

# Stratigraphic range extension of the turtle *Boremys pulchra* (Testudinata, Baenidae) through at least the uppermost Cretaceous

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## Abstract

New material of the derived baenid turtle *Boremys pulchra* from the Hell Creek Formation of Montana extends the stratigraphic range of the taxon through at minimum the latest Maastrichtian. Previously, the species was constrained to the Campanian of Montana and Alberta, so this extension constitutes at least 5 million years. Due to fossil reworking at the Bug Creek Anthills assemblage, where Maastrichtian and Paleocene deposits are mixed, a definitive extension for *B. pulchra* cannot currently include Paleocene strata. However, the presence of *B. pulchra* in latest Cretaceous strata, previous identification of Paleocene *Boremys* sp. and the general success of baenid taxa across the K–Pg boundary, make it quite plausible that *B. pulchra* survived the extinction event and that previously described Maastrichtian and Paleocene *Boremys* sp. material probably represents a new taxon. A stratigraphic extension beyond the Campanian indicates that *B. pulchra* survived the paleoenvironmental conditions of the latest Cretaceous, where adaptation to locally heterogeneous aquatic habitats and paleotemperature fluctuations may have facilitated latest Cretaceous and K–Pg survivorship. Additionally, ectoparasitic bore marks on the *Boremys pulchra* specimen described here can be attributed to the ichnotaxon *Karethraichnus lakkos*.

## Key Words

Biostratigraphy, Bug Creek Anthills, Hell Creek Formation, *Karethraichnus lakkos*, K–Pg boundary, Montana

## Introduction

*Boremys* Lambe, 1906a is a genus of eubaenine baenoid turtle known primarily from the Campanian of Utah (Kaiparowits Formation [Fm.]) and New Mexico (upper Kirtland Formation), as well as the Judith River Group in Alberta and Montana (Lambe et al. 1906a; Lambe 1914; Gilmore 1920; Parks 1933; Gaffney 1972; Brinkman and Nicholls 1991; Hutchison et al. 2013; Sullivan et al. 2013; Joyce and Lyson 2015). Of particular interest presently, Lyson and colleagues (2011) referred material to *Boremys* sp. from the Maastrichtian Hell Creek Formation of North Dakota and eastern Montana and the Paleocene Fort Union Formation of North Dakota (Puercan North American land mammal “age” [NALMA]), but did not reach a species designation due to missing key areas of the shell (Lyson et al. 2011; Joyce and Lyson 2015).

A partial eubaenine nuchal from the early Paleocene Denver Basin of Colorado has also been attributed to *Boremys* sp. (Hutchison and Holroyd 2003; Joyce and Lyson 2015). Additionally, undescribed partial specimens of *Boremys* sp. (e.g. RSKM P3135.68, RSKM P3143.36, RSKM P3150.41, RSKM P3173.11, RSKM P3174.16, RSKM P3174.37, RSKM P3175.14, RSKM P3176.25 and RSKM 2618.44) from the Maastrichtian Frenchman Fm. of southern Saskatchewan, which is coeval with the Upper Hell Creek Fm., could correspond with the *Boremys* sp. described by Lyson et al. (2011). Several other published referrals of *Boremys* were not supported by the comprehensive baenid review of Joyce and Lyson (2015) and I follow their assessment of this material. No *Boremys pulchra* material was identified in the survey of Montana Hell Creek/Fort Union Formation turtle faunas by Holroyd et al. (2014) and the total number of referred

*B. pulchra* specimens is small, suggesting that it was a rare turtle, as proposed for *B. grandis* in New Mexico and Utah (Lively 2016).

Previously, all *Boremys* specimens were synonymised into *B. pulchra*, distributed from Alberta to New Mexico, including *Boremys albertensis* Gilmore 1920 from the Belly River Group of Alberta (Gaffney 1972; Joyce and Lyson 2015). Currently, *Boremys* is comprised of two valid species, the northern Laramidian *Boremys pulchra* Lambe, 1906a and southern Laramidian *Boremys grandis* Gilmore, 1935, which differ systematically (Brinkman and Nicholls 1991; Joyce and Lyson 2015). The most dramatic difference is shell size, with *B. grandis* nearly twice as large as *B. pulchra* (Brinkman and Nicholls 1991; Joyce and Lyson 2015). Sandy crevasse splays, followed by channels, were determined as the preferred paleoenvironment inhabited by *Boremys* sp., based on the material evaluated by Lyson et al. (2011). A paleobiogeographical analysis of Cretaceous baenids suggests that a southern *B. grandis* and *B. pulchra* in Montana are the result of an allopatric speciation event, with subsequent southern dispersal of *B. grandis* and *B. pulchra* into Alberta (Lively 2013).

## Geological setting

The turtle specimen described here (RAM 27109) was discovered in 1994 in the Bug Creek Anthills assemblage (Locality V-1994096), near the Cretaceous-Paleogene (K-Pg) boundary in McCone County, Montana (Lofgren 1995) (Fig. 1). Unlike similarly-aged exposures in nearby Garfield County, where the Hell Creek-Tullock Formation contact approximates the K-Pg boundary, the upper part of the Hell Creek Formation in McCone County is Paleocene (Lofgren 1995). Fossils at Bug Creek Anthills locality V-1994096 (Fig. 1) occur in abundance as disarticulated elements within a pebble conglomerate, which is composed of clay-mud clasts with a light brown to tan sandstone matrix. The fossiliferous conglomerate-sandstone is scoured into a grey sandstone with red-brown ironstone lenses. Conglomerate is exposed along the north-facing side of a prairie-capped flat area, 0.6–1.5 m (2–5 ft) below the prairie cap.

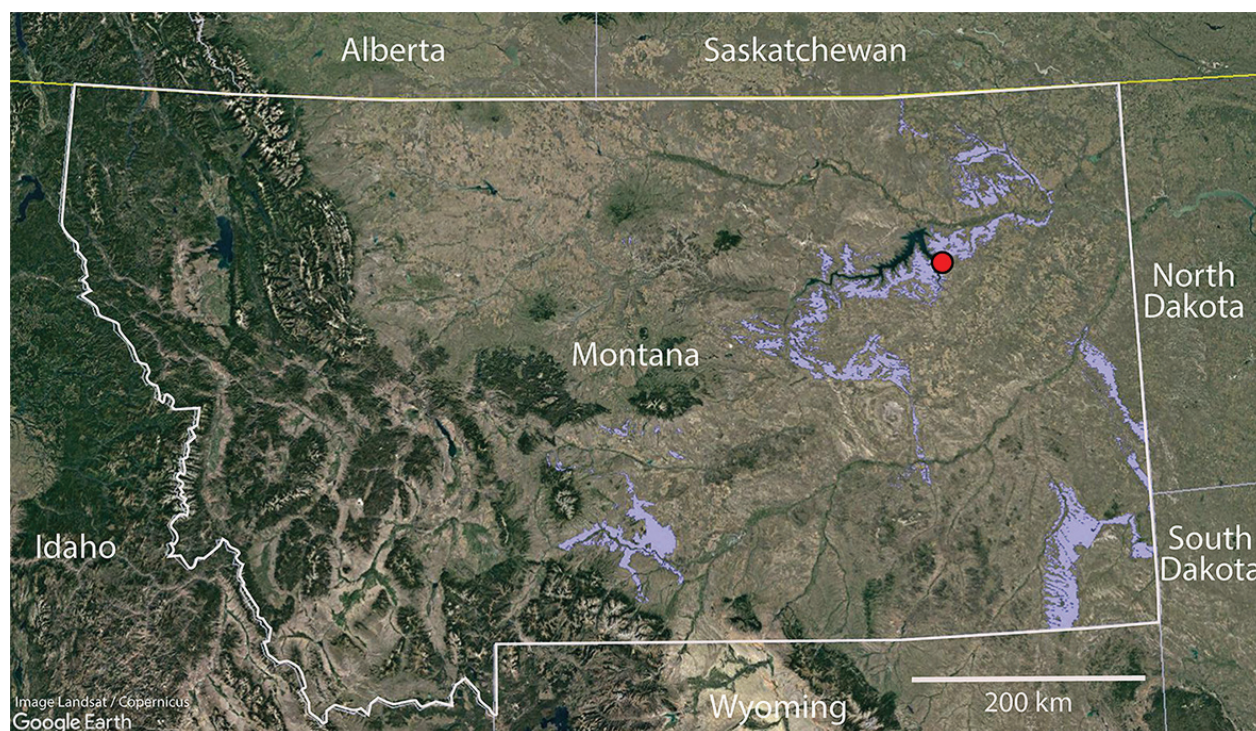
The greater Bug Creek assemblages are comprised of several localities that have been historically challenging to categorise temporally, due to reworking of their fossils—see detailed history in Lofgren (1995) and summary in Cifelli et al. (2004). One of these assemblages, Bug Creek Anthills, was originally described as the oldest in a series of three (followed by Bug Creek West and Harbicht Hill) (Cifelli et al. 2004). Extensive fossil reworking in these strata was determined to be caused by the incision of large Paleocene sandstone channels into fossiliferous Cretaceous strata, resulting in older (uppermost Maastrichtian) fossils that are present as sedimentary particles in younger channel fills deposited during the Puercan NALMA (Lofgren 1995; Cifelli et al. 2004). Central to the age

determination of Bug Creek Anthills is the presence of the “archaic ungulate” index taxon *Protungulatum donnae* Sloan and Van Valen, 1965 as the FAD (First Appearance Datum) for the advent of the initial interval zone of the Puercan NALMA (Archibald 1981, 1982; Archibald and Lofgren 1990; Cifelli et al. 2004). Lithofacies analyses of the Bug Creek localities show exclusive association with lag deposits of large channel facies, which are deeply entrenched into older floodplain deposits yielding in situ dinosaur remains (Lofgren 1995). Channel facies are arranged within a complex stratigraphic interval and locally traceable erosion surfaces were formed within channelling events (Lofgren 1995). The channels can only rarely be ordered temporally, based on superposition or crosscutting relationships (Lofgren 1995).

Some North American fossil sites near the K-Pg transition represent restricted and homogenous habitats, with faunal and floral content that can vary with depositional facies (see the Gryde Local Fauna of the Frenchman Formation in Saskatchewan; Storer 1991). This is the case in the Bug Creek assemblages of the Hell Creek Formation, where faunal remains are restricted to large, sandy channel fillings that reflect multiple episodes of deep channel entrenchment into older floodplains (Fastovsky 1987; Lofgren 1995). As in many terrestrial microvertebrate localities formed by fluvial regimes, the majority of bone material at Bug Creek is concentrated into lags in channel facies and abrupt faunal and floral changes in these strata may be, at least in part, artefacts of the depositional system (Fastovsky 1987; Eaton et al. 1989). Fluvial sedimentation also produces patterns of lenticular, interfingering and laterally discontinuous facies, none of which has extensive spatial or temporal continuity (Fastovsky 1987). Individual channels at Bug Creek are frequently lithologically and petrographically indistinguishable, sedimentary hiatuses are numerous and correlation between discontinuous outcrops is often uncertain, as the scale of the gaps between exposures can exceed that of the predicted scale of the fluvial components (Fastovsky 1987). Taphonomic analysis assessing the degree of abrasion on fossil specimens from reworked sediments may approximate distance of transport or the energy and abrasive capacity of a channel, but cannot distinguish between heterochronous faunas (Eaton et al. 1989). Overall, the depositional history of the Hell Creek Formation at Bug Creek Anthills presents a complex suite of depositional and taphonomic biases that confound characterisation and limit detailed channel and paleoenvironmental reconstructions.

Baenidae is represented by at least 11 taxa in the Hell Creek Formation, accounting for much of the diversity in the considerable turtle assemblage of the unit (Lyson et al. 2019). At least seven other family level clades of turtles are also known from the Hell Creek Fm.: Adocidae, Chelydridae, Kinosternoidea, Macrobaenidae, Nanshiungchelyidae, Pleurosternidae and Trionychidae (see faunal list of Holroyd et al. 2014: table 2). As previously stated, no specimens of *Boremys pulchra* were identified





**Figure 1.** Index map of locality V-1994096 in the Hell Creek Formation, northeast Montana. Blue areas indicate Hell Creek Formation exposures in Montana and the red dot indicates the Bug Creek Anthills assemblage. Base satellite map generated with Google Earth V 7.3.4.8248. (March 20, 2022). Montana, United States. Camera: 929 km, 46°54'58"N, 109°48'21"W. Landsat/Copernicus 2022. <http://www.earth.google.com> [20 March 2022].

in past surveys of Hell Creek Fm. turtles, despite being readily identifiable (Holroyd et al. 2014). Besides RAM 27109, the only other turtles identifiable from Bug Creek Anthills locality V-1994096 are from indeterminate trionychid (softshell turtle) fragments. However, the coeval small mammal assemblage from Bug Creek Anthills is exceptional in diversity and abundance, with numerous multituberculate (11 genera), marsupial (6 genera) and eutherian (9 genera) taxa identified to species level—see faunal list of Lofgren (1995: 70) and relevant taxonomic updates in Wilson (2014: table 1). According to RAM collections records, indeterminate crocodilian, champsosaurid, amphibian and squamate material has also been recovered from locality V-1994096, as well as a presbyornithid bird. Finally, chondrichthyan and osteichthyan fishes are represented, including Actinopterygii, Amiidae and Lepisosteidae.

## Materials and methods

Screenwashing techniques described by McKenna (1965) were employed at Bug Creek Anthills locality V-1994096 in 1994; however, the size of the specimen (larger than ~ 1 cm<sup>2</sup>) indicates it was probably surface collected (Lofgren, pers. comm.). Linear measurements were taken using Neiko (China) #01417A 6" Digital Calipers and depth measurements were performed with an iGaging (USA) # 35-125 Digital Electronic Indicator. Some distances and angles were measured from high quality digital

photographs using IMAGEJ (Rasband 1997–2016). The plot and regression line of anterior plastral lobe measurements were generated in Microsoft EXCEL (v. 2203). I use the taxonomic scheme of turtles presented by Joyce (2007, 2017) unless otherwise specified and I adhere to Phylocode guidelines (e.g. Laurin et al. 2005; Joyce et al. 2020, 2021). Following Hutchison and Bramble (1981) and most modern authors, the two pairs of scales present on the anterior plastron are termed gular and extragular scales, where the gulars are located anteromedially to the extragular scales and both sets of scales are anterior to the entoplastron. Classification of ichnological pits follows Hutchison and Frye (2001).

## Institutional abbreviations

**CMN**, Canadian Museum of Nature (formerly NMC), Ottawa, Canada; **NMC**, National Museum of Canada, Ottawa, Canada; **PTRM**, Pioneer Trails Regional Museum, Bowman, North Dakota, USA; **RAM**, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; **ROM**, Royal Ontario Museum, Ontario, Canada; **RSKM**, Royal Saskatchewan Museum, Saskatchewan, Canada; **TMP**, Royal Tyrell Museum of Palaeontology, Alberta, Canada; **UALVP**, University of Alberta Laboratory of Vertebrate Paleontology, Alberta, Canada; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA; **USNM**, National Museum of Natural History, Washington D.C., USA.

## Systematic paleontology

**Testudinata Batsch, 1788** (sensu Joyce, Parham & Gauthier, 2004)

**Paracryptodira Gaffney, 1975** (sensu Joyce, Parham, Anquetin, Claude, Danilov, Iverson, Kear, Lyson, Rabi & Sterli, 2020)

**Baenidae Cope, 1873** (sensu Joyce, Anquetin, Cadena, Claude, Danilov, Evers, Ferreira, Gentry, Georgialis, Lyson, Pérez-García, Rabi, Vitek & Parham, 2021)

### *Boremys* Lambe, 1906b

*Boremys pulchra* Lambe, 1906a

**Type specimen.** CMN 1130, a plastron and anterior half of carapace (Lambe 1902: fig. 8; Lambe 1906a: pls. 3.4, 4).

**Type locality and stratum.** Near the mouth of Berry Creek, Red Deer River, Dinosaur Provincial Park, Alberta, Canada; Dinosaur Park (formerly Judith River) Formation, Judith River Group, Campanian, Late Cretaceous (Lambe 1906a; Brinkman and Nicholls 1991; Eberth and Hamblin 1993).

**Material.** RAM 27109, a near-complete anterior plastral lobe, comprised of co-ossified entoplastron, epiplastron and partial hyoplastra (Fig. 2).

**Description.** RAM 27109 is a well preserved, mostly complete anterior plastral lobe (Fig. 2). The pattern of sulci at the anterior end of the ventral side of the lobe closely matches that of *Boremys pulchra*, as reconstructed by Brinkman and Nicholls (1991: fig. 7B) (Fig. 2A–C). The epiplastron, entoplastron and hyoplastra of RAM 27109 are completely fused, with no visible sutures (Fig. 2A, C). Archibald (1977) considered lack of shell fusion a derived character in *Boremys*, but most *Boremys pulchra* shells examined by Brinkman and Nicholls (1991) were fused. Considering that baenid turtles exhibit determinate growth and co-ossify as adults and that RAM 27109 is similar in size and proportions to other *B. pulchra* specimens, RAM 27109 can be considered a nearly full-sized adult (Hutchison 1984) (Fig. 3, Table 1). Smaller size is a primary diagnostic character for this species and Brinkman and Nicholls (1991) regard 320 mm as the maximum mid-line carapace length for *B. pulchra*. Similarly, Joyce and Lyson (2015) found 300 mm as the carapace length dividing *B. pulchra* from the congeneric *B. grandis*. Using the proportions of the reconstructed shell of *B. pulchra* from Brinkman and Nicholls (1991), the mid-line carapace length of RAM 27109 is estimated to be ~200 mm, similar to Campanian *B. pulchra* specimens (Brinkman and Nicholls 1991; Joyce and Lyson 2015) (Fig. 3, Table 1). The presence of anterior plastral scalloping (lateral epiplastral projections) and straight extragular-humeral sulci further differentiate RAM 27109 from *B. grandis* (Gilmore 1935). I consider the reconstruction of Brinkman and Nicholls (1991: fig. 7B)

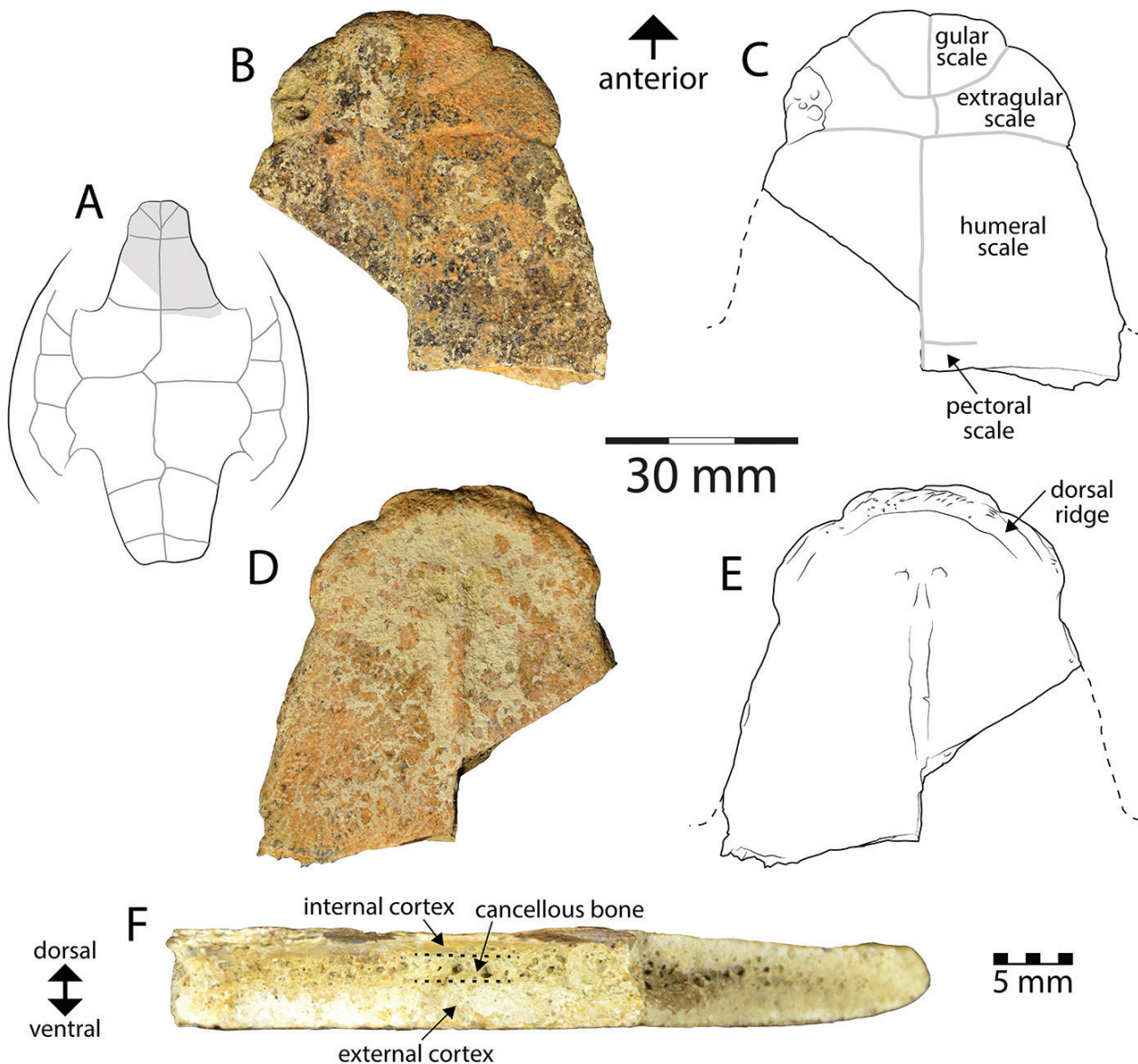
probably more representative than that presented by Gaffney (1972: fig. 40) because it is more recent and based on more specimens (NMC 2281, ROM 5115, TMP 90.119.6, UALVP 9, UCMP 130155). The current specimen and reconstructions of *B. pulchra* vary in the degree of curvature between the gular-extragular and extragular-humeral sulci, as well as the degree of lateral projection on the epiplastron (Gaffney 1972; Brinkman and Nicholls 1991). Given the uncertainty regarding sutures due to shell fusion, I interpret these last minor morphological differences as probable individual variation (Gaffney 1972; Brinkman and Nicholls 1991).

RAM 27109 is subtriangular in shape with a bilateral pair of rounded lobes (the anterior of which is smaller) projecting laterally from the epiplastron to form distinct anterior plastral scalloping (Fig. 2B–E). Each laterally projecting lobe is upturned dorsally and protrudes slightly beyond a rounded ridge on the dorsal surface of the plastron which runs along the bases of the lobes (Fig. 2D–E). This 3–4 mm wide ridge likely marked the transition between the scale-covered lobes and the body wall (Fig. 2E). The dorsal surface of the anterior plastral lobe is otherwise flat and even, apart from a ~1 mm tall ridge along the posterior portion of the anterior plastral lobe mid-line, which likely represents a reduced homologue of the posterior process of the entoplastron that is present in basal testudinates (Gaffney 1990: figs. 91–92; Szczygielski and Sulej 2019: fig. 6) (Fig. 2D–E). The mid-line ridge reaches a maximum width of 4.3 mm and it diminishes anteriorly across the inferred length of the entoplastron, terminating at approximately the anterior end of this bone (Fig. 2D–E). At this level, there is a small round pit (diameter = ~3 mm) on each side of the mid-line ridge (Fig. 2D–E). Anterior to the hyoplastra, the muscles supracoracoideus anterior and deltoideus clavicularis possibly attached to the anterior plastral lobe near the mid-line (Zhu 2011). The functions of these muscles are adduction and retraction of the humerus, which are important in aquatic locomotion of turtles (Walker 1973; Zhu 2011).

**Table 1.** Measurements of anterior plastral lobes (maximum lengths and widths) of *Boremys pulchra* Lambe, 1906a specimens. Additional data from Brinkman and Nicholls (1991: table 2). Graph ID numbers correspond with those in Figure 3. All measurements are from specimens collected in Dinosaur Provincial Park, Alberta (Dinosaur Park Formation, middle Campanian), except RAM 27109. All measurements in mm.

Graph ID	Specimen	Length mm	Width mm
1	RAM 27109	54	61
2	NMC 2281	64	57
3	USNM 8803	64	94
4	UALVP 9	56	59
5	TMP 88.36.111	52	50
6	TMP 90.119.6	68	80
7	TMP 74.10.1	55	56
8	TMP 75.11.46	53	61
9	TMP 88.2.10	65	75

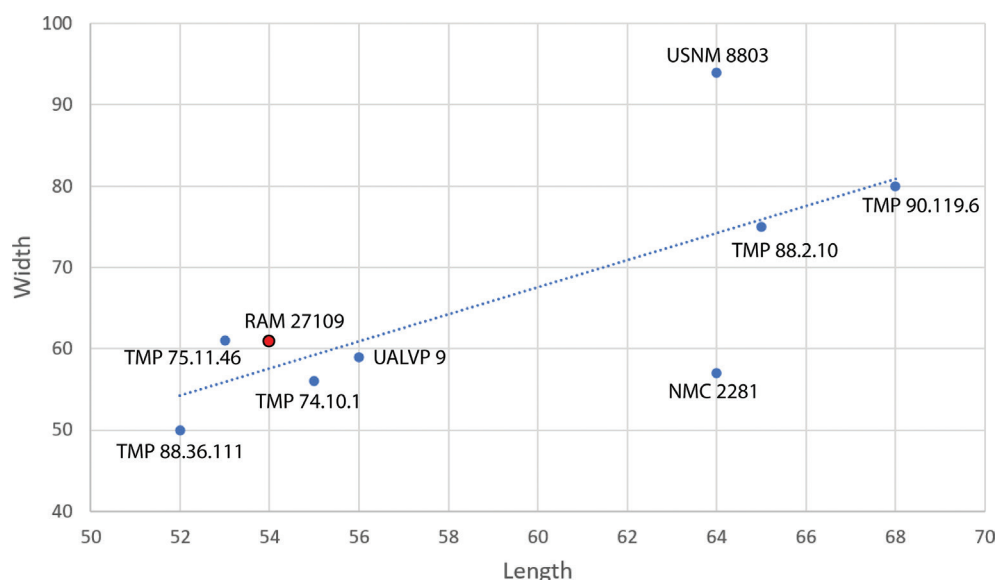




**Figure 2.** RAM 27109, anterior plastral lobe of *Boremys pulchra* Lambe, 1906a. **A.** Reconstructed *B. pulchra* carapace of Brinkman and Nicholls (1991), with shaded area representing RAM 27109; **B.** Photograph in ventral view; **C.** Line drawing in ventral view; **D.** Photograph in dorsal view; **E.** Line drawing in dorsal view; **F.** Proximal (broken) cross section of anterior plastral lobe. Light grey lines represent sulci and dashed lines in **C** and **E** show missing edges. In **F**, dotted lines indicate boundaries between interior bone layers. 5 mm scale applies to **F** only.

The posterior end of the anterior plastral lobe is broken cleanly in an approximately straight line perpendicular to the mid-line on the left side (Fig. 2F). On the right side, the break angles anterolaterally at approximately  $53^\circ$  from the mid-line (Fig. 2B–E). Both breaks provide a view into the interior anatomy of the anterior plastron, but few details of the microanatomy can be assessed (Fig. 2F). The bone exhibits a diploë structure typical of turtles, with compact external and internal cortices enclosing an interiormost region of cancellous bone (Scheyer 2007) (Fig. 2F). The primary comparative data available regarding baenid shell histology is from carapacial and plastral material of *Boremys* sp. from the Late Cretaceous Dinosaur Park Formation in Alberta, Canada (Scheyer 2007). Compared to *Neurankylus* sp. and *Plesiobaena*

sp., *Boremys* sp. (and *Chisternon* sp.) is reported to have less compact bone, thinner cortices and a well-developed cancellous interior, with larger marrow cavities in cancellous bone and higher vascularisation in compact bone (Scheyer 2007). Such detailed microanatomical morphology cannot be ascertained from RAM 27109; however, there is distinct cancellous bone with prominent marrow cavities in the interiormost region of approximately the middle third of the lobe (Fig. 2F). Trabeculae are larger towards the mid-line and are generally round to ovoid and the lateral plastral margins consist of only compact bone, without a cancellous interior (Fig. 2F). Near the mid-line, the well-developed external cortex is approximately 2.7 times thicker than the internal cortex (Fig. 2F). This disparity between external and internal cortical thickness



**Figure 3.** Maximum length/width (mm) plot of the anterior plastral lobe in *Boremys pulchra* Lambe, 1906a specimens (Brinkman and Nicholls 1991: table 2). Values are provided in Table 1. All measurements, except RAM 27109 (in red), are from specimens collected in Dinosaur Provincial Park, Alberta (Dinosaur Park Formation, middle Campanian). For the dotted blue regression line,  $R^2 = 0.5246$ .

is similar to that of a costal from *Denazinemys nodosa* Gilmore, 1916 in the late Campanian Fruitland Formation, where the exterior cortex is significantly thicker than the internal cortex and trabeculae are mostly small and circular (Lichtig and Lucas 2017).

## Results

The posterior half of the posterior lobe of anterior scalloping (lateral epiplastral projection) on the right ventral side of RAM 27109 exhibits distinct pits, which are interpreted as a cluster of at least four ectoparasitic bore marks (Figs 2A, B, 4). The marks are shallow (non-penetrative) and have simple profiles and rounded hemispherical termini (Fig. 4A). They can be classified as Type II pits according to the classification of Hutchison and Frye (2001), which are circular to ovoid with rounded bottoms (Fig. 4A). Measurements for individual marks are provided in Table 2. Pit dimensions range from 1.2–2.8 mm in diameter and from 1.8–3.2 mm in depth (Fig. 4, Table 2). The marks are adjacent to each other along the slope of a bevel at the plastral margin and only on the ventral side. Abraded areas, lateral and anterior to the cluster, may have contained additional small marks, but their borders have been taphonomically obscured (Fig. 4A). Mark #1 is the only pit that has an unabraded border and, thus, a more precise depth, but the remaining pits occur along a curved surface with worn edges, making their depths (and hence diameter/depth ratios) less reliable (Fig. 4, Table 2).

The morphology and size of the bore marks on RAM 27109 are consistent with *Karethraichnus lakkos* Zonneveld, Bartels, Gunnell and McHugh, 2016, a common ectoparasitic ichnotaxon on turtles and tortoises from Cretaceous and Tertiary deposits in North America and Africa (Zonneveld et al. 2016, 2021; Adrian et al.

**Table 2.** Measurements of bore marks (in mm) on ventral surface of RAM 27109 (see Fig. 4). Marks are attributed to the ectoparasitic ichnotaxon *Karethraichnus lakkos* Zonneveld, Bartels, Gunnell & McHugh, 2016.

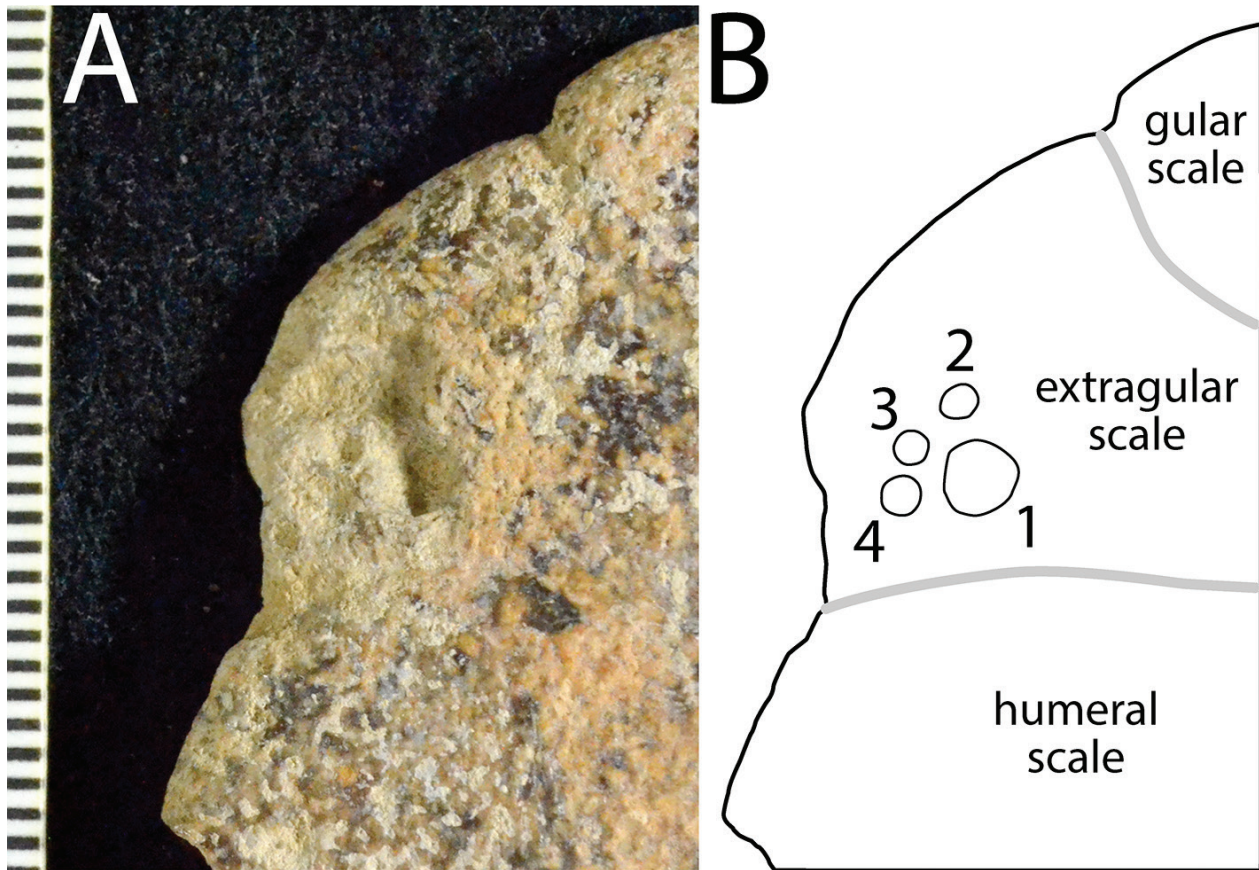
Mark #	Diameter mm	Depth mm	Diameter/Depth
1	2.8	1.8	1.56
2	1.3	2.0	0.65
3	1.2	3.2	0.38
4	1.4	2.3	0.61

2021). Congeneric ichnospecies are also known from a Campanian dermochelyid (marine) turtle in Japan and from Late Pleistocene armadillos in Brazil (Sato and Jenkins 2020; Moura et al. 2021). Tracemakers usually associated with *K. lakkos* include leeches and ixodid arthropods (ticks), which are known to feed on blood sinuses within shell bone, especially at sulci between epidermal scales (Siddall and Gaffney 2004; Zonneveld et al. 2016, 2021). Bore marks of *K. lakkos* are only emplaced in locations accessible on living turtles—external surfaces of the carapace and plastron, especially at marginal or lip areas (Zonneveld et al. 2016). Thus, *K. lakkos* is associated with the activities of parasites instead of postmortem scavengers or synmortem predators (Zonneveld et al. 2016).

## Discussion

### Taxonomic and temporal assignment of RAM 27109, and stratigraphic range extension

Though *Boremys pulchra* is primarily known from the Campanian, fossil material attributable to *Boremys* sp. has also been reported from Maastrichtian deposits of North Dakota, eastern Montana and southern Saskatchewan, the Paleocene of North Dakota (Lyson et al. 2011)



**Figure 4.** Ectoparasitic bore traces attributed to the ichnotaxon *Karethraichnus lakkos* Zonneveld, Bartels, Gunnell and McHugh, 2016. **A.** Close-up photograph under oblique lighting; **B.** Line drawing. Grey lines indicate sulci and measurements of marks are provided in Table 2.

and the Paleocene of Colorado (Hutchison and Holroyd 2003). For the *Boremys* material described by Lyson et al. (2011), species designation was not possible due to the presence of open sutures and central plastral fontanelles between the mesoplastra, which could be indicators of skeletal immaturity or possible autapomorphies for a new Maastrichtian/Puercean taxon.

The only character in the phylogenetic matrix of Lyson et al. (2011) that is coded differently between *Boremys pulchra* and *Boremys* sp. is a carapacial trait (#44, vertebral scale shape) and, thus, cannot be applied to the plastral specimen RAM 27109. This makes body size within *Boremys* an established morphological difference between its species that is not reflected in the phylogenetic matrix of Lyson et al. (2011). Carapace size is considered (#40) in the more recent baenid matrix of Lyson et al. (2016), but *Boremys* sp. is not included, so the character only distinguishes between *B. pulchra* and *B. grandis*. The remarkable overall similarity between the coding for *B. pulchra* and *Boremys* sp. in multiple baenid matrices makes shell size the only published diagnostic difference between the two taxa, as applicable to the plastron. Shell size is, therefore, the only morphological basis available in the current study to differentiate RAM 27109 from the *Boremys* sp. of Lyson et al. (2011). The only published carapace length of *Boremys* sp. (PTRM 16156, 31.8 cm) is above the upper threshold (30 cm) of

*B. pulchra* body size and probably represents a juvenile individual, due to large plastral fontanelles and open sutures (Lyson et al. 2011; Joyce and Lyson 2015). Thus, the adult size of *Boremys* sp. is not known and may be closer to the larger *B. grandis* than *B. pulchra* (Lyson et al. 2011). The consistency of size between RAM 27109 and *B. pulchra* (Table 1), coupled with high similarity of their anterior plastral pholidoses, allows referral of the current specimen to that taxon. However, there is a margin of uncertainty due to the lack of other diagnostic morphology in the partial RAM 27109. Future discoveries (i.e. the skull or more complete shells of *Boremys* sp.) and analysis of other undescribed Maastrichtian *Boremys* sp. material may clarify our understanding of the lineage following the Campanian and additional stratigraphic revisions may be necessary.

RAM 27109 is referred to *B. pulchra*, based on its small adult size and anterior plastral morphology, consistent with Campanian representatives of the species (Gaffney 1972; Brinkman and Nicholls 1991). Its presence in the uppermost Cretaceous deposits of the Hell Creek Formation at Bug Creek Anthills makes it the youngest known specimen of *B. pulchra*, although extensive reworking of uppermost Maastrichtian rocks in this unit only allows for definitive attribution to rocks which are latest Maastrichtian in age (Lofgren 1995). However, the presence of the genus above the K–Pg boundary, the



presence of *B. pulchra* in the latest Maastrichtian (established here) and the known survival of most Hell Creek Fm. baenids into the Paleocene (Lyson and Joyce 2009b; Lyson et al. 2011; Holroyd et al. 2014; Joyce and Lyson 2015), suggests that *B. pulchra* also survived the K–Pg extinction event. Generally, turtles fared well during the K–Pg extinction event, with a survival rate of 84% at the generic level (Hutchison and Archibald 1986; Lofgren 1995; Lyson et al. 2011; Holroyd et al. 2014).

## Pathologies

Haematophagous leeches are the most common ectoparasites of modern aquatic reptiles and amphibians, including freshwater turtles (Sawyer 1986; Readell et al. 2008). Leeches can cause anaemia and bacterial and fungal infections in captive hosts and are also known vectors for haematoparasites, which can be transmitted intra- and interspecifically (Telford 1984; Readell et al. 2008). Leech loads vary significantly between modern turtle species and are higher on bottom-walking taxa, which live in close contact with the substrate inhabited by leeches and ponds with high turbidity (Ryan and Lambert 2005; Readell et al. 2008). Some studies have reported higher leech intensity (or associated haemogregarine parasites) in female turtles, possibly due to their frequently larger body size (McKnight et al. 2021). Despite common hypotheses, mean leech intensity in modern taxa is not affected by aerial basking and does not vary with turtle abundance, amount of edge vegetation or number of available basking sites (Readell et al. 2008; McKnight et al. 2021). Baenids, in general, are considered bottom-dwelling turtles that favoured running water and articulated specimens are found predominantly in sandy sediments (Hutchison and Archibald 1986; Holroyd and Hutchison 2002; Lyson et al. 2021). *Karethraichnus*, in particular, has also been reported on baenid fossils from the Eocene Green River Basin in Wyoming and Uinta Formation of Utah, though it has been more frequently documented in the geoemydids *Echmatemys* and *Bridgeremys* (Zonneveld et al. 2016; Adrian et al. 2021). Considered together, these factors suggest that *B. pulchra* may have been exposed to more parasite-bearing substrate due to potential bottom-walking, but its leech loads may have been mitigated by a higher energy, fluvial depositional setting. Further studies should examine the effect of haematophagous parasites on the health, behaviour and physiology of wild turtles, as well as the morphology of modern parasitic traces on turtle shell bone.

## Conclusions

The presence of *Boremys pulchra* in the Bug Creek Anthills assemblage of Montana establishes the taxon through the latest Maastrichtian and also potentially extends the stratigraphic range of the taxon through the K–Pg boundary into the Puercan NALMA. Due to temporal uncertainty at Bug Hills Anthills localities caused by reworking of Paleocene

fossils into the uppermost Maastrichtian deposits, this extension can only include the latest Cretaceous deposits, consistent with prior treatment of turtle taxa from Bug Creek Anthills (see Holroyd and Hutchison 2002). Thus, the current study extends the stratigraphic range of *B. pulchra* by at least 5 million years. Further, considering that multiple specimens of *Boremys* sp. have been identified from Paleocene deposits (Hutchison and Holroyd 2003; Lyson et al. 2011; Joyce and Lyson 2015) and the high rate of baenid survivorship through the K–Pg extinction event (Hutchison and Archibald 1986; Lyson and Joyce 2009b; Lyson et al. 2011; Holroyd et al. 2014), the present study increases the likelihood that *B. pulchra* also survived the K–Pg boundary. Given the exclusively southern distribution of the large-bodied *B. grandis*, the consistently northern range of the small *B. pulchra* and the reconstructed ancestral range of *Boremys* in Montana (Lively 2013), it is probable that the larger *Boremys* sp. material described by Joyce and Lyson (2011) represents a new northern taxon of intermediate size.

If *Boremys pulchra* did, indeed, survive the K–Pg extinction, it would be the tenth surviving baenid taxon to do so, joining *Neurankylus eximius* Lambe, 1902, *Cedrobaena brinkman* Lyson & Joyce, 2009b, *Cedrobaena putorius* Lyson & Joyce, 2009b, *Palatobaena cohen* Lyson & Joyce, 2009a, *Eubaena cephalica* Hay, 1904, *Stygiochelys estesi* Gaffney & Hiatt, 1971, *Goleremys mckennai* Hutchison, 2004, *Saxochelys gilberti* Lyson, Saylor & Joyce, 2019 and *Boremys* sp. (Lyson et al. 2011; Joyce and Lyson 2015). Survival of aquatic vertebrates across the K–Pg boundary has been related to adaptation in mutable, locally heterogeneous aquatic environments that experienced fluctuating paleotemperature patterns, which characterise the latest Cretaceous deposits in the northern Great Plains of North America (Fastovsky 1990; Holroyd and Hutchison 2002; Holroyd et al. 2014). Additional confirmed Maastrichtian *B. pulchra* specimens may allow more robust comparison between Campanian and later forms. Specific adaptations to post-Campanian paleoenvironments, such as swimming ability, feeding ecology or bottom walking, may also be elucidated by additional morphological study. Finally, further collection of turtle fossils in localities near the Cretaceous/Paleocene transition and detailed examination of specimens currently in collections (including material from microvertebrate sites) may alter the stratigraphic ranges of other north Laramidian turtles, including those that are small and/or rare, like *B. pulchra*.

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