found in the Corral Bluffs study area (DMNH EPV.134085) was found as float and its lithology/depositional environment could not be determined.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788 (sensu Joyce, Parham, Anquetin, Claude, Danilov, Iverson, Kear, Lyson, Rabi, and Sterli, 2020)

PAN-TRIONYCHIDAE Joyce, Anquetin, Cadena, Claude, Danilov, Evers, Ferrera, Gentry, Georgalis, Lyson, Perez-Garcia, Rabi, Sterli, Vitek, and Parham, 2021

PLASTOMENIDAE Hay, 1908 (sensu Joyce, Anquetin, Cadena, Claude, Danilov, Evers, Ferrera, Gentry, Georgalis, Lyson, Perez-Garcia, Rabi, Sterli, Vitek, and Parham, 2021)

PLASTOMENUS Cope, 1873

Type Species—*Trionyx thomasi* Cope, 1872.

PLASTOMENUS THOMASII (Cope, 1873)

Type Specimen—AMNH 3948 (syntype), shell fragments (Cope, 1884); USNM 4092, 4093, 5838 (syntypes), shell fragments

(Cope, 1884); AMNH 6018 (“temporary replacement type”, see Vitek and Joyce, 2015:208), nearly complete shell (Hay, 1908).

Type Locality and Age—AMNH 3948 (“SW Wyoming”), USNM 4092 (“Upper Green River”), USNM 4093, 5838 (“Cottonwood Creek”), Wyoming, USA (but see Vitek and Joyce, 2015); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, Eocene.

Referred Material—See referred material and range in Vitek and Joyce (2015).

PLASTOMENUS VEGETUS, nov. comb. (Gilmore, 1919)

Type Specimen—USNM 8539, partial carapace and plastron.

Type Locality and Age—Section 35, T 23 N, R 9 W, San Juan County, New Mexico, USA (Gilmore, 1919); Nacimiento Formation, Puercan NALMA, Danian, Paleocene (Simpson, 1959).

PLASTOMENUS JOYCEI, sp. nov.
(Figs. 2, 3)

Type Specimen—DMNH EPV.95454 (Fig. 2), a mostly complete, articulated shell, fore- and hind limbs, shoulder and pelvic girdle, cervical and caudal vertebrae, and lower jaws.

Type Locality and Age—The holotype specimen is from DMNH Loc. 6517 in the Corral Bluffs study area. The Corral Bluffs study area is situated east of Colorado Springs, El Paso County, Colorado (more detailed locality information is available upon request; Fig. 1) in the southern Denver Basin. The type locality is located in the D1 sequence of the Denver Formation, earliest Danian, early Paleocene. Biostratigraphically, the holotype occurs in the Pu II NALMA and pollen zone 2 (Fig. 1). See Table 1 for stratigraphic placement, age of locality for each of the GPTS 2012 and Clyde et al. (2016) age models, elements preserved, and depositional environment for the type specimen of *P. joycei*.

Diagnosis—*Plastomenus joycei* sp. nov. can be diagnosed as a representative of Pan-Trionychidae by the absence of peripherals, pygals, and scutes, presence of a boomerang-shaped entoplastron, and presence of sculpturing that covers all metaplastic portions of the shell bones. *Plastomenus joycei* can be diagnosed as a representative of Plastomenidae by the presence of a curved entoplastron, enlarged costal VIII, and xiphiplastra that contact one another along their entire length. *Plastomenus joycei* can be diagnosed as a representative of *Plastomenus* by the presence of a broad midline contact between the hypo- and xiphiplastra, presence of metaplastically ossified hyoplastral shoulders (i.e., anteriorly protruding lappets), presence of spike-like epiplastra, small size, and presence of sinusoidal raised ridges on the carapace. *Plastomenus joycei* differs from *Plastomenus vegetus* (USNM 8539) by the presence of large costals VIII that are much longer than wide rather than being subequal in length, the presence of a straight posterior edge of the carapace, the presence of a hypoplastron where the anteromedial edge is subequal in length to the posteromedial edge which increases the area of contact between the hypoplastra, the presence of costals VII

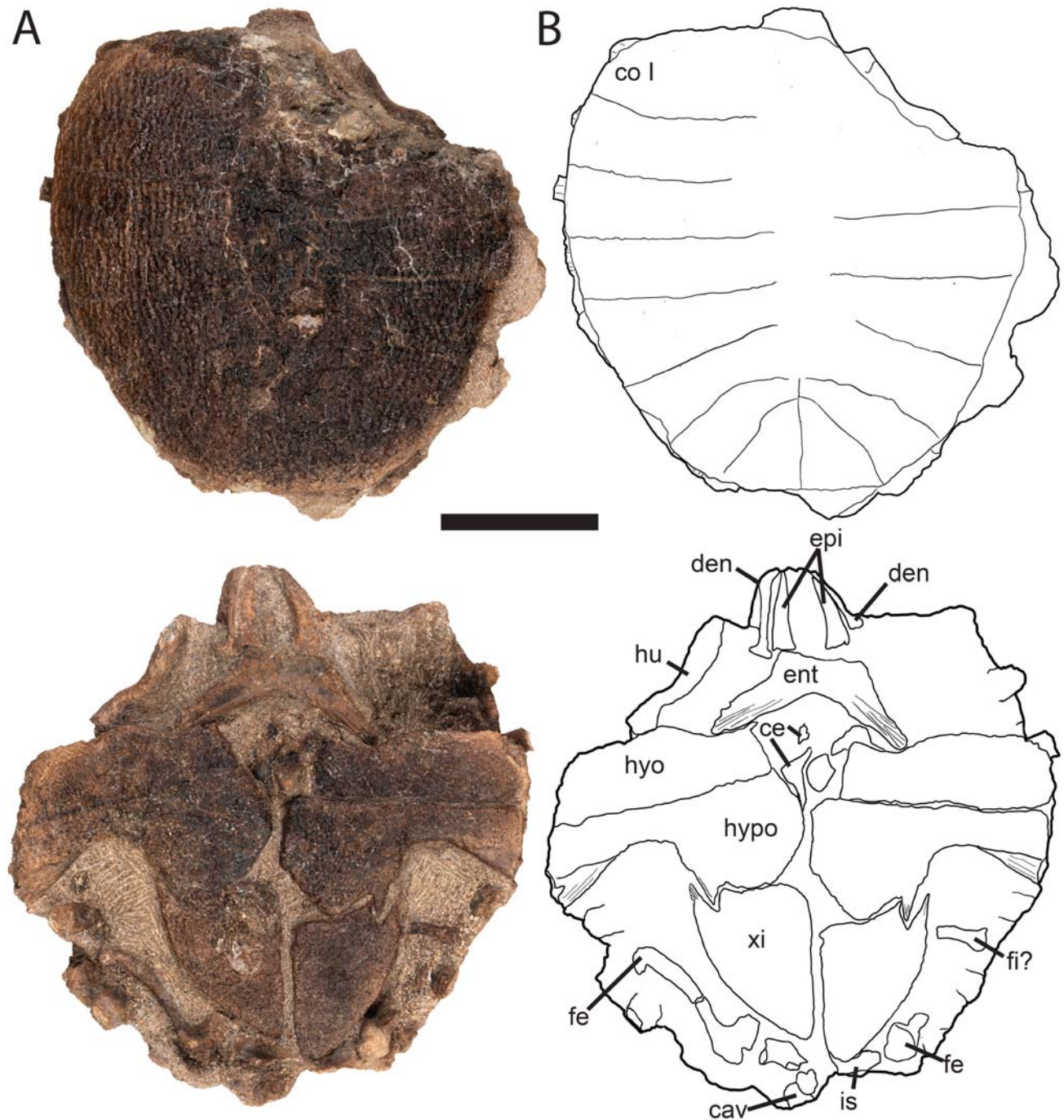


FIGURE 2. *Plastomenus joycei*, sp. nov., DMNH EPV.95454, holotype, skeleton. **A**, **B**, photograph (**A**) and line drawing (**B**) in dorsal (top) and ventral (bottom) views. Scale bar equals 5 cm.

that contact another along their entire length, and is smaller, but has a more ossified plastron including lateral metaplastic ossification that nearly covers the posterior hyoplastral process and medial metaplastic ossification covers all medial hyo- and hypoplastral processes. *Plastomenus joycei* differs from *Plastomenus thomasi* (AMNH 6018 and UCMP 158800) in lacking an entoplastral callosity, presence of a fenestra between hypo- and xiphiplastra, xiphiplastra that are not sutured to the hypoplastra, less developed metaplastically ossified hyoplastral shoulders (i.e., anteriorly protruding lappets), lack of a hypoplastral callosity

that rolls over the lateral process, and a narrower posterior plastral lobe lacking parallel sides (Table 2).

Referred Material—DMNH EPV.130989 (DMNH Loc. 8432), a nearly complete fused left hyo/hypoplastron and right costal VIII and left costal VII, both costal elements with distinctive raised sinusoidal ridges (Fig. 3); DMNH EPV.134085 (DMNH Loc. 7317), costal fragments with distinctive raised sinusoidal ridges; DMNH EPV.45114 (DMNH Loc. 2398), four costals (right V–VII and putative right IV) and putative neural IV, all with distinctive sinusoidal raised ridges.

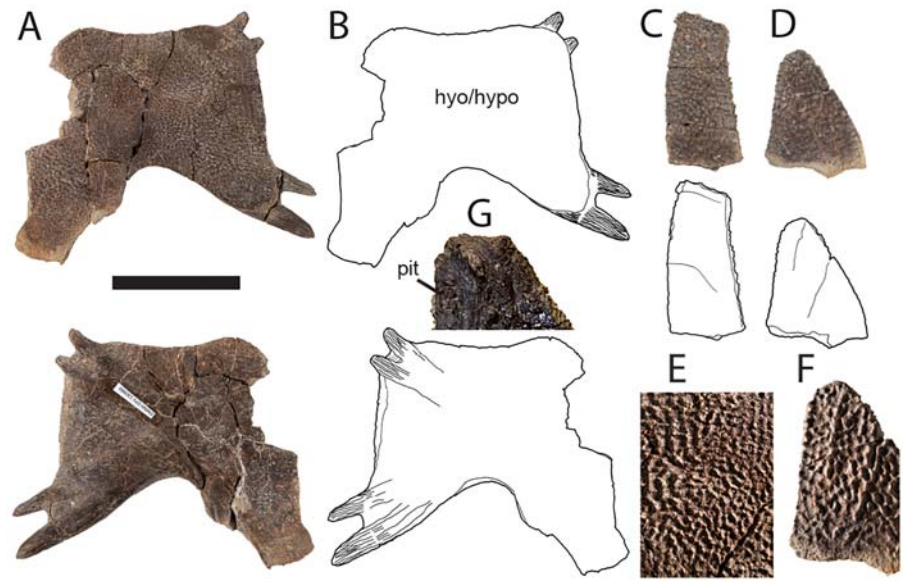


FIGURE 3. *Plastomenus joycei*, sp. nov., DMNH EPV.130989 fused left hyo- and hypoplastron, right costal VIII, and left costal VII. **A, B**, photograph (**A**) and line drawing (**B**) of fused hyo- and hypoplastron in dorsal (top) and ventral (bottom) views. **C**, photograph (top) and line drawing (bottom) of left costal V. **D**, photograph (top) and line drawing (bottom) of right costal VIII. **E, F**, close-up photograph of metaplastic ossification from the hyo- and hypoplastron (**E**) and costal V (**F**). **G**, inner surface of costal VIII showing circular pit here interpreted to represent the point of contact with the ilium. Scale bar for A–D equals 5 cm.

TABLE 2. Comparison of morphological characters used to diagnose species of *Plastomenus* and *Gilmoremys*. **Abbreviations:** L, length; W, width.

	<i>P. joycei</i>	<i>P. vegetus</i>	<i>P. thomasi</i>	<i>G. lancensis</i>	<i>G. gettyspherensis</i>
Carapace shape (dorsal view)	round	oval	round	oval	?
Ridges on carapace	depressions	depressions	depressions	depressions	raised
Size of 8th costals	L > W	W > L	W > L	W > L	W > L
Posterior edge of carapace	rounded	flat	rounded	flat	flat
# of hyoplastral prongs	2	2	2	2	2
Epiplastra shape	?	spike	spike	?	?
# of plastral callosities	6	6?	7	6?	6?
Hypoplastral callosity rolls onto posterolateral edge	present	absent	present	absent	absent
Costals VII contact another along their entire length	present	absent	absent	absent	?

Referred Material Age—Two (DMNH EPV.130989; DMNH Loc. 8432 and DMNH EPV.134085; DMNH Loc. 7317) of the three referred specimens are from the Corral Bluffs study area and were found geographically and stratigraphically near the type specimen (Fig. 1). See Table 1 for stratigraphic placement, age of locality for each of the GPTS 2012 and Clyde et al. (2016) age models, elements preserved, and depositional environment for each specimen of *P. joycei*. An additional specimen (DMNH EPV.45111; DMNH Loc. 2398) is from the earliest Paleocene portion of the D1 sequence of the Denver Formation in the Denver Basin. This specimen was found in Arapahoe County, Colorado. There is no other biostratigraphic or chronostratigraphic information for this specimen. The specimen was found as float below a large, coarse-grained sandstone channel.

Etymology—The eponym ‘joycei’ is named in honor of W. G. Joyce, prominent turtle paleontologist and friend and colleague to T. R. Lyson.

DESCRIPTION

The holotype specimen (DMNH EPV.95454) is preserved in a phosphatic concretion or nodule, an unusual mode of preservation in terrestrial environments that is common in the Corral Bluffs study area (Lyson et al., 2019b). The specimen is preserved three-dimensionally in a coarse-grained sandstone. The skull, neck and limbs are all retracted inside the shell and therefore hidden from view. The appendicular elements all appear to be

articulated, indicating rapid burial after death. Unlike most trionychid turtles, which have flat shells, the shell resembles that of other plastomenid and cyclanorbine turtles in being high-domed, analogous to box turtles. The distal limbs (manus, ulna/radius, and pes) and most of the caudal vertebrae were eroded prior to collecting (Fig. 2).

Carapace—The carapace is mostly complete, except for the nuchal region and anterior portion of the right edge of the carapace which are missing. The metaplastically ossified portion of the carapace is thin throughout the length of the costals, usually only 3–4 mm thick. The carapace is slightly oblong, with the maximum length estimated to be 155 mm, while the maximum carapace width is 148 mm—both measured along carapacial disc and not including ribs that extend laterally. The posterior edge of the carapace lacks a notch and is broad and flat. The carapace has a netted sculpture pattern and has distinctive sinusoidal raised ridges that cross the costals anteroposteriorly. Similar ridges are also found in Cretaceous and Paleogene plastomenid trionychids such as *Gilmoremys gettyspherensis* (Joyce et al., 2018), *Gilmoremys lancensis* (Gilmore, 1919), *Hutchemys acupictus* (Hay, 1907), *Plastomenus thomasi*, and *Plastomenus vegetus*. Sinusoidal raised ridges are also commonly found in juvenile trionychid turtles (Vitek and Joyce, 2015). Sinusoidal raised ridges are found on all referred specimens of *P. joycei*, including DMNH EPV.130989 (Fig. 3), which is the largest specimen. In addition to being large, this specimen has a fused hyo- and hypoplastral suture, which we interpret as indicating an

adult specimen. Thus, sinusoidal ridges are here interpreted as an adult feature of *P. joycei*.

The carapace is highly fractured, particularly along the midline, making it impossible to identify the neural and neural/costal sutures. The remaining portion of the carapace is less fractured and sutures between the costals can be easily identified (Fig. 2). As in other turtles, eight pairs of costals are present. The distal edges of the costals are not split, as is typified in *Huchemys* spp. (Joyce et al., 2009). As in *Gilmoremys* spp. (Joyce and Lyson, 2011; Joyce et al., 2018), all eight ribs extend well beyond the edge of the metaplastically ossified portion of the costal bones. Costals VII and VIII contact one another along the midline. Costal VIII is large, as in *P. thomasi*, *Gilmoremys* spp., and *P. vegetus*. In addition, costal VIII is longer than wide (Figs. 2 and 3). A small (3–5 mm circumference), rugose pit is present medially on the underside of costal VIII, here interpreted to represent the point of contact with the ilium (Fig. 3).

Plastron—All elements of the plastron are preserved. However, the lateral edges of the hyo/hypoplastron are damaged due to erosion in the holotype specimen (DMNH EPV.95454) (Fig. 2). The lateral edges of the hyo/hypoplastron are preserved in referred specimen DMNH EPV.130989 (Fig. 3). The plastron extends along the majority of the length of the carapace with the paired hyoplastra processes terminating at costal III, and perhaps extending anteriorly to costal II, and the paired hypoplastra extending to costal V. In addition, metaplastically ossified bone is present laterally between the paired hypoplastra and paired hypoplastral processes and contacts the distal ribs of costals III–V.

The paired epiplastra are preserved as elongated spikes that taper anteriorly, similar to those reported for *P. thomasi* (Hutchison, 2009). The epiplastra lack the posterolateral processes typical of other trionychids that posteromedially contact the lateral margin of the entoplastron. The epiplastra therefore do not have a J-shape. Instead, the epiplastra form a flat posterior contact along the anterolateral corners of the entoplastron. The epiplastra lack callosities and striations and are smooth along their entire length. The lack of callosities and connectivity suggests a highly kinetic joint between the epiplastra and the entoplastron, similar to that in *P. thomasi*. The epiplastra are located directly below the retracted mandible/cranium, but the cranium is not visible (Fig. 2).

The entoplastron lacks a callosity and has a broad anterior edge. The anterior edge is as wide as the lateral processes of the entoplastron are long. The wide anterior edge creates an obtuse angle between the two lateral edges of the entoplastron. The inside, or posterior edge, of the entoplastron forms a broad, rounded margin lacking distinct angles. The lateral processes of the entoplastron are finely striated and their posterior edges contact the anteromedial edges of the hyoplastra.

The hyo-, hypo-, and xiphoplastra are all covered by broad callosities and are sculptured with a worn, netted pattern. The medial edges of the hyoplastra do not broadly contact one another, creating a rhomboidal fenestra framed by the entoplastron and hyoplastra. The strap-like process that comprises the deep-tissue component of the hyoplastra is exposed laterally and two small striated processes are present laterally. The hypoplastral callosity is rectangular in shape and shows an anterior lappet that embraces the entoplastron and that is intermediate in morphology between the Cretaceous *Gilmoremys* spp. with a modest anterior lappet and the early Eocene *P. thomasi* where the entoplastron is fully encapsulated by the anterior lappets of the hyoplastra. No medial processes are visible and this area appears to be fully covered by metaplastic bone. The hyo- hypoplastra suture is open and visible in DMNH EPV.95454, but fully fused and not visible in the larger specimen, DMNH EPV.130989.

The strap-like process that comprises the deep-tissue component of the hypoplastra is fully exposed laterally and two

large striated processes are present posterolaterally and two faintly developed processes are present posteromedially for articulation with the xiphoplastra. No medial processes are visible. Unlike the broadly rounded medial edge of the hypoplastra in *Gilmoremys* spp., there are two subequal medial edges in the hypoplastra in *P. joycei*. The anterior edges of the hypoplastra contact one another medially and the posterior edges of the hypoplastra, along with the xiphoplastra, form a small, triangular fenestra along the midline of the plastron. A similar, albeit larger, triangular fenestra is present in *Gilmoremys* spp., and the fenestra is absent in *P. thomasi* where the hypoplastra fully contact one another along the midline.

The xiphoplastra are relatively large, are much longer than wide, and contact one another along the entire length of their midline. Anteriorly, they form a broad contact with the hypoplastra. The xiphoplastra have two anterolateral processes that interdigitate with the hypoplastral processes and a single posteromedial process. While the carapace completely covers the pelvic girdle, the posterior portion of the ischia is visible along the posterolateral edge of the xiphoplastra (Fig. 2).

Few details can be gleaned from the appendicular and pelvic/shoulder girdle elements. The right femur is 46.8 mm long and the right humerus is 46.4 mm long. The dentary is broken at the posterior edge of the symphysis and it is unknown whether or not it is greatly elongated as found in *G. lancensis* and *P. thomasi*. A tall coronoid process is present.

PHYLOGENETIC ANALYSIS

In order to investigate the phylogenetic affinity of *Plastomenus joycei*, we scored the holotype (DMNH EPV.95454) and one referred specimen (DMNH EPV.130989) in the published character/taxon matrix of Joyce et al. (2018) (Supplemental Data 1). This matrix focuses on fossil and extant trionychids and is largely based on composite entries and the latest iteration of the sequential phylogenetic analyses of Meylan (1987), Joyce et al. (2009), Joyce and Lyson (2010, 2011, 2017), and Brinkman et al. (2017). We do not add characters to this matrix (95 characters), but in addition to *P. joycei* we added another Pu II NALMA plastomenid turtle, *Plastomenus vegetus* (USNM 8539), that is morphologically similar to our taxon to bring the total number of taxa analyzed to 39. We changed character scores for *Plastomenus thomasi* (characters 15, 25), *Atoposemys superstes* (Russell, 1930) (characters 8, 21, 88, 91), and *Aspideretoides foveatus* (Leidy, 1856) (character 91). See Table S1 for a list of all changes (Supplemental Data 2).

We followed the analytical protocol outlined in Joyce et al. (2018). Phylogenetic analysis was performed in the program TNT, version 1.5 (Goloboff et al., 2008). Following Joyce et al. (2018) characters 1, 3, 5, 14, 20, 22, 41, 54, 79, 81, and 94 were ordered, the backbone topology was constrained using the molecular tree for extant trionychids of Le et al. (2014), and all fossil taxa were allowed to float freely. We used implied weighting ($k = 12$) in concordance with Joyce et al. (2018), who, in turn, followed the suggestion of Goloboff et al. (2018). We analyzed the matrix using ‘traditional search’ (100,000 replications) and the tree bisection-reconnection (TBR) swapping algorithm. We allowed 1000 trees per replication to be saved, because at lower numbers (10 and 100 trees) we encountered replication overflow. This analysis recovered 429 most parsimonious trees with a best TBR score of 13.26552. We report the 50% majority consensus tree in Fig. 4. A set of the full strict consensus (Fig. S1 in Supplemental Data 2), 50% majority consensus (Fig. S2 in Supplemental Data 2), and bootstrap trees (2000 replications, standard bootstrap, nodes with support < 5% collapsed) (Fig. S3 in Supplemental Data 2) can be found in the supplemental data (Supplemental Data 2).

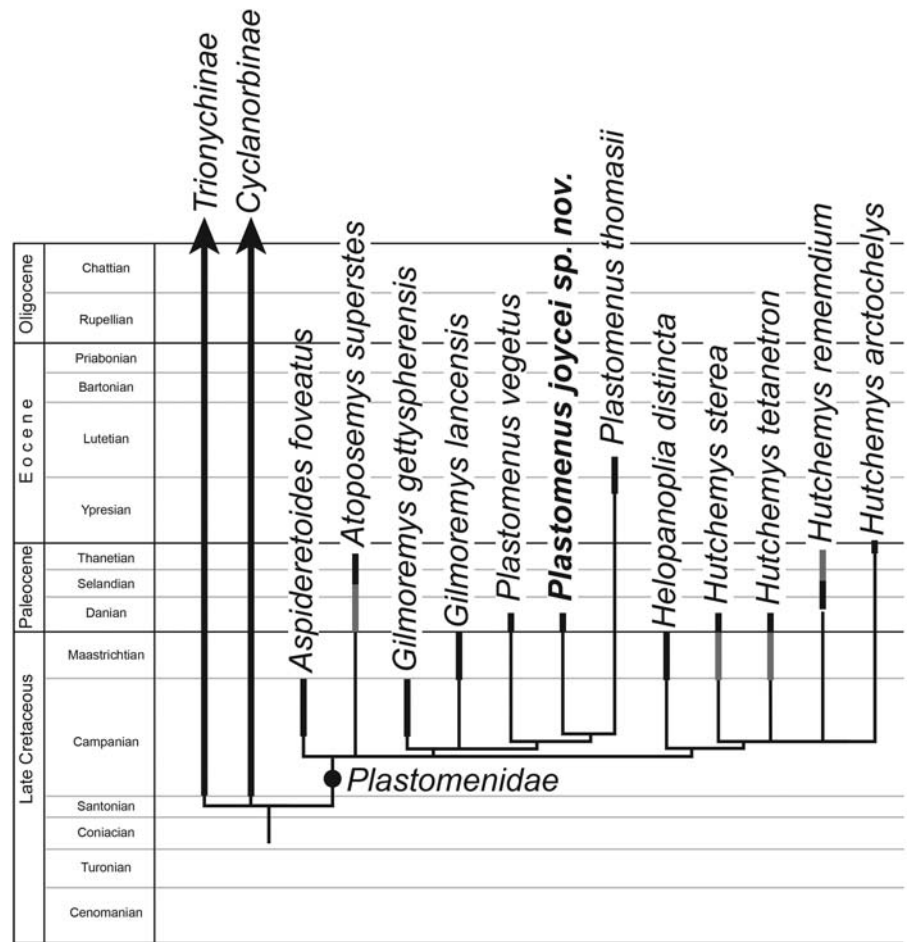


FIGURE 4. Cladogram of Plastomenidae mapped against the stratigraphic ranges for each taxon (bold lines; black = holotype, gray = referred material). 50% majority rule tree from 429 most parsimonious trees (see Phylogenetic Methods).

DISCUSSION

Alpha Taxonomy

Several trionychid species have been named from earliest Danian sediments occurring in the Puercan NALMA and of these available names nine are considered valid (Vitek and Joyce, 2015), including *Atoposemys superstes* (Russell, 1930), *Axestemys montinsana* (Vitek, 2012), *Hutchemys sterea* (Hutchison, 2009), *H. tetanetron* (Hutchison, 2009), *Plastomenus vegetus* (Gilmore, 1919), ‘*Trionyx*’ *admirabilis* (Hay and Wortman, 1905), ‘*T.*’ *eloisae* (Gilmore, 1919), ‘*T.*’ *reesidei* (Gilmore, 1919), and ‘*T.*’ *singularis* (Hay, 1907). Of these, *A. montinsana*, ‘*T.*’ *eloisae*, ‘*T.*’ *reesidei*, and ‘*T.*’ *singularis* all have large, 200+ mm diameter carapaces, small eighth costals, and costals with worn distal edges. In addition, of these taxa, the plastra of *A. montinsana* and ‘*T.*’ *singularis* are also known and are poorly ossified with little contact along the midline between the hyo-, hypo-, and xiphiplastra and have one hyoplastral process. All of these features are found in trionychines, and more specifically *Axestemys* spp. (Vitek, 2012; Joyce et al., 2019), and can easily be differentiated from the small, well-ossified *P. joycei*. ‘*Trionyx*’ *admirabilis* is based on a single large skull that resembles that of *Axestemys* spp. (Vitek, 2012; Joyce et al., 2019) and can be differentiated from *P. joycei* based on size alone.

The remaining named valid taxa from the earliest Danian of North America are widely regarded as belonging to

Plastomenidae (Vitek and Joyce, 2015; Joyce et al., 2018) and include: *A. superstes*, *Hutchemys* spp., and *P. vegetus*. *Plastomenus joycei* sp. nov. resembles *A. superstes* (as described by Russell, 1930, and based on referred specimen DMNH EPV.97075) in overall size and presence of a broad entoplastron that lacks a callosity. *Plastomenus joycei* can be diagnosed from *A. superstes* based on the presence of large eighth costals that are taller than wide, sinusoidal ridges on the carapace, ribs that extend well beyond the carapacial disc, spike-like epiplastra, shoulder lappets on the hyoplastra, two lateral processes on the hyoplastra, and xiphiplastra that contact one another for their entire length.

Plastomenus joycei sp. nov. resembles *H. sterea* (as described by Hutchison, 2009) in overall size, high-domed carapace, and presence of large eighth costals that are taller than wide. *Plastomenus joycei* can be diagnosed from *H. sterea* based on numerous features, including: oval-shaped carapace with sinusoidal ridges, thin shell, distal ribs that project beyond the carapacial rim, lack of a lateral projection on the distal ends of costals II and III, thin shell, spike-like epiplastra without callosities, free entoplastron that lacks a callosity, midline fenestra between the hypo- and xiphiplastra, hypo- and xiphiplastra not sutured together, hypo- and hyoplastral processes not fully embedded in metaplastral bone, and two hyoplastral processes.

Plastomenus joycei sp. nov. resembles *H. tetanetron* in overall size and presence of large eighth costals. *Plastomenus joycei* can be diagnosed from *H. sterea* based on numerous features, including: carapace with sinusoidal ridges, thin shell, distal ribs

that project beyond the carapacial rim, thin shell, spike-like epiplastra without callosities, free entoplastron that lacks a callosity, midline fenestra between the hypo- and xiphiplastra, hypo- and xiphiplastra not sutured together, and xiphiplastra longer than wide.

The morphology of *Plastomenus joycei* sp. nov. broadly overlaps with that of *P. vegetus*, including presence of sinusoidal ridges on the carapace, large eighth costals, hyoplastral lappets or ‘shoulders’, two lateral hyoplastral processes, and a fenestra between the hypo- and xiphiplastra. However, while *P. joycei* is smaller than *P. vegetus*, it has a more heavily ossified plastron—lateral metaplastic ossification covers more of the posterior hyoplastral process in *P. joycei* compared to that in *P. vegetus* and medial metaplastic ossification covers all medial processes of the hypo- and hypoplastra in *P. joycei*. In addition, *P. joycei* can be further diagnosed from *P. vegetus* by its oval shell, eighth costals that are much longer than wide, having a straight posterior edge of the carapace, and the anteromedial edge of the hypoplastron is subequal in length to the posteromedial edge of the hypoplastron which increases the area of contact between the hypoplastra and reduces the size of the hypo-/xiphiplastra fenestra.

In addition to the valid Danian trionychid taxa, we also compare *Plastomenus joycei* sp. nov. to North American Maastriichtian trionychid taxa currently considered valid (Vitek and Joyce, 2015). Currently there are six valid taxa from North America (Vitek and Joyce, 2015): *Axestemys infernalis* (Joyce et al., 2019), *Gilmoremys lancensis* (Gilmore, 1919), *Helopanoplia distincta* (Hay, 1908), *Hutchemys sterea* (Hutchison, 2009), *Hutchemys tetanetron* (Hutchison, 2009), and ‘*Trionyx*’ *beecheri* (Hay, 1904). Comparisons were already made above to *Hutchemys* spp., which are also present in the Danian. *Plastomenus joycei* can be diagnosed from *A. infernalis* based on its small size, presence of sinusoidal ridges on the carapace, large eighth costals, spike-like epiplastra, broad entoplastron, broad contact between the hypo-, hypo-, and xiphiplastra, two lateral hyoplastral processes, and large xiphiplastra. *Plastomenus joycei* can be diagnosed from *Helopanoplia distincta* (as described by Joyce and Lyson, 2017) by its smaller size, presence of sinusoidal ridges on the carapace, thin shell, distal ends of ribs extending well beyond carapacial disc, large eighth costals, lack of lateral metaplastic ossification on the lateral edges of the hypo-/hypoplastra, and two lateral hyoplastral processes. *Plastomenus joycei* can be diagnosed from ‘*T.*’ *beecheri* by its smaller size, presence of sinusoidal ridges on the carapace, thin shell, spike-like epiplastra, broad entoplastron, broad contact between the hypo-, hypo-, and xiphiplastra, two lateral hyoplastral processes, and large xiphiplastra.

The morphology of *Plastomenus joycei* sp. nov. broadly overlaps with that of *Gilmoremys lancensis*, including presence of sinusoidal ridges on the carapace, distal ends of ribs that extend well beyond the carapacial disc, thin shell, large eighth costals, hyoplastral lappets or ‘shoulders’, two lateral hyoplastral processes, and a fenestra between the hypo- and xiphiplastra. *Plastomenus joycei* can be diagnosed from *G. lancensis* by its small size, oval-shaped shell, eighth costals that are much taller than wide, having a straight posterior edge of the carapace, and the anteromedial edge of the hypoplastron is subequal in length to the posteromedial edge of the hypoplastron which increases the area of contact between the hypoplastra and reduces the size of the hypo-/xiphiplastra fenestra.

Our taxon most closely resembles the Upper Cretaceous (Campanian and Maastriichtian) *Gilmoremys* spp., early Paleocene *Plastomenus vegetus* (Danian) (differentiated above) and the early Eocene (Ypresian/Lutetian) *Plastomenus thomasii*. *Plastomenus joycei* resembles *Gilmoremys* spp. in having a thin carapace, sinusoidal ridges on the carapace, all distal ends of ribs extend beyond the carapacial disc, large eighth costals, broad entoplastron, presence of a hyoplastral shoulder lappet

or ‘shoulder’, two lateral hyoplastral processes, and large xiphiplastra that broadly contact one another. *Plastomenus joycei* can be diagnosed from *Gilmoremys* spp. by its smaller size, eighth costals much longer than wide, and larger midline contacts between the hypo-, hypo-, and xiphiplastra which reduces the anterior and posterior midline plastral fenestrae. *Plastomenus joycei* resembles *P. thomasii* in its overall size, sinusoidal ridges on the carapace, eighth costals much longer than wide, spike-like epiplastra, broad entoplastron, presence of a hyoplastral shoulder lappet or ‘shoulder’, two lateral hyoplastral processes, and large xiphiplastra that broadly contact one another. *Plastomenus joycei* can be diagnosed from *P. thomasii* by having distal rib ends that extend well beyond the carapacial disc, lack of callosity on the entoplastron, hypo- and xiphiplastra not sutured together, and presence of a fenestra between the hypo- and xiphiplastra. The available morphologic data support the naming of a new species of plastomenid turtle from the Danian of North America, herein *Plastomenus joycei*.

Phylogenetic Relationships, Ecology, Shell Evolution, and Biogeography

Our phylogenetic analysis resulted in 2459 most parsimonious trees. We report the 50% majority consensus tree in Figure 4, while the strict consensus, full 50% majority consensus, and bootstrap trees can be found in the supplemental data (Supplemental Data 2). The 50% majority consensus tree broadly resembles that of previous phylogenetic analyses (e.g., Joyce and Lyson, 2011, 2017; Joyce et al., 2018). A polytomy between *Aspideretoides foveatus*, *Atoposemys superstes*, a clade composed of *Gilmoremys* spp. and *Plastomenus* spp., and a clade composed of *Helopanoplia distincta* (Hay, 1908; as described by Joyce and Lyson, 2017) and *Hutchemys* spp. is present at the base of Plastomenidae (Fig. 4). *Plastomenus vegetus* is analyzed in a phylogenetic framework for the first time and it is sister to *P. joycei* and *P. thomasii*. *Plastomenus vegetus* and *P. joycei*, as well as *Gilmoremys* spp., break up the long-hypothesized ghost lineage of *P. thomasii* present in previous analyses (Joyce and Lyson, 2011, 2017; Joyce et al., 2018), creating a tree in closer agreement with stratigraphic data by suggesting shorter ghost lineages (Fig. 4). An implication of this new topology is that the cranial features listed by Joyce and Lyson (2010) no longer diagnose all plastomenid turtles, but rather only the *Plastomenus* spp. and *Gilmoremys* spp. clade, the only two plastomenid turtles with described crania. In addition to the cranial features that now diagnose this clade, *Gilmoremys* spp. and *Plastomenus* spp. share a number of important features in their shell that supports the notion that they are closely related, including two hyoplastral processes and distinct sinusoidal ridges on the surface of the carapace. Finally, it is worth noting that *Plastomenus vegetus* and *P. joycei* shared more features with *P. thomasii* than *Gilmoremys* spp., including their smaller size, well ossified plastron, and highly domed carapace and we thus placed both taxa within the genus *Plastomenus* rather than *Gilmoremys*. Thus, the change from *Gilmoremys* to *Plastomenus* across the K/Pg boundary does not represent an unusual macroevolutionary change, but rather the subjective nature of delineating genera.

Plastomenus joycei broadly resembles both the Upper Cretaceous *Gilmoremys* spp. and the Eocene *P. thomasii* (see diagnosis above), and shows intermediate morphology between these taxa. *Plastomenus* spp. and *Gilmoremys* spp. have two lateral hyoplastral processes, an anterior hyoplastral lappet or ‘shoulder’, and a broad midline contact between the xiphiplastra. The intermediate morphology exhibited in *P. joycei* relates to ossification of the plastron: the hyoplastral anterior lappets are better developed than in *Gilmoremys* spp., but not as well ossified as in *P. thomasii* where the entoplastron is more integrated into the plastron by the expansion of the anterior lappets of the hyoplastral lappets; the hypoplastra form a larger contact in *P. joycei*

than in *Gilmoremys* spp., which reduces the size of the fenestra and this fenestra is fully closed in *P. thomasi* as a result of the full midline contact between the hypo- and xiphiplastra. These changing morphologies result in a general trend from a less ossified plastron with large anterior and posterior midline fenestrae in *Gilmoremys* spp. to a more ossified plastron with smaller anterior and posterior midline fenestrae in *P. joycei*, to a fully ossified plastron where the hypo-, hypo-, and xiphiplastra all suture together to obliterate the posterior fenestra in *P. thomasi*.

A decrease in size, an increase in doming of the shell, and the initial increase in ossification of the *Gilmoremys/Plastomenus* lineage corresponds with the K/Pg boundary. This correlation may be related to ecosystem changes from large-bodied dinosaurs to small- to medium-sized mammals. We hypothesize that the rapid spread of increasingly efficient mammalian predators following the K/Pg mass extinction event may have selected for smaller, better ossified plastomenid turtles. The presence of increasingly ossified plastomenid turtles (i.e., *P. thomasi*, *Hutchemys rememidium* [Joyce et al., 2009], and *Hutchemys arctochelys* [Joyce et al., 2009]) in the Paleocene and Eocene suggests this directional selective process continued throughout the Paleocene and into the early Eocene. This same selective pressure was hypothesized by Lyson and Joyce (2009a) to be responsible for the decrease in upper temporal emargination found in the crania of Cretaceous to Eocene baenid turtles. Here, at least four lineages of Cretaceous to Paleocene baenid turtles independently close their upper temporal emarginations. Cretaceous taxa have large upper cranial emarginations rimmed by thin parietals and the supraoccipital. The cranial emarginations are reduced in the early Paleocene baenid lineages that survive the K/Pg mass extinction by an expansion and thickening of the parietals and supraoccipital and early Eocene baenid lineages largely lack upper temporal emarginations altogether. Baenid turtles are incapable of fully retracting their head and neck into their shells, but may have been able to laterally tuck in their head and neck into their shells (Werneburg et al., 2015), which Lyson and Joyce (2009a) hypothesized was a disadvantage in the early Cenozoic mammalian-dominated world and the closure of the upper temporal emargination was in response to increased mammalian predation. Here a similar increase in mammalian predation may be responsible for an increase in ossification found in the shells of Cretaceous through Eocene plastomenid turtles. It stands to reason that within latest Cretaceous/early Paleogene North American turtles, the only group of hard-shelled turtles incapable of retracting their necks/skulls (baenid turtles) and soft-shelled turtles would be most impacted by an increase in small- to medium-sized mammalian predators.

While the sample size is low, it is noteworthy that the two associated skeletons of *P. joycei* (DMNH EPV.95454 and DMNH EPV.130989) are both found in bodies of coarse, thick-bedded sandstone. Lithology has been used in other fossil ecosystems (e.g., Hell Creek and Denver formations) to help determine paleoecology, including environment, of dinosaurs, mammals, and turtles (Holroyd and Hutchison, 2002; Lyson and Longrich, 2011; Lyson et al., 2019a, 2019b). In the Corral Bluffs study area, coarse, thick-bedded sandstone facies is interpreted to represent river/stream complexes (Lyson et al., 2019b; Table 1), suggesting *P. joycei* may have inhabited riverine environments. Within the Corral Bluffs study area, *Hoplochelys* sp. is largely found in fine-grained sediments interpreted to represent ponded water or overbank environments, while baenid turtles are largely found in coarse, thick-bedded sandstone facies interpreted to represent river/stream complexes (Lyson et al., 2019b). A riverine paleoenvironmental interpretation for *P. joycei* differs from that of *Gilmoremys* spp., both of which are largely found in sediments interpreted to represent ponded water environments (Joyce and Lyson, 2011, Joyce et al., 2018).

There are biogeographic patterns within early Paleocene plastomenid turtles. *Plastomenus* spp. are present in the southern basins (Denver and San Juan Basins), but not in the Williston Basin. *Hutchemys sterea* and *Atoposemys superstes* dominate further to the north in the Williston Basin. A specimen referable to *Hutchemys* spp. is present in the Denver Basin (Hutchison and Holroyd, 2003), but this group does not dominate this turtle assemblage as it does in the Williston Basin. More fieldwork in each of these basins, as well as more taxonomic work on existing specimens, needs to be conducted to determine the veracity of this hypothesis.

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ORCID

Tyler R. Lyson  <http://orcid.org/0000-0003-4391-9044>

Holger Petermann  <http://orcid.org/0000-0002-3847-2244>

Ian M. Miller  <http://orcid.org/0000-0001-6783-8105>

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