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ARTICLE

A NEW BAENID TURTLE, *PALATOBAENA KNELLERORUM* SP. NOV., FROM THE LOWER PALEOCENE (DANIAN) DENVER FORMATION OF SOUTH-CENTRAL COLORADO, U.S.A.

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ABSTRACT—Baenidae are the most diverse clade of turtles from the latest Cretaceous and earliest Paleogene of North America. *Palatobaena* species have a distinctive cranial bauplan within baenid turtles and we herein describe a new species, *P. knellerorum*, based on a complete cranium from the lower Paleocene Denver Formation in the Denver Basin, Colorado. *Palatobaena knellerorum* differs from other *Palatobaena* species in the extreme degree of its dorsally oriented orbits, as well as the presence of a broad pentagonal midline crest formed by the supraoccipital and parietals. It can be further diagnosed from other species of *Palatobaena* by the following unique combination of characters: having a broadly rounded cranium, presence of upper temporal emargination that extends well anterior to the otic chamber, a broad exposure of the supraoccipital on the dorsal skull roof, a broadly rounded 'tongue groove' between the maxillae and premaxillae, and a deeply emarginated nasal region that exposes the underlying premaxillae in dorsal view. *Palatobaena knellerorum* most closely resembles the Maastrichtian/Danian taxon *Palatobaena cohen* and the Danian taxon *P. bairdi*. A phylogenetic analysis places *P. knellerorum* as sister to *P. bairdi*, and these taxa are sister to *P. cohen*. *Palatobaena knellerorum* overlaps in time with *P. cohen*, but the two are separated geographically with *P. knellerorum* restricted to the Denver Basin and *P. cohen* restricted to the Williston Basin. Cranial anatomical data and sedimentological data suggest *Palatobaena* spp. were bottom dwelling turtles living in shallow water environments that used a putative proboscis to prey upon freshwater-shelled invertebrates.

http://zoobank.org/urn:lsid:zoobank.org:pub:3552FD8C-FDDA-4158-9134-0EF7DD0F1766

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

INTRODUCTION

Baenid turtles are a speciose group of turtles that are endemic to North America. The group arose in the early Cretaceous, diversified in the late Cretaceous, and went extinct in the Eocene (Hay, 1908; Gaffney, 1972; Joyce and Lyson, 2015). All baenid species are thought to have been aquatic (Hutchison, 1984; Holroyd and Hutchison, 2002; Holroyd et al., 2014; Lyson et al., 2019a) and most species have determinate growth, as determined by the complete obliteration of the sutures in the shell (Hutchison, 1984). These two factors likely contribute to the group's remarkable fossil record – complete shells with fused sutures and crania are common in upper Cretaceous and lower Paleogene rocks (Hay, 1908; Gaffney, 1972; Joyce and Lyson, 2015). Over the past several decades, numerous studies have documented the anatomy, taxonomy, and diversity of this group from the Early Cretaceous (Gaffney, 1972; Lipka et al., 2006; Joyce et al., 2020a), the Late Cretaceous Campanian (Brinkman and Nicholls, 1991; Brinkman, 2003, 2005; Hutchison, 2004; Sullivan et al., 2013; Lively, 2015, 2016), the Late Cretaceous Maastrichtian (Gaffney and Hiatt, 1971; Holroyd and Hutchison, 2002; Lyson and Joyce, 2009a, 2009b, 2010, 2011; Holroyd et al., 2014; Lyson et al., 2019a), Paleocene (Archibald and Hutchison, 1979; Hutchison, 2004; Lyson et al., 2011; Lyson et al., 2016), and Eocene (Hay 1908; Gaffney, 1972; Hutchison

1996; Hutchison and Storer 1998; Lichtig and Lucas 2015). In addition, the abundant fossil material from single localities has provided insights into intraspecific variation within the shell and crania for several species, making baenids one of the best understood groups of Late Cretaceous and early Paleocene turtles (Brinkman, 2003; Lyson and Joyce, 2009a; Lyson et al., 2019a).

Arguably the most unusual baenid turtle is *Palatobaena*, which has a broadly rounded cranium, massive triturating surfaces, dorsally oriented orbits, and a sulcus around an enlarged external narial opening uncritically thought to be the origin of muscles for a moveable proboscis (Archibald and Hutchison, 1979). Currently, three *Palatobaena* species are recognized – *P. cohen* from the latest Cretaceous Maastrichtian and earliest Paleocene Danian (Lyson and Joyce, 2009a), *P. bairdi* from the early Paleocene Tiffanian North America Land Mammal Age (NALMA) (Gaffney, 1972), and *P. gaffneyi* from the early Eocene Wasatchian NALMA (Archibald and Hutchison, 1979). We here describe a fourth species of *Palatobaena* based on cranial material from the early Paleocene Puercan NALMA, place the new taxon in a phylogenetic analysis, and discuss the paleobiogeography and paleoecology of this enigmatic taxon.

Institutional Abbreviations—**CCM**, Carter County Museum, Ekalaka, Montana, U.S.A.; **DMNH**, Denver Museum of Nature & Science, Denver, Colorado, U.S.A.; **UCM**, University of Colorado Museum, Boulder, Colorado, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **YPM-PU**, Yale Peabody Museum of Natural History (Princeton University Collection), New Haven, Connecticut, U.S.A.

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Anatomical Abbreviations—**bo**, basioccipital; **bs**, basisphenoid; **ex**, exoccipital; **fpp**, foramen palatinum posterius; **fpcci**, foramen posterior canalis carotici interni; **fst**, stapedial foramen; **fr**, frontal; **ju**, jugal; **mx**, maxilla; **na**, nasal; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pr**, prootic; **pt**, pterygoid; **qj**, quadratojugal; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal; **vo**, vomer.

GEOLOGICAL SETTING AND AGE CONTROL

The Corral Bluffs study area is located in the southwestern Denver Basin, which hosts Upper Cretaceous through Eocene synorogenic sediments that were deposited immediately east of the Colorado Front Range during the Laramide orogeny (Fig. 1). The synorogenic sediments in the basin occur in two unconformity-bound packages informally named the D1 and D2 sequences (Raynolds, 1997, 2002). The D1 sequence, which is exposed in the Corral Bluffs study area, is comprised of the latest Cretaceous–earliest Paleocene-aged Denver Formation and the Paleocene-aged sediments of the Dawson Formation. It overlies the lower Maastrichtian Laramie Formation and is overlain by the D2 sequence comprised of Eocene-aged sediments of the Dawson Formation (Raynolds and Johnson, 2003; Fig. 1). The D1 sequence accumulated in the Denver Basin between ca. 68 and 64 Ma and is composed of reworked Mesozoic and Paleozoic sediments as well as Precambrian basement rock shed during the Laramide uplift of the Front Range (Raynolds, 1997, 2002; Raynolds and Johnson, 2003). The D1 sequence exposed in the Corral Bluffs study area, from which specimens of *P. knellerorum* were recovered, contains sandstone and mudstone beds interpreted to be channel and overbank deposits that formed in a floodplain setting (Fuentes et al., 2019; Lyson et al., 2019b). Both specimens of *P. knellerorum* were found as float, but were preserved in phosphatic concretions that also incorporate coarse-grained sand. The coarse-grained sand in the concretions suggests they precipitated in and eroded from channel deposits. As a result, we interpret the environment in which *P. knellerorum* lived as dominated by fast-flowing rivers on a high gradient floodplain draining the Laramide highlands to the west-southwest (Lyson et al., 2019b).

Using the chronostratigraphic framework developed for the Corral Bluffs study area by Fuentes et al. (2019), we obtained precise ages for the stratigraphic horizons at which *P. knellerorum* occurs (Table 1). This framework is derived from identifying three paleomagnetic chron boundaries (C30n/C29r, C29r/C29n, and C29n/C28r) in the section, the stratigraphic
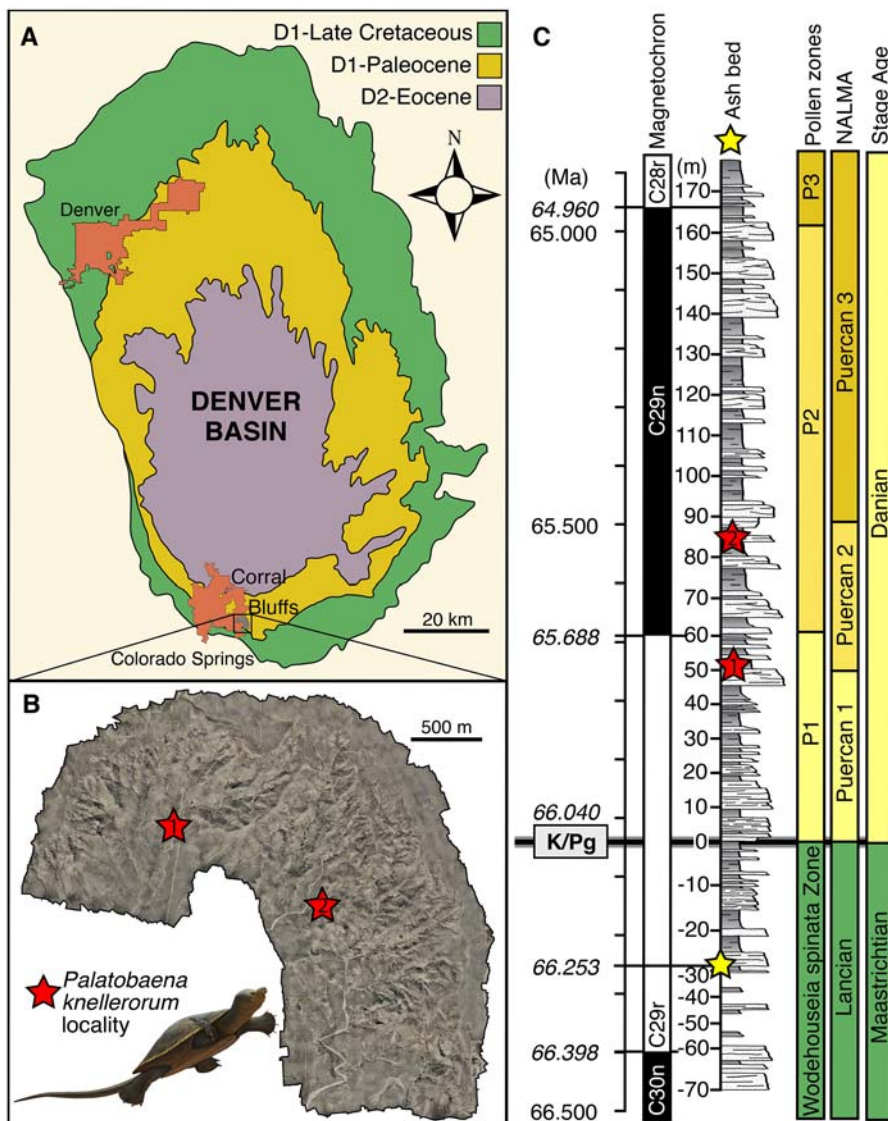

FIGURE 1. Geographic, magnetostratigraphic, lithostratigraphic, chronostratigraphic, and biostratigraphic placement of localities at which specimens of *Palatobaena knellerorum* occur. **A**, map of the Denver Basin showing the location of the Corral Bluffs study area (highlighted by box and enlarged 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. knellerorum* (denoted by red stars): 1 – DMNH EPV.134081/DMNH Loc. 8729 (holotype specimen); 2 – DMNH EPV.130980/DMNH Loc. 6984. **C**, magnetostratigraphic, lithostratigraphic, chronostratigraphic, and biostratigraphic logs showing stratigraphic placement of localities at which *P. knellerorum* (denoted by red stars) occur. Stratigraphy is tied to the Geomagnetic Polarity Time Scale (GPTS 2012, Gradstein et al., 2012) using remnant magnetization of the rocks in the Corral Bluffs study area, two CA-ID-TIMS U-Pb-dated volcanic ash (denoted by 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. Modified from Lyson et al. (2021).

TABLE 1. Stratigraphic placement, age of locality using two age models, element preserved, lithology, and depositional environment for each specimen of *Palatobaena knellerorum*

DMNH Specimen#/ locality#	Stratigraphic position (m) above K/Pg boundary	Age model GPTS 2012 (Ma)	Age model Clyde et al. 2016 (Ma)	Element	Lithology	Depositional environment
EPV.134081/ Loc. 8729	51.7	65.74	65.84	Complete cranium	Sandstone	River channel
EPV.130980/ Loc. 6984	85.0	65.52	65.59	Partial cranium	Sandstone	River channel

location of the palynologically defined Cretaceous/Paleogene (K/Pg) boundary, and two chemical abrasion isotope dilution thermal ionization mass spectrometry (CA-ID-TIMS) ^{206}Pb/^{238}U dates on zircons separated from thin (ca. 2–3 cm thick) tonstein beds preserved in lignite beds (Fig. 1). The tonstein beds are interpreted as volcanic ash falls. These temporal benchmarks were used to calculate average sedimentation rates and interpolated ages for the section (Fuentes et al., 2019; Lyson et al., 2019b). We provide two estimates for the age of each of our *P. knellerorum* specimens based on slight differences in the estimates for the age of magnetochron boundaries and the K/Pg boundary—one using Geomagnetic Polarity Time Scale (Gradstein et al., 2012; Ogg, 2012) and the other using recent estimates from Denver Basin sediments (Clyde et al., 2016). These are 65.74 and 65.84 Ma for specimen EPV.134081, respectively; and 65.52 and 65.59 Ma for specimen EPV.130980, respectively (Table 1). While precise ages are provided for both specimens, it should be noted that both were found on the surface as float. Because each specimen is mostly complete, we hypothesize they were not transported far. Given the specimens moved down section via the forces of gravity, the ages provided here represent maximum age estimates.

Considering recent biostratigraphic and magnetostratigraphic work in the section at Corral Bluffs, we note that both specimens of *Palatobaena knellerorum* were recovered from localities within the Puercan (Pu) II NALMA, identified by the presence of the mammals *Carsioptychus coarctatus* (Cope, 1883) and *Ectoconus ditrigonus* (Cope, 1884) (Lofgren et al., 2004). Furthermore, the specimens were recovered from sediments that span the uppermost *Momipites inaequalis–Discoidites parvistriatus* (P1) pollen zone and *Momipites wyomingensis–Kurtzipites trispissatus* pollen zone (P2) (Nichols and Fleming, 2002; Lyson et al., 2019b) (Fig. 1). All known specimens of *P. knellerorum* cluster around the C29r/29n boundary.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788 Joyce, Parham, Anquetin, Claude, Danilov, Iverson, Kear, Lyson, Rabi, and Sterli, 2020b
PARACRYPTODIRA Gaffney, 1975 Joyce, Parham, Anquetin, Claude, Danilov, Iverson, Kear, Lyson, Rabi, and Sterli, 2021
BAENIDAE Cope, 1873 Joyce, Parham, Anquetin, Claude, Danilov, Iverson, Kear, Lyson, Rabi, and Sterli, 2021
BAENODDA Brinkman, 2003 Joyce, Parham, Anquetin, Claude, Danilov, Iverson, Kear, Lyson, Rabi, and Sterli, 2021
PALATOBAENA Gaffney, 1972

Type Species—*Palatobaena bairdi* Gaffney, 1972.
Included Species—*Palatobaena bairdi* Gaffney, 1972; *Palatobaena gaffneyi* Archibald and Hutchison, 1979; *Palatobaena cohen* Lyson and Joyce, 2009a

PALATOBAENA BAIRDI Gaffney, 1972
(Fig. 2)

Type Specimen—A partially distorted right half of a cranium, YPM-PU 16839.

Type Locality and Age—Cedar Point Quarry, Bighorn Basin, Wyoming; Fort Union Formation, early Tiffanian (late Paleocene).
Referred Material—See Lyson and Joyce, 2009a for lists of referred material based on synapomorphies or equivalent stratigraphy.

PALATOBAENA GAFFNEYI, Archibald and Hutchison, 1979
(Fig. 2)

Type Specimen— Nearly complete cranium, UCMP 114529.
Type Locality and Age—Sweetwater County, Wyoming; main body of Wasatch Formation, Wasatchian (early Eocene).
Referred Material—See Lyson and Joyce, 2009a for list of referred material based on equivalent stratigraphy.

PALATOBAENA COHEN, Lyson and Joyce, 2009a
(Fig. 2)

Type Specimen— A complete uncrushed cranium, mandible, and shell, YPM 57498.
Type Locality and Age—Bucklin Township, Slope County, northwest of Marmarth, North Dakota; Hell Creek Formation (latest Maastrichtian), approximately 57 meters below the Hell Creek/Fort Union formational contact.
Referred Material—See Lyson and Joyce (2009a) for lists of referred material based on synapomorphies or equivalent stratigraphy. We herein remove three specimens from the referred material of Lyson and Joyce (2009a) based on further examination of the material and the discovery of more complete material of *Cedrobaena putorius* (Lyson et al., 2019b). Further examination of UCM 37738 (cranium and jaw fragments), UCM 49229 (left dentary), and UCM 49230 (right and left dentary) suggests these specimens, all of which were collected from the Corral Bluffs study area (Fig. 1), may belong to either *Palatobaena* spp. or *C. putorius*, both of which have broadened triturating surfaces. The preserved material from these three localities is not complete enough to differentiate between these taxa and are thus removed from the list of referred material for *P. cohen*.

PALATOBAENA KNELLERORUM, sp. nov.
(Fig. 3)

Type Specimen—A complete cranium, DMNH EPV.134081 (Fig. 3).
Type Locality and Age—The holotype specimen is from DMNH Loc. 8729 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; Table 1) in the southern Denver Basin. The type locality is located in the Denver Formation, Danian, lower Paleocene. Biostratigraphically, the holotype occurs in the Pu II NALMA and within pollen zone 2 (Fig. 1). See Table 1 for stratigraphic placement, age of locality for each
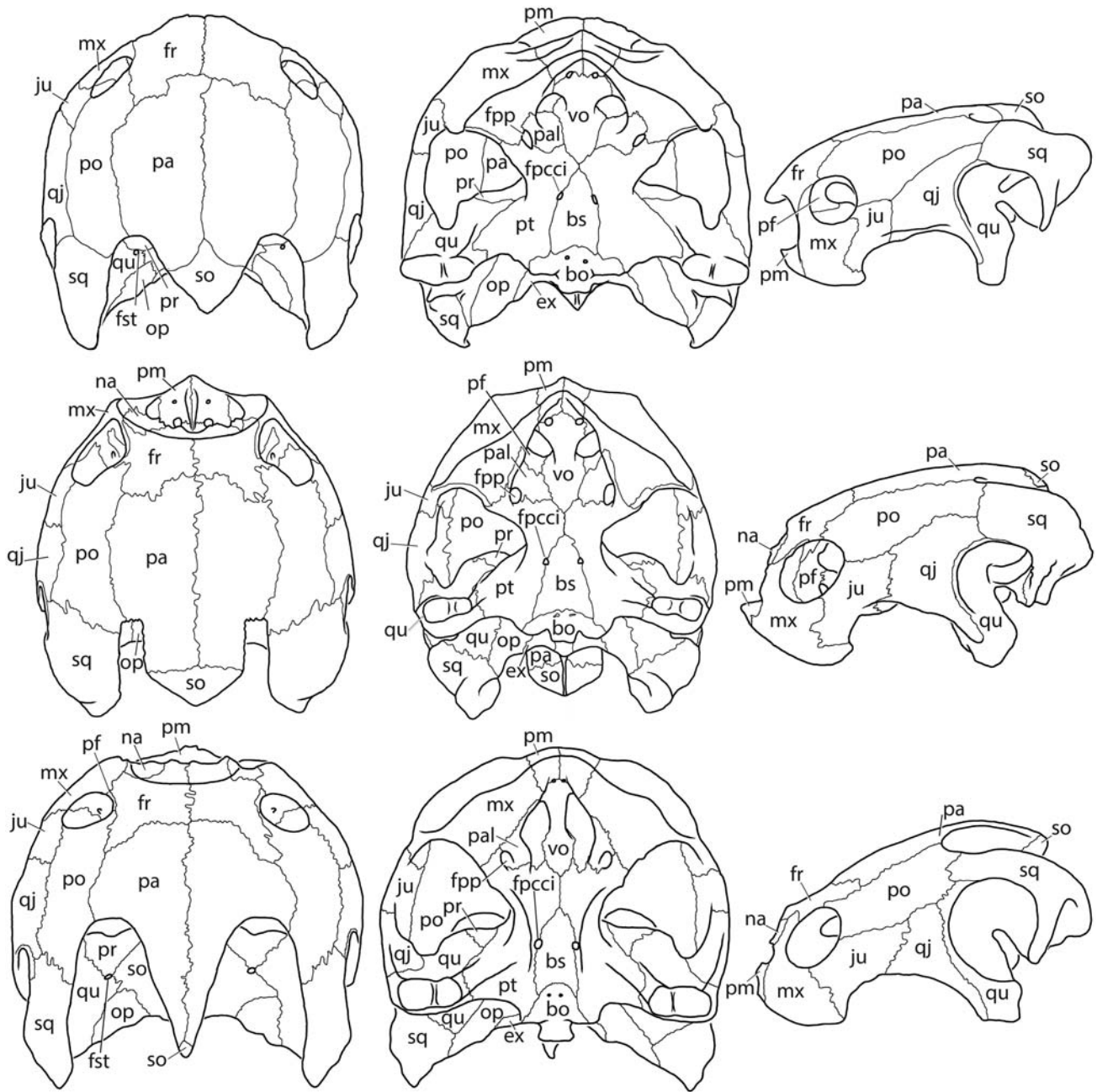
FIGURE 2. Line drawings of the crania in dorsal (left), ventral (middle), and left lateral (right) views of recognized *Palatobaena* taxa. *Palatobaena gaffneyi* (top) is based on the holotype specimen UCMP 114529 (Archibald and Hutchison, 1979), *Palatobaena bairdi* (middle) is based on referred specimen CCM 77-11 (Archibald and Hutchison, 1979), and *Palatobaena cohen* (bottom) is based on the holotype specimen YPM 57498 (Lyson and Joyce, 2009a). Line drawings for *P. bairdi* and *P. gaffneyi* modified from Archibald and Hutchison (1979) and line drawings for *P. cohen* modified from Lyson and Joyce (2009a).

of the GPTS 2012 and Clyde et al. (2016) age models, elements preserved, and depositional environment for the type specimen of *P. knellerorum*.

Diagnosis—*Palatobaena knellerorum* sp. nov. can be diagnosed as a representative of Paracryptodira by the placement of the foramen posterior canalis carotici interni (sensu Rollot et al., 2018) halfway between the suture of the basisphenoid and the pterygoid and the absence of an interpterygoid vacuity. *Palatobaena knellerorum* can be diagnosed as a representative of Baenidae by the presence of posteriorly expanded triturating surfaces with a posteriorly reduced lingual ridge, a well-developed basioccipital contact, and a small dorsal lappet of the prefrontal. *Palatobaena knellerorum* can be diagnosed as a representative of *Palatobaena* by the greatly reduced preorbital skull length and overall round shape of the cranium, dorsally oriented orbits, the greatly reduced processus pterygoideus externus, the absence of a lingual ridge on the triturating surface of the maxillae, swollen maxillae, an obtuse angle formed by the two maxillae, and no midline contact between the nasals. *Palatobaena knellerorum* differs from all other
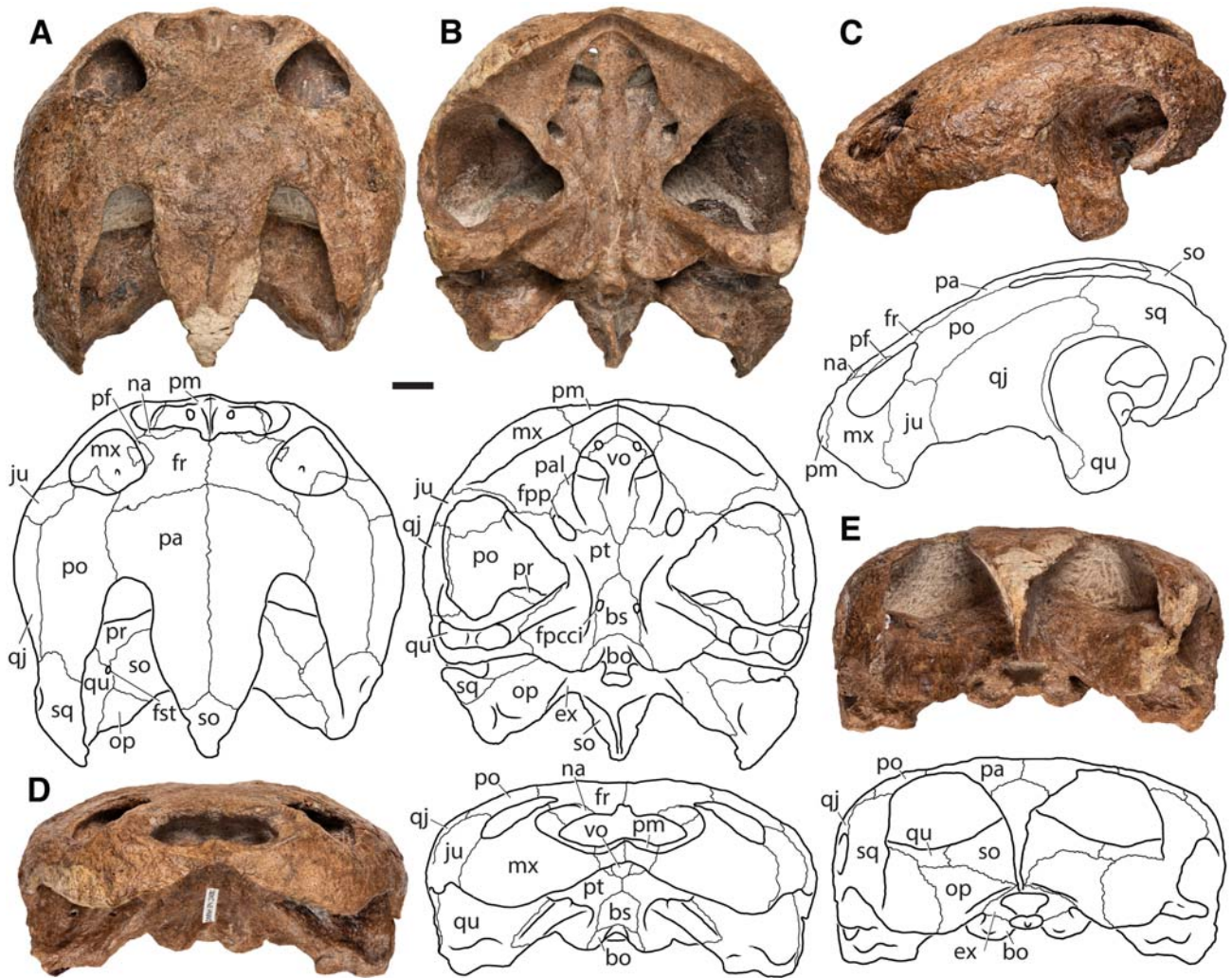
FIGURE 3. *Palatobaena knellerorum*, sp. nov., DMNH EPV.134081, holotype, cranium. **A–C**, photograph (top) and line drawing (bottom) in dorsal (left), ventral (middle), and left lateral (right) views. **D**, photograph (left) and line drawing (right) in anterior view. **E**, photograph (top) and line drawing (bottom) in posterior view. Scale bar equals 1 cm.

species of *Palatobaena* in having orbits that are much more dorsally oriented (see dorsal and lateral views; Figs. 2, 3) and the greater degree of upper temporal emargination (Table 2). *Palatobaena knellerorum* differs from *P. cohen* (YPM 57498) in the presence of a broad, pentagonal midline crest formed by the supraoccipital and parietals, a broad dorsal exposure of the supraoccipital on the skull roof, and a broadly rounded arc formed by the premaxillae, maxillae, and palatines (i.e., "tongue groove"). *Palatobaena knellerorum* differs from *P. bairdi* (CCM 77-11) in overall skull proportions where maximum width is greater than maximum length, a broadly rounded skull lacking a pronounced anterior projection, a strong anteroposterior slope of skull roof in lateral view, and the presence of deep upper temporal emarginations. *Palatobaena knellerorum* differs from *P. gaffneyi* (UCMP 114529) in the broad, pentagonal midline crest, the presence of deep upper temporal emarginations, the overall skull proportions where maximum width is greater than maximum length, the reduction of the nasal/frontal region with underlying premaxillae exposed in dorsal view, a broad midline contact between the pterygoids, and a strong anteroposterior sloped skull roof in lateral view (Figs. 2, 3; Table 2).

Referred Material— A fragmentary cranium, DMNH EPV.130980 (DMNH Loc. 6984; Fig. S1), that exhibits a greatly reduced preorbital skull length, an overall rounded cranium, dorsally oriented orbits, deep upper temporal emarginations, greatly swollen maxillae, and a broad, pentagonal midline crest, which combined allow referral to *P. knellerorum* (Fig. S1).

Referred Material Age— The only referred specimen is from the Corral Bluffs study area and was found geographically and stratigraphically near the type specimen (Fig. 1). See Table 1 for stratigraphic placement.

Etymology— The eponym "knellerorum" is named in honor of Stephen and Mary Lynne Kneller for their interest and continued support of K/Pg mass extinction and post-K/Pg recovery research at the Denver Museum of Nature & Science.

DESCRIPTION

The holotype specimen DMNH EPV.134081 (Fig. 3) consists of a large, exceptionally well-preserved cranium with no distortion. A second specimen consists of a partial cranium with poor preservation of the bone surface, which obscures many of the sutures. Both specimens were preserved in phosphatic

TABLE 2. Distribution of cranial characters that diagnose each species of *Palatobaena*.

	P. knellerorum	*P. cohen*	*P. bairdi*	*P. gaffneyi*
skull shape	round	round	oval	round
orientation of orbits	dorsal	dorsolateral	dorsolateral	dorsolateral
midline crest shape	broad, pentagonal	triangular	broad, pentagonal	triangular
upper emargination relative to otic capsule	anterior	anterior	posterior	posterior
emargination of nasal region/exposure of underlying premaxillae	present	present	present	absent
pterygoid contact	broad	broad	broad	narrow
'tongue groove'	broadly rounded	V-shaped	broadly rounded	broadly rounded
supraoccipital exposure in dorsal view	broad	narrow	broad	broad

concretions, an unusual mode of preservation in terrestrial environments (Lyson et al., 2019b). The description of the cranium is based on the holotype specimen DMNH EPV.134081. The cranium is broadly rounded with the maximum width exceeding the maximum length. The maximum width of the cranium is between the orbits and the anterior extent of the upper temporal emargination. The orbits are oriented dorsally, much more so than in other species of *Palatobaena*. The dorsally oriented orbits are broadly round in dorsal view, but are narrow crescent-shaped when viewed laterally (Fig. 3). The upper temporal emargination extends well anterior of the otic capsule, deeper than in other species of *Palatobaena*. The external narial opening is large with a distinct sulcus on the bones that form the external narial opening – premaxillae, maxillae, nasals, and frontals. The nasals/frontals are reduced and, in dorsal view, the underlying premaxillae are broadly exposed. In lateral view, the skull roof slopes upward posteriorly as in *P. cohen* and the lateral cheek embayment is deep, extending dorsal to the floor of the orbit.

Nasal—The nasals are greatly reduced and are slender elements, wider than long, that form the dorsolateral margin of the external narial opening (Fig. 3). The nasals contact the frontals posteriorly and form a small contact with the maxillae anterolaterally. The nasals do not contact one another along the midline.

Prefrontal—The prefrontals are composed of a dorsal horizontal plate and a vertical descending plate (Fig. 3). The dorsal plate of the prefrontal has a small exposure on the dorsal skull roof, but this exposure is greater in *P. knellerorum* compared with that of other species of *Palatobaena*. The dorsal plate of the prefrontals contact the frontals medially and form a small contact with the maxillae anterolaterally. The descending process of the prefrontals forms the fossa nasalis posterolaterally and the fossa orbitalis anteromedially. The descending process of the prefrontals contacts the frontal dorsally, the maxilla laterally, and the vomer and palatine ventrally.

Frontal—The maximum width of each frontal exceeds its maximum length, and combined they have an hourglass shape (Fig. 3). The frontals form a portion of the external narial opening anteriorly, as well as contribute to the posteromedial rim of the orbital margin. The contribution of the frontals to the orbital margin prevents the prefrontals from contacting the postorbitals. A distinct notch is present between the frontals along the external narial opening. The frontals contact one another along the midline, the nasals, maxillae, and prefrontals anterolaterally, the parietals posteriorly, and the postorbitals posterolaterally. The frontals, as well as the nasals, are reduced anteriorly to such a degree that the underlying premaxillae are broadly exposed in dorsal view.

Parietal—The parietals are anteroposteriorly elongate elements that are slightly notched posterolaterally as a result of the deep upper temporal emargination (Fig. 3). The parietals contact one another medially, the postorbitals laterally, the frontals anteriorly, and the supraoccipital posteriorly. The parietal/postorbital suture is laterally convex and terminates posteriorly just lateral to the deepest point of the upper temporal emargination. The parietals form a large portion of the broad, pentagonal midline crest above the supraoccipital, a feature that diagnoses *P. knellerorum* from other species of *Palatobaena*. Sulci for scales, present in other species of *Palatobaena*, are not visible on the dorsal surface of the parietals or any other cranial roof element.

Postorbital—The postorbitals are large rectangular bones that contribute to the posterior edge of the orbital margin and the lateral edge of the upper temporal emargination (Fig. 3). The postorbital contacts the frontal and parietal medially, the jugal and quadratojugal laterally, and the squamosal posteriorly. The orbit is inset in the postorbital, creating two thin ridges: a horizontal ridge that overhangs the orbit and a dorsoventral ridge within the orbit (Fig. 3D). Within the orbit, the dorsoventral ridge of the postorbital and the jugal form a distinct ridge that demarcates the posterior portion of the orbit.

Jugal—The jugals are large plate-like elements that form the posteroventrolateral wall of the fossa orbitalis. The jugals form a portion of the orbital margin (Fig. 3). Within the orbit the jugal contacts the maxilla and pterygoid, but not the palatine. The jugals form the anterior margin of the lower temporal emargination. In ventral view the jugal contacts the postorbital anteriorly, the quadratojugal posteriorly, the maxilla anteriorly, and forms a small contact with the pterygoid medially. Along with the quadratojugal, the jugal forms much of the lower temporal emargination.

Quadratojugal—The quadratojugals are large elements that form 'C'-shaped structures in lateral view. The quadratojugal forms much of the lower temporal emargination. The quadratojugals contact the jugal anteriorly, the postorbital anterodorsally, the quadrate posteriorly, and the squamosal posterodorsally. The ventral most portion of the quadratojugal that forms the lower temporal emargination is thickened and at the thickest point is gently concave (Fig. 3).

Squamosal—The squamosals are situated on the posterolateral corner of the cranium (Fig. 3). The squamosals house the large antrum postoticum and form the posterodorsal portion of the antrum postoticum. The squamosals form the posterior margin of the cavum tympani. In dorsal view the squamosals form the posterolateral margin of the upper temporal emargination and contact the postorbital and quadratojugal anteriorly and the quadrate ventrally. In ventral view the squamosal contacts the opisthotic medially.

Premaxilla—Much of the premaxillae are exposed in dorsal view due to the reduction of the dorsal skull roof (Fig. 3). The premaxillae are blocky rectangular elements that contact the maxilla laterally and the vomer posteriorly. The premaxillae form the ventral margin of the apertura narium externa. The foramina praepalatina are located between the premaxillae and the vomer. The ventral portion of the premaxillae forms the robust

edge of the labial ridge. The labial ridge formed between the premaxillae forms an obtuse angle and creates a broadly rounded arc formed by the premaxillae, maxillae, and palatines (i.e., "tongue groove").

Maxilla—The maxillae are robust rectangular elements that can be divided into vertical and horizontal plates. The vertical portion forms a broad rectangular sheet of bone below the orbit (Fig. 3). Anteromedially the vertical plate forms a large portion of the external narial opening. An anterodorsal ramus of the maxilla extends dorsally, anterior of the orbits, to contact the frontal and prefrontal. Posteriorly the vertical plate of the maxilla contacts the jugal. The horizontal plate of the maxillae is greatly swollen ventrally, which creates a robust wedge-shaped labial ridge. In ventral view, the horizontal plate of the maxillae forms the vast majority of a broad, flat triturating surface. A lingual ridge is completely absent. In ventral view the maxilla contacts the premaxilla anteriorly, the palatine medially, and the jugal and pterygoid posteriorly. Within the orbit, the supramaxillary foramen is formed entirely by the maxilla (Fig. 3A).

Vomer—The vomer is a single, anteroposteriorly elongate element. In ventral view, the anterior portion of the vomer is flat, contacts the premaxillae anteriorly, and forms the posterior margin of the foramina praepalatina (Fig. 3). The anterior portion of the vomer forms the medial margin of the apertura narium interna. The vomer tapers posteriorly to form a rounded point that terminates at the midline contact between the pterygoids. The vomer contacts the palatines posterolaterally and the prefrontal posterodorsally.

Palatine—The palatines are broad elements that form the posterolateral walls of the apertura narium interna. In ventral view, the palatines contact the vomer medially, the pterygoids posteriorly and the maxillae laterally (Fig. 3). The palatine forms the medial edge of the foramen palatinum posterior. The palatine and pterygoid form the foramen palatinum posterior with no contribution from the maxillae. The palatines do not contribute to the triturating surfaces. Within the orbit, the palatines contact the descending process of the prefrontal anterodorsally. The horizontal plate of each palatine contacts the descending process of the parietal dorsally.

Pterygoid—The pterygoids are broad elements on the palate that combined are shaped like butterfly wings. There is a broad midline contact between the pterygoids (Fig. 3). The pterygoids contact the vomer anteromedially, palatine and maxilla anteriorly, basisphenoid and basioccipital posteromedially, and the quadrate posterolaterally. The pterygoid-quadrate suture is located on the ramus leading up to the condylus mandibularis on the quadrate. The pterygoids form the lateral margin of the foramen posterior canalis carotici interni (sensu Rollot et al., 2018), which is situated midway between the pterygoid-basisphenoid suture. The pterygoids form the posterolateral half of the foramen palatinum posterior. A medially arced crest, interpreted as the insertion point for the pterygoideus musculature, is present lateral to the pterygoid-basisphenoid suture. The pterygoids have a poorly developed processus pterygoideus externus on the lateral edge of the pterygoid and a vertical flange is not present. The pterygoids extend posteriorly, forming a large posterior process that floors the cavum acustico-jugulare and extends posteriorly to the neck of the occipital condyle. The posterior process extends laterally and terminates at the ramus leading up to the condylus mandibularis, where a small pocket is present interpreted as the insertion point for the pterygoideus musculature.

Epipterygoid—It cannot be determined if an epipterygoid is present.

Quadrate—The quadrates are stout vertical elements that, in lateral view, contact the quadratojugal along an anteriorly convex suture. As in other turtles, the quadrates form most of the cavum tympani. In posterior view, the quadrates form the incisura columellae auris, which is open posteriorly. In ventral view, the quadrates form a robust condylus mandibularis and contact the pterygoid medially, prootic anteromedially, quadratojugal anterolaterally, opisthotic posteriorly, and squamosal posterolaterally. The quadrates form the lateral margin of the stapedial foramen. In ventral view, a robust processus trochlearis oticus, made up equally by the quadrate and prootic, projects anteriorly.

Prootic—The prootics are small elements that form the anterior portion of the otic capsule. The deep upper temporal emargination exposes the prootics in dorsal view. Within the upper temporal emargination the prootics contact the supraoccipital posteromedially, the quadrate laterally, and the parietal anteromedially. The prootics form a small margin of the stapedial foramen. The prootic forms the medial half of a very robust processus trochlearis oticus.

Opisthotic—Much of the opisthotics are visible in dorsal view due to the presence of a deep upper temporal emargination (Fig. 3). The quadrate-supraoccipital contact excludes the opisthotics from the foramen stapedio-temporale. In dorsal view the opisthotic contacts the quadrate anterolaterally and the supraoccipital anteromedially. In ventral view the opisthotic contacts the squamosal posterolaterally and the exoccipitals medially. The opisthotic roofs the fenestra postotica and forms the lateral margin of the foramen jugulare posterius.

Supraoccipital—The supraoccipital forms the dorsal-most portion of the foramen magnum. In dorsal view the supraoccipital is broadly exposed and forms the posterior tip of the midline crest (Fig. 3). The supraoccipital has transverse contacts with the parietals, creating a large rhomboidal dorsal exposure of the supraoccipital. The crista supraoccipitalis is tall and extends well beyond the foramen magnum. The supraoccipital contacts the parietals anterodorsally, the prootic anterolaterally, the opisthotic laterally, and the exoccipital posteriorly.

Exoccipital—The exoccipitals are paired elements that frame the foramen magnum laterally (Fig. 3). The exoccipitals contact the opisthotic laterally, supraoccipital dorsally, pterygoid ventrolaterally, basioccipital ventrally, and basisphenoid ventromedially. It is unclear if the exoccipitals contribute to the occipital condyle. The foramen jugulare posterior is located exoccipital-opisthotic suture. The exoccipital forms the medial margin of the fenestra postotica.

Basioccipital—The basioccipital forms a broad contact with the pterygoids posterolaterally, contacts the exoccipitals dorsally and the basisphenoid anteriorly. The basioccipital floors the foramen magnum (Fig. 3).

Basisphenoid—The basisphenoid is an elongate, posteriorly concave hexagon that contacts the pterygoids laterally and the basioccipital posteriorly. The foramen posterior canalis carotici interni is located between the suture of the basisphenoid and the pterygoid. A broad midline contact between the pterygoids prevents the basisphenoid from contacting the vomer anteriorly (Fig. 3).

PHYLOGENETIC ANALYSIS

The analysis of the phylogenetic position of *Palatobaena knellerorum* was based on the modified and expanded data matrix from Lyson and Joyce (2011). We chose this matrix over the more recent Lyson et al. (2019a) matrix because the former has a more well-resolved phylogenetic tree compared with the latter. Both the current analysis and the Lyson et al. (2019a) phylogenetic matrix were based on modified versions of the Lyson and Joyce (2011) analysis. Lyson et al. (2019a) tried to achieve a species level cladogram and added several characters and taxa to the Lyson and Joyce (2011) analysis, which ultimately resulted in a poorly resolved phylogenetic tree. Thus,
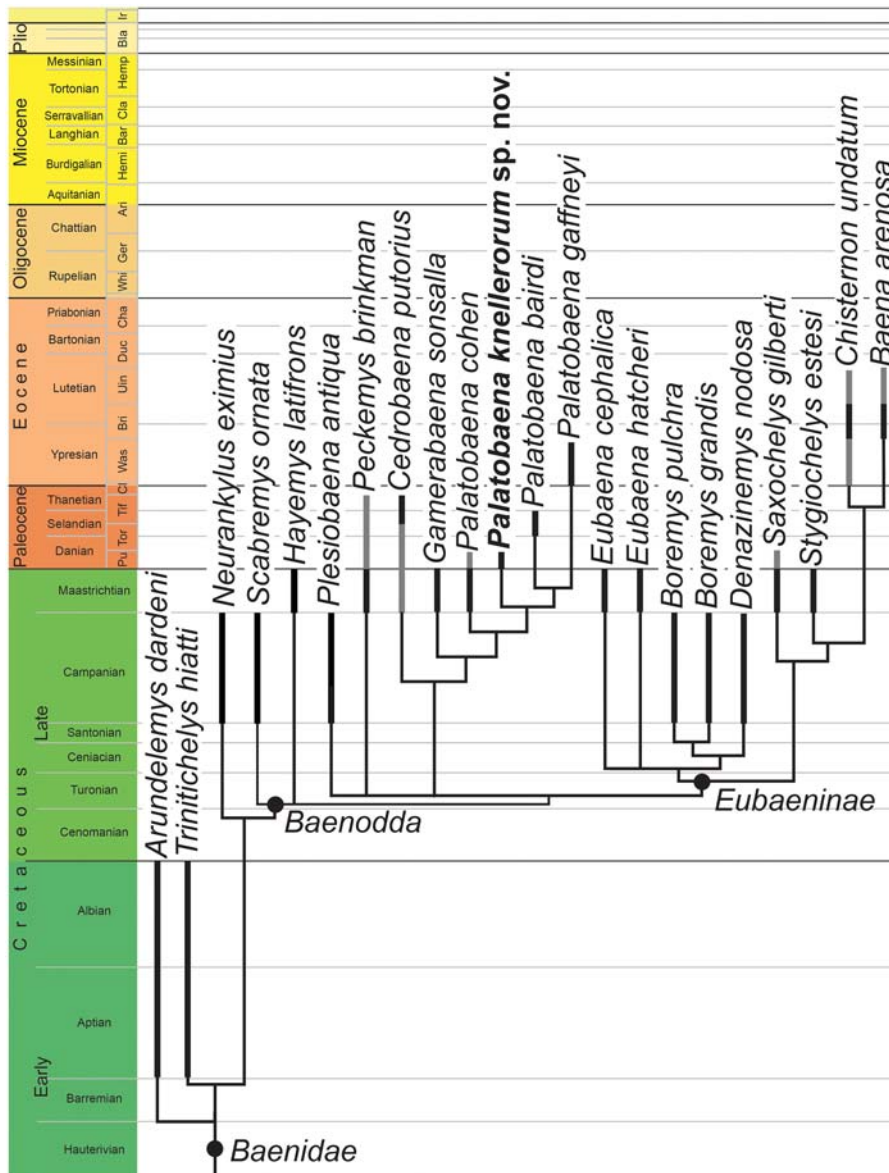
FIGURE 4. Cladogram of Baenidae mapped against the stratigraphic ranges for each taxon (bold lines; black = holotype, gray = referred material). Strict consensus tree from five most parsimonious trees (see Phylogenetic Methods). **Abbreviations**: **Ari**, Arikareean; **Bar**, Barstovian; **Bla**, Blancan; **Bri**, Bridgerian; **Cha**, Chadronian; **Cl**, Clarkforkian; **Cla**, Clarendonian; **Duc**, Duchesnean; **Ger**, Geringian; **Hemi**, Hemingfordian; **Hemp**, Hemphillian; **Ir**, Irvingtonian; **Plio**, Pliocene; **Pu**, Puercan; **Tif**, Tiffanian; **Tor**, Torrejonian; **Uin**, Uintan; **Was**, Wasatchian; **Whi**, Whitneyan.

P. knellerorum was integrated into the Lyson and Joyce (2011) matrix and no other additions or edits were made to the matrix. The final matrix included 106 morphological characters and 30 taxa. Ten characters were considered to form a morphocline and, therefore, run ordered (characters 1, 6, 14, 16, 18, 28, 33, 36, 67, 70). The remaining characters were run unordered and all characters were left unweighted. *Proganochelys quenstedti* and *Kayentachelys aprix* were specified as the outgroup taxa. We performed a 'traditional search' in the program TNT version 1.5 (Goloboff et al., 2008) with 100,000 replications and using the tree bisection-reconnection algorithm (retaining 1000 trees per replication), which resulted in 5 most parsimonious trees with a tree length of 266 steps (CI = 0.459; RI = 0.731). The strict consensus tree of Baenidae (outgroup and non-baenid paracryptodires are not shown here, but the entire tree can be found in Figure S2) is reported in Figure 4. Support for each node was measured by calculating bootstrap frequencies, with 2000 bootstrap replicates, and these results can be found in Figure S3. Synapomorphies mapped onto

the Baenodda portion of the strict consensus tree are also included in Figure S4. The analysis broadly resembles that of past analyses that evaluated baenid relationships (Lyson and Joyce, 2009a, 2009b, 2011; Lyson et al., 2016, 2019a; Lively, 2015, 2016).

DISCUSSION

Alpha Taxonomy, Biogeography, Phylogenetic Relationships, and Paleoecology

Hutchison and Holroyd (2003) first recognized *Palatobaena* in the Denver Basin based on fragmentary cranial and lower jaw material from three UCM localities within the Corral Bluffs study area (Fig. 1). Lyson and Joyce (2009a) referred this material to *Palatobaena cohen*. However, reexamination of this fragmentary material, as well as the discovery of several complete *Cedrobaena putorius* crania from the Corral Bluffs study area (Lyson et al., 2019b; also see Hutchison and Holroyd,

2003) makes us question this referral. The new *C. putorius* material shows that this taxon, like *Palatobaena* spp., has a very broad triturating surface on the palate of the skull and massive lower jaws – two features that were used by Hutchison and Holroyd (2003) and Lyson and Joyce (2009a) to refer this material to *Palatobaena* (see Systematic Paleontology section above). Given the broad similarities in triturating surfaces and lower jaws between *Palatobaena* spp. and *C. putorius* and the fragmentary nature of the material, we herein recognize that the specimens from the three UCM localities could belong to either taxon. However, regardless of the referral of these specimens, it is clear that both *Palatobaena* and *Cedrobaena* were part of the earliest Danian (ca. 66–65 Ma) fauna at Corral Bluffs.

In general, less is known about the earliest Danian turtle fossil record compared with that of the Late Cretaceous Campanian or Maastrichtian records. Faunal studies from the Campanian and Maastrichtian are often based on complete shells and crania (Holroyd and Hutchison, 2002; Brinkman, 2005; Hutchison et al., 2013; Sullivan et al., 2013), compared with the more fragmentary material from the earliest Danian (e.g., Hutchison and Weems, 1998; Hutchison and Holroyd, 2003). Much of the earliest Danian fragmentary turtle fossils are recovered from microvertebrate localities. Shell fragments are sufficient for higher taxonomic studies (Hutchison and Weems, 1998; Hutchison and Holroyd, 2003; Holroyd et al., 2014), but are usually insufficient for species-level analyses, particularly within the speciose baenid clade where species-level identifications often require complete material as species are diagnosed by unique character combinations within the shell and cranium (Lyson and Joyce, 2010; Joyce and Lyson, 2015). Based on fragmentary material, Hutchison and Holroyd (2003) recognized three baenid taxa from the lower Danian of the Denver Basin: *Plesiobaena* (referred by Lyson and Joyce 2009b to *Cedrobaena*), *Stygiochelys*, and *Palatobaena*. The recent discovery of exceptionally complete mammal, crocodilian, and turtle fossils preserved in phosphatic concretions (Lyson et al., 2019b) will undoubtedly increase the diversity of baenid turtles, as well as other turtles (Lyson et al., 2021), from the lower Danian of the Denver Basin. While diversity will undoubtedly increase, an interesting observation based on the known baenid taxa to be present in the lower Danian of the Denver Basin is that each baenid taxon has a broad triturating surface and short face and is thought to be a durophagous predator (Archibald and Hutchison, 1979; Lyson and Joyce, 2009a, 2009b; Joyce and Lyson, 2015). Several of the baenid lineages that survived the K/Pg mass extinction are hypothesized to have been durophagous predators (Lyson and Joyce, 2009b). Lyson and Joyce (2009b) hypothesized this ecological adaptation was advantageous in surviving the K/Pg mass extinction and these durophagous predators thrived in the early post-extinction environments. The presence of several durophagous taxa at Corral Bluffs (e.g., the crocodilian cf. *Navajosuchus*, the baenid turtles *Cedrobaena putorius* and *P. knellerorum*, etc.), as well as the abundance of these taxa, provides tangential evidence for this hypothesis.

Specimens of *Palatobaena* have also been recovered from the lower Danian Fort Union Formation of Montana (Lyson and Joyce, 2009a). At least two lower Danian Fort Union specimens, UCMP 131953 and UCMP 131952, have a pointed midline crest and dorsolaterally oriented orbits that most closely resemble *P. cohen* (Lyson and Joyce, 2009a). With the description of *P. knellerorum*, there are now two recognized *Palatobaena* taxa from the early Danian – *P. cohen* from the Williston Basin in the northern part of the U.S.A. and *P. knellerorum* from the more southerly Denver Basin. Given the degree of spatial niche partitioning recognized in baenids within the Hell Creek Formation wherein stratigraphically equivalent localities separated by ~400 meters and interpreted to represent different fluvial paleoenvironments support distinct assemblages of baenid turtles (Lyson et al., 2019b), it is not surprising to have two contemporaneous *Palatobaena* taxa in the earliest Danian that are separated by more than 700 kilometers, as baenids appear to have a high degree of habitat specificity. *Palatobaena knellerorum* is the southernmost occurrence of *Palatobaena* spp., as this taxon is not known from the well-documented more southern San Juan Basin or any other basin, including those in Mexico.

The phylogenetic analysis resulted in five most parsimonious trees and we present the results of the strict consensus tree in Figure 4. The results from our study broadly overlap with those from the less-resolved phylogenetic tree of the Lyson et al. (2019a) study, as well as those of the Lyson and Joyce (2011) analysis. The distinctive rounded cranium, extreme preorbital shortening of the face, dorsally oriented orbits, and several other synapomorphies unite the four *Palatobaena* species and position this clade as sister to *Cedrobaena putorius* and *Gamerabaena sonsalla*; both taxa share broad triturating surfaces with *Palatobaena* spp. (see Supplemental Data 1 for list of synapomorphies). Like previous analyses, our analysis suggests multiple acquisitions of a broad triturating surface and inferred durophagous diet—in the *Cedrobaena*/*Gamerabaena*/*Palatobaena* clade and in the Eubaeninae lineage (e.g., *Eubaena cephalica*, *Saxochelys gilberti*, *Stygiochelys estesi*).

The cranium of *Palatobaena* spp. differs significantly from that of other baenids and provides clues to the paleoecology of this enigmatic taxon. The orbits of *Palatobaena* spp., particularly *P. knellerorum*, are dorsally oriented indicating this taxon may have been a bottom dweller. In addition, the massive jaws, extreme preorbital shortening, and other modifications to the skull and lower jaws provide strong evidence that *Palatobaena* spp. was a durophagous predator (Archibald and Hutchison, 1979; Lyson and Joyce, 2009a). Finally, Archibald and Hutchison (1979) speculated that the distinctive sulcus that surrounds the narial opening in *Palatobaena* spp. was likely the origination point for a proboscis (Archibald and Hutchison, 1979). Sedimentological data from the type locality of *P. cohen*, which contains multiple shells and crania of *P. cohen*, suggests this taxon lived in an ephemeral pond or shallow stream environment (Lyson and Joyce, 2009a), whereas the sedimentological data from *P. knellerorum* suggests this taxon lived in riverine environments. Combined, these data suggest *Palatobaena* spp. was a bottom-dwelling turtle living in ponded water and riverine environments that used its proboscis to search and prey upon freshwater shelled invertebrates such as mollusks and gastropods.

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