NEW BAENID TURTLES FROM THE CRETACEOUS

KAIPAROWITS FORMATION OF SOUTHERN

UTAH: IMPLICATIONS FOR LARAMIDIAN

BIOGEOGRAPHY

by

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ABSTRACT

Recent discoveries demonstrate that Campanian dinosaur assemblages across the western North American subcontinent (Laramidia) exhibit basin-scale endemism, with each sedimentary basin possessing its own unique assemblage, and an apparent higher-level biogeographic boundary between northern and southern Laramidia. Subsequently, during the Maastrichtian, most taxa are present in multiple basins, with some forms supporting the presence of distinct northern/southern provinces, whereas others are more cosmopolitan. Despite these dinosaur biogeographic data, little attention has been paid to other vertebrate groups. To test these biogeographic hypotheses, I examined the alpha taxonomy, evolution, and paleobiogeography of the paracryptodiran turtle clade Baenidae using a newly-generated species-level phylogeny. Baenids were one of the most diverse and abundant turtle clades during the Late Cretaceous, are restricted to North America, and have a well-sampled fossil record, making them an ideal study system for examining Laramidian biogeography.

I first assessed the taxonomic affinities of newly discovered baenid turtles from the Upper Cretaceous (Campanian) Kaiparowits Formation of southern Utah. I found that at least five distinct baenid species inhabited the Kaiparowits Basin during the Campanian. These taxa include *Denazinemys nodosa*, previously known from Texas and New Mexico, *Boremys grandis*, previously known from New Mexico only, and three new

taxa that appear to have been endemic to southern Utah. These newly described taxa include two new species of *Neurankylus* and a morphologically unique pig-nosed taxon. Using new morphologic data from the Kaiparowits specimens, I conducted a comprehensive phylogenetic analysis on the clade, utilizing 106 characters and 32 ingroup taxa.

Based on occurrences alone, Campanian baenid assemblages display distinct northern and southern provinces with no taxonomic overlap. To investigate the evolutionary patterns of this biogeographic signal, I applied a dispersal-extinction-cladogenesis model to the strict consensus tree and three randomly selected most parsimonious trees from my phylogenetic analysis. This study reveals that the ancestral ranges for basal baenid branches were cosmopolitan across either Laramidia or all of North America. More derived baenids (i.e., subclade Baenodda) possessed ancestral ranges in the area of Montana, Wyoming, and the Dakotas, and the analysis reconstructs multiple individual lineages then dispersing to southern Laramidia and Alberta.

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CHAPTER 1

A PIG-NOSED BAENID TURTLE FROM THE KAIPAROWITS

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Abstract

I describe a newly discovered baenid turtle specimen from the middle Campanian Kaiparowits Formation of southern Utah as a new taxon. The specimen consists of a nearly complete articulated skeleton and shell, and the skull was scanned using micro-computed tomography (μCT) to gain a better understanding of its internal anatomy. This baenid possesses two distinct external nares separated by a bony septum, an autapomorphic feature among known baenid taxa. The skull is wedge-shaped with a broad rostrum and laterally expanded nasals. Although the shell is similar to that of *Plesiobaena antiqua*, a phylogenetic analysis places this new taxon as sister to *Hayemys latifrons* from the Maastrichtian Lance Formation of Wyoming, emphasizing the importance of the skull/shell association. These taxa are relatively basal within the sub-clade Baenodda. This phylogenetic placement for the new taxon suggests that the general shell morphology exhibited by *Plesiobaena antiqua* and other suggested closely related taxa may actually represent the plesiomorphic state for Baenodda, and is not phylogenetically significant for baenodd interrelationships or alpha taxonomy.

Introduction

Baenidae is an extinct clade of freshwater turtles that was restricted to the Cretaceous– Eocene of North America (e.g., Gaffney, 1972; Hutchison, 1984; Holroyd and Hutchison, 2002; Brinkman, 2003). Along with Pleurosternidae and and other baenoid taxa such as *Dinochelys whitei* (e.g. Gaffney, 1979; Brinkman et al., 2000), *Compsemys victa* (e.g., Lyson and Joyce, 2011), and *Uluops uluops* (e.g., Bakker, 1988), baenids are members of the extinct clade Paracryptodira (Joyce, 2011; Lyson and Joyce, 2011). The oldest-known and most basal baenid, *Arundelemys*, occurs in the Potomac Formation of Maryland (Lipka et al., 2006; Lyson and Joyce, 2011). However, all other known baenids are restricted to the Western Interior of North America. During the Campanian and Maastrichtian, baenids were one of the most speciose and abundant freshwater turtle clades in Laramidia (Lyson and Joyce, 2010). This clade survived into the Paleogene and finally went extinct during the Eocene (Gaffney, 1972). Gaffney (1972) provided the first comprehensive review and revision of the taxonomy systematics of Baenidae. Several synonymies from this work have been reassessed by Brinkman and Nichols (1991), Larson et al. (2012), Sullivan et al. (2012), and Lyson and Joyce (2009a, 2009b, 2010, 2011) described number of new taxa and additional taxonomic revisions. However, their efforts have focused on the baenids of the Maastrichtian–Paleocene Hell Creek Formation of northern Laramidia. Limited attention has been dedicated to the baenids from the Campanian of southern Laramidia, and the focus of the few available publications is largely restricted to the San Juan Basin, New Mexico (Lucas and Sullivan, 2006; Sullivan et al., 2012).

Recent research into the vertebrate assemblage of the Campanian Kaiparowits Formation in Grand Staircase-Escalante National Monument (southern Utah) over the past decade has greatly increased our understanding of southern Laramidian Late Cretaceous nonmarine ecosystems. Although previous works had published faunal lists (e.g., Eaton et al., 1999), Hutchison et al. (in press) were the first to describe the turtle assemblage of the Kaiparowits Formation. Among baenids, they recognized two distinct but unnamed species of *Neurankylus*, *Denazinemys nodosa*, *Boremys grandis*, and *Plesiobaena* sp. *Plesiobaena*, Gaffney 1972 included two named species: *Plesiobaena antiqua* from the Campanian of Montana and Alberta and *Plesiobaena putorius* from the Maastrichtian of North and South Dakota and the Paleocene of Wyoming (Gaffney, 1972; Lyson and Joyce, 2009b). Brinkman (2003) noted clear differences between Campanian (Alberta) and Maastrichtian (Montana, Colorado, Wyoming) specimens ascribed to *P. antiqua*, but did not erect a new taxon for the latter material. Lyson and Joyce (2009b) revised *Plesiobaena*, finding that the taxon was paraphyletic and restricted the genus to *P. antiqua* from the middle Campanian Dinosaur Park and Oldman formations of Alberta. Maastrichtian members of the species were assigned to the new taxon *Peckemys brinkman*, whereas members of *"Plesiobaena" putorius* were placed in the new genus *Cedrobaena* (Lyson and Joyce, 2009b). Most of the diagnostic characters for these taxa were based on skull morphology, because only one shell is known for *P. brinkman* and none are known for *C. putorius*. Because of similarities between *P. antiqua*, *P. brinkman*, and *Palatobaena cohen*, Lyson and Joyce (2009a,b) concluded that although it is possible to identify *P. antiqua*, distinguishing between Maastrichtian using only shells was not possible.

Hutchison et al. (in press) identified *Plesiobaena* sp. from the Kaiparowits Formation based on two shell specimens preserving only the carapace and plastron, with no cranial material. However, a third, nearly complete articulated specimen has recently been discovered that includes a skull, shell, and numerous postcranial elements. The purpose of this study is to describe the morphology of this taxon, evaluate its taxonomic identity, and determine its phylogenetic position within Baenidae.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York City; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **MRF**, Marmarth Research Foundation, Marmarth, North Dakota; **ND**, North Dakota Heritage Center, Bismark, North Dakota; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; **TMP**, Royal Tyrrell Museum of Paleontology, Drumheller, Alberta; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; **UMNH**, Natural History Museum of Utah, University of Utah, Salt Lake City, Utah; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut.

Geologic Setting

The specimens described here were found in the Upper Cretaceous Kaiparowits Formation of the Kaiparowits Plateau in southern Utah. The 860 m thick formation was deposited in a prograding clastic wedge extending from the Sevier orogenic belt in the

west, to the Western Interior Seaway to the east (Roberts, 2007). The formation is interpreted to represent deposition in a low relief, alluvial/coastal plain setting, and is characterized by channel sandstones and overbank deposits. Abundant fluvial and paludal paleoenvironments, along with a diverse flora and fauna, suggest a humid climatic regime for this basin, similar to that of the Gulf Coast region today (Roberts, 2007). ^{40}Ar/^{39}Ar ages from throughout the Kaiparowits Formation found that it was deposited between 76.49 ± 0.14 and 74.69 ± 0.18 Ma (Roberts et al., in press; Roberts et al., 2005), which indicates a late Campanian age for the formation and places it in the Judithian Land Mammal Age (Lillegraven and McKenna, 1986). This correlates the Kaiparowits Formation with fossil-bearing portions of the Dinosaur Park, Judith River, and Two Medicine formations to the north and partially correlative with the Aguja Formation to the south (Roberts et al., in press; Roberts et al., 2005). The Kaiparowits Formation is also partly correlative with the Fruitland Formation and older than the Kirtland Formation in the nearby San Juan Basin of northwestern New Mexico (Roberts et al., in press; Roberts et al., 2005).

The Kaiparowits Formation is informally divided into the lower, middle and upper members (Roberts, 2007). For the most part, vertebrate remains have been recovered from the lower and middle units. The holotype of the new taxon described here was recovered from approximately 170 m above the base of the formation, within the middle member. This stratigraphic position places it between bentonite beds KDR-05 and KP-07 (Roberts et al., 2005). The former has produced an ^{40}Ar/^{39}Ar age of 76.46 ± 0.14 Ma; the latter produced an ^{40}Ar/^{39}Ar age of 75.97 ± 0.14 Ma and U-Pb age of 76.19 ± 0.05 Ma (Roberts et al. in press). The locality that produced this specimen (UMNH VP

locality 951) consists of a fine-grained, overbank deposit capped by a thick fluvial

sandstone. The specimen was excavated from a medium-grained bed within this

sandstone sequence. The quarry also produced a nearly complete associated skeleton of

the hadrosaurid dinosaur *Gryposaurus* sp., a disarticulated ankylosaurid dinosaur

skeleton, a partial ornithomimid skull, a nearly complete alligatoroid skeleton (Irmis et al.

in press), a partial indeterminate baenid skeleton, and numerous gastropods and

pelecypods.

Methods

The specimen was collected, prepared, and curated using standard paleontological

techniques. The articulated nature of the holotype skull means that adequate observations

of the palate, triturating surface, and mandible could not be made even after preparation.

Therefore, I utilized micro-computed tomography (μCT) to image the skull, digitally

remove matrix, digitally disarticulate the lower jaw, and reconstruct the cranial

morphology in three dimensions. I scanned the articulated cranium, mandible, atlas, and

axis on February 16, 2011 at the Small Animal MRI Imaging Facility at the University of

Utah Health Sciences Center Core Research facility. Scanning was conducted at 97

micron intervals with a voltage of 80 kVp and 500 uA of current. A 1.5 mm lead filter

was used to better image the interior of the specimen. I digitally segmented and

reconstructed the specimen using Siemens Inveon Research Workplace v.3.0 software.

This included the cranium, mandible, and first two cervical vertebrae. Where definite

sutures could not be distinguished in the CT slices or using surface morphology, multiple

bones were segmented as a single complex. This was especially true for portions of the skull roof, basicranium, palate, and otic capsule.

Systematic Paleontology

TESTUDINES Linnaeus, 1758, *sensu* Joyce et al., 2004

PARACRYPTODIRA Gaffney, 1975, *sensu* Lyson and Joyce, 2011

BAENOIDEA Williams, 1950, *sensu* Lyson and Joyce, 2011

BAENIDAE Cope, 1882, *sensu* Lyson and Joyce, 2011

BAENODDA Gaffney and Meylan, 1988, sensu Lively, this volume (see chapter III)

NEW TAXON

Plesiobaena sp. Hutchison et al., in press

Holotype. UMNH VP 21151, a partial skull and mandible, nearly complete carapace, complete plastron, nearly complete right forelimb, partial right hindlimb, and incomplete cervical and caudal vertebral series.

Type horizon and locality. Upper Cretaceous (Campanian) Kaiparowits Formation, approximately 170 m above the base of the formation. This places it within the informal middle unit of the formation, with an age between 76.60 and 76.14 Ma. The specimen was discovered at UMNH VP locality 951 (Horse Mountain Gryposaur Quarry) in Grand Staircase-Escalante National Monument, Kane County, Utah, USA.

Etymology. The genus name is derived from '*arvina*', Latin for bacon, referring to the pig-like snout of the holotype; and '*chelys*', Latin for tortoise. The specific epithet honors Jerry Golden, volunteer preparator at the Natural History Museum of Utah, who

has skillfully prepared numerous NHMU holotypes and other important specimens, including the holotype of the new taxon described here.

Diagnosis. Diagnosed by the following autapomorphies (indicated by asterisk) and unique combination of characters: two distinct external nares*; narrow triturating surface on the mandible with a small or absent lingual ridge*; including a wedge-shaped skull, as in all other baenodds and *Neurankylus* spp., and differing from *Trinitichelys hiatti*; broad rostrum, as in *Hayemys latifrons*, differing from the tapered rostrum of all other members of Baenodda; sagitally horizontal tubercula basioccipitale as in *Palatobaena cohen* and *Palatobaena bairdi*, differing from the blocky morphology of other baenids; a strongly scalloped posterior carapace margin, as in *Denazinemys nodosa* and *Boremys* spp., differing from the weakly scalloped posterior of *Neurankylus baueri*, *"Denazinemys" ornata*, *"Baena" hayi*, *Eubaena cephalica*, *Chisternon undatum*, *Baena arenosa*, and the unscalloped posterior of all other known baenids;   a subtriangular anterior plastron with a blunt tip in some specimens, as in *Plesiobaena antiqua*, *Peckemys brinkman*, and *P. cohen*, differing from the more rectangular anterior plastral lobe of other baenids; lingual ridge developed anteriorly only, a lack of epiplastral processes, and well-developed axillary and inguinal buttresses as in all other baenids; and the presence of a pygal notch and the contribution of the fifth vertebral to the posterior carapace margin as in all other baenodds, differing from *Neurankylus* spp. and *Thescelus* spp.

Referred specimens. UMNH VP 20451, a nearly complete shell, missing only part of the left posterolateral carapace; UMNH VP 20183, a partial carapace and plastron.

Distribution. Upper Cretaceous (Campanian) Kaiparowits Formation, southern Utah, USA.

Description

The holotype preserves a nearly complete skull, a nearly complete shell, cervical and caudal vertebrae, right scapula and coracoid, complete right distal forelimb, pelvic girdle, both femora, and partial hindlimb; most of these elements were found articulated. After preparation, the skull is still articulated with the mandible, the first two cervical vertebrae and a partial hyoid. This portion of the specimen is slightly dorsoventrally crushed; the distortion is most apparent in the ventromedial rotation of the right maxilla and the fragmentation of the triturating surface, which is visible in 3-D digital reconstructions of the skull. Three other partial cervical vertebrae are preserved in articulation with each other. The carapace is missing most of the posterior and left margins. The plastron is nearly complete, missing only a portion of the right posterolateral margin. The shell overall is mediolaterally crushed, affecting the carapace most conspicuously. The right scapula and coracoid are articulated and mostly in place. The distal portion of the right humerus is preserved in articulation with the radius, ulna, and pes. The left half of the pelvis is visible and in articulation with the femur. The right femur is also preserved, along with a partial right pes. Four caudal vertebrae are also preserved in articulation.

Skull

The skull is approximately 5.2 cm wide at its greatest extent just anterior to the cavum tympanum and is just under 5 cm (4.964 cm) long from snout to occipital condyle. The skull is wedge-shaped, similar to other members of Baenodda; however, unlike other baenodds, which possess a tapered snout, the rostrum is mediolaterally broad (Fig. 1.1C), as in *Hayemys latifrons* (AMNH 6139). Unlike all other baenids, which have a single external narial opening, The new taxon possesses two distinct external nares separated by a bony septum formed by the contact between the premaxillae and nasals along the midline (Figs. 1.1B; 1.2C). The external nares are oriented slightly laterally and are each sub-equal in size with the orbits. This gives the new taxon a pig-like snout. It is possible that a similar morphology was present in *H. latifrons*, but the specimen is crushed and therefore the orientation and shape of the external narial opening(s) cannot be assessed. The most important of these features, the bony septum, is not preserved in *H. latifrons*. It is evident that *H. latifrons* and the new taxon possessed the largest external narial opening(s) relative to the size of the skull of any baenid.

The orbits appear to be laterally oriented. However, if the post-mortem ventromedial rotation of the maxilla is taken into consideration, the orbit was most likely oriented slightly dorsally. This is only seen in *Cedrobaena putorius* (YPM-PU 20600), *Gamerabaena sonsalla* (ND 06-14.1; Lyson and Joyce, 2010), *Palatobaena* spp. (YPM 57498; YPM-PU 16039; UCMP V71238/114529), and *Eubaena cephalica* (MRF 571). Another shared similarity with *C. putorius*, *G. sonsalla*, and *Palatobaena* spp. is that the orbit appears inset into the maxilla in dorsal view because of the presence of a minor lateral ridge on the dorsolateral portion of the maxilla. This gives the dorsal surface of the
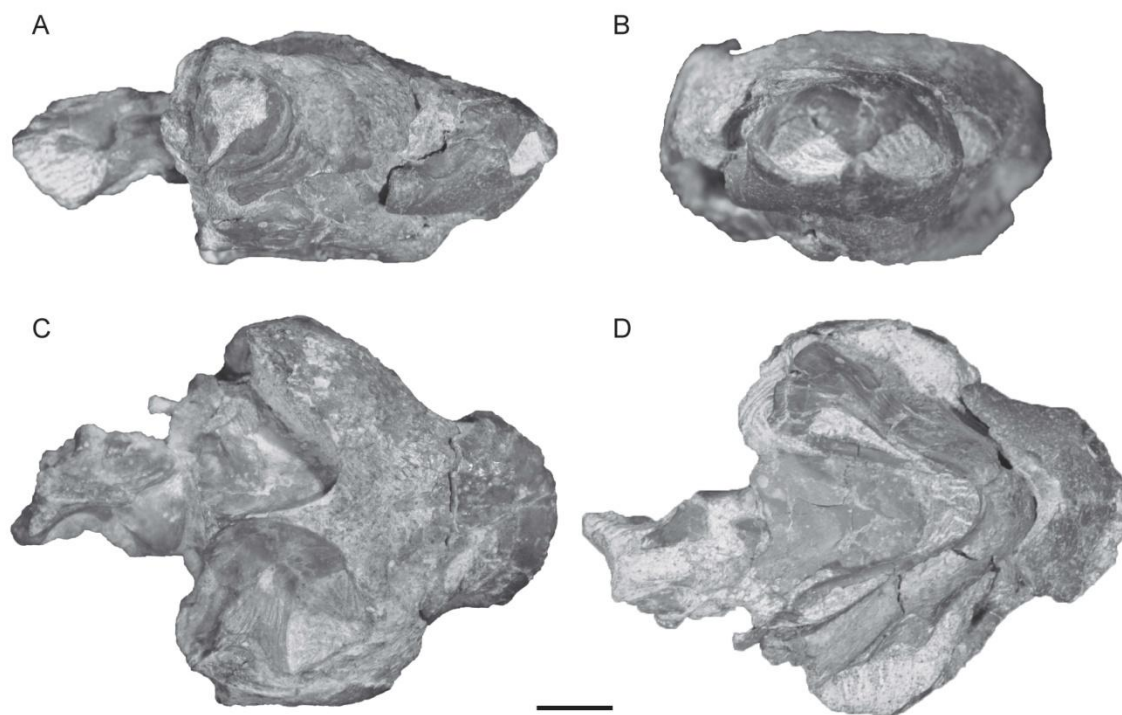
Figure 1.1. Photographs of articulated cranium, mandible, atlas, and axis of the holotype specimen (UMNH VP 21151) in A, right lateral; B, anterior; C, dorsal; and D, ventral views. Scale bar equals 1 cm.
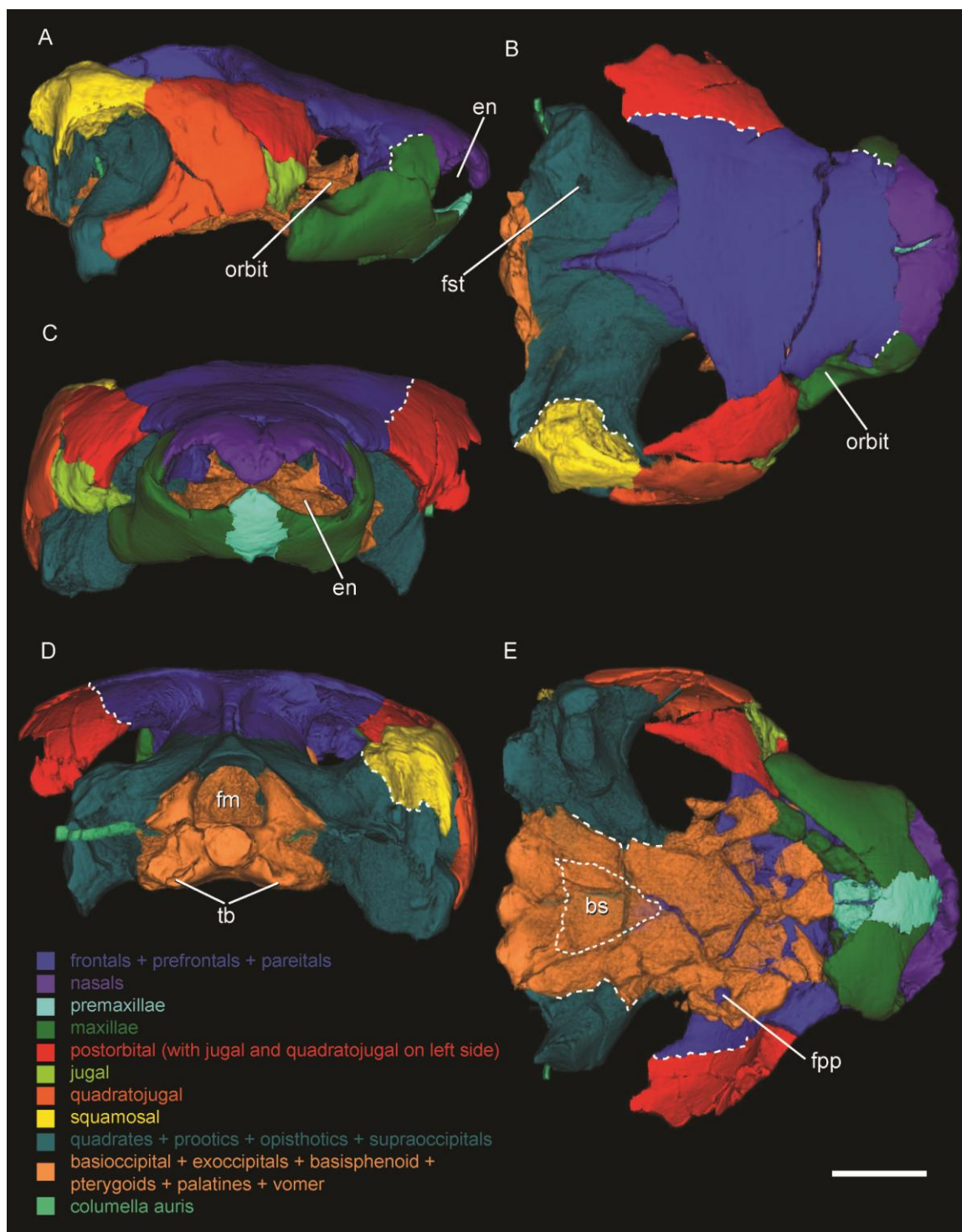
Figure 1.2. Three-dimensional reconstruction of the cranium of the holotype specimen (UMNH VP 21151) based on μCT scanning: A, lateral; B, dorsal; C, anterior; D, posterior; and E, ventral views. Abbreviations: fst, foramen stapedio-temporale; fpp, foramen posterius palatinum. White dashed lines represent inferred sutures. Scale bar equals 1 cm.

maxilla a concave appearance, differing from the flat surface observed in most baenids. The width between the orbits is greater relative to skull length than in most baenids, such as *Plesiobaena antiqua* (TMP 1994.012.0274), *Peckemys brinkman* (MRF 231), *Denazinemys nodosa* (BYU 19123), *Eubaena cephalica* (MRF 571), and *Stygiochelys estesi* (AMNH 2601); however, it is relatively smaller compared to *Palatobaena bairdi* (YPM-PU 16039), *P. cohen* (YPM 57498), *H. latifrons* (AMNH 6139), and *Neurankylus* spp (NMMNH P-57874; UCMP V84043/131700).

The exposure of the nasals on the roof of the skull is exceptionally large compared to most other baenids; they are widest medially and taper laterally. These elements contact the frontals/prefrontals posteriorly, the maxillae posterolaterally, and form the roof of the fossa nasalis. The nasals are wider medially and taper laterally. The two elements contribute to an anteroventrally directed septum that nearly meets a dorsally projecting process from the premaxillae. This almost forms a complete separation between the two external nares. Within baenids, nasals this large relative to skull length are only present in *Trinitichelys hiatti* (MCZ 4070), *Neurankylus* sp. (NMMNH P-57874), and *H. latifrons* (AMNH 6139). Both *H. latifrons* and the new taxon share laterally expanded nasals, due to a wide preorbital rostrum.

The maxillae, in their preserved form, are separated by an approximately 88° angle. This angle is greater than that of most baenids, but less than that of *Palatobaena* spp., which exhibit maxillae separated by greater than 90°.Ventrally, the triturating surface is not well preserved, possibly because dorsoventral crushing and rotated the maxillae. It does appear that a lingual ridge is present only anteriorly and that the triturating surface would have expanded posteriorly. The palatine contributes to the

posterior portion of this surface. The labial ridges of the maxillae are gracile compared to the more robust labial ridge of *Palatobaena* spp. Therefore, it is very unlikely that this animal would have been as specialized for durophagy, as suggested for *Palatobaena* spp. (Lyson and Joyce, 2009a).

The frontal-parietal sutures and the frontal-prefrontal sutures could not be distinguished thought the CT slices. This set of elements contacts the nasals anteriorly, the maxillae anterolaterally, the postorbitals laterally, the otic capsules posteroventrally, and the pterygoid ventrally. Although the posterior margins of the parietals are slightly eroded, it is still apparent that the upper temporal emargination is deep, exposing the anterior margin of the otic capsule. Contact with the squamosal is prevented by a deep upper temporal emargination and wide exposure of the postorbital along this margin. The crista supraoccipitalis is not as developed as that of other baenids and does not reach the foramen magnum posteriorly. A subvertical plate that is presumably the prefrontal forms the posterolateral margin of the fossa nasalis and the anteromedial portion of the fossa orbitalis. Posteriorly, this contacts the palatine. As in other baenids, the parietal is made up of two components: a dorsal horizontal plate that forms a portion of the skull roof and a vertical plate that contacts the pterygoid and otic capsules ventrally and posteroventrally.

The lateral portion of the skull (Fig. 1.1A) is made up of the postorbital, jugal, and quadratojugal. It is unclear whether or not the jugal contributes to the orbital margin, because the postorbital bar is missing. It does appear, thought, that the bar between the orbit and the cheek emargination would have been roughly half the width of the orbit. The cheek emargination is similar to other baenodds in being deep, reaching a level even

with the ventral margin of the orbit. The jugal contacts the postorbital dorsally and the quadratojugal posteriorly. The postorbital possesses a broad exposure on the lateral surface of the skull, contacting the quadratojugal posterolaterally, the jugal ventrally, and the frontal/parietal medially. Due to missing bone, it is unclear whether the postorbital contacted the squamosal or whether the quadratojugal prevented this by being exposed on the rim of the upper temporal emargination. However, the former is most likely based on the morphology of other baenids. The suture with the parietal was traced through the specimen first via a suture visible in the transverse CT slices and then by a distinct indentation in the bone posteriorly. Due to a large, transverse crack just posterior to the orbit, the shape of the anterior portion of this suture cannot be confidently determined. The quadratojugal is a thin, c-shaped element that forms the anterior rim of the cavum tympanum. It extends dorsally above the cavum tympanum where it contacts the squamosal, as in all baenids except *Baena arenosa* (USNM 18102) and *Chisternon undatum* (AMNH 5961; AMNH 25554; USNM 12839). The cavum tympanum, which is rimed anteriorly by the quadratojugal and dorsally by the quadratojugal and squamosal, is circular in shape and larger than the orbit. The squamosal forms the posterolateral dorsal corner of the skull, contacting the otic capsule ventromedially, and the postorbital and quadratojugal anteriorly. As in other baenids, this cone-shaped element possesses a shallow fossa posteroventrally that serves as the dorsal attachment of the M. depressor mandibulae (Gaffney, 1982). Ventrally, a dorsal continuation of the cavum tympanum known as the antrum postoticum is capped by the squamosal.

The otic capsules are mostly oriented mediolaterally in the new taxon, especially compared to those of *P. cohen* (YPM 57498) and *D. nodosa* (BYU 19123), which are

slanted posterolaterally. The nature of the contacts between individual elements of the otic capsule cannot be determined because sutures are closed in this of this portion of the skull. The bones that comprise this region of the skull in baenids are the quadrate, opisthotic, prootic, and supraoccipital (Gaffney, 1982). The ventral processus articularis of the quadrate bears the condylus mandibularis, the articular surface for the lower jaw. The relative size of the mandibular condyle is smaller than that of most baenids (see Appendix VI). The ratio of the size (length x width) of the condyle to skull length is similar to that of *P. antiqua* (TMP 1986.36.49; TMP 1994.12.273), *P. brinkman* (MRF 231), *T. hiatti* (MCZ 4070), *Arundelemys dardeni* (USNM 497740), and the paracryptodire *Glyptops plicatulus* (AMNH 336), being 0.352:4.954 for the new taxon. This is significantly smaller than the same ratio for *P. cohen* (YPM 57498), which is 1.6:6.4. The otic capsule contacts the squamosal dorsolaterally, the quadratojugal laterally, the parietal anterodorsally, the basicranium ventrally, and the pterygoid anteroventrally.

The bones of the otic capsule, in concert with the pterygoid, form the walls of the incisura columella auris and the bony middle ear. The otic capsule houses the columella auris, or stapes. The medial portion of the stapes, the basis columella, is conical in shape. This element becomes more rod-like laterally and eventually anterior-posteriorly compressed at its lateral-most extent. The stapes does not appear to vary from that of other pan-cryptodire Testudines.

The palate and basicranium were segmented as a single structure, because this region is filled with cracks and definite sutures were not visible. However, a faint outline of the basisphenoid can be seen on the ventral surface. The processus externus

pterygoideous is a pointed, posterolaterally curved flange (Fig. 1.2E). This differs from the condition seen in *Palatobaena* spp., which possess reduced external pterygoid processes. Due to suture closure, it is unclear whether or not the pterygoids contribute to the foramen palatinum posterius. Both sides of the specimen possess symmetrical cracks through this foramen that may have formed preferentially along the suture between the pterygoids and palatines. The basisphenoid is pentagonal in shape, with the foramen posterior canalis carotici internus being located in just anterior to the inflection of the basisphenoid-pterygoid suture. Based on the observable size of the basisphenoid, it is likely that the new taxon possessed a relatively wide interpterygoid suture, especially compared to *D. nodosa* (BYU 19123), *Stygiochelys estesi* (AMNH 2601; UCMP V73023/113316), and *C. undatum* (AMNH 5961; AMNH 25554; USNM 12839). The basioccipital tubercles exhibit a similar morphology to those of *P. cohen* in possessing a flat, horizontal flange posteriorly (sagitally horizontal basioccipital tubercles, sensu Lyson and Joyce, 2010, character 66). The occipital condyle is short and rounded. It differs from that of *H. latifrons* (AMNH 6139), which is extended more posteriorly and possesses a distinct neck.

The anterior horns of the hyoid apparatus are preserved in vivo in the holotype specimen. Each side of this portion of the hyoid is made up of two rami: one oriented subhorizontally and the other projecting posterodorsally. Both of these are rod-like in shape with a circular cross section. The angle between these two rami is approximately 113°.

Mandible

Figure 1.3 shows both lateral and dorsal views of the mandible. As with several

other regions of the skull, due to suture closure and taphonomy, the individual bones of

the mandible could not be discerned and the structure was segmented as one element. The

coronoid process is much taller relative to the length of the mandible than in any other

baenid. Most baenids appear to possess a prominent development of the coronoid

process, with the exception of *E. cephalica* (MRF 766), *D. nodosa* (BYU 19123), and

Boremys pulchra (TMP 1988.02.10; TMP 2001.12.36), but the condition in the new

taxon is particularly exaggerated compared to the typical baenid condition.

Anteriorly, the mandible possesses a prominent symphysial hook. The two rami of the

mandible come together at approximately an 88° angle, suggesting the angle measured

for the upper jaw has not been seriously affected by crushing. The mandible possesses a

narrow triturating surface. Although the labial ridge is prominent, the new taxon appears

to lack a lingual ridge on the mandible. Because of this, the triturating surface slopes

ventromedially. This state is unknown in any other baenid and is proposed as an

autapomorphy for this taxon. Laterally, a distinct tubercle is present on the anterior

portion of the coronoid process. This feature is also seen in *Palatobaena* spp. (Lyson and

Joyce, 2009a), *S. estesi* (UCMP V73023/113316), and *B. arenosa* (AMNH 5971).

Posterior to this tubercle, a large fossa is present on the lateral surface of the mandible.

This, coupled with the aforementioned tubercle, may have provided an articulation

surface for a massive M. adductor mandibulae, the main muscle for jaw closure. This

may suggest a powerful bite force, as has been inferred for *Palatobaena* spp. (Lyson and
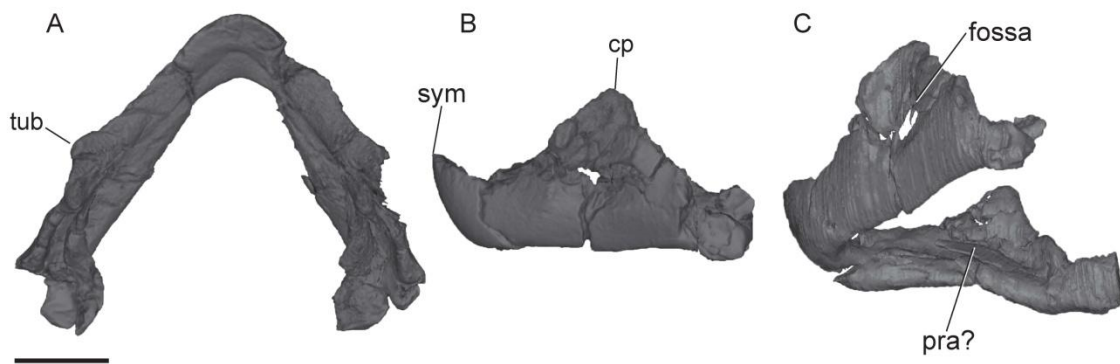
Figure 1.3. Three-dimensional reconstruction of the mandible of the holotype specimen (UMNH VP 21151) based on μCT scanning: A, dorsal; B, lateral; and C, posteroventrolateral view. The latter view is a surface rendering and best displays the large, lateral fossa on the mandible. The scale bar is 1 cm.

Joyce, 2009a). However, unlike *Palatobaena*, the new taxon did not possess an expanded triturating surface.

Carapace

All three specimens of the new taxon preserve a relatively complete shell (Figs. 1.4 & 1.5), but the carapace of UMNH VP 20451 is best preserved, and provides the basis for most of the shell's description here (Fig. 1.4C). Overall, the carapace is very similar to that of *P. antiqua*, with a few key differences; it is rounded anteriorly, lacking the nuchal projection of *P. antiqua* (TMP 1992.36.681) and *P. cohen* (YPM 57498; MRF 123, Lyson and Joyce, 2009a), which is less prominent in the former. Posterior to the inguinal buttress, the carapace is subtriangular, as in *P. antiqua*. This gives the carapace an almost torpedo shape in dorsal view. The widest point of the carapace is at the inguinal buttress. Minor scalloping is present along the anterior and lateral margins, similar to, but much more subdued than that of *D. nodosa*. The posterior margin is strongly scalloped, as in *D. nodosa* (UMNH VP 20447) and *Boremys* spp. (TMP 1981.28.01; USNM 12979). This differs from the smooth to very lightly-scalloped to smooth posterior margin of *P. antiqua* (TMP 1976.06.35) and the smooth margin of *P. cohen* (YPM 57498). As in other members of Baenodda, a pygal notch is present posteriorly, though shallow.

A mid-dorsal ridge runs the length of the carapace, as in *P. antiqua* (TMP 1976.06.35), *D. nodosa* (BYU 19123), and *B. pulchra* (TMP 1981.28.01). Posteriorly on this ridge, three prominent bumps are present, making the keel more pronounced. The surface of the shell is smooth, with the exception of a few low, circular nodes on the
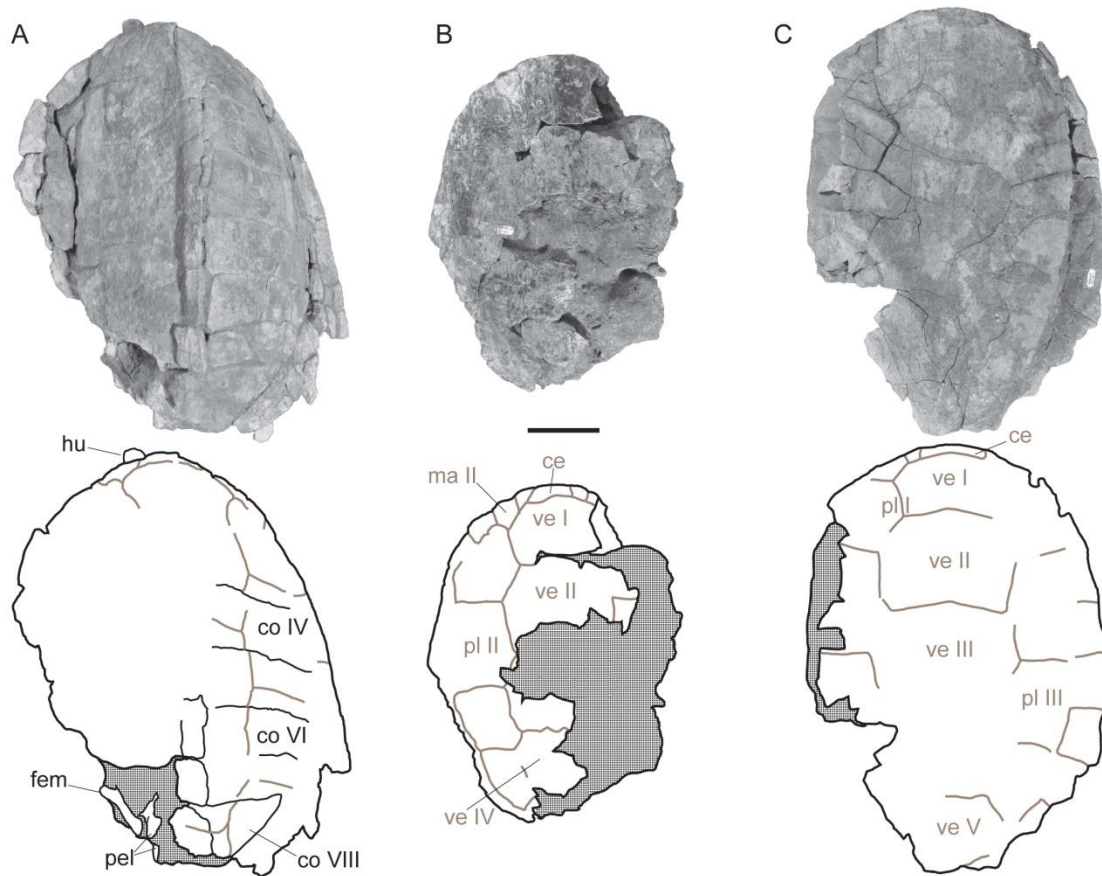
Figure 1.4. Carapace photographs (top) and line drawings (bottom) of A, UMNH VP 21151; B, UMNH VP 20183; C, UMNH VP 20145. Black lines represent bones and gray lines represent scale sulci. Abbreviations: ce, cervical scute; co, costal; fem, femur; hu, humerus; ma, marginal scute; pl, pleural scute; pub, pubis; ve, vertebral scute. Scale bar equals 5 cm.
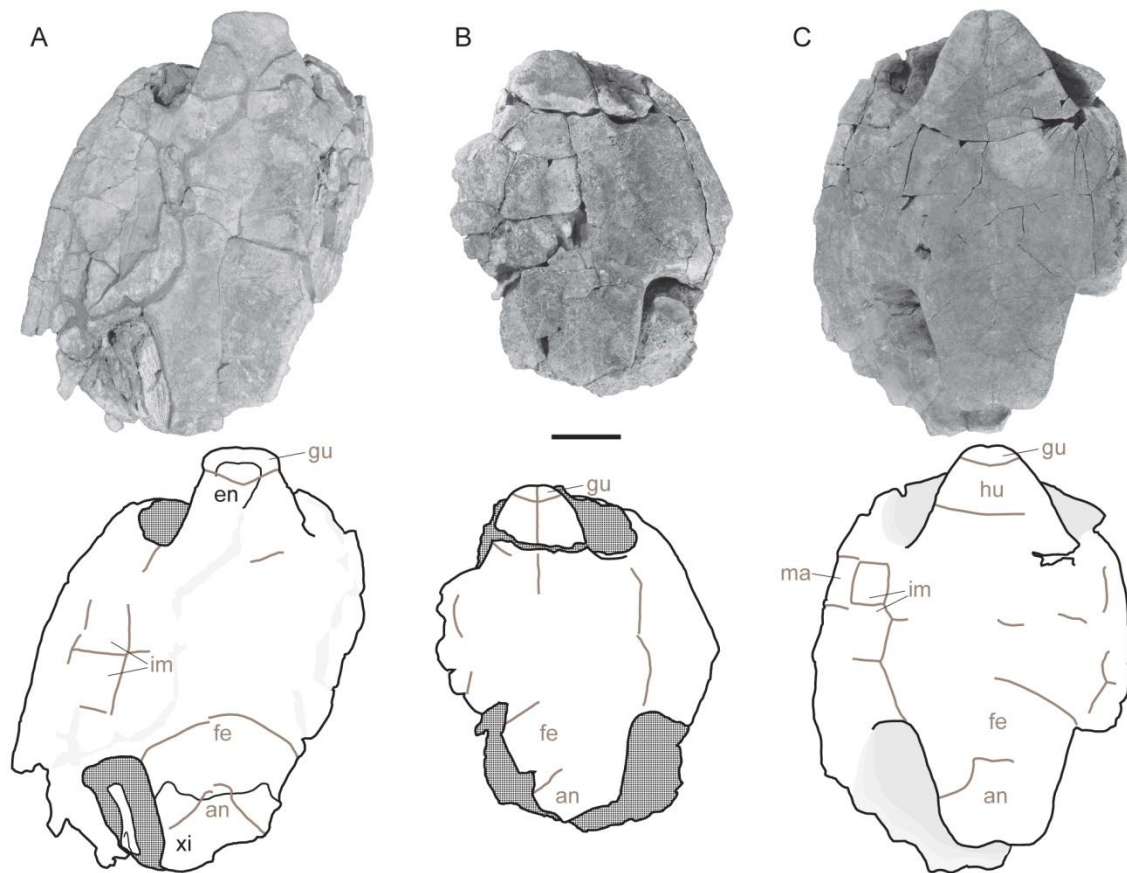
Figure 1.5. Plastron photographs (top) and line drawings (bottom) of A, UMNH VP 21151; B, UMNH VP 20183; C, UMNH VP 20145. Black lines represent bones and gray lines represent scale sulci. Abbreviations: an, anal scutes; en, entoplastron; fe, femoral scutes; gu, gular scutes; hu, humeral scutes; im, inframarginal scutes; ma, marginal scute; xi, xiphiplastra. Scale bar equals 5 cm.

costals that are not as pronounced as in *D. nodosa*, *Boremys* spp., or *"Denazinemys"* *ornata*. For the most part, sutures between the carapace bones are closed in all specimens of the new taxon; however, in the type specimen, crushing of the shell appears to have reopened several sutures, particularly between the posterior neurals and most of the costals on the right side (Fig. 1.4A). The posterior neurals are longer than they are wide, as in all other baenids.

The cervical scute is much wider than it is long and is not subdivided. A similar condition is present in *Thescelus* spp., *"Denazinemys" ornata* (USNM 13229), *P. antiqua* (TMP 1976.06.35), and *P. cohen* (YPM 57498). This differs from the narrow, rectangular scute of basal baenids such as *T. hiatti* (MCZ 4070) and *Neurankylus* spp. and the subdivided cervical scutes of *B. arenosa* (AMNH 5971), *C. undatum* (AMNH 5961), *D. nodosa* (UCMP V95087/159703), *Boremys* spp., *"Baena" hayi* (USNM 6728), and *"Baena" hatcheri* (AMNH 106). The first marginal is small and rectangular. Marginal II is larger and subrectangular, with a slight dorsal projection. As in other baenids with scalloping along the posterior margin of the carapace, the posterior marginal scales lie on a single serration, with intermarginal sulci lying between these projections.

The vertebral scutes are wider than they are long, as in *T. hiatti* (MCZ 4070), *Neurankylus* spp., *Thescelus* spp., *"Denazinemys" nodosa* (USNM 13229), *P. antiqua* (TMP 1976.06.35), *P. brinkman* (UMMP 20490; Lyson and Joyce, 2009b), and *P. cohen* (YPM 57498). The first two vertebrals are hexagonal in shape, and vertebral II narrows slightly anteriorly. The sulci of the third vertebral are not completely preserved for UMNH VP 20451 or 20183, but it appears to be hexagonal as well. As in all baenids with preserved shells except *T. hiatti*, *Neurankylus* spp., *and Thescelus* spp., the fifth vertebral

is exposed on the posterior margin of the carapace. This has traditionally been used to distinguish members of the clade Baenodda. The size of the pleural scutes is restricted due to the wide vertebrals. Pleural II possesses the largest exposure amongst this series of scutes. Prepleural scutes are absent, as in all baenids except *D. nodosa* (UCMP V95087/159703), *Boremys* spp., *S. estesi* (UCMP V73023/113316), *Baena* spp., and *C. undatum* (AMNH 5961).

Plastron

The anterior lobe of the plastron appears to exhibit some variation across specimens assigned to the new taxon. The type specimen exhibits a morphology similar to some specimens of *D. nodosa* (e.g., BYU 19123) in being subtriangular posteriorly, then becoming broader and more rounded anteriorly (Fig. 1.5A). In contrast, UMNH VP 20451 and 20183 possess a triangular anterior plastron with a blunt tip (Fig. 1.5B & C), nearly identical to the morphology observed in *P. antiqua* (TMP 1985.58.45), *P. brinkman* (UMMP 20490; Lyson and Joyce, 2009b), and *P. cohen* (YPM 57498). I attribute these differences in plastron shape to individual variation, with the holotype simply possessing a slightly broader anterior plastron. Another difference between the holotype and other two referred specimens is the size of the humeral scutes, which are significantly smaller in UMNH VP 20451 and 20183 than in the type and most other baenids, with the humeral-pectoral sulcus located well anterior to the axillary buttress. The holotype is similar in size to UMNH VP 20451, so ontogenetic variation does not explain these disparities in plastral morphology. Other than these differences, the shells

of the three specimens are indistinguishable. The sutures of the entoplastron and

epiplastra are visible on the holotype and exhibit the typical morphology of other baenids.

The posterior plastral lobe is larger than the anterior, as in all other baenids except two

new species of *Neurankylus* from the Kaiparowits Formation. The posterior plastron is

subrectangular in shape. A distinct xiphiplastral notch is present on UMNH VP 20451.

The axillary buttress is well-developed as in other baenids, contacting the first dorsal rib,

forming a distinct neck shield (sensu Lyson and Joyce, 2011b). A well developed

inguinal buttress contacts the fifth dorsal rib. As in the shells of other members of

Baenodda, the suture between the hypoplastron and xiphiplastron is z-shaped laterally.

The intergular scutes are absent, as in *P. brinkman* (UMMP 20490; Lyson and

Joyce, 2009b), *P. cohen* (YPM 57498), and some specimens of *P. antiqua*. The gular-

humeral sulcus is posteriorly triangular. The pectoral and abdominal scutes exhibit a

similar morphology to other baenids. The morphology of the inframarginals appears to

vary from specimen to specimen; inframarginal III possesses a broad contact with the

pectoral scute in UMNH VP 20451, whereas this contact is small on UMNH VP 20183.

The mediolateral width of the inframarginals is similar to that of the ventral exposures of

the marginal scutes, as in *Neurankylus eximius* (TMP2003.12.171), *Thescelus*

hemispherica (USNM 12818), *Boremys grandis* (USNM 12979), and *S. estesi* (UCMP

V73023/113316). This differs from *Neurankylus wyomingensis* (USNM 7581),

Neurankylus baueri (USNM 8344), *T. hiatti* (MCZ 4070), and *"Baena" hayi* (USNM

6728), which have narrower inframarginals than marginals; the inframarginals of *P.*

antiqua (TMP 2007.12.01), *P. brinkman* (UMMP 20490; Lyson and Joyce, 2009b), *D.*

nodosa (UMNH VP 20447), and *B. arenosa* (AMNH 5970) differ in being wider than the

ventral marginals The anal scute possesses an anterior projection with a truncated margin in all three specimens. This projection crosses the hypoplastron-xiphiplastron suture, as in all baenids except *Neurankylus* spp., *T. hiatti* (MCZ 4070), and *Boremys* spp.

Vertebrae

As with other baenids (Brinkman and Nichols, 1991; Lyson and Joyce, 2009b), the atlas is made up of four separate elements: two paramedian elements that comprise the neural arch, an anterior intercentrum, and a posterior centrum. Similar to *P. brinkman*, but differing from *B. pulchra*, there do not appear to have been cervical ribs attached to the atlas (Brinkman and Nichols, 1991; Lyson and Joyce, 2009b). However, it is possible that these may have disarticulated prior to burial. The neural arches of the atlas are each made up of two plates: a flat dorsal plate that would have joined with the same structure of the other neural arch element dorsal to the spinal cord and a ventrally-directed plate. The latter possesses articular surfaces that appear to have contacted the occipital region of the cranium just lateral to the condyle. Extending posteriorly from the neural arches are postzygopophyseal flanges that contact the axis. The centrum of the atlas is slightly concave posteriorly and possesses distinct fossae laterally.

The axis is similar to that described for *P. brinkman* (Lyson and Joyce, 2009b). The neural spine possesses an anterodorsal projection that extends nearly halfway along the atlas. The prezygopophyses are prominent, extending forward from the lower portion of the neural arch to articulate with the atlas. The centrum of the axis is keeled ventrally. The anterior surface of the centrum is relatively flat and slopes posteroventrally. The transverse processes are short and robust, providing an articulation point for the tubercle

of the rib. The holotype's axis is preserved with both cervical ribs *in situ*. These are

relatively flat elements with broad rib heads that taper rapidly posteroventrally down the

shaft of the rib.

Three other incomplete cervical vertebrae of unknown position are also preserved.

The presence of a ventral keel on the cervicals cannot be confirmed because the elements

are weathered. Keeled centra are present on the fourth and fifth cervicals of *P. brinkman*

(Lyson and Joyce, 2009b), the fourth cervical of *B. pulchra* (Brinkman and Nichols,

1991), and on a cervical of unknown position of *Neurankylus* sp. nov. from the

Kaiparowits Formation (see Chapter II). These vertebrae suggest that at least a few of the

centra in the cervical series were acoelous. The transverse process is short and robust and

is displaced anteriorly from the center of the centrum. As in other baenids, the neural

spine appears to be robust. The prezygopophyses are prominent.

Four distal caudal vertebrae of unknown position are preserved. These are rod-

like elements, lacking neural spines, haemal arches, and transverse processes. All four are

approximately 1 cm long and 0.5 cm tall. These are similar in size and general

morphology to the caudals XVII and XIX figured by Brinkman and Nichols (1991) for *B.
pulchra*.

Shoulder girdle

The entire shoulder girdle is preserved in place in the holotype of the new taxon,

though portions of it are concealed by matrix. The scapular and acromion processes of

the scapula are separated by an angle greater than 100°. This is greater than that of most

baenids, whose scapula processes are typically approximately 90° apart, but less than that

of *C. undatum* (AMNH 5904), whose scapular and acromion processes are separated by approximately 125°. Anteriorly, the acromion process expands into a club-shaped structure, a state unknown amongst other baenids. The coracoid is articulated with the scapula, exhibiting the typical testudinian morphology of being narrow laterally and expanding in to a broad, thin blade medially.

Forelimb

The holotype specimen preserves a nearly complete distal right forelimb and manus in articulation with the distal portion of the humerus (Fig. 1.6). As in other baenids, a groove along the dorsomedial dorsal face of the distal portion of the humerus represents the entepicondylar canal. Only one side of the radius and ulna are exposed, and they appear very similar to those of other baenids. The metacarpals appear to be shifted proximally, along with matrix, they cover most of the carpal bones. A portion of what appears to be the intermedium is present between the distal radius and ulna. The intermedium appears to have been in a broad articulation with the medial facet of the ulna as in *P. brinkman* (Lyson and Joyce, 2009b). A blocky bone just beyond the ulna is identified here as to be the ulnare, and is shifted slightly lateral to its normal position. Two distal carpals are exposed; the medial element is blocky with an irregular shape, and the is being rounded, similar to distal carpals II and III of *D. nodosa* (BYU 19123). Metacarpal I is the shortest and most robust of all of the metacarpals. The second metacarpal is very distinct from those of *D. nodosa* and *P. brinkman* because it possesses a prominent proximal expansion, compared to the more rod-like elements in the other two taxa. Metacarpals III and IV are the longest in the manus, and are relatively longer
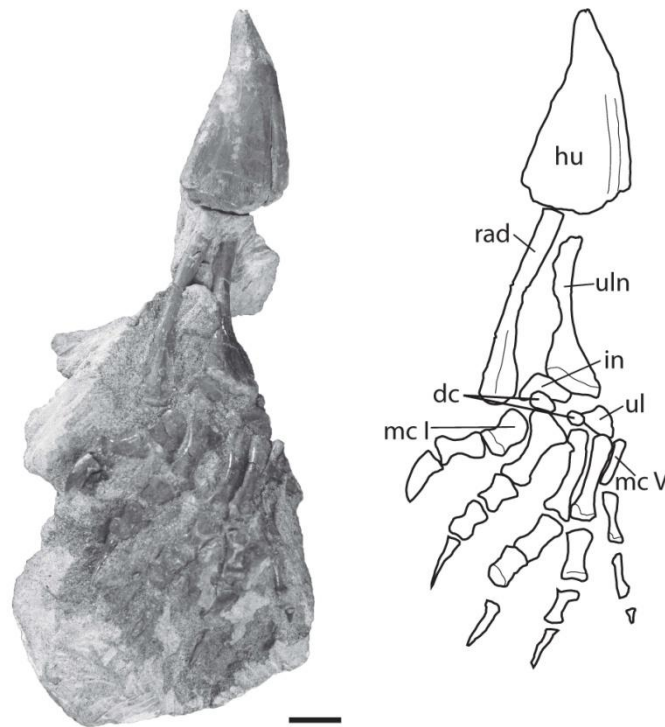
Figure 1.6. Photograph (left) and line drawing (right) of the right forelimb and manus of the holotype (UMNH VP 21151) in ventral view. Abbreviations: dc, distal carpals; hu, humerus; in, intermedium; mc, metacarpal; rad, radius; uln, ulna; ul, ulnare. Scale bar equals 1 cm.

compared to those of *D. nodosa*. In contrast, the fifth metacarpal of the new taxon is comparatively shorter. The phalangeal formula is 2:3:3:3:3; the fourth digit is the longest. The second phalanx of digit V is extremely gracile when compared to the same element of *D. nodosa*. As with other baenids, the unguals are slightly curved and sharp. The fifth ungual is much smaller than those from the first four digits.

Pelvis

Nearly the entire left pelvis of the holotype is visible in place on the holotype specimen. The ilial shaft has a straight, subvertical anterior margin. Dorsally, the ilium expands into a broad blade, directed posteroventrally. This is similar to most other baenid specimens that preserve the ilium, with the exception of *P. brinkman*, whose ilial blade expands both anteriorly and posteriorly at the dorsal end. The ischium possesses a sharp, posterior projecting boot as in other baenids. The pubic apron is not exposed; but the ventral pubic tubercles are visible, and are rounded and robust.

Hind limb

Both femora of UMNH VP 21151 are visible in limited views. The left femur is in situ, still articulated with the acetabulum, whereas the right femur is visible only posteriorly. The femur is relatively straight and only slightly sigmoidal. As in other baenids, the medial and lateral trochanters are prominent, with a U-shaped intertrochanteric line separating the two.

Proximal and distal tarsals are not preserved or visible in the holotype specimen. Although not all elements of the pes are present, observations of all of the digits can be

made based on external molds of some of the phalanges preserved in the sandstone matrix of the specimen (Fig. 1.7). Metatarsals I–IV are present. The first metatarsal is a robust element that is the shortest of the first four metatarsals. However, compared to the same element figured by Lyson and Joyce (2009b) for *P. brinkman*, this element is proportionally longer. It is approximately twice as wide as any of the other metatarsals. Metatarsals II–IV are gracile elements, the longest of which is metatarsal III. As in *P. brinkman*, metatarsals II and IV are subequal in length. The phalangeal formula is 2:3:3:3:2, as in other baenids with preserved feet. Digit I is the shortest and digit III is the longest. Phalanx I of digit V is especially long compared to phalanx I of any other digit, as is the case in *P. brinkman*.

Phylogenetic Analysis

I performed a phylogenetic analysis incorporating nearly all valid baenid taxa to determine the phylogenetic relationships of the new taxon. Thirty-three total species were included in the analysis, including one outgroup taxon, the paracryptodire *Glyptops plicatulus* (e.g., Gaffney, 1979). In contrast to Lyson and Joyce (2009a, 2009b, 2010, 2011), but similar to Larson et al. (2012), multiple species of *Neurankylus* were coded separately in the analysis. The three recognized species of *Thescelus*, sensu Sullivan et al. (2012) were also included. A total of 106 characters were used in the analysis, incorporating those from Lyson and Joyce (2009a, 2009b, 2010, 2011), Larson et al. (2012), and 11 new characters. The complete character list is provided in Appendix B. An explanation of the characters used and deleted from previous analyses is provided in Chapter 3. Characters 7, 14, 16, 18, 28, 33, 36, 69, and 106 form morphoclines and were
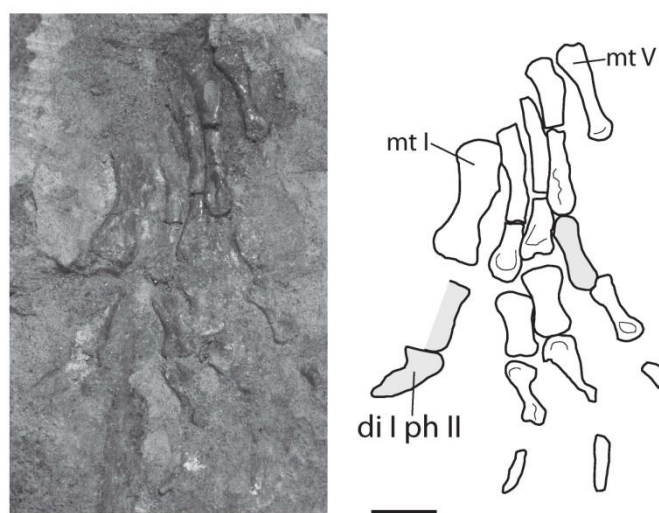
Figure 1.7. Photograph (left) and line drawing (right) of the partial right pes of the holotype (UMNH VP 21151) in ventral view. Abbreviations: di I ph II, digit I phalanx II; mt, metatarsal. Shaded areas represent missing elements that were traced from external molds on the specimen. Scale bar equals 1 cm.

ordered in the analysis. All other characters were left unordered, and all characters were weighted equally. The complete character matrix is provided in Appendix C. A maximum parsimony analysis was performed on the dataset using a traditional heuristic search with three bisection-reconnection and 1000 random addition search replicates in the program Tree analysis using New Technology (TNT) v. 1.1 (Goloboff et al., 2008). Bootstrap frequencies (Felsenstein, 1985) and Bremer support values (Bremer, 1994) were calculated in TNT to test support for each node.

My phylogenetic analysis recovered 18 most-parsimonious trees, with a length of 259 steps. The new taxon is found to be the sister taxon to *Hayemys latifrons* from the Maastrichtian Lance Formation of Wyoming. These taxa are united by the lateral expansion of the nasals (character 97 = 1). The new baenid and *H. latifrons* are placed within the clade Baenodda. "*Denazinemys*" *ornata*, and the clade of the new taxon+*Hayemys* form successively more nested branches at the base of Baenodda; above this, *Plesiobaena antiqua* is much more highly-nested, as the sister group of a clade including *"Baena" hayi*, *Stygiochelys*, *Baena*, *Chisternon*, and *Boremys*. Other taxa previously assigned to *Plesiobaena* (e.g., *Cedrobaena* and *Peckemys*) are spread paraphyletically between the new taxon and *P. antiqua*. Baenodda is united by the presence of scalloping on the posterior margin of the carapace (character 36 = 1,2), the contribution of the fifth vertebral to the posterior carapace margin (character 37 = 1), and the presence of a pygal notch (character 57 = 1).

Overall, bootstrap frequencies were low across the phylogeny with most nodes below 50%; other than the value for Baenidae (100%), the highest bootstrap value was for the clade including *Denazinemys nodosa* and *Boremys* spp. (54%). Bremer support

values were almost universally 1 within Baenidae, with the exceptions of *Thescelus* spp. + Baenodda (3), *D. nodosa* + *Boremys* spp. (2), and *Boremys grandis* + *Boremys pulchra* (3). These low support values likely reflect the moderate character/taxon ratio (~3:1), high levels of homoplasy among baenids, and the often conflicting phylogenetic signal between skulls and shells of the same taxa. These data are more fully discussed in Chapter 3.

Because material of the new taxon was previously assigned to *Plesiobaena* sp., I tested the suboptimality of constraining a topology with the clade of this new baenid and *Plesiobaena antiqua*. This requires 4 additional steps, recovering 2457 most parsimonious trees with a length of 263 steps. I also tested the suboptimality of constraining the topology of a monophyletic clade of *P. antiqua* + *Peckemys brinkman* + *Cedrobaena putorius* + *Gamerabaena sonsalla* + *Palatobaena* spp., *sensu* Lyson and Joyce (2009a; 2009b; 2010) and Lyson et al. (2011). This requires only one additional step, recovering 36 most parsimonious trees with a length of 260 steps. The resulting topology is similar to that of Lyson and Joyce (2011) in which *P. antiqua* and *P. brinkman* form a polytomy with the clade *C. putorius* + *G. sonsalla* + *Palatobaena* spp.

Discussion

Lyson and Joyce (2009b) recognized that turtles formerly assigned to the genus *Plesiobaena*, including *Plesiobaena antiqua*, a previously unnamed Maastrichtian taxon, and *P. putorius* actually represented a paraphyletic group, with placed on successively nested branches along the stem to *Palatobaena* spp. Because of this, they suggest that Maastrichtian taxa (i.e. *Peckemys brinkman*, *Cedrobaena putorius*, and *Palatobaena*

cohen) are not as easily diagnosed by shell morphology, but that Campanian shells of the "*Plesiobaena* grade" could still be diagnosed as belonging to *P. antiqua* (Lyson and Joyce, 2009b). Nonetheless, the results of the above phylogenetic analysis suggest otherwise. Until Hutchison et al. (in press) identified "*Plesiobaena* sp." shells from the Kaiparowits Formation, *Plesiobaena* was known only from northern Laramidia, but the discovery of skull material for this taxon suggests that it is more closely related to *Hayemys latifrons*. The phylogenetic analyses of Lyson and Joyce (2009a, 2009b, 2010) indicated weak support for a monophyletic clade that included *P. antiqua, P. brinkman*, *C. putorius*, *Gamerabaena sonsalla*, and *Palatobaena* spp. In contrast, my analysis provides weak support for *P. antiqua* being more closely related to the clade including *Baena arenosa* and *Boremys pulchra*. The topology of Lyson and Joyce with *P. antiqua* more closely related to *Palatobaena* than *Boremys* requires only one more additional step. This, coupled with the phylogenetic placement of the new taxon, indicate that the general shell morphology previously attributed to *Plesiobaena* spp. actually represents a grade spread throughout the basal portion of the clade Baenodda. This makes generic identification of even Campanian taxa based solely on shell material increasingly difficult, though there are a couple of characters that distinguish the shell of the new baenid from *P. antiqua*. If differences in the morphology of the anterior plastron between the holotype and referred specimens of the new taxonare found to be taxonomically significant in the future (i.e., following the discovery of a skull associated with this shell morphotype that is distinct from the skull of the holotype of the new taxon), then these phylogenetic and morphologic hypotheses will require reassessment.

Lyson and Joyce (2010) suggest the skull-based taxon *H. latifrons* is the junior synonym of the shell morphotype named *Thescelus insiliens* based on both stratigraphic and phylogenetic evidence. However, no directly associated specimen of this skull and shell has been discovered. My analysis predicts instead that *H. latifrons* may have possessed a "*Plesiobaena*-grade" shell, rather than a *Thescelus*-like shell. Key similarities that link *Hayemys* with the new taxon include a wedge-shaped skull, a laterally-expanded rostrum, and premaxillae that do not extend beyond the anterior margin of the skull roof. The presence of two distinct external nares in *H. latifrons* cannot be assessed because of the crushed nature of the holotype specimen. There are also some key differences between the skulls of these two taxa, including adult size. Although the skull sutures of the new taxon's holotype are almost all completely closed, suggesting it was nearing adulthood (Hutchison, 1984), the sutures of the skull of *H. latifrons* are completely open even though it approximately 40% larger than the new taxon. Hutchison (1984) demonstrated that size is taxonomically significant when comparing adult specimens in baenids because they exhibit determinate growth. Additionally, the morphology the basioccipital tubercles of the new taxon more closely resembles that of *Palatobaena cohen* than *Hayemys*. Finally, the occipital condyle of *H. latifrons* is more prominent with a weakly-formed "neck" anterior to the condyle. It is possible, therefore, that the cranial morphology shared by the new taxon and *Hayemys*, like "*Plesiobaena*-type" shells, may also represents a grade of baenid skull within Baenodda. Therefore, the synonymy of *H. latifrons* and *T. insiliens* cannot be ruled out, but it is not supported by available data and should not be assumed in phylogenetic analyses (e.g., Larson et al., 2012).

H. latifrons, from the Maastrichtian Lance Formation of Wyoming, has historically possessed a temporally long ghost linage, given its basal position outside Baenodda according to previous phylogenetic analyses (Lyson and Joyce, 2010). This new taxon partially fills this gap by extending the fossil record of the lineage into the late Campanian, 10 million years earlier than the age of *Hayemys*. This new taxon also extends the geographic range of this lineage into southern Laramidia.

Latitudinal differences in vertebrate assemblages during the Late Cretaceous have been proposed for several decades (e.g., Lehman, 1987; 1997). Recent investigations into the dinosaur assemblage of the Kaiparowits Formation (e.g., Sampson et al., 2010) have supported this hypothesis, demonstrating the presence of disparate, but stratigraphically coeval assemblages in northern and southern Laramidian basins. Thus far, six baenid taxa are known from the Kaiparowits Formation of southern Utah, with five being diagnosable to recognized or new species: the new taxon, *Denazinemys nodosa*, *Boremys grandis*, two new species of *Neurankylus*, and an indeterminate species of *Thescelus* (see Chapter II). Of those identifiable species, only *D. nodosa* and *B. grandis* are known from outside of the Kaiparowits Basin, and both are restricted to southern Laramidia. The new taxon, along with the two new species of *Neurankylus*, is currently unknown from outside of southern Utah. This provides further support for the hypothesis of basin-scale endemism and differences overall between northern and southern Laramidian fossil assemblages from the Campanian.

Conclusions

This baenid taxon described herein represents a new, morphologically disparate taxon from the Kaiparowits Formation of southern Utah. Unlike any other baenid, is possesses a pig-like snout with two external nares separated by a bony septum. The morphology of the mandible suggests it likely had a powerful bite, though it is unlikely it fed on molluscs and crustaceans, as has been suggested for *Palatobaena* spp. (Archibald and Hutchison, 1979; Lyson and Joyce, 2009a). Its phylogenetic placement supports the idea that that shells previously assigned to the genus *Plesiobaena* actually represent a basal grade within the clade Baenodda. The new taxon, which is unknown outside of southern Utah, also provides additional evidence for basin-scale endemism during the Campanian on Laramidia.

CHAPTER 2

BAENID TURTLES OF THE KAIPAROWITS FORMATION

(UPPER CRETACEOUS: CAMPANIAN)

OF SOUTHERN UTAH

Abstract

In this paper, I describe the assemblage of baenid turtles found in the Campanian

Kaiparowits Formation of southern Utah and compare them with baenids from other

basins across Laramidia. Baenids were one of the most diverse and abundant fresh water

turtle clades during the Late Cretaceous. They were restricted to North America, with all

except the basal-most taxon (*Arundelemys*) restricted to Laramidia. During the

Campanian, baenids were conspicuous parts of the turtle assemblages of Alberta,

Montana, and New Mexico. The baenids of the Kaiparowits Formation are critical in that

they provide an assemblage from southern Laramidia that is correlative with those from

northern Laramidia, allowing for more accurate testing of biogeographic hypotheses. My

comprehensive review of collected material indicates that five baenid taxa are present in

the formation, including three new species, *Denazinemys nodosa*, and *Boremys grandis*.

While the three new taxa have not been identified outside of the Kaiparowits Basin, *D.

nodosa* and *B. grandis* are both known from younger sediments of the San Juan Basin of

New Mexico. These taxa provide support for both basin-scale endemism and north-south provincialism across Laramidia during the Campanian.

Introduction

Baenidae is an extinct clade of Cretaceous through Eocene paracryptodiran turtles that is restricted to North America (Gaffney, 1972; Hutchison, 1984; Holroyd and Hutchison, 2002; Brinkman, 2003; Joyce 2007). Most taxa are from the Western Interior of North America (Laramidia) ,although the basal-most baenid is from Maryland (Lipka et al., 2006; Lyson and Joyce, 2011). Baenids first evolved in the early Cretaceous, reached their greatest diversity in the latest Cretaceous, and went extinct during the Eocene (Gaffney, 1972; Lyson and Joyce, 2010). Not only was this group one of the most speciose turtle clades during the Late Cretaceous (e.g., Lyson and Joyce, 2010), but they were also one of the most abundant (Hutchison and Archibald, 1986). The North American endemism and high diversity of baenids during the Late Cretaceous, baenid turtles provide an excellent study system for testing Laramidian biogeographic hypotheses.

Gaffney (1972) was the first to thoroughly address the systematics of Baenidae. Recent work on the taxonomy and systematics of this clade by Lyson and Joyce (2009a, 2009b, 2010, 2011) has provided an excellent basis for understanding the evolution of the clade. These studies have focused on baenid taxa from the northern portion of Laramidia, in particular, those from the Maastrichtian-Paleocene Hell Creek Formation. However, limited attention has been devoted to understanding the systematics of baenids from older

strata in southern Laramidia, and has been largely restricted to the San Juan Basin of New Mexico (Lucas and Sullivan, 2006; Sullivan et al, in press).

The Campanian Kaiparowits Formation is restricted to the Kaiparowits Plateau within Grand Staircase-Escalante National Monument of southern Utah. Research into the vertebrate fauna of the formation is still in its infancy relative to other Upper Cretaceous strata across the Western Interior. However, a diverse array of new vertebrate taxa has been discovered, including saurischian dinosaurs (Zanno and Sampson, 2005; Carr et al., 2011; Zanno et al., 2011), ornithischian dinosaurs (Gates and Sampson, 2007; Sampson et al., 2010), crocodyliforms (Irmis et al., in press), squamates (Nydam, in press), amphibians (Gardner et al., in press; Roček et al., in press), and fish (Brinkman et al., in press; Kirkland et al, in press). This research has placed renewed focus on Campanian biogeographic hypotheses (e.g., Sampson et al., 2010) first proposed by Lehman (1997, 2001), proposing 1) on one level, the presence of two distinct biogeographic provinces during the Late Campanian and 2) basin-scale endemism of some species. In their survey of nonmarine Campanian vertebrate taxa, Gates et al. (2010) indicate that, with our current extent of sampling, the observed Campanian vertebrate distribution across Laramidia may represent either 1) a continuous latitudinal gradient or 2) two distinct biogeographic provinces with a medial faunal mixing zone. However, the authors recognize that these hypotheses can be best tested at the level of individual clades in an evolutionary context (Gates et al., 2010).

Kaiparowits Formation baenid turtles represent key data for the future tests, but have not been systematically described. Eaton et al. (1997) listed three turtles now included within Baenidae from the Kaiparowits Formation: *Boremys pulchra*, *"Baena"*

nodosa, and *Neurankylus* sp. Hutchison et al. (in press) were the first to fully assess the turtle fauna of the Kaiparowits Formation. They recognized five baenid taxa within the formation: two indeterminate species of *Neurankylus*, *Plesiobaena* sp., *Denazinemys nodosa*, and *Boremys grandis*. The authors provided preliminary descriptions of specimens and did not attempt to resolve the alpha taxonomy of the indeterminate species.

The purpose of this paper is to provide in-depth descriptions of the baenid taxa from the Kaiparowits Formation and to place them within a systematic context. Three of the five species present are novel taxa; two new species of the basal baenid genus *Neurankylus* are named and described herein. The third taxon will be named in a different work (Chapter 1). In addition, I provide the first description of the cranial anatomy of *Denazinemys nodosa*, based on a new specimen from the Kaiparowits Formation. The baenids of the Kaiparowits Formation are then compared to those from penecontemporaneous strata from Montana and Alberta and slightly younger specimens of the San Juan Basin. These data provide a basis for an evolutionary biogeographic study of Late Cretaceous Baenidae (see Chapter III).

Institutional Abbreviations

AMNH, American Museum of Natural History, New York City; **BYU**, Brigham Young University Museum of Paleontology, Provo, Utah; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **MRF**, Marmarth Research Foundation, Marmarth, North Dakota; **ND**, North Dakota Heritage Center, Bismark, North Dakota; **NMMNH**, New Mexico Museum of Natural History and

Science, Albuquerque, New Mexico; **TMP**, Royal Tyrrell Museum of Paleontology, Drumheller, Alberta; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; **UMNH**, Natural History Museum of Utah, University of Utah, Salt Lake City, Utah; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut.

Geologic Setting

For much of the Late Cretaceous, high sea levels divided the North American continent into two separate landmasses (Roberts and Kirschbaum, 1995): Appalachia to the east and Laramidia to the west. The Kaiparowits Formation was deposited in a prograding clastic wedge at the southern end of the Cordilleran foreland basin of Laramidia (Roberts, 2007). This position allowed it to be tectonically influenced by both the Sevier orogenic belt to the west and the Mogollon Highlands to the south, providing for some of the highest sedimentation rates in the western interior (Goldstrand, 1992; Lawton et al., 2003; Roberts, 2007).

Outcrops of the Kaiparowits Formation are restricted to the Kaiparowits Plateau within Grand Staircase-Escalante National Monument, in southern Utah. This formation is conformably underlain by the early-middle Wahweap Formation (Jinnah et al., 2009) and is unconformably overlain by the Canaan Peak Formation (Roberts et al., 2005; Roberts, 2007). The Kaiparowits Formation itself is divided into three informal units: the lower, middle, and upper members (Roberts, 2007). The maximum total thickness of the Kaiparowits Formation is approximately 860 meters (Roberts et al., 2005). In general, the

lower and upper units are characterized by fluvial channel sandstone facies, while the middle unit is dominated by muddier, over-bank deposits. The formation is interpreted to represent deposition in a low relief, alluvial/coastal plain setting, with only one interval within the lower middle unit that may be tidally influenced (Roberts, 2007). Abundant fluvial and paludal paleoenvironments suggest a humid paleoclimatic regime for the region.

Roberts et al. (2005) radioisotopically dated using the ^{40}Ar/^{39}Ar method four of the eight known bentonite layers within the Kaiparowits Formation and determined that the formation spans roughly 76.46 to 74.69 Ma, assigning it to the late Campanian (Judithian North American Land Mammal Age). This correlates the Kaiparowits Formation with the fossil-bearing strata of the Dinosaur Park, Judith River, and Two Medicine formations to the north and partially correlative with the Aguja Formation to the south. There is likewise some overlap with the Fruitland and Kirtland formations of the San Juan Basin of northwestern New Mexico; however, the primary fossil-bearing strata of these formations are slightly younger than those of the Kaiparowits, where vertebrate fossils are mostly found in the lower and middle units (Roberts et al., 2005).

Systematic Paleontology

TESTUDINES Linnaeus, 1758, sensu Joyce et al., 2004

PARACRYPTODIRA Gaffney, 1975, sensu Lyson and Joyce, 2011

BAENOIDEA Williams, 1950, sensu Lyson and Joyce, 2011

BAENIDAE Cope, 1882, sensu Lyson and Joyce, 2011

Neurankylus Lambe, 1902

Diagnosis

Autapomorphies include: large size in comparison to other baenid taxa; rounded, upturned margins of the carapace forming dorsolateral gutters along the peripherals; distinct shell ornamentation consisting of fine, vermicular texture with anastomosing ridges and pits; opisthotic, quadrate, and prootic enter the foramen stapedio-temporale, while the supraoccipital does not (Larson et al., in press); and a relatively straight humerus compared to more derived baenids. *Neurankylus* possesses a nuchal that is slightly recessed anteriorly, but not as deeply emarginated as in *Thescelus* spp. As in *Glyptops plicatulus*, *Thescelus* spp., but differing from all other baenids, the fifth vertebral does not contribute to the posterior margin of the carapace. The skull is wedge shaped, as in members of Baenodda, differing from the oblong-shaped skull of *Glyptops plicatulus* and *Trinitichelys hiatti*. There are large dorsal exposures of the prefrontals on the skull roof, as in *Hayemys latifrons* and *Arundelemys dardeni*, but differing from all other baenids. The intergulars prevent contact between the gular scutes, as in *G. plicatulus* and *T. hiatti*, differing from the condition in other baenids where the gulars exhibit a medial contact due to smaller or absent intergulars.

Remarks

Larson et al. (in press) provide a framework for classifying species within the genus, including characters related to the shape of marginal IV and morphology of the intergular and gular scutes (Larson et al., in press). I recognize several other characters that help to diagnose species of *Neurankylus*, including the shape of the carapace, development of the mid-dorsal ridge, number of marginal scutes, relative proportions of

the anterior and posterior lobes of the plastron, and the shape of the anterior margin of the plastron.

Type species

Neurankylus eximius Lambe, 1902

Neurankylus sp. nov. A

Holotype

UCMP V93118/154450, a carapace and plastron missing one third of the right side, two cervical, two sacral vertebrae, two caudal vertebrae, both scapulae, humerus, and complete pelvis.

Type horizon and locality

Upper Cretaceous (Campanian) Kaiparowits Formation, approximately 280 m above the base of the formation. This places it within the informal middle unit of the formation. The type locality is within Grand Staircase-Escalante National Monument, Garfield County, Utah, USA.

Diagnosis

Neurankylus sp. nov. A differs from all other species of *Neurankylus* by the presence of: a high-domed, laterally rounded carapace, whereas all other members of the genus have a low-domed carapace with relatively parallel lateral margins; thirteen marginal scutes; second marginal with a prominent dorsal projection between vertebral I

and pleural I; marginal VIII greatly expanded laterally; marginals V-XI are exceptionally wide; adult size approximately 90 cm; ilial shaft sloped posteriorly; flange present on anterior rim of acetabulum, fossa faces posteroventrally. *N.* sp. nov. A is similar to *N.* sp. nov. B. in the presence of a rounded anterior plastral lobe that is larger than the posterior plastral lobe. A possible autapomorphy for the species is the presence of mediolaterally compressed dorsal vertebrae with prominent ventral keels (Hutchison et al., in press).

Referred specimen

UCMP V95083/194122, a first peripheral.

Distribution

Middle unit, Upper Cretaceous (Campanian) Kaiparowits Formation, southern Utah, USA.

Description

Carapace. The carapace of the holotype (Fig. 2.1A) is missing the right half, but the left half is well preserved with sulci lightly impressed on the surface. Sutures are fused, preventing description of the carapace bones. Hutchison (1984) recognized that maximum adult size is a diagnostic character of baenid species because they exhibit determinate growth. The carapace of *Neurankylus* sp. nov. A is larger than any known baenid, approximately 91 cm in length. Other than *Neurankylus* sp. nov. B (see discussion below), the largest examples of other species of the genus are around 60 cm in length. *Neurankylus* sp. nov. A's carapace is highly domed, while all other *Neurankylus*
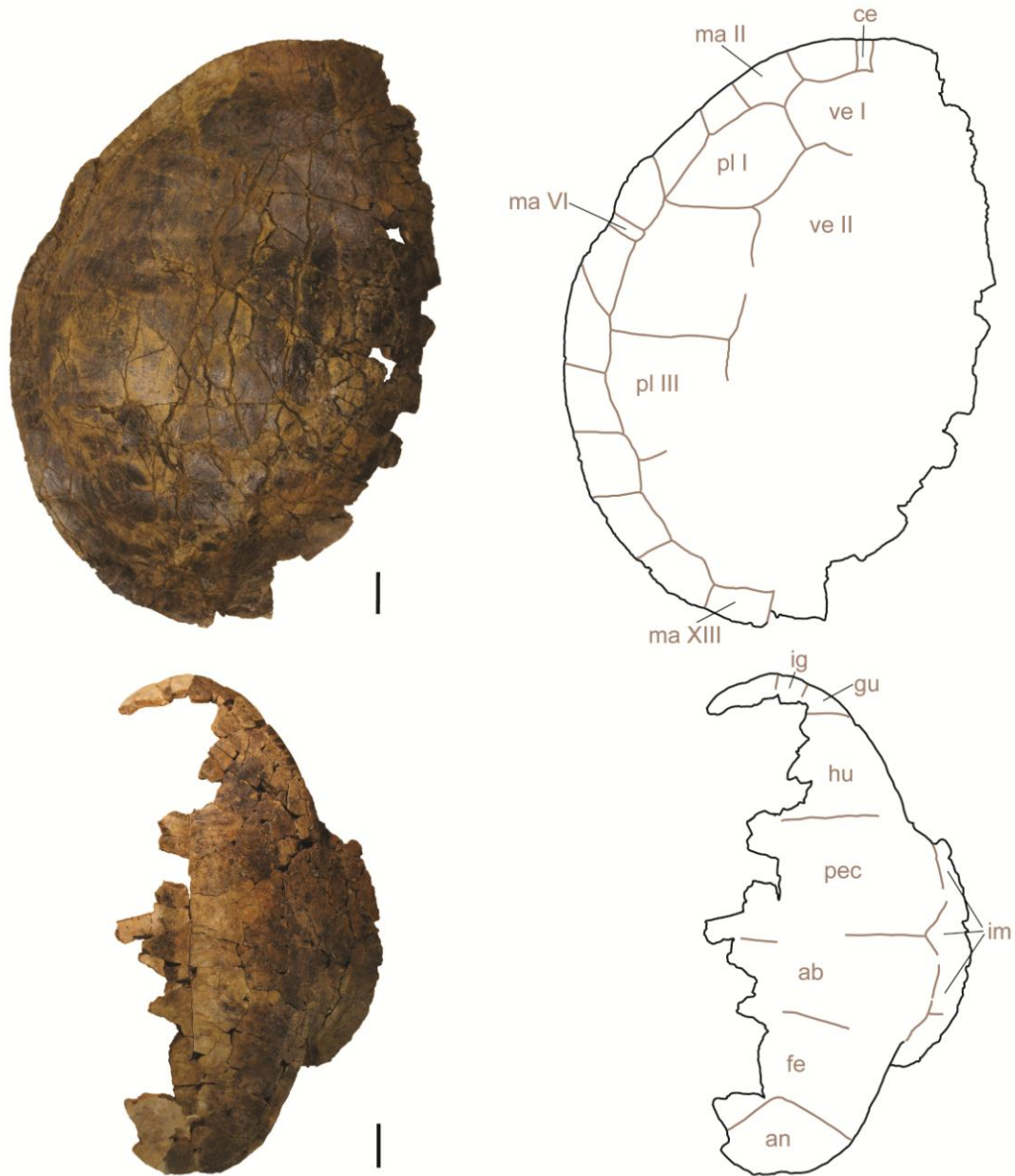
Figure 2.1. *Neurankylus* sp. nov. A (UCMP V93118/154450) holotype photographs (left) and line drawings (right) of the A, carapace and B, plastron. Abbreviations: ab, abdominal scutes; an, anal scute; ce, cervical scute; fe, femoral scutes; gu, gular scute; hu, humeral scute; ig, intergular scute; im, inframarginal scutes; ma, marginal scutes; pec, pectoral scutes; pl, pleural scutes; ve, vertebral scutes. Scale bar equals 5 cm.

possess a low domed, relatively streamlined silhouette in lateral view. *Neurankylus* sp.

nov. A also possesses a laterally rounded carapace, whereas all other members of the

genus possess a more ovoid shape with relatively parallel lateral margins. The widest

point on the carapace is roughly even with the fourth trunk vertebra. At this point, the

shell is approximately 90 cm wide. As in other members of the genus (Larson et al., in

press), the nuchal is slightly recessed anteriorly. The midline is preserved along the entire

length of the carapace, and a mid-dorsal keel is present only posteriorly. This condition is

also seen in *N. eximius* (TMP.012.0171) and *Neurankylus* sp. nov. B, whereas *N. baueri*

(USNM 8344) possesses a ridge along the entire length of the shell. Dorsally, the axillary

buttress contacts the first dorsal, forming a distinct neck shield. The inguinal buttress also

extends well onto the costals – both of these states are synapomorphies of Baenidae

(Lyson and Joyce, 2011).

As in other members of the genus (with the exception of one unnamed taxon from

the Lance Formation of Wyoming), the cervical scute is longer than it is wide. However,

the cervical of *Neurankylus* sp. nov. A is longer relative to those of *N. baueri* and *N.

eximius*. In the latter taxa, the cervical is approximately half as long as the first marginal

scute is deep; the cervical of *Neurankylus* sp. nov. A is as long as marginal I. Vertebral I

is sub-hexagonal in shape, with a wider anterior than posterior. Similar to other species of

Neurankylus, the second vertebral tapers considerably anteriorly. The sulci for the

remaining vertebrals are not well preserved. Only the marginals are exposed along the

posterior margin of the carapace. The entire marginal series is preserved on the left side.

Thirteen marginals are present on the holotype specimen. The sixth marginal is a thin

scute that may represent an anomalous addition in this individual, a condition that is well

documented in modern populations of turtles on the Iberian Peninsula (Velo-Anton et al., 2011). Until additional specimens prove otherwise, the presence of thirteen pairs of marginals are an autapomorphy of the species. The second marginal is relatively square in shape, with the exception of a prominent, tapering dorsal projection that partially divides the first vertebral from the first pleural. The fourth marginal scute has a curved dorsal margin, with the tallest point being in the middle of the scute. This state is also observed in *N. eximius*, and differs from *N. baueri*, *Neurankylus* sp. nov. B, and a new species from the Milk River Formation, which possess trapezoidal fourth marginal scutes that widen posteriorly. Marginals V through XII are significantly wider than those of other members of the genus. The eighth marginal widens laterally, which constricts the width of marginal VII.

Plastron. The plastron of the holotype (Fig. 2.2B) is 66 cm in length – longer than the carapace of most other species of *Neurankylus*. The anterior lobe is approximately 1 cm longer and 2 cm wider at the buttress than the posterior plastral lobe. A larger anterior plastral lobe is only observed in *Neurankylus* sp. nov. B and *Glyptops plicatulus*. This lobe is subrectangular in shape and is rounded along the anterior margin. The gular region is incompletely preserved; however, it is apparent that the gular scutes were significantly larger than the intergulars. Both the humeral-pectoral and the pectoral-abdominal sulci are transversely horizontal. The true sizes of the inframarginals are difficult to access due to disarticulation of the plastron from the carapace, but it is apparent that inframarginal I is the most narrow and IV is the widest. All four are narrower than the ventral exposures of the marginals, as in other species of *Neurankylus*. The abdominal-femoral sulcus is slightly anteriorly convex, as in other baenids.

Posteriorly, the plastron is sub-rectangular in shape with no prominent xiphiplastral notch. The anal scute possesses a simple anterior projection at the midline.

Vertebrae. Two cervical vertebrae (cervical A and B) of unknown position are preserved with the holotype specimen (Fig. 2.2A). Both are strongly keeled ventrally, similar to cervicals two to eight in *Boremys pulchra* (Brinkman and Nicholls, 1991) and *Plesiobaena antiqua* (Brinkman, 2003). The neural spines are robust and expand dorsally. Both vertebrae possess prominent prezygopophyses. The centrum of cervical A is 10.6% longer than cervical B, but the centra are of near equal height. Cervical A possesses a biconvex (amphicoelous) centrum. The anterior articulation is teardrop shaped, tapering ventrally. The posterior articulation is ovoid in shape, 32% taller than wide. This condition is similar to that reported for the fourth cervical of *B. pulchra* (Brinkman and Nicholls, 1991). The transverse processes are not preserved on this vertebra, but appear to have been halfway along the anterior-posterior length of the neural arch, as in cervical B. These processes are robust and shorter than those of the proximal caudal vertebrae. The centrum of cervical B (Fig. 2.2A) is procoelous, with a circular articulation anteriorly and a tall and narrow posterior articulation. This morphology likely favored movement of the head from side to side as opposed to dorsoventral movement (Hutchison et al., in press). The neural spine of cervical B is significantly shorter than that of cervical A. Instead of terminating in a robust, concave knob as in the latter vertebra, the neural spine of this one terminates in a coronally flattened plate with two small tubercles dorsally and broad postzygopophyses ventrally. Similar tubercles are seen on cervicals three to five of *B. pulchra* (Brinkman and Nicholls, 1991)
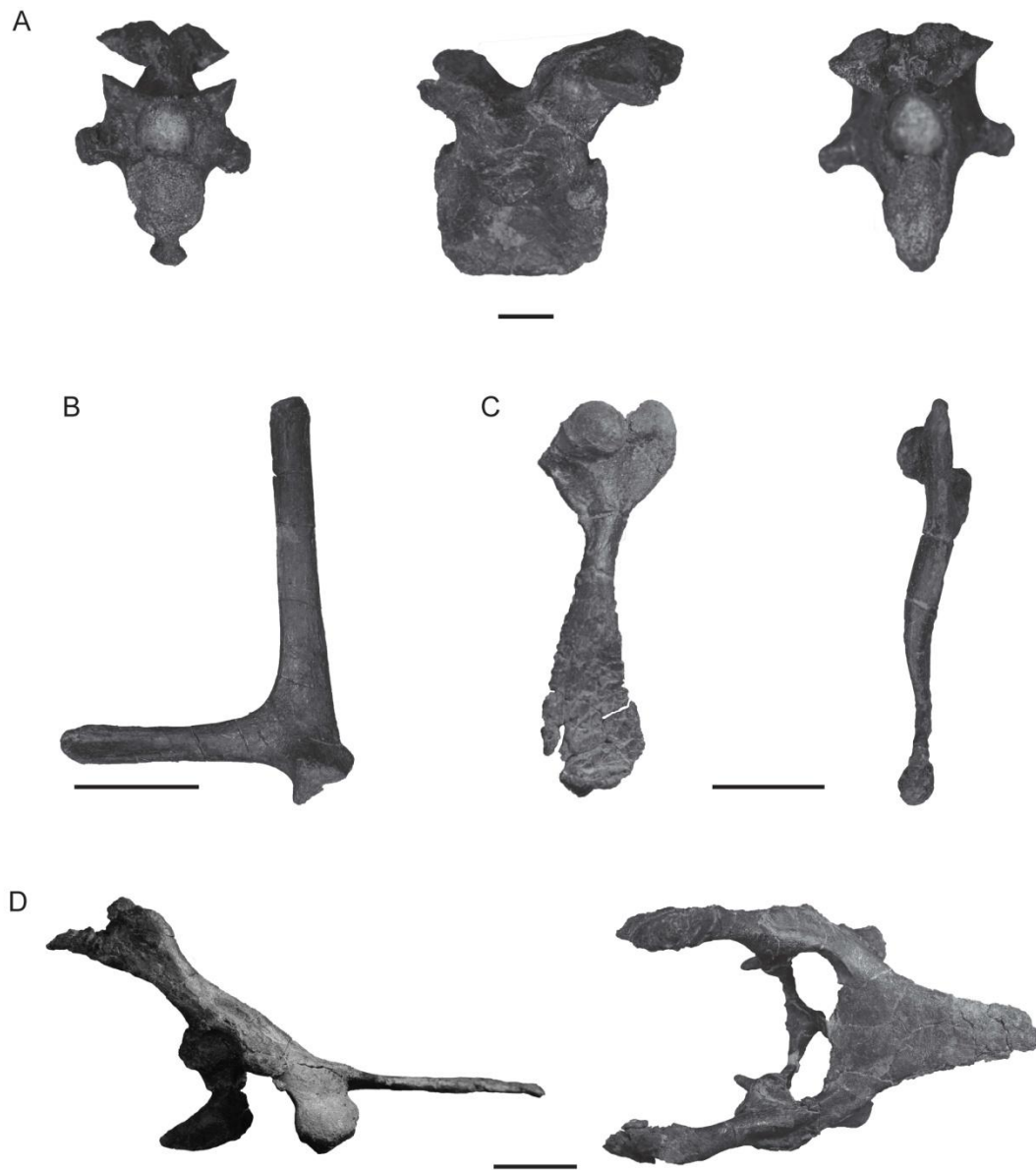
Figure 2.2. Postcranial elements of *Neurankylus* sp. nov. A, UCMP V93118/154450: A, cervical vertebra in anterior (left), lateral (middle), and posterior (right) views – scale bar equals 1 cm; B, scapula – scale bar equals 5 cm; C, humerus in dorsal (left) and posterior (right) views – scale bar equals 5 cm; D, pelvis in lateral (left) and dorsal (right) views – scale bar equals 5 cm.

The trunk vertebrae were described by Hutchison et al. (in press) to be laterally compressed compared to those of other baenids, suggesting that this may be an autapomorphy for the species. This appearance is likely, in part, due to a prominent ventral keel, especially on the anterior half of the column.

The two sacral vertebrae follow the general pattern of other baenids. The anterior sacral vertebra is partially preserved. The centrum is procoelous, as in other baenids such as *Chisternon undatum*. The transverse processes are robust, expanding laterally toward the articulations with the ilium. The second sacral vertebra has a shallow procoelous articular surface. The transverse processes are gracile and curve anteriorly to articulate with the expanded transverse processes of sacral I. The posterior centrum is platycoelous, and wider than tall.

Only one complete caudal vertebra is preserved. The centrum possesses a shallow procoelous articulation. The transverse processes are approximately twice as long as those of cervical B and are positioned slightly anterior to center of the centrum. The neural spine is a short, robust process.

Scapula. Both scapulae are preserved in this specimen, including a complete right side (Fig. 2.2B) and partial left. Unlike the scapular process of other baenids, which are typically rodlike and circular in cross section, the scapular process of *Neurankylus* sp. nov. A is slightly mediolaterally compressed, with an anterolateral groove running the length of the top half of the process. This is likely an autapomorphy for this species, as all other *Neurankylus* scapulae are circular in cross section. The scapular process is approximately 25% longer than the acromion process. The acromion process possesses a

medial shelf that expands anteriorly. A depression on the lateral side of the anterior end of the process gives the appearance of a dorsal ridge on the acromion.

Humerus. The left humerus of the holotype is preserved (Fig. 2.2C). As in other specimens of *Neurankylus*, such as TMP 1994.129.0001 from the Campanian Oldman Formation of Alberta, the humerus is slightly sigmoidal but straighter than the humeri of derived baenids. The humeral head is rounded in shape, being nearly circular in outline. The lateral humeral trochanter is much larger than the medial trochanter, being expanded and rounded along the lateral margin. The two trochanters are spaced widely apart, creating a wide intertrochanteric fossa. As in other baenids, the humerus expands distally, with an entepicondylar groove present on the dorsal surface of the element. Both the radial head and ulnar groove are preserved.

Pelvis. Anteriorly, the pelvis possesses a narrow, subtriangular pubic apron that makes up approximately half of the inominate length (Fig. 2.2D). The pubic tubercles are robust, projecting anteroventrally from the acetabulum. The ilia slope posterodorsally from the acetabulum, at an approximately 142° angle measured dorsally from the pubic apron (Fig. 2.2E), while those of other baenids typically form a 105-115° angle. This is likely an autapomorphy related to the highly domed nature of the carapace. Dorsally, the ilia expand posteroventrally into the ilial blade. The ilium is much more robust in this animal, possibly related to its large size. The acetabulum is subtriangular shaped, as in most baenids. However, the acetabular fossa is elongated more in the anterior-posterior direction than in any other observed baenid. In addition to this, there is a shelf along the anterodorsal margin of the acetabulum, another possible autapomorphy for the taxon. This causes the acetabulum to face more posteroventrally than the normally lateral facing

fossa of other baenids. These characters possibly coupled to limit the dorsal movement of the femur compared to other baenids, with the lengthening of the acetabulum allowing for more anterior-posterior movement.

Remarks

Neurankylus sp. nov. A was possibly the largest non-marine turtle during the Late Cretaceous of North America, rivaled only by *Basilemys* (Hutchison et al., in press). *Neurankylus* sp. nov. A was first recognized as a distinct taxon by Hutchison et al. (in press), based on size, shell shape, wide marginal scutes, and strongly keeled trunk vertebrae; however, they did not classify it beyond being an unidentified species of *Neurankylus*. Thus far, fossils of this turtle are only known from the middle unit of the Kaiparowits Formation, in strata that are between approximately 76.24 and 75.36 Ma. This correlates with the fossil-bearing portions of the Dinosaur Park and Judith River formations, which contain *N. eximius*.

Neurankylus sp. nov. A possesses a very disparate morphology compared to other members of the genus. Other than its enormous size, the most notable of these features is the highly domed nature of the carapace. No other known species of *Neurankylus* preserves a similar morphology. The pelvis is also autapomorphic within Baenidae. The ilial shaft slopes posteriorly much more than that of any other baenid. This is likely related to the highly-domed carapace and the ability for articulation with the sacral vertebrae. The ilia are also much more robust than those of other baenids. Another aspect of the pelvis that is unique to *Neurankylus* sp. nov. A is the orientation of the acetabulum.

While all other known baenids possess a laterally-facing acetabulum, the acetabular fossa of *Neurankylus* sp. nov. A is directed more posteroventrally.

Neurankylus sp. nov. B sp. nov.

Holotype

BYU 12001, an almost complete carapace and plastron.

Type horizon and locality

Middle (?) unit, Upper Cretaceous (Campanian Kaiparowits Formation, Grand Staircase-Escalante National Monument, southern Utah, USA.

Diagnosis

Distinguished from other species of *Neurankylus* based on a unique combination of characters: adult carapace size approximately 75 cm in length, larger than *N. eximius* and *N. baueri*, but smaller than *Neurankylus* sp. nov. A; a mid-dorsal keel is present posteriorly only, as in *Neurankylus* sp. nov. A and *N. eximius*; the posterior margin of the carapace lacks scalloping, as in all members of the genus except *N. baueri*; the fourth marginal is shaped like an asymmetrical trapezoid, expanding posteriorly as in *N. baueri* and the Milk River *Neurankylus*; anterior lobe of the plastron is larger than the posterior lobe, as in *N.* sp. nov. A; the anterior margin of the carapace is rounded, as in *Neurankylus* sp. nov. A and *Neurankylus* sp. from the Hell Creek Formation; the intergular scutes are curved to sigmoidal laterally, as in *N. eximius* and Hell Creek

Neurankylus sp.; the intergulars share a wide sulcus with the humerals, as in *N. baueri* and the Milk River *Neurankylus*.

Referred specimens

BYU 9411, a shell with only the plastron visible.

Distribution

Upper Cretaceous (Campanian) Kaiparowits Formation, southern Utah, USA.

Description

Carapace. The holotype possesses a nearly complete carapace, missing only the anteromedial margin and a portion of the right lateral margin (Fig. 2.3A). All sutures are fused, making it impossible to observe the relationships of individual carapace elements but this does indicate the specimen is at adult size, and can be compared with adult specimens of other members of the genus. The carapace of BYU 12001 is 75 cm in length, which is larger than all other known baenid species except *Neurankylus* sp. nov. A. The general shape of the carapace is similar to most other species of *Neurankylus* in being ovoid with relatively parallel margins. In profile, the shell is low-domed, as in all

Neurankylus except *Neurankylus* sp. nov. A. Similar to all other members of the genus except *N. baueri*, the posterior margin lacks strong scalloping. All *Neurankylus* possess a mid-dorsal keel on the carapace, the extent of which varies from species to species. *Neurankylus* sp. nov. B possesses a ridge only along the posterior portion of the
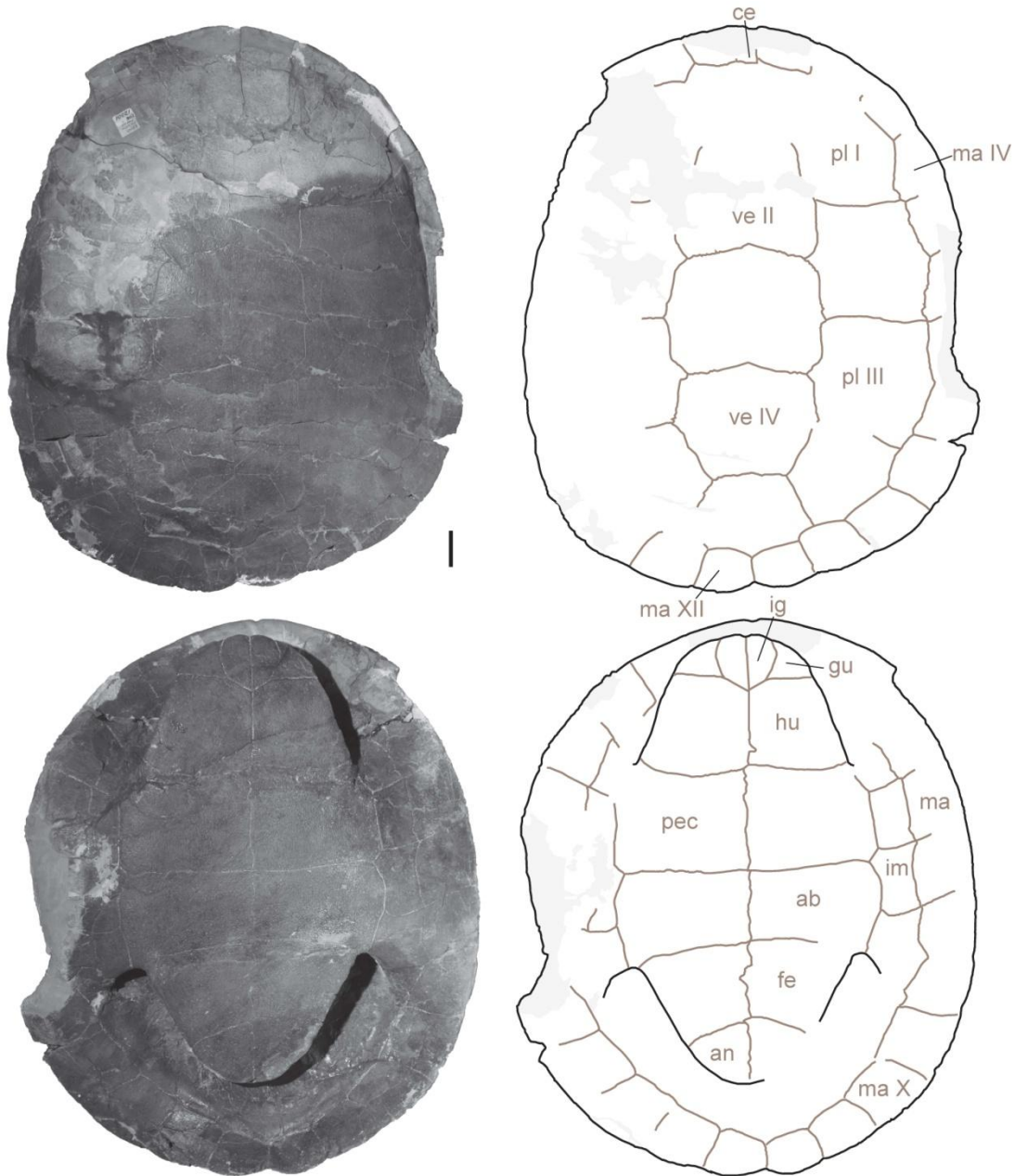
Figure 2.3. *Neurankylus* sp. nov. B (BYU 12001) photographs (left) and line drawings (right) of the A, carapace and B, plastron. Abbreviations: ab, abdominal scutes; an, anal scute; ce, cervical scute; fe, femoral scutes; gu, gular scute; hu, humeral scute; ig, intergular scute; im, inframarginal scutes; ma, marginal scutes; pec, pectoral scutes; pl, pleural scutes; ve, vertebral scutes. Scale bar equals 5 cm.

carapace, as in *Neurankylus* sp. nov. A and *N. eximius*. The latter differs in possessing a much more prominent keel. In contrast, *N. baueri* and *Neurankylus* sp. from the Hell Creek Formation possess a mid-dorsal ridge that runs the entire length of the carapace.

The cervical scute is not fully preserved, but it does appear to be longer than wide. The vertebral scutes are wider than long, a plesiomorphic state for Baenidae observed in all members of the genus. The first three vertebrals are hexagonal in shape. The first vertebral tapers posteriorly, while vertebral II tapers anteriorly. Vertebral IV also tapers posteriorly. Yet another plesiomorphic condition among baenids observed in this and other species of *Neurankylus* is the lack of exposure of the fifth vertebral on the posterior margin of the carapace, as the shell's posterior is ringed with marginal scutes. *Neurankylus* sp. nov. B possesses 12 marginals, as in all species of *Neurankylus* except *Neurankylus* sp. nov. A. A character noted by Larson et al. (in press) to be an important diagnostic character is the shape of the fourth marginal. As in *N. baueri* and the Milk River *Neurankylus*, this scute was shaped like an asymmetrical trapezoid, with the posterior end mediolaterally expanded. The width of the fifth marginal then tapers posteriorly.

Plastron. The relative dimensions of the two plastral lobes differ from all other species of *Neurankylus* except *Neurankylus* sp. nov. A in that the anterior lobe is large than the posterior lobe (Fig. 2.3B). The anterior lobe is rounded as in *Neurankylus* sp. nov. A and specimens of the genus from the Hell Creek Formation. This differs from the truncated morphology of *N. eximius*, *N. baueri*, and the Milk River *Neurankylus*. The posterior lobe, though shorter comparatively, possesses a triangular shape similar to that of other members of the genus. A xiphiplastral notch is absent. Both the inguinal and

axillary buttresses exhibit the typical baenid morphology; they are well developed, and possess a long articulation with the ventral carapace.

Neurankylus sp. nov. B exhibits the typical basal baenid/paracryptodire morphology of gular scutes that are separated from each other by posterior extension of the intergulars. The morphology of the intergular scutes appears to be unique among *Neurankylus*. The lateral margins of the intergulars are curved, as in *N. eximius*; however, the intergular-gular sulci of *Neurankylus* sp. nov. B are not as sigmoidal. This differs from the intergulars of *N. baueri* and the Milk River *Neurankylus*, which possess straight lateral margins. The intergular-humeral sulcus is of similar relative width to that of *N. baueri*, which is smaller than that of the Milk River *Neurankylus*. *N. eximius* differs in possessing little to no intergular-humeral contact. Figure 2.4 shows the differences in the morphology of the anterior plastron amongst several species of *Neurankylus*. The humeral, pectoral, and abdominal scutes do not differ in morphology when compared to other members of the genus. As in other species of *Neurankylus*, the pectoral scutes contact inframarginals I-III, whereas the abdominal scutes contact inframarginals III and IV. The inframarginals themselves are approximately half the width of the ventral exposures of the marginals. Inframarginal III does not possess a prominent medial process. This restricts the sulcus between the pectoral scute and inframarginal III, which is much wider in other species of *Neurankylus*. This narrower sulcus may represent an autapomorphy for *Neurankylus* sp. nov. B; but this is tentative due to the low sample size of specimens for this taxon.
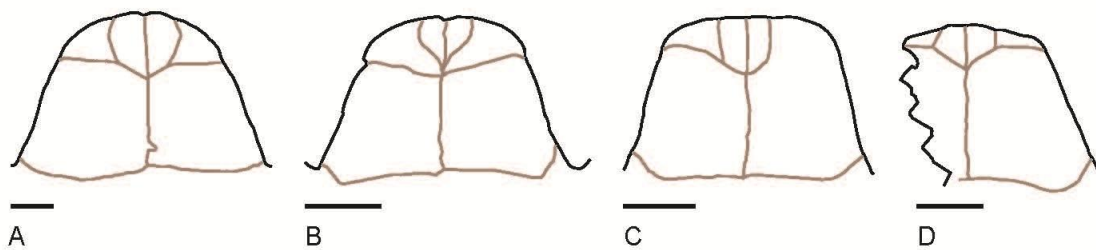
Figure 2.4. Comparative line drawings of the anterior plastra of species of *Neurankylus*: A, BYU 12001; B, *N. eximius* (TMP 2003.012.0171); C, *N. baueri* holotype (USNM 8344); D, Milk River Formation *Neurankylus* sp. holotype (TMP 2007.035.0045). Each scale bar equals 5 cm.

Remarks

Hutchison et al. (in press) recognized *Neurankylus* sp. indeterminate A (*Neurankylus* sp. nov. B) as a distinct species from their *Neurankylus* sp. indeterminate B (*Neurankylus* sp. nov. A) and indicated that it differed from *N. baueri* and *N. eximius* in the proportions of the two plastral lobes and the shape of the anterior margin of the plastron. They observed that *N.* sp. nov. B was similar to *N. baueri* in possessing a reduced mid-dorsal keel, compared to *N. eximius*. It should be noted, however, that *N. baueri* possesses a ridge that runs the length of the carapace, whereas this ridge is present only posteriorly on *Neurankylus* sp. nov. A. The two also differ in carapace length (*Neurankylus* sp. nov. B is larger), the absence of posterior scalloping in *N.* sp. nov. B, and the shape of the intergular-gular sulcus. Based on the alpha-taxonomic scheme of Larson et al. (in press), and with the addition of new distinguishing characters for various species of *Neurankylus*, the separation of *Neurankylus* sp. nov. B as a new species from other members of the genus is well-supported.

With the addition of *Neurankylus* sp. nov. A and *Neurankylus* sp. nov. B, there are now six recognized species of *Neurankylus*, all with consistent, disparate morphologies. Four of these species, including *N. baueri*, *N. eximius*, *Neurankylus* sp. nov. A, and *N. baueri* lived during the late Campanian, with the first three being contemporaneous based on radioisotopically-constrained correlation of fossil zones (Roberts et al., 2005; Roberts et al., in press).

BAENODDA Gaffney and Meylan, 1988, sensu Lively (Chapter 3)

New pig-nosed taxon (Chapter 1)

Holotype

UMNH VP 21151, a nearly complete skull and mandible, nearly complete carapace, complete plastron, nearly complete right forelimb, partial right hindlimb, and incomplete cervical and caudal vertebral series.

Type horizon and locality

Upper Cretaceous (Campanian) Kaiparowits Formation, approximately 170 m above the base of the formation. This places it within the informal middle unit of the formation, with an age of between 76.60 and 76.14 Ma. The specimen was discovered in Grand Staircase-Escalante National Monument, Kane County, Utah, USA.

Diagnosis

See Chapter 1.

Referred specimens

UMNH VP 20145, a nearly complete carapace and plastron; UMNH VP 20183, a partial carapace and plastron.

Distribution

Upper Cretaceous (Campanian) Kaiparowits Formation, Utah, USA.

Description

See Chapter 1.

Remarks

Hutchison et al. (in press) recognized the presence of a baenid with similar morphology to *P. antiqua* within the Kaiparowits, which they referred to *Plesiobaena* sp. Differences they recognized between this taxon and *P. antiqua* include a strongly serrated posterior carapace, wider vertebral scutes, and a mid-dorsal ridge spanning the length of the carapace. UMNH VP 21151 reveals more differences from *Plesiobaena*, including a broad rostrum, large nasals, and external nares separated by a bony septum – a character unique . My phylogenetic analysis (see Chapter 1) reveals that this is a taxon distinct from *P. antiqua*, most closely related to *Hayemys latifrons*. This new taxon is only known from the Campanian Kaiparowits Formation of Utah, while *H. latifrons* is known only from the Maastrichtian Lance Formation of Wyoming.

Denazinemys Lucas and Sullivan, 2006

Type and only species

Denazinemys nodosa (Gilmore, 1916)

Revised diagnosis

Autapomorphies for *Denazinemys* in relation to other baenids: a tall crista supraoccipitalis that extends beyond the occipital condyle; a sub-triangular shaped carapace; a nodular carapace texture consisting of prominent, rounded, lobate to circular nodes that are tightly packed, more so than in *Boremys* spp.; Diagnosed by a unique combination of characters including: a wedge-shaped skull that is longer than wide, as in *Eubaena cephalica*; otic capsules that slant posterolaterally from the braincase, as in *E.*

cephalica and *Palatobaena* spp. and differing from all other baenids, which possess

mediolateral-trending capsules; the exclusion of the jugal from the orbital margin as in

Arundelemys dardeni, *Trinitichelys hiatti*, *Boremys pulchra*, *E. cephalica*, and

Plesiobaena antiqua; the exclusion of the opisthotic from the foramen stapedio-temporale

as in *Hayemys latifrons*, *B. pulchra*, *E. cephalica*, *P. antiqua*, *Peckemys brinkman*,

Cedrobaena putorius, and *Palatobaena* spp.; the foramen posterius palatinum rimed only

by the palatine as in *H. latifrons*, *Stygiochelys estesi*, and some specimens of *Chisternon*

undatum, differing from all other baenids in which both the palatine and pterygoid

contribute to the foramen; a short medial contact between the pterygoids due to a long,

pentagonal basisphenoid, as in some specimens of *E. cephalica*, *S. estesi*, *C. undatum*,

Baena arenosa, and *Palatobaena gaffneyi*, differing from the broad contact of other

baenids; a lateral narrowing of costal V, as in *Boremys pulchra*; the presence of a

prepleural (i.e. anterior supernumerary pleural scute) as in *Baena arenosa*, *Chisternon*

undatum, *Boremys* spp., *'Baena' hatcheri*, and *'Baena' escavada*; the absence of both a

postpleural (i.e., posterior supernumerary pleural scute) and supramarginal scutes, as in

all baenids except *Boremys* spp.

Distribution

Upper Cretaceous (Campanian) Kaiparowits Formation, southern Utah, USA;

Upper Cretaceous (Campanian) Aguja Formation, Texas, USA; Upper Cretaceous

(Campanian) Fossil Forest Member, Fruitland Formation, New Mexico, USA; Upper

Cretaceous (Campanian) Hunter Wash and De-na-zin members, Kirtland Formation, New

Mexico, USA

Denazinemys nodosa (Gilmore, 1916)

Holotype

USNM 8345, an almost complete carapace and plastron.

Type horizon and locality

Upper Cretaceous (Campanian) De-na-zin Member, Kirtland Formation, San Juan Co., New Mexico, USA.

Referred specimens

BYU 19123, a partial skeleton including a nearly complete skull, shell, and partial left forelimb; UMNH VP 20447, a nearly complete, partially crushed shell; UMNH VP 20446, a shell with a partial carapace and complete plastron; UMNH VP 16872, a partial shell; UMNH VP 9545, carapace fragments; UCMP V94039/194342, a partial anterior carapace and plastron; UCMP V94028/194335, right anterolateral carapace fragment and anterior plastron; UCMP V93096/194271, partial carapace; UCMP V93084/194248, costal fragments; UCMP V93070/194207, left anterolateral quarter of carapace; UCMP V95087/159703, partial anterior carapace; UCMP V99441/159399, partial carapace; for referred specimens from the San Juan Basin, see Sullivan et al. (in press) and Gaffney (1972).

Description

Skull. BYU 19123 includes a skull associated with a shell of *D. nodosa*, the first such association recognized. The skull (Fig. 2.5) is uncrushed and nearly complete,
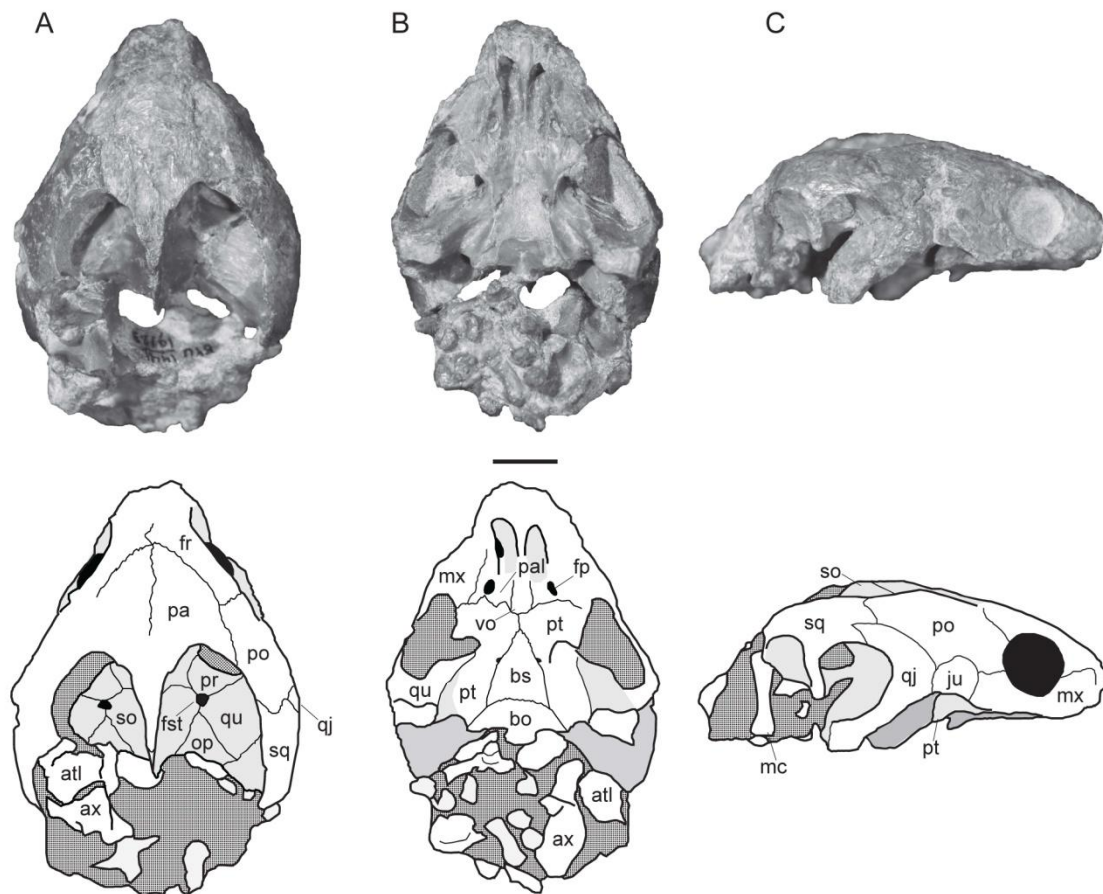
Figure 2.5. Photographs (top) and line drawings (bottom) of the skull of *Denazinemys nodosa* (BYU 19123) in A, dorsal; B, ventral; and C, lateral views. Abbreviations: atl, atlas; ax, axis; bo, basioccipital; bs, basisphenoid; fp, foramen palatinum posterius; fr, frontal; fst, foramen stapedio-temporale; ju, jugal; mc, metacarpal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; po, postorbital; pr, prootic; pt, pterygoid; qu, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; vo, vomer. Scale bar equals 1 cm.

missing only the anterior rostrum (nasals and premaxillae) and the ventral portions of the maxillae. Overall, the skull is wedge-shaped with a constriction of the skull roof in the middle of the orbit, which gives the appearance of a rectangular rostrum. This constriction is also present in the same position in *Peckemys brinkman*, *Goleremys mckennai*, and *Eubaena cephalica*, whereas it is located more toward the anterior margin of the orbit in *Boremys pulchra* and *Plesiobaena antiqua*. Though most of the rostrum is missing, the skull is longer at the midline than it is wide at the otic capsules (the skull's widest point). The presence of an elongated rostrum, observed in *B. pulchra* and *E. cephalica*, cannot be confirmed because the tip of the rostrum is missing. The orbits are circular and oriented laterally. They are slightly smaller than the cavum tympani. The interorbital width is narrow relative to the length of the skull, more so than in any other baenid observed in this study. The cheek region is deeply emarginated, almost to the level of the ventral margin of the orbit. This emargination is much deeper than that seen in *Trinitichelys hiatti*, but is not as deep as that of *P. brinkman*. The otic capsules slant posterolaterally from the braincase. This condition differs from *B. pulchra* and *P. antiqua* and most other baenids where the otic capsules are more or less perpendicular to the sagittal plane. The otic capsules of *Palatobaena* spp. also exhibit this morphology.

The frontals contact the prefrontals and maxillae anterolaterally, the postorbitals posterolaterally, and the parietals posteriorly. The frontals exhibit a large contribution to the dorsal orbital margin. As with many derived baenids, the contribution of the frontal to the postorbital skull roof is greatly reduced. The frontal-parietal suture is greatly notched, with the parietal extending anteriorly nearly to the midpoint of the orbit, a state also seen in *B. pulchra* and *Chisternon undatum*. Laterally, the frontals extend to the posterior

margin of the orbit. As in all baenids except *Baena arenosa* and *C. undatum,* the parietals are longer than their combined maximum width. In BYU 19123, the parietals are well over twice as long as their combined width. The parietals contact the frontals anteriorly, the postorbitals laterally, the supraoccipital posteroventrally, the prootic ventrally, and each other medially. The upper temporal emargination extends beyond the otic capsule, which prevents any contact between the squamosal and parietal. The crista supraoccipitalis is pointed and extends posterior to the occipital condyle. The supraoccipital possesses a small exposure on the dorsal skull roof.

The jugal has a small exposure on the lateral portion of the skull and is excluded from the orbital margin by a small contact between the maxilla and the postorbital, as in *B. pulchra*. It contacts the maxilla anteriorly, the postorbital dorsally, and the quadratojugal posteriorly. The quadratojugal is a comma-shaped element that possesses an expansion that extends dorsal to the cavum tympanum, as in all baenids except *Baena arenosa* and *Chisternon undatum*. The quadratojugal contacts the jugal anteriorly, the postorbital dorsally, the squamosal posterodorsally, and the quadrate medially. The postorbital is a rectangular element with a large exposure within the upper temporal emargination. Medially, it contacts the parietal with a relatively straight suture that does not diverge much from the midline. There is a small contact with the frontal anteromedially. The postorbital contacts the squamosal posteriorly, the quadratojugal and jugal ventrally, the maxilla anteroventrally, and is exposed in the orbital margin anteriorly. A contact between the maxilla and postorbital, preventing exposure of the jugal within the orbital margin, is seen also observed in *A. dardeni*, *T. hiatti*, *P. antiqua*, *G. sonsalla*, *B. pulchra*, and *E. cephalica*. The squamosal is exposed on the posterolateral

corner of the dorsal skull roof. There is a distinct fossa on the posteroventral portion of the element just posterior to the cavum tympanum, a likely attachment site for the M. depressor mandibulae (Gaffney, 1982). The squamosal contacts the quadrate ventrally, the quadratojugal anteroventrally, the postorbital anteriorly, the opisthotic ventromedially, and is exposed along the rim of the temporal emargination medially.

Although the maxillae are weathered, enough of the element is preserved to determine that the triturating surface expands slightly posteriorly. The presence of a lingual ridge anteriorly cannot be determined, but it is absent posteriorly. The vomer is a long element that expands posteriorly, where it contacts the palatines laterally. The vomer possesses a straight suture with the pterygoids posteriorly, as in *A. dardeni*, *T. hiatti*, *C. putorius*, *E. cephalica*, *C. undatum*, and *G. mckennai*. The palatines are lightly exposed on the triturating surface. As in other baenids (Gaffney, 1982), the palatine forms the posterior border of the foramen orbito-nasale. Medial to this, the palatine contacts the prefrontal. Posterior to the aperture narium interna, the palatine possesses a shallow but wide sulcus that flattens out before the suture with the pterygoid is reached. The contact between to palatines and pterygoids is straight medially and then curves posterolaterally. This suture does not enter the foramen palatinum posterius, a condition similar to that of *Stygiochelys estesi* but differing with *B. pulchra*. The processus pterygoideus externus is a pointed flange that curves posterolaterally. These flanges project ventrally, and are visible below the rest of the palate in lateral view. The pterygoids contact the vomer and palatine anteriorly, each other medially, the basisphenoid posteromedially, the basioccipital posteriorly, and the quadrate dorsolaterally. The basisphenoid is a long, pentagonal-shaped element that greatly restricts the medial contact of the pterygoids, as

in *S. estesi* and *C. undatum*. This differs from the basisphenoids of *B. pulchra* and most other baenids, which are pentagonal but relatively short, providing for a longer interptergyoid contact. The foramen posterius canalis caroticus internus is located halfway along the suture between the basisphenoid and the pterygoid, as in all baenids. Posterior to this foramen, the groove that would have housed the internal carotid expands posteriorly to half a centimeter lateral to the basioccipital.

The basioccipital possesses paired ventral tubercles that project posteriorly. These exhibit the typical baenid morphology of being blocky in shape, in contrast to the flattened tubercles of *Palatobaena* spp. and the new pig-nosed taxon. The basisphenoid contacts the pterygoids anterolaterally and the exoccipitals dorsolaterally. The exoccipitals each contain a foramen jugulare posterius, which is approximately the same size as the foramen posterius canalis caroticus internus. The opisthotic contacts the exoccipitals ventromedially, the supraoccipital dorsomedially, and the quadrate laterally. The opisthotic is excluded from the margin of the foramen stapedio-temporale by a narrow bar formed by the contact between the supraoccipital and quadrate. These two bones and the prootic enter the margin of the stapedial foramen. This is similar to the condition seen in *B. pulchra*, where the opisthotic is also separated from the stapedial foramen by a thin bar. The opisthotic is also excluded from the stapedial foramen in *H. latifrons*, *P. antiqua*, *P. brinkman*, *C. putorius*, *G. sonsalla*, *Palatobaena* spp., and *E. cephalica*. Lateral to this foramen, the dorsal surface of the quadrate is highly rugose. A similar texture was described by Brinkman (2003) just lateral to the suture of the prootic and quadrate on *Plesiobaena antiqua*. This was described as the articulation point with the carilago transiliens – the sliding sesamoid cartilage at the contact between the

processus trochlearis oticus and the tendon of the external adductor muscle (Gaffney, 1972). The supraoccipital contacts the parietals anterodorsally, the opisthotic ventrolaterally, the exoccipitals ventrally, and the prootic anterolaterally. The supraoccipital has a slight exposure on the dorsal skull roof. The crista supraoccipitalis is mediolaterally thin posteriorly, but broad in lateral view, and therefore greatly dorsoventrally expanded compared to other baenids. Both stapes are visible through the fenestrae postotica and appear to exhibit the typical turtle morphology.

Mandible. Only the posterior portion of the right side of the mandible is preserved in BYU 19123. It is very similar in overall morphology to that of *B. pulchra* (Brinkman and Nicholls, 1991) in possessing a relatively low coronoid process and a well developed retroarticular process. Unlike *B. pulchra*, which is described by Brinkman and Nicholls (1991) as having a v-shaped suture between the dentary and squamosal, *D. nodosa* possesses a straight, vertical suture between these two elements.

Carapace. A large percentage of *Denazinemys nodosa* shells are taphonomically distorted. However, based on the holotype and UMNH VP 20447, it appears that the carapace is typically subtriangular in outline, with a tapered anterior end. Variation is seen in the mediolateral shape of the posterior margin, ranging from relatively flat in the holotype to rounded in other specimens. Any variation in this shape not attributable to distortion could be individual variation, ontogeny, or sexual dimorphism, as there are no other characters that distinguish the specimens of *Denazinemys* within the Kaiparowits Formation or San Juan Basin. Though it is often accentuated by crushing, many specimens of *D. nodosa* appear to have a more highly-domed carapace compared to other

baenids such as *Neurankylus eximius* and *Plesiobaena antiqua*. Figure 2.6 shows several *D. nodosa* shells from the Kaiparowits.

Minor scalloping is present on the anterolateral margin of the carapace in all specimens of *D. nodosa*. In some specimens, such as BYU 19123, scalloping similar to that of *Boremys* spp. is present on the nuchal. Though most of the posterior serrations are reconstructed on the holotype of *Denazinemys*, UMNH VP 20447 confirms that the posterior carapace margin was strongly scalloped, with at least five serrations on each side. As in most baenodds, a prominent pygal notch is present medially on the posterior carapace margin.

The ornamentation of *D. nodosa* is very distinct and may be used to distinguish it from other ornate baenids such as *"Denazinemys" ornata* and *Boremys* spp. Compared to the ornamentation of *B. grandis*, *D. nodosa* exhibits more tightly-packed, prominent nodes. Although the distribution of ornamentation varies from individual to individual, the nodes are typically ovate to circular in shape. Lateral to the neural series, there are three rows of nodes oriented anterior-posterior that are elongate and ovoid. This differs from the dorsal ornamentation of *"Denazinemys" ornata*, which possesses more ridge-like nodes that are not as rounded as those of *D. nodosa*. Towards the lateral edge of the carapace, the nodes are typically circular to ovate in shape, with any ovate nodes oriented mediolaterally. On specimens of *"Denazinemys" ornata* this area is typified by rows of alternating ridge-like and circular nodes, some of which are at oblique angles to the midline. In contrast, the lobate nodes of *D. nodosa* and *Boremys* spp. are typically perpendicular to the midline on the lateral carapace. Anteriorly, on the nuchal and first costals, the ornamentation of *D. nodosa* is typically characterized by small circular nodes
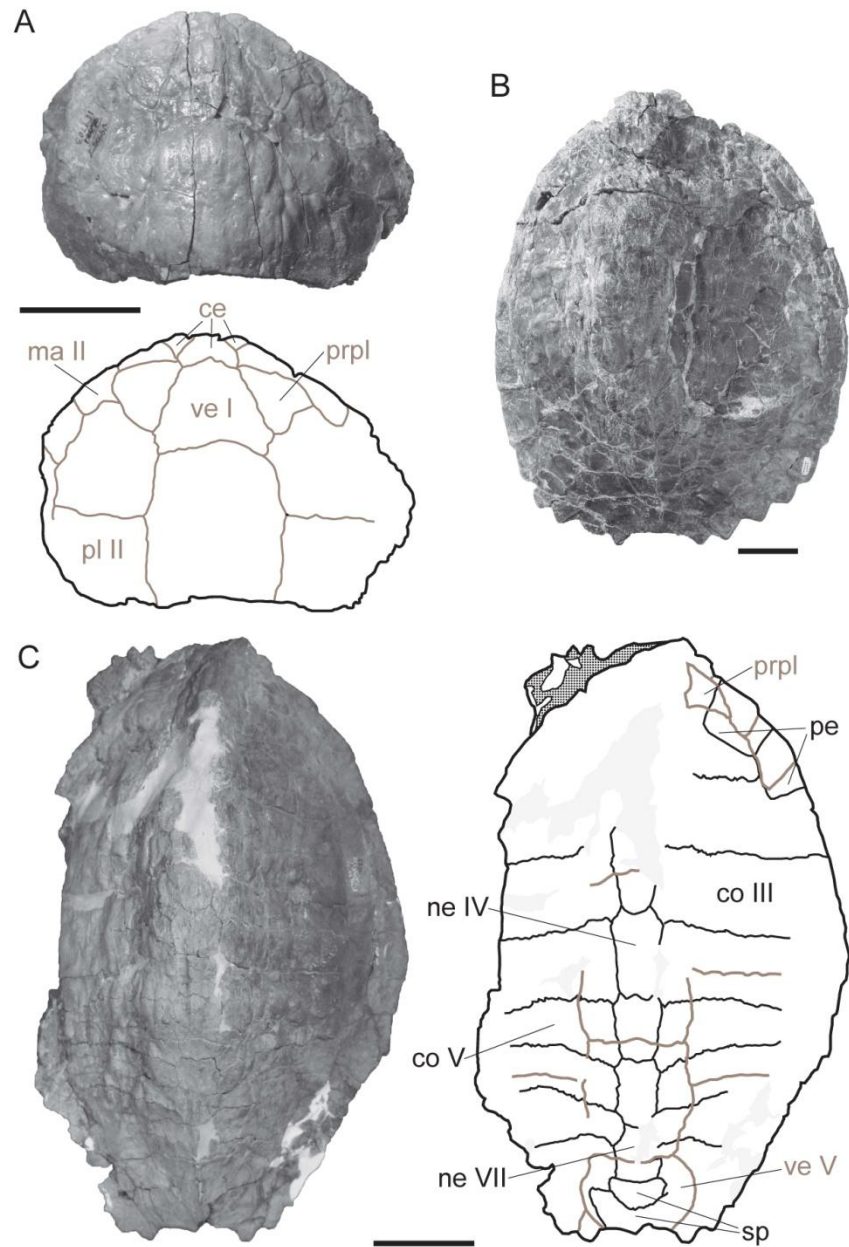
Figure 2.6. Carapace of *Denazinemys nodosa*. A, Photograph (top) and line drawing (bottom) of the UCMP V95087/159703 displaying sulci of the anterior carapace; B, Carapace of UMNH VP 20447 demonstrating the general shape of *D. nodosa*; C, Photograph (left) and line drawing (right) of BYU 19123 showing elements of the carapace and overlying scale pattern. Abbreviations: ce, cervical scutes; co, costals; ma, marginal scutes; ne, neural; pe, peripheral; pl, pleural scutes; prpl, prepleural; sp, suprapygal; ve, vertebral scutes. Scale bars equal 5 cm. Bone sutures and labels are in black while scale sulci and labels are in gray.

that are tightly packed, particularly in the area under the posterolateral portion of vertebral I. Similar ornamentation in this area is also seen in *"Denazinemys" ornata*. A simple mid-dorsal keel is present along the posterior half of *D. nodosa*, from neural IV to the pygal notch. Specimens of *Boremys* spp. also possess a posterior mid-dorsal keel. *"Denazinemys" ornata* exhibits a mid-dorsal ridge made up of three rows of ornamentation ridges clustered at the midline anteriorly. This becomes a single ridge posteriorly.

Although most known specimens of *D. nodosa* are adult and do not preserve sutures in the shell, BYU 19123 appears to be a subadult and sutures are identifiable where the carapace is well preserved. As with other baenids, the nuchal bone contributes to the anterior margin of the carapace. The nuchal expands anteriorly. Neurals I and II are not fully preserved on BYU 19123, and the presence of a preneural is uncertain in this specimen. However, a preneural is present on NMMNH P-41229 from the Kirtland Formation of New Mexico. The length of the first neural is reduced relative to the same element in *Plesiobaena antiqua*, likely because it is subdivided to form the preneural. The first neural is slightly longer than it is wide. Neurals II-VI are all longer at the midline than they are the wide. The third neural is hexagonal in shape with a longer posterior, giving the element a coffin shape, as in other baenids. Neural III possesses a narrow contact with costal II and a broader contact with costal III. The anterior end of neural IV is concave due to a posterior extension of the third neural. Neural IV has a narrow contact with costal III and a broad contact with costal IV. The fifth neural follows a similar pattern, but is shorter relative to neurals III and IV. Neural V has a slight anterior projection that excavates a portion of neural IV. The sixth neural is sub-

octagonal in shape, contacting costals V, VI, and VII, with the broadest contact being with costal VI. Neural VII is slightly shorter than it is wide and is subtriangular in shape with a tapered anterior end. It contacts costals VII and VIII. Neural VIII is twice as wide as it is long, and only contacts costal VIII, neural VII, and the first suprapygal.

As in all other baenids except *Stygiochelys estesi* (Brinkman and Nicholls, 1991), two suprapygals are present. The first suprapygal is a small element that is larger than the eight neural and is subrectangular in shape. The second suprapygal is much larger than the first, being more than twice as wide. It is constricted medially by the anterior suprapygal and the pygal notch, making it appear like a bow-tie shape.

For the most part, the costals are relatively regular in shape, with sutures between the anterior elements being mostly parallel, trending mediolaterally. The third costal is the widest; it is 25% wider than the fourth costal and over 64% wider than the sixth. Costal V narrows laterally, being constricted due to the anterolateral trend of the sixth costal. This accommodates the anterior-posterior widening of the seventh costal, which is 71% wider laterally than it is at its medial contact with neurals VI and VIII. A similar pattern is described for *Boremys pulchra* (Gilmore, 1919).

The cervical scute of *D. nodosa* is consistently subdivided into three scutes on all known specimens. Other baenids with subdivided cervical scutes are *Boremys* spp., *S. estesi*, *C. undatum*, *B. arenosa*, *B. hatcheri*, and *"Baena" hayi*. The central scute varies from subrectangular to heart-shaped, always possessing a tapered end that opens onto the anterior margin of the carapace. Two smaller scutes are anterolateral to the central scute, subequal in size to one another, and vary from ovate to subtriangular in shape. These are referred to here as portions of a subdivided cervical as opposed to the first marginal

because of their small size and restriction to the nuchal bone. Between one half and one third of marginal I is located on the nuchal, with the rest of it lying on the first peripheral. Marginal II expands posteriorly and is positioned on peripherals I and II, with 60-80% of it located on peripheral II. Subsequent marginals follow a similar pattern, straddling the suture between the corresponding peripheral and the one anterior to it, with the majority of each marginal residing on the corresponding peripheral (e.g., most of marginal IV resides on peripheral IV). In both specimens where sutures are well preserved, BYU 19123 (Kaiparowits Fm) and NMMNH P-41229 (Fruitland Fm), the posterolateral margin of the carapace is not preserved beyond peripheral VII, except for the posterior-most margin in BYU 19123. Therefore, the number of peripherals and the relationships with the overlying marginal scutes cannot be determined. The entire last marginal and half of the second-to-last marginal reside on the last peripheral. Based on complete specimens such as UMNH VP 20447 and USNM 8345, there are 13 sets of marginal scutes present, so marginals XII and XIII are on the last peripheral. The marginal scutes as well as the subdivided cervical outline both the anterior and posterior serrations on *D. nodosa*.

D. nodosa possesses a supernumerary scute anterior to the first pleural scute and lateral to the first vertebral; this will be referred to herein as the prepleural scute (sensu Hutchison et al., in press; anterior supernumerary pleural scutes, sensu Lyson and Joyce, 2009a). This scute is subtriangular in shape and overlies portions of the nuchal, costal I, and peripheral I. This scute is also observed in *Boremys* spp., *Chisternon undatum*, *Baena arenosa*, and *Baena hatcheri*. The presence of this scute restricts the anterior portion of the first vertebral scute, giving this scale a subtriangular hexagonal shape. The shape of

the sulcus between vertebral I and the prepleural varies in curvature from straight in some specimens to slightly convex or concave laterally. The first vertebral overlies portions of the nuchal, costal I, neural I, and the entire preneural. Unlike *Boremys* spp., a nuchal scute (i.e., a subdivision of vertebral I lying entirely on the nuchal bone) is not present in *D. nodosa*. Vertebral scutes II, III, and IV are all rectangular in shape and are longer than they are wide. Vertebral II overlies neurals I, II, and III and costals I-III. The third vertebral overlies neurals III-V and costals III-V. Vertebral IV overlies neurals V-VII and costals V-VIII. The sulcus between the fourth and fifth vertebrals overlies the suture between neurals VII and VIII. As in all other baenodds, the fifth vertebral scute exhibits an exposure on the posterior margin of the carapace. It overlies neural VIII, both suprapygals, and a portion of costal VIII and the last peripheral.

Plastron. Figure 2.7 illustrates the plastron of BYU 19123. As with other derived baenids, there is a broad distance between the posterior carapace and the plastron. The axillary buttress extends dorsally to meet the first dorsal vertebra, forming a distinct neck shield. The inguinal buttress is also well developed, extending onto the ventral surface of the costals. Both of these traits are synapomorphies of Baenidae (Lyson and Joyce, 2011) and have been observed by the author in all other baenids. As with all other baenids except *Neurankylus* sp. nov. A and *Neurankylus* sp. nov. B from the Kaiparowits Formation, the anterior lobe of the plastron is smaller than the posterior lobe. The plastron thickens medial to both the axillary and inguinal buttresses, the latter of which is an apomorphy of Paracryptodira (Lyson and Joyce, 2011). The anterior lobe is typically subrectangular in shape, though it can be slightly subtriangular in some specimens. The
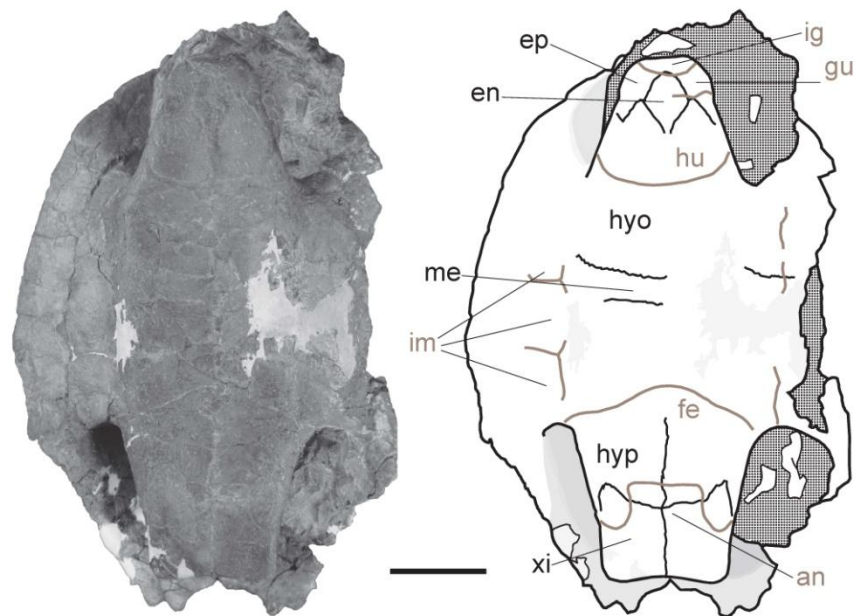
Figure 2.7. Photograph (left) and line drawing (right) of the plastron of *Denazinemys nodosa* (BYU 19123), displaying bones and scales. Abbreviations: an, anal scutes; en, entoplastron; ep, epiplastron; fe, femoral scutes; gu, gular scutes; hu, humeral scutes; hyo, hyoplastra; hyp, hypoplastra; ig, intergulars; im, inframarginals; me, mesoplastron; xi, xiphiplastra. Scale bar equals 5 cm. Bone sutures and labels are in black while scale sulci and labels are in gray.

anterior margin is broadly rounded in all specimens, regardless of whether the shape is more triangular or rectangular. The posterior lobe of the plastron is subtriangular proximally, with an inflection point near the sulcus between the femoral and anal scutes. Posterior to the point, the lateral margins are parallel. Anterior to this inflection point, the posterior lobe is greatly thickened laterally. This state is seen in all other baenids, but this area is especially thick in *D. nodosa*. This distinct morphology of the posterior plastral lobe is observed in *D. nodosa*, *Boremys* spp., and *E. cephalica.* A shallow xiphiplastral notch is present in most specimens.

The suture between the epiplastra and the entoplastron/hyoplastra is z-shaped. The mesoplastra meet at the midline, with their anterior-posterior length tapering medially. As in other baenodds, the suture between the hypoplastra and xiphiplastra is strongly z-shaped, as described by Lyson and Joyce (2010).

The gular scutes contact each other medially posterior to the intergular scutes. The size of the gular series varies slightly, but the intergulars are typically of similar size to the gulars. The intergulars overlap slightly onto the entoplastron, but are otherwise restricted to the epiplastra. The sulcus between the gulars and humeral scutes varies in shape from a simple posteriorly convex curve to undulatory, possessing paired posterior projections. As with many specimens of *Boremys* spp., some specimens of *D. nodosa* possess distinct notches in the plastron where the sulci of the gular series scales meet the margin. The shape of the sulcus between the femoral and anal scales varies slightly. In some specimens, an anterior projection of the anal scutes is present and the anterior margin is truncated. In other specimens, this projection is undulatory anteriorly, with up to three sub-projections. This anterior projection of the anal scute laps onto the

hypoplastron. There are four inframarginals in the bridge area of the shell. These are all pentagonal in shape except for the third, which is hexagonal. Marginals IV-VII are also exposed on the ventral bridge area. The inframarginals are slightly larger (~20%) than the ventral exposure of these marginal scutes.

Forelimb. The nearly complete lower left forelimb and manus of BYU 19123 are preserved in ventral view (Fig. 2.8); only the proximal ends of the radius and ulna, the distal portion of the ulna, and the proximal half of metacarpal I are missing, but the latter's size can be assessed because an external mold of the element is still present on the specimen. The intermedium, centralae, and radiale are not exposed on the surface of the specimen. The ulnare is a large blocky element with a depression on the dorsal side. Distal to this, a small ovoid block of bone is preserved that I identify as the pisiform. The pisiform figured for *Peckemys brinkman* in Lyson and Joyce (2009, Fig. 10) is proportionally much larger than that of *D. nodosa* compared to other elements of the manus. The first four distal carpals are preserved, increasing in size laterally. Distal carpal I is a small lateral-medial rectangular element. Distal carpals II and III are each spheroid in shape and are approximately the same size. This differs from *P. brinkman*, in which the third is slightly larger than the second (Lyson and Joyce 2009, Fig. 10). The fourth distal carpal is larger and blocky. Metacarpal I is a short, robust element that is wider than the other metacarpals. The remaining metacarpals are more slender, with metacarpal III being the longest. Unlike the new pig-nosed taxon, the second metacarpal of *D. nodosa* is not significantly wider than the shaft of the element. The third and fourth metacarpals of *D. nodosa* are longer than the other metacarpals, but not as proportionally long as the same elements of the pig-nosed baenid. Metacarpal V is a short, slender bone
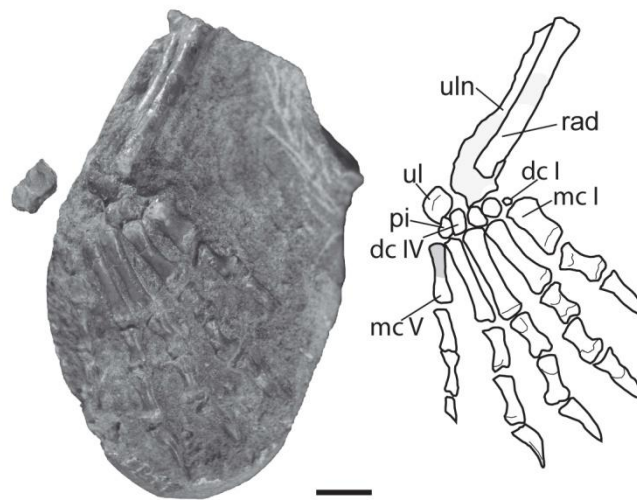
Figure 2.8. Photograph (left) and line drawing (right) of the left forelimb and manus of *Denazinemys nodosa* (BYU 19123). The ulnare, pisiform, and distal carpal IV are in a separate piece of sandstone from the rest of the manus (far left). These elements are reflected into place in the line drawing. The light gray areas represent reconstructed areas on the specimen, whereas the dark gray area of the proximal metacarpal V is reconstructed from an external mold. Abbreviations: dc, distal carpals; mc, metacarpals; pi, pisiform; rad, radius; ul, ulnare; uln, ulnare. Scale bar equals 1 cm.

and is the forth longest of the metacarpals. The phalangeal formula is 2:3:3:3:3, which appears to be consistent across all baenid taxa with preserved forelimbs. The proportions of the digits are similar to those of the new taxon, in that the fourth digit is the longest, followed by digit III, II, V, and I. However, digit I of BYU 19123 is slightly longer than the same digit of the holotype of the new taxon, whereas all other digits are consistently 0.5 to 2 mm shorter in BYU 19123. The slightly curved and pointed unguals are similar to other baenids. The unguals on digits I-IV are subequal in length, but the ungual on digit V is approximately half the length of the others. This condition is also observed in the new pig-nosed taxon.

Pelvis. Various pelvic and hindlimb elements are exposed posterior to the left inguinal buttress in matrix, but the only identifiable bone is the ilium. Because it is out of context from the other pelvic elements, its orientation relatively to the acetabulum cannot be assessed. Dorsally, the ilium expands into a broad blade with both anterior and posterior projections. Therefore, unlike other baenids such as *P. antiqua* and *Neurankylus* sp. nov. A where the anterior shaft and blade of the ilium is relatively straight, the anterior edge of the ilium in *D. nodosa* slants anterodorsally to form the anterior portion of the expansion. This state is also seen in *P. brinkman*.

Remarks

Denazinemys nodosa was first described by Gilmore (1916) based on shells from the San Juan Basin of New Mexico. As with many other new baenid taxa described during the early 20th century, it was originally classified as a species of *Baena*. In his review of baenid systematics, Gaffney (1972) did not reclassify *"Baena" nodosa* because

no associated skull was known at the time. Lucas and Sullivan (2006) erected the genus *Denazinemys* for the species *"Baena" nodosa*, and also referred the San Juan Basin taxon *"Baena" ornata* to the genus. The authors united these species based only on the presence of a nodular texture and strongly scalloped posterior margin of the carapace; however, no other characters unite these two taxa, and other taxa, such as *Boremys* spp., possess these characters as well. Phylogenetic analysis of paracryptodiran and baenid relationships published by Lyson and Joyce (2011) and Lyson et al. (2011) demonstrated that the genus is polyphyletic and that *Denazinemys nodosa* is the sister taxon to *Boremys* spp., not *"Denazinemys" ornata*. This is supported by the new phylogenetic analysis of Baenidae by Lively (Chapter III).

Despite the discovery of *D. nodosa* nearly a century ago, this work offers the first description of a clearly associated skull for this taxon. The skull shares several characteristics with those of *Boremys pulchra* and *Eubaena cephalica* including a reduced frontal with a greatly curved posterior suture with the parietal, exclusion of the jugal from the orbital margin, and exclusion of the opisthotic from the stapedial foramen. Though the anterior rostrum is not preserved in BYU 19123, it does appear that a significant portion is missing, and therefore that *D. nodosa* possessed a lengthened preorbital skull, as in *B. pulchra* and *E. cephalica*. *D. nodosa* differs from *B. pulchra*, but is similar to *E. cephalica* in the presence of a narrow medial contact between the pterygoids and a foramen posterius palatinum that is rimed only by the palatine. The similarities between *D. nodosa* and these other two taxa are to be expected based on the phylogenetic analysis of Lyson and Joyce (2011) that found *D. nodosa* to be sister taxon to *Boremys* spp., with *E. cephalica* the sister to the clade formed by these two taxa.

Known occurrences of *D. nodosa* are restricted to the Kaiparowits Formation of southern Utah, the Fossil Forest Member of the Fruitland Formation, and the Hunter Wash and De-na-zin members of the Kirtland Formation of the San Juan Basin in New Mexico. The temporal range of these occurrences is approximately 76.46 to 73.0 Ma (Roberts et al., 2005). *D. nodosa* is noticeably absent from well-studied, correlative formations in northern Laramidia such as the Judith River and Dinosaur Park formations. This is supported by the highly recognizable ornamentation that allows even small shell fragments to be attributed to *D. nodosa*. Sullivan et al. (in press) claim that the ornamentation of *D. nodosa* is not diagnostic enough to distinguish it from *Boremys* or *"Denazinemys" ornata*. While this may be true for pieces of the lateral carapace, my observations suggest a great disparity in the ornamentation of these three taxa toward the midline. The ornamentation of this taxon differs from *Boremys* spp. in being much more tightly packed; it differs from *"Denazinemys" ornata* in being less ridge-like and more ovoid and lobate.

Boremys Lambe, 1906b

Type species

Boremys pulchra (Lambe, 1906a)

Referred species

Boremys grandis Gilmore, 1935

Revised diagnosis

A member of Baenodda distinguished from all other taxa by the following combination of characters: subdued, widely-scattered, lobate and circular ornamentation on the surface of the carapace; the presence of both prepleural and postpleural scutes; and the presence of supramarginal scutes. The presence of postpleurals and supramarginals are synapomorphies for the genus.

Boremys grandis Gilmore, 1935

Holotype

USNM 12979, a nearly complete carapace and plastron.

Type horizon and locality

Upper Cretaceous (Campanian) Hunter Wash Member, Kirtland Formation, San Juan County, New Mexico, USA.

Diagnosis

Boremys grandis differs from *Boremys pulchra* and other baenids based on a number of autapomorphies observed consistently in all specimens assigned to the taxon: the cervical scute is subdivided into three subequal scales, whereas in *B. pulchra*, it remains either undivided or divided into a larger central scute and smaller lateral scutes (as in *D. nodosa*). *B. grandis* possesses up to nine supramarginal scales arranged in two uneven rows, while *B. pulchra* is characterized by only three or four supramarginals restricted to one anterior-posterior row. Adult *B. grandis* are significantly larger than

those of *B. pulchra* (Brinkman and Nicholls, 1991), which is taxonomically significant according to Hutchison (1984) because baenids possess determinate growth.

Referred specimens

UCMP V94009/151773, a nearly complete carapace and plastron; UCMP V97098/156997, the left anterolateral portion of the carapace; UMNH VP 18628, a left peripheral fragment; for those from the San Juan Basin, see Sullivan et al. (in press) and Gaffney (1972).

Distribution

Upper Cretaceous (Campanian) Kaiparowits Formation, Utah, USA; Upper Cretaceous (Campanian) Hunter Wash Member, Kirtland Formation, New Mexico, USA.

Description

All sutures are fused in UCMP V94009/151773 and UCMP V97098/156997. The most complete specimen (UCMP V94009/151773) consists of a partial carapace and plastron with a surface weathered anterior and a more intact posterior (Fig. 2.9).

Carapace. The carapace (Fig. 2.9) is ovoid in shape, similar to *B. pulchra*. However, *B. grandis* is much larger; the type specimen's carapace is over 45 cm in length, whereas all specimens of *B. pulchra* are less than 32 cm in length at the midline (Brinkman and Nicholls, 1991). The anterior margin of the carapace is lightly scalloped, but not as much so as in some specimens of *B. pulchra* (e.g., UCMP V82222/130155). The posterior margin of the carapace is scalloped, similar to many members of Baenodda;
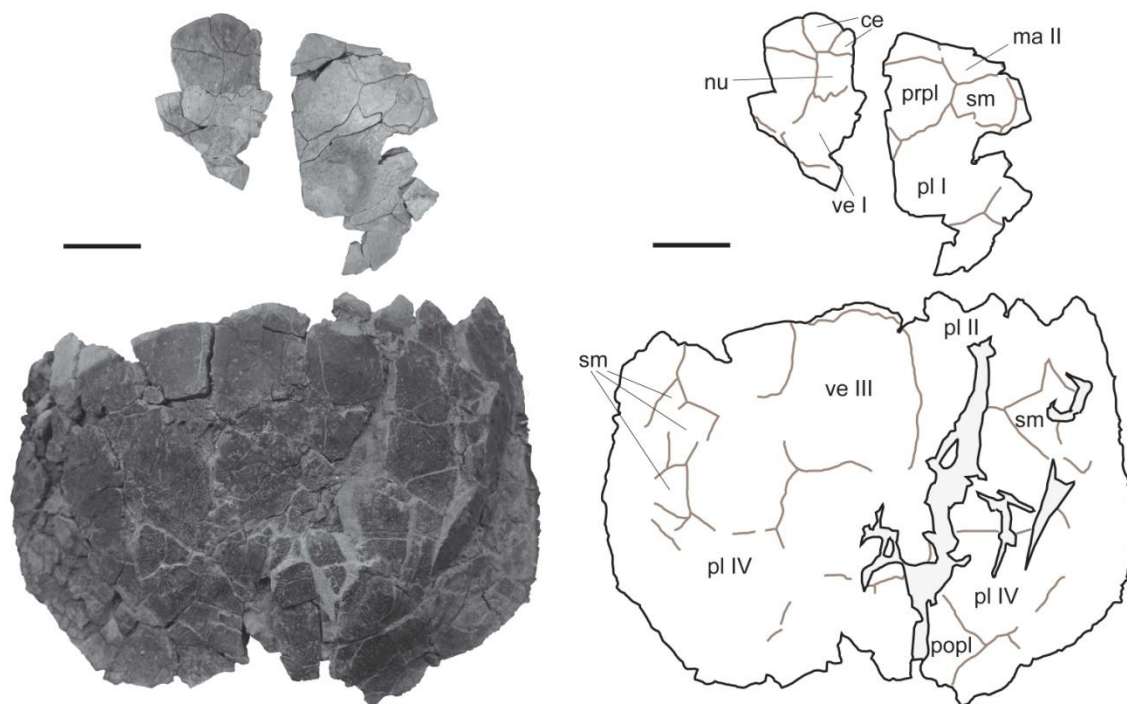
Figure 2.9. Photograph (left) and line drawing (right) of the carapace of *Boremys grandis* (UCMP V94009/151773). Abbreviations: ce, cervical scutes; ma, marginal scute; nu, nuchal scute; pl, pleural scutes; popl, postpleural scute; prpl, prepleural scute; sm, supramarginal scutes; ve, vertebral scutes. Scale bar equals 5 cm.

the development of these serrations is comparable to *Denazinemys nodosa* and *B. pulchra*. A prominent pygal notch is present posteromedially. Ventrally, as in other baenids, the axillary buttress extends dorsally to form a distinct neck shield.

Ornamentation is present on the dorsal surface of the carapace in the form of large, ovate knobs, as well as smaller, circular nodes. In this regard, the ornamentation is similar to *D. nodosa* and *B. pulchra*, but differs from *"Denazinemys" ornata* in not being characterized by prominent, straight ridges. The ornamentation is similar to *B. pulchra* because it is subdued and more widely scattered compared to the prominent, tightly-packed nodes of *D. nodosa*. A particularly large, prominent node is present underneath pleural I. Anteriorly and laterally, this ornamentation is smaller, consisting of lobate and circular nodes. *B. grandis* lacks the large, tightly-packed nodes and ridges that are present along the midline of *D. nodosa*. This region of *B. grandis* is relatively smooth. Differences in the nature of the ornamentation allows for easy field identification of these two taxa based solely on carapace fragments.

Like the type specimen of *B. grandis* from the San Juan Basin, the cervical scute of the Kaiparowits Formation specimens are subdivided into three subequal scales, with the central scute being slightly smaller than the lateral scales; the central scale is sub-triangular, tapering anteriorly, while the lateral scutes taper posteriorly. This pattern differs from all other baenids with a subdivided cervical. In particular, *D. nodosa* differs in having a larger medial scute that tapers anteriorly and two smaller, circular scutes anterolateral to it. Some specimens of *B. pulchra* possess a similar pattern to *D. nodosa*; however, Brinkman and Nicholls (1991) note great variation in the cervical morphology

of *B. pulchra*. The first vertebral is subdivided into a nuchal scute anteriorly, which among baenids is only seen in *Boremys* spp. and *Chisternon undatum*. Posteriorly, vertebrals III-V are also well preserved. As in *Boremys pulchra*, *D. nodosa*, *Baena arenosa*, *C. undatum*, and *"Baena" hatcheri*, the third vertebral is sub-rectangular in shape and is longer than it is wide – a derived character state amongst baenids. The area around the fourth vertebral is slightly more fragmented, but it appears to be slightly wider than it is long. The fifth vertebral, as in all derived baenids, is exposed on the posterior margin of the carapace.

The nuchal scute and the first vertebral are constricted anteriorly by the presence of prepleurals. These are triangular scales that taper posteromedially and are also present in *D. nodosa*, *C. undatum*, *Baena arenosa*, and *"Baena" hatcheri*. The pleural series scutes are restricted in size because of proliferation of supramarginal scutes laterally. Postpleural scutes (sensu Hutchison et al., in press; posterior supernumerary pleural scutes, sensu Lyson and Joyce, 2009a) are present lateral to the fifth vertebral. This is a pair of scutes only see in the genus *Boremys*. These scutes are large and trapezoidal in shape.

The precise number of supramarginals is difficult to assess because the anterior portion of the shell of UCMP V94009/151773 is fragmented. However, it is clear that the number of supramarginals is much higher than in *B. pulchra* and appears to exhibit a similar pattern to *B. grandis* from New Mexico. The first supramarginal is located lateral to the prepleural, contacting it, pleural I, and marginals II and III. It is rounded with a jagged sulcus dividing it and pleural I. Portions of the second and possibly third supramarginals are also visible on fragments from the anterior carapace. Posteriorly,

portions of four to five supramarginals in two uneven rows are present. The proliferation of supramarginals is an autapomorphy for the taxon that distinguishes it from *B. pulchra*.

Marginal I of *B. grandis* possesses a posteromedial projection that contacts the nuchal scute and divides the lateral cervical scales from the prepleural. Marginals II and III each possess minor medial projections and appear subtriangular in shape. The marginals in the middle portion of the carapace are not well preserved. The posterior marginals appear to be much wider than those from the anterior portion of the carapace.

Plastron. The anterior lobe of the plastron is subrectangular in shape with a broadly round margin. Scute sulci are not preserved; however, the margin of the plastron is notched, as in other *Boremys* specimens, presumably where the gular and intergular sulci meet the plastral margin. This indicates that the intergulars are large and of similar size to the gulars. The remainder of the carapace is weathered, and sulci are not preserved. The posterior lobe is subtriangular in shape. As in other baenids, the lateral margins are thickened; however, as in other specimens of *Boremys* and *D. nodosa*, this area is exceptionally thick.

Remarks

Boremys pulchra was first described by Lambe (1906a) as *"Baena" pulchra*, based on a suite of differences between it and *"Baena" hatcheri* and *"Baena" (Plesiobaena) antiqua*. He later erected the genus *Boremys* for this new species (Lambe, 1906b). Gilmore (1919) named a second species, *B. albertensis* based on a specimen from the (Campanian) Dinosaur Park Formation. The major difference between *B. albertensis* and *B. pulchra* was the presence of four instead of three supramarginals. This

taxon was synonymized with *B. pulchra* by Gaffney (1972). Other workers have upheld this synonymy, attributing this difference to individual variation (Brinkman and Nicholls, 1991 and references within). Gilmore (1935) named *B. grandis* from the San Juan Basin of New Mexico based on the holotype's larger size and proliferation of supramarginals. This taxon was provisionally synonymized with *B. pulchra* by Gaffney (1972), though he noted that it may represent a distinct taxon due to the aforementioned differences. More recent workers have supported the validity of *B. grandis* (Brinkman and Nicholls, 1991; Sullivan et al., in press).

Hutchison et al. (in press) described the anterior portion of the carapace of *Boremys grandis* from the Kaiparowits Formation based on two specimens, UCMP V94009/151773 and UCMP V97098/156997. The former consists of surface weathered fragments of the anterior third of the carapace and plastron. However, the posterior portion of this specimen's shell remained unprepared and undescribed until now. This newly exposed anatomical information helps to definitively assign this specimen to *B. grandis* based on similarities with the holotype.

The two specimens confidently attributed to *B. grandis* from the Kaiparowits Formation represent the only occurrences of this taxon outside of the San Juan Basin. Previously, this taxon had been restricted stratigraphically to the Hunter Wash Member of the Kirtland Formation. The presence of *B. grandis* in the Kaiparowits Formation demonstrates that this taxon occurred contemporaneously with *B. pulchra*, which is restricted to the Judith River and Dinosaur Park formations of Montana and Alberta. Based on the stratigraphic correlations of Roberts et al. (in press), *B. grandis* has a known geologic range from approximately 76.46 to 74.5 Ma. Lyson et al. (2011) demonstrated

that an indeterminate species of *Boremys* survived the K/T mass extinction, because it is present in the Puercan (earliest Paleocene) Fort Union Formation of North Dakota, 14 m above the boundary. They also recognized specimens from near the base of the Maastrichtian Hell Creek Formation, indicating that the genus persisted for at least 11 Ma beyond the previously known last appearance of either named species of *Boremys* (Lyson et al., 2011). Sullivan et al. (in press) suggest that *B. grandis* must have been a relatively rare taxon in the San Juan Basin, based on a low relative abundance compared to *Denazinemys* and other turtle taxa. A similarly low number of specimens representing this taxon have been recovered from the Kaiparowits Formation of Utah. Although it is possible that this pattern may be a taphonomic bias, as suggested by Lyson et al. (2011) for the thin-shelled Maastrichtian and Puercan specimens, *B. grandis* appears to have had a robust shell suggesting a fairly high preservation potential similar to other baenid taxa.

Discussion

Roberts et al. (in press) demonstrated, based on ^{40}Ar/^{39}Ar dates from throughout the formation, that the fossil-bearing portions of the Kaiparowits Formation are contemporaneous in age with the fossil-bearing strata of the Two Medicine, Judith River, and Dinosaur Park formations that were deposited in northern Laramidia. This makes it possible to test hypotheses of region provinciality and basin-scale endemism of vertebrates without the hindrance of time transgression. The baenids found in the Dinosaur Park and Judith River formations are *Neurankylus eximius*, *Plesiobaena antiqua*, and *Boremys pulchra*. Although two genera of baenids found in Montana and Alberta are also found in the Kaiparowits basin, there are no overlapping species. *N.*

eximius differs from the Kaiparowits species, *Neurankylus* sp. nov. A and *Neurankylus* sp. nov. B, in size, characters of the anterior plastron, and other features. *B. pulchra* differs from *B. grandis* of the Kaiparowits and Kirtland formations in size and the number of supramarginal scutes. Though it was originally thought that an indeterminate species of *Plesiobaena* was found in the Kaiparowits Formation, a recently discovered specimen has demonstrated that material referred to this genus is a distinct genus. *Denazinemys nodosa*, one of the most distinguishable turtles from the Kaiparowits, is noticeably absent from the Campanian strata of Montana and Alberta. At present, there are no overlapping taxa at the species level between the Kaiparowits Basin and northern Laramidia, though two genera are shared.

The slightly younger Fruitland and Kirtland formations of New Mexico's San Juan Basin share two baenid species with the Kaiparowits Formation: *D. nodosa* and *B. grandis*. *D. nodosa* is known from the Fossil Forest Member of the Fruitland Formation and the Hunter Wash and De-na-zin members of the Kirtland Formation. *B. grandis* is known only from the Hunter Wash Member of the Kirtland Formation (Sullivan et al., in press). Other baenids known from these formations include *Neurankylus baueri* (Hunter Wash and De-na-zin members, Kirtland Formation), *Thescelus rapiens* (Hunter Wash and De-na-zin members, Kirtland Formation), *Thescelus hemispherica* (Hunter Wash Member, Kirtland Formation), and *"Denazinemys" ornata* (Hunter Wash Member, Kirtland Formation). Thus far, none of these taxa are known from the Kaiparowits Formation, though to two basins do share the genus *Neurankylus*. This may be a result of either true endemism or the difference in stratigraphic position of strata in the two basins. *Thescelus* specimens are rare, but are also known from the Campanian Mesa Verde

Group in northern Utah (UFH.V.54.14.1; Lively, pers. obs.) and the Maastrichtian Lance

Formation of Wyoming. It is possible that members of this genus migrated south

following deposition of the Kaiparowits or that it was exceedingly rare and has yet to be

discovered in southern Utah.

Sullivan et al. (in press) argue that latitudinal differences in the distribution of

individual turtle species are simply a product of a lack of temporal overlap of strata

sampled and that similarities at the generic level disprove geographic variation. The

inclusion of taxa from the Kaiparowits Formation into the biogeographic framework of

baenids severely weakens this interpretation, as the fossil-bearing portions of the

Kaiparowits are contemporaneous with those of the Two Medicine, Judith River, and

Dinosaur Park formations and contain taxa that are different at both the species and

generic level. Even so, there is no a priori reason why species-level differences should be

any less important for biogeographic patterns than generic differences. Also, their

assumption of similar temperatures across Laramidia at this time is erroneous (e.g.,

Coulson et al., 2011).

Finally, this study calls into question the validity of the Kirtlandian land

vertebrate "age" (Sullivan and Lucas, 2006). Two baenids that they propose as

Kirtlandian index fossils, *D. nodosa* and *B. grandis*, are also found in the Kaiparowits

Formation, which clearly has a Judithian age by Roberts et al. (in press). This is a clear

example of the problems of making biostratigraphic conclusions in the absence of

independent age constratints (e.g., Irmis et al., 2010, 2011). Therefore, until other

purported index fossils such as *"Denazinemys" ornata* and *N. baueri* are found in similar

aged strata from other regions of the Western Interior, caution should be exercised in recognizing the validity of the "Kirtlandian" biostratigraphic zone.

Conclusions

The Kaiparowits Formation preserves five different baenid species and four genera. Three of these taxa are new and have not been found outside of the Kaiparowits Basin: *Neurankylus* sp. nov. A; *Neurankylus* sp. nov. B; and the new pig-nosed taxon. The other two species, *Denazinemys nodosa* and *Boremys grandis*, are only otherwise known from the San Juan Basin of New Mexico. This supports the findings of Gates et al. (2010) and Sampson et al. (2010) that 1) two biogeographic provinces were present during the late Campanian on the Laramidian subcontinent and 2) many taxa exhibited basin-scale endemism. *D. nodosa* and *B. grandis* are examples of regional baenid endemism, with the former being found in southern Utah, New Mexico, and Texas, whereas the latter has only been identified from southern Utah and New Mexico. The Kaiparowits Formation provides a southern contemporaneous counterpart to fossil-bearing strata of Montana and Alberta (Roberts et al., 2005) and this allows for better testing of Laramidian biogeographic hypotheses, as previous results were preliminary because the fossil-bearing strata in the Fruitland and Kirtland formations of New Mexico were of a younger age than those in northern Laramidia. Further work in central Utah and Wyoming will help more rigorously test these hypotheses and determine the nature of the boundary between the two biogeographic provinces (i.e., a sharp vs. gradational boundary).

CHAPTER 3

TESTING LARAMIDIAN PALEOBIOGEOGRAPHIC HYPOTHESES:

EVIDENCE FROM THE EVOLUTION OF BAENID TURTLES

Abstract

During the Late Cretaceous, North America was bisected by an epicontinental

seaway, forming two subcontinents: Appalachia and Laramidia to the east and west,

respectively. Evidence from dinosaur biogeography suggest the presence of two distinct

biogeographic provinces during the Campanian stage, with lineages from the south

dispersing north during the Maastrichtian. Most taxa of the turtle clade Baenidae were

restricted to Laramidia and were one of the most abundant and diverse groups of turtles

during the Late Cretaceous, making them an excellent study system for biogeography. To

test these biogeographic hypotheses, I reconstructed the evolutionary history of baenid

turtles, and analyzed the paleobiogeography of Cretaceous baenid taxa. My phylogeny

includes new taxa and morphologic data from the Campanian Kaiparowits Formation of

southern Utah. This analysis supports a number of key relationships: a monophyletic

Neurankylus; a new Kaiparowits taxon as the sister to the Maastrichtian *Hayemys*

latifrons; and a paraphyletic relationship of *Plesiobaena antiqua*, *Peckemys brinkman*,

and *Palatobaena* spp. I used both strict and smooth temporally-calibrated trees from both

the strict consensus and several randomly-chosen most parsimonious trees in a maximum likelihood biogeographic analysis applying a dispersal-extinction-cladogenesis model. Although baenids do display basin-scale and regional endemism, southern taxa are instead well-nested within clades of predominately northern baenids. This contrasts with the biogeography interpretations of some Campanian dinosaur phylogenies (e.g., ceratopsids). Baenids conform to the provinciality hypothesis, possibly reflecting disparate northern and southern climatic regimes during the Campanian stage.

Introduction

A combination of elevated global sea level and tectonics lead to the bisection of North America by the Western Interior Seaway during most of the Late Cretaceous, approximately 100–70 Ma (Roberts and Kirschbaum, 1995). This formed two sub-continents: Appalachia to the east and Laramidia to the west. Laramidia was characterized by the Sevier fold and thrust belt running most of the length of this north-south 'island' and narrow alluvial and coastal plains along the western margin of the epicontinental seaway (Blakey, 2009). Despite this small area between the mountains to the west and the seaway to the east, this area supported a diverse nonmarine vertebrate fauna.

Most work on Late Cretaceous Laramidian biogeography over the past two decades has focused on dinosaurs (e.g., Lehman, 1987, 1997; Gates et al., 2010). Lehman (1997) hypothesized that, during the Campanian, two distinct faunal provinces were present across Laramidia: a northern fauna characterized by taxa from Montana and Alberta, and a southern fauna represented by organisms from New Mexico and Texas.

The recently described fauna of the Kaiparowits Formation of southern Utah has supported this claim, where the vast majority of dinosaurian remains identifiable to species are distinct from their counterparts in other penecontemporaneous basins (e.g., Gates and Sampson, 2007; Sampson et al., 2010; Zanno and Sampson, 2005; Zanno et al., 2011; Carr et al., 2011). The phylogenetic position of these taxa generally support the idea of northern and southern regional provinces. In contrast, Sullivan and Lucas (2006) and Sullivan et al. (in press) criticized these biogeographic hypotheses because they argued that the relevant strata from different basins were not actually correlative. This is partially true, as the traditional southern sedimentary basin used in biogeographic studies – the Fruitland and Kirtland formations of the San Juan Basin in New Mexico – is slightly younger than northern Laramidian strata, such as the Dinosaur Park and Judith River formations (Roberts et al., 2005). The Kaiparowits Formation of southern Utah has resolved this issue, as the fossil-bearing strata are penecontemporaneous with the fossil-bearing portions of northern Laramidian basins (Roberts et al., 2005). Recently, Gates et al. (2010) more broadly surveyed the distribution of Campanian nonmarine vertebrates and concluded that two biogeographic hypotheses were possible during the Campanian: 1) two biomes, one to the north (i.e., Alberta and Montana) and one to the south (i.e., Utah, New Mexico, and Texas) with a broad zone of mixing in between; or 2) a continuous latitudinal gradient. However, the authors acknowledge that in addition to examining all clades during a single time slice, workers should examine evolutionary biogeography clade-by-clade (Gates et al., 2010).

Though these biogeographic hypotheses have been evaluated using various dinosaur clades, none have applied a quantitative phylogenetic biogeographic approach,

and these questions have not been examined for non-dinosaurian vertebrate clades, many of which have greater sample sizes both in terms of number of taxa and number of specimens. An ideal group for such a test is Baenidae, a clade of freshwater paracryptodiran turtles that originated in the early Cretaceous and went extinct during the Eocene (Gaffney, 1972; Hutchison, 1984; Holroyd and Hutchison, 2002; Brinkman, 2003). Despite intermittent connections with Asia during the Late Cretaceous and the interchange of North American and Asian turtle faunas (Hutchison, 2000), baenids are restricted to North America, with no representative having been found north of Dinosaur Provincial Park (Brinkman, 2003). With the exception of the basal-most baenid *Arundelemys* (Lyson and Joyce, 2011; this study), all baenids are restricted to western North America. Because this clade of turtles is well sampled, has a high abundance, and extraordinary taxonomic diversity during the latest Cretaceous (Lyson and Joyce, 2010), baenids are the perfect study system for testing Laramidian biogeographic hypotheses.

The goals of this study are threefold. First, the phylogeny of Baenidae was revised using character observations and new material from the Campanian Kaiparowits Formation of southern Utah. Second, the hypothesis of Campanian basin-scale provinciality was tested by examining distribution of baenid taxa across Laramidia, incorporating the new taxa from Utah. Finally, utilizing temporally-calibrated versions of the new phylogeny, I performed an evolutionary biogeographic analysis of Cretaceous taxa to understand the nature of ancestral ranges for lineages within Baenidae and to determine how the distribution of baenids has changed through the Cretaceous.

Phylogenetic Analysis

Methods

My new phylogenetic analysis of Baenidae consists of 33 species-level operation taxonomic units and 106 characters. The taxa analyzed included 32 baenid species and one outgroup taxon, the Jurassic pleurosternid *Glyptops plicatulus* from the western interior of North America. This taxon was chosen as the outgroup because it is closely related to baenids (Lyson and Joyce, 2011) and I had access to a number of specimens (AMNH 336; AMNH 6099; YPM 1784; YPM 4717). The Early Cretaceous paracryptodiran taxon *Arundelemys dardeni* was included as part of the ingroup because this taxon was found by Lyson and Joyce (2011) to be a member of Baenidae. Representatives of nearly every species in the phylogenetic analysis were personally observed by the author (see list of specimens, Appendix A, with the lone exception being *Gamerabaena sonsalla*, which was coded from the literature (Lyson and Joyce 2010). Following Larson et al. (in press) but in contrast to Lyson and Joyce (2009a, 2009b, 2010, 2011), the genus *Neurankylus* was broken into its separate constituent species to better understand the evolution of this clade, which has recently been revised by other workers (e.g., see Chapter 2; Larson et al., in press; Sullivan et al., in press) and recognized as being more diverse than previously thought (e.g., Gaffney, 1972). New taxa included in this phylogenetic analysis of Baenidae for the first time include *Neurankylus* sp. nov. A, *Neurankylus* sp. nov. B, and a new pig-nosed taxon. An unnamed species of *Neurankylus* from the Maastrichtian Hell Creek Formation was also included to better understand the interrelationships of the genus.

The majority of characters in the analysis were derived from previous

phylogenetic analyses by Lyson and Joyce (2009a, 2009b, 2010, 2011) and Larson et al.

(in press). Several of these characters were amended based on observations made during

the study; explanations for this changes are given below. Eleven novel characters were

also added to these previous analyses. The taxon-character matrix,was assembled in

Mesquite v. 2.75 (see Appendix C for the matrix). A maximum parsimony analysis was

performed on the dataset using a traditional heuristic search with three bisection-

reconnection and 1000 random addition search replicates in the program Tree analysis

using New Technology (TNT) v. 1.1 (Goloboff et al., 2008). Characters 7, 14, 16, 18, 28,

33, 35, 69, 86, 87, and 106 form logical morphoclines and were ordered in the analysis.

The analysis included 1000 random addition search replicates. Bootstrap frequencies

(Felsenstein, 1985) and Bremer support values (Bremer, 1994) were also calculated in

TNT. Bootstrap frequencies were calculated using 1,000 replicates, collapsing zero-

length branches. Bremer support calculations included 1,000 replicates, and the number

of trees saved per replicate was 10,000.

Character analysis

Of the 106 characters scored for in this study, a total of 86 were derived at least in

part from the works of Lyson and Joyce (2009a, 2009b, 2010, 2011). The characters used

by Lyson and Joyce (2009a, 2009b, 2010) for their phylogenetic analyses of Baenidae

were used in their entirety with the exception of their character 60 (shape of the sulcus

between vertebral scutes IV and V), which appears to show intraspecific variation among

multiple specimens of the same species in several baenid taxa. Additional characters from

Lyson and Joyce's (2011) assessment of the evolutionary relationships of Paracryptodira were used in this study when relevant to diagnosing Baenidae and the phylogenetic relationships within the clade; these include their characters 75,77, 78, 79, 81, 83, 84, 87, 89 (in part), 90, 95, 96, 97, 101, and 105.

Character 2 (Lyson and Joyce, 2009a) evaluates whether the width of the skull roof between the orbits (i.e., the interorbital width) is wide or narrow. Because the authors did not specify the parameters of what constitutes 'wide' or 'narrow', for known baenid skulls, I plotted the width of the interorbital area relative to the length of the skull at the midline, from snout to tip of crista supraoccipitalis or occipital condyle (see Appendix F). This graph clearly shows that a few taxa display a disparately wide interorbital dorsal skull roof. However, the baenid taxa scored as having a 'wide' interorbital area by Lyson and Joyce (2009a) is much more inclusive than those that are differentiated in the plot. In fact, several of the taxa previously scored as possessing a wide interorbital skull roof actually have some of the relatively narrowest skulls among Baenidae (e.g., *Plesiobaena antiqua*, TMP 1994.12.273). Taxa that were clearly outliers, on the plot, with higher ratios of interorbital widths to skull length, were classified as having a 'wide' skull roof, while all others were scored as having 'narrow' interorbital skull roofs. The taxa with clearly distinct wide interorbital widths include *Hayemys latifrons* (AMNH 6139), *Palatobaena bairdi* (YPM-PU 16839), *Palatobaena cohen* (YPM 57498; UCMP V85083/131953), and *Neurankylus* sp. (NMMNH P-57874).

The character describing the shape of the posterior margin of the carapace (character 38 of Lyson and Joyce, 2009a) were slightly altered for several reasons. Previously, this character was described as either 'rounded' or 'flattened to concave'.

However, the posterior margin of the carapace can often be fragmented or deformed during taphonomy. Therefore, I found it more useful to distinguish between rounded/flattened margins and sub-triangular margins, as the latter state may have united *Plesiobaena antiqua* and the new pig-nosed taxon(diagnosed as *Plesiobaena* sp. by Hutchison et al., in press). The 'concave' morphology mentioned by Lyson and Joyce in this state is duplicative because it is expressed by the presence or absence of the pygal notch in character 57 (see also Lyson and Joyce, 2010).

Character 50 describes the shape of the anterior lobe of the plastron (Lyson and Joyce 2009a), either triangular or sub-rectangular in shape. Larson et al. (in press) revise the scorings of several taxa, such as *Boremys pulchra*, based on inconsistencies of scorings in the previous studies. My analysis finds that the shape of the anterior plastron varies intraspecifically in taxa such as *Denazinemys nodosa* (UMNH VP 20447; BYU 19123) and *B. pulchra* (TMP 1988.02.10; TMP 1981.28.001), with some possessing a rectangular anterior plastron with a rounded margin and other specimens possessing a subtriangular anterior lobe. The latter state differs consistently from the triangular anterior plastron of *P. antiqua* (TMP 1990.119.001), *Peckemys brinkman* (UMMP 20490, Lyson and Joyce, 2009b), and *P. cohen* (YPM 57498, Lyson and Joyce, 2009a) in that it does not come to a blunt tip and is, instead, broadly rounded. Therefore, a third state was erected for this character for those that possess a subtriangular anterior plastron with a slightly expanded and rounded anterior margin.

The utility and distribution of character states was tested quantitatively for character 68, the size of the mandibular condyle. This was done by multiplying the length and width of the condyle to calculate a proxy for the area of the condyle, and plotting this

number against the length of the skull at the midline (see Appendix F). *P. cohen* (YPM 57498), *P. bairdi* (YPM-PU 14984), *Goleremys mckennai*, (UCMP V99042/179519) and *Neurankylus* sp. (NMMNH P-57874) were found to be outliers and suggest that a large condyle may be phylogenetically significant. Lyson and Joyce (2010) score only *P. cohen*, *P. bairdi*, and *Palatobaena gaffneyi* as exhibiting this character state. However, my measurements indicate that *P. gaffneyi* (UCMP V71238/114529) does not possess a significantly larger condyle area compared to other baenids, while the other two taxa do.

Character 80 assesses the surface texture of the carapace. This character in Lyson and Joyce (2011) includes states for a smooth texture, distinct tubercles (i.e., pustulose texture of *Glyptops plicatulus*), and large, distinct knobs. I added a fourth character state for those taxa possessing a vermicular texture, which is characteristic of most species of *Neurankylus*.

Character 87 is a combination of characters 73 and 88 of Larson et al. (in press). This character captures the morphology of the nuchal bone along the anterior margin of the carapace. These characters were combined for ease of scoring and to set up a morphocline that preserves the homology of having some sort of nuchal emargination regardless of its size. A slight recession in the nuchal is present in most species of *Neurankylus*, and a deep nuchal emargination is restricted to *Thescelus* spp. and unites the recognized species of this genus. In contrast, a nuchal projection is present in other baenids, including *P. antiqua* (TMP 1990.119.001) and *P. cohen* (YPM 57498, Lyson and Joyce, 2009a), with this projection being best developed in the latter taxon. *D. nodosa* was not scored as possessing a nuchal projection because the overall shape of the carapace in well-preserved specimens (e.g., USNM 83445) is triangular, tapering

anteriorly. I do not consider this state homologous to the oval carapaces of *P. antiqua* and *P. cohen* that possess nuchal projections.

Characters 90-100 are new characters not used in previous analyses. The two states of character 90 describe the morphology of the anterior margin of the plastron in baenids possessing a rectangular anterior plastral lobe, where the margin is either broadly rounded or truncated (Fig 3.1). The truncated (i.e., squared-off) anterior plastron is present in *Neurankylus baueri* (USNM 8344; USNM 8531), *Neurankylus eximius* (TMP 2003.12.171), and a new taxon from the Milk River Formation of Alberta (TMP 2007.35.45). A more rounded morphology is observed in *Neurankylus* sp. nov. A (UCMP V93118.154450), *Neurankylus* sp. nov. B (BYU 12001; BYU 9411), and an unnamed taxon from the Hell Creek Formation of Montana (UCMP V84010/129724; UCMP V86075/132057). Character 91 evaluates the relative anterior extent of the plastron and carapace; *Thescelus* spp. possess a plastron that extends beyond the anterior margin of the carapace in dorsal view.

Character 92 assesses the shape of the posterior lobe of the plastron. In *Eubaena cephalica* (UCMP V73023/107617; UCMP V88020/133929), *D. nodosa* (BYU 19123), *Boremys* spp. (TMP 1988.02.10; USNM 12979), *Chisternon undatum* (AMNH 5904), and *Baena hatcheri* (AMNH 106), the posterior plastral lobe is subtriangular anteriorly, tapering posteriorly, and then becomes rectangular posterior to an 'inflection point' (Fig 3.2). Though all baenids possess a thickened posterolateral plastron, this feature is exceptionally thick anterior to this inflection point in these taxa.
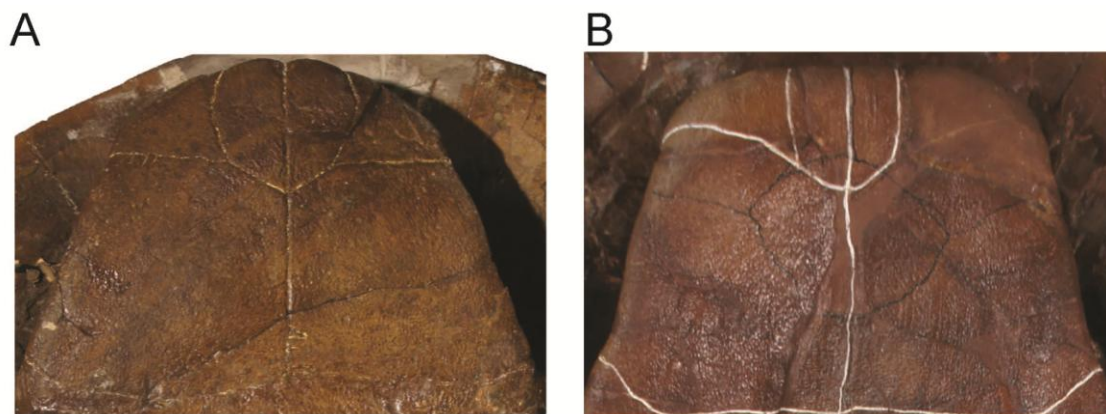
Figure 3.1. Possible states for character 90 (shape of anterior plastral lobe if rectangular): A, rounded anterior margin (*Neurankylus* sp. nov. B, BYU 12001); B, truncated anterior margin (*Neurankylus baueri* holotype, USNM 8344).
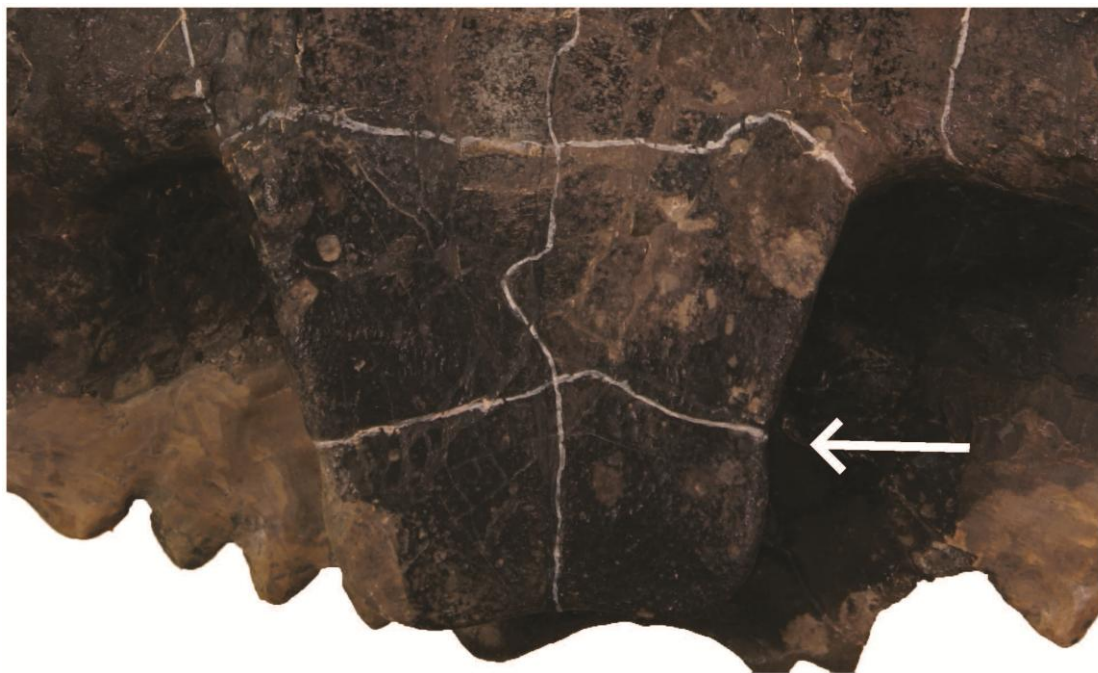
Figure 3.2. Character 92, state 1, posterior plastron sub-triangular anteriorly, with parallel margins posteriorly. This state is observed here on *Denazinemys nodosa* (USNM 83445). The arrow points to the inflection point on the plastron where it becomes more rectangular posteriorly.

The presence and extent of a longitudinal mid-dorsal keel on the carapace is described by character 93. Although Larson et al. (in press) assess the presence/absence of a mid-dorsal keel; they do not differentiate whether the ridge is present along the entire carapace or just along the posterior portion. Based on my observations, the development of a mid-dorsal keel is taxon-specific and may be phylogenetically significant.

Character 94 examines the extent of the nodular texture present in some baenid taxa. I recognize distinct differences in the distribution and morphology of these knobs that are intraspecifically consistent. *Denazinemys nodosa* (BYU 19123) and *"Denazinemys" ornata* (USNM 13229) possess the most prominent ornamentation, with tightly-packed nodes and ridges. *Boremys grandis* (USNM 12979) and *Boremys pulchra* (TMP 1988.02.10) possess more subdued ornamentation that is more widely scattered across the carapace than in the other two taxa. The nodes present on *D. nodosa* are ovate and circular, as in *Boremys* spp., whereas the ornamentation of *"Denazinemys" ornata* is more ridge-like, with fewer circular nodes. The shape of the ornamentation in these three taxa was not expressed in a character, as the latter morphology is an autapomorphy of *"Denazinemys" ornata*, and therefore not phylogenetically informative.

In those taxa with a wedge-shaped skull (character 1), the point where the dorsal skull roof no longer tapers anteriorly and becomes more rectangular in shape is considered here the rostral constriction (character 96); this is a feature that has not been previously assessed for baenids. The position of this rostral constriction varies, and is either towards the posterior end or middle of the orbit, or anterior to the orbit. When the latter character state is present, the orbits face forward more so than the orbits of baenids.

Character 99, the height of the coronoid process relative to the rest of the mandible, was also added as a character. Until now, only the presence/absence of a dorsolateral tubercle on the dentary and the size of the splenial are captured by phylogenetic characters. A prominent coronoid process is observed in most baenids that preserve a lower jaw, but this process is significantly smaller in *E. cephalica* (MRF 766), *D. nodosa* (BYU 19123), and *B. pulchra* (TMP 1988.01.10), along with the outgroup taxon *G. plicatulus* (AMNH 336).

Results

Figure 3.3 displays the strict consensus of 18 most parsimonious trees (MPT), with a length of 260 steps. The tree is generally well-resolved; almost all polytomies occur within monophyletic genera (*Neurankylus*, *Thescelus*, and *Palatobaena*); the only exception is a polytomy at the node that includes *Goleremys mckennai*, *"Baena" hayi*, a clade including taxa closely related to *Baena arenosa*, and a clade including taxa closely related to *B. pulchra*. *Arundelemys dardeni* is found to be the basal-most baenid, with *Trinitichelys hiatti*, *Neurankylus* spp., and *Thescelus* spp. being successive ingroups. *"Denazinemys" ornata* is found to be the basal-most member of the subclade Baenodda. The topology of Baenodda is similar to that of Lyson and Joyce (2011) and Lyson et al. (2011), with the exception of *Plesiobaena antiqua* and *Peckemys brinkman*, which were found in previous analyses to be more closely related to *Cedrobaena putorius*, *Gamerabaena sonsalla*, and *Palatobaena* spp. Bremer support values were low, being almost universally '1', with the exception of the nodes that include Baenodda + *Thescelus* spp. (3), *D. nodosa* + *Boremys* spp. (2), and *B. grandis* + *B. pulchra* (3). The following
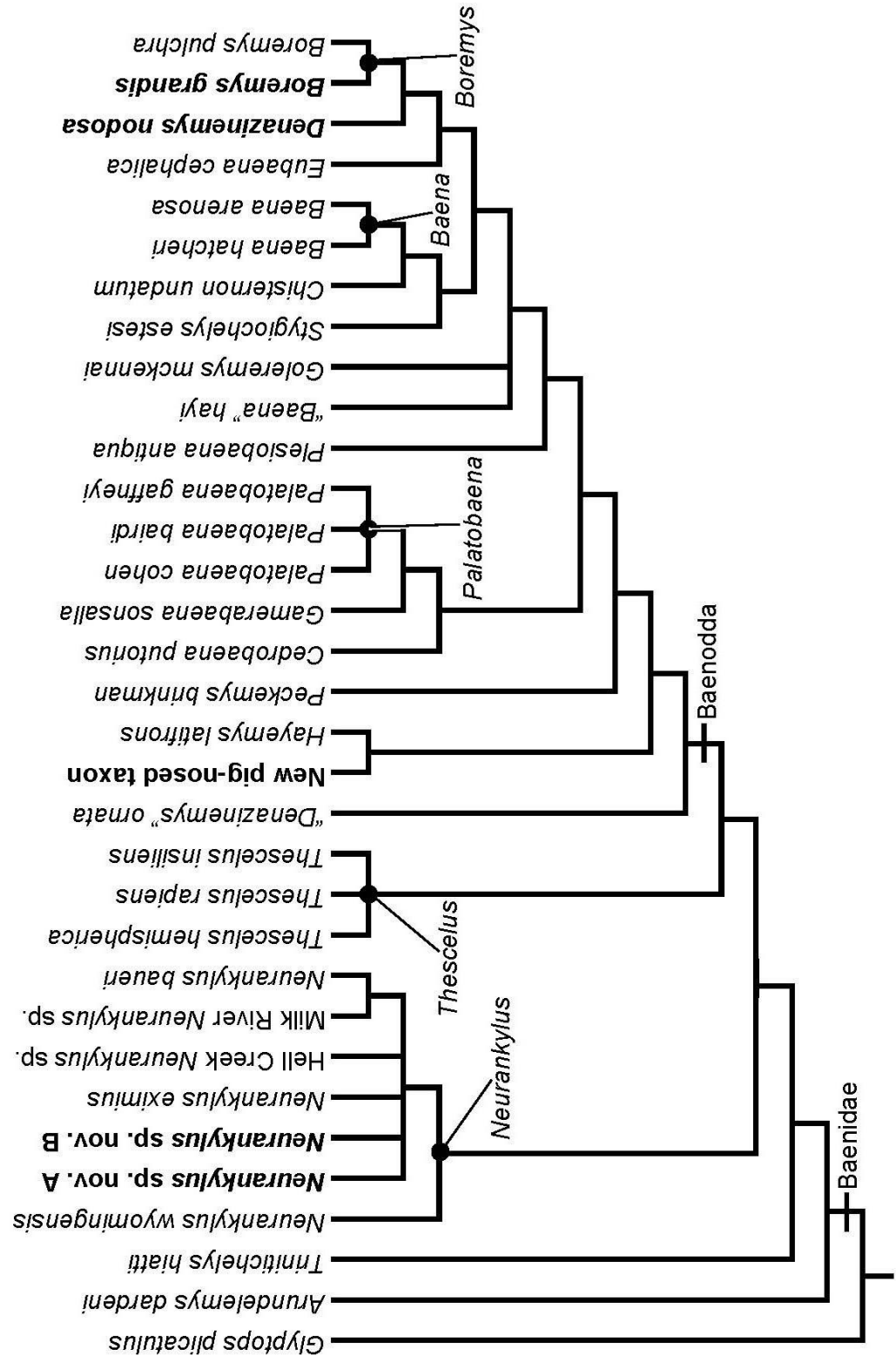
Figure 3.3. Strict consensus cladogram of Baenidae.

describes the synapomorphies that optimize the various nodes of the consensus tree and defines the contents and phylogenetic relationships of clades within Baenidae

Clade diagnosis and character evolution

Here, I describe the synapomorphies that diagnose each clade in the recovered phylogeny and revise the phylogenetic taxonomy for Baenidae.

TESTUDINES Linnaeus, 1758, sensu Joyce et al., 2004

PARACRYPTODIRA Gaffney, 1975, sensu Lyson and Joyce, 2011

BAENOIDEA Williams, 1950, sensu Lyson and Joyce, 2011

BAENIDAE Cope, 1882, sensu Lyson and Joyce, 2011

Baenidae was phylogenetically defined by Lyson and Joyce (2011) as: "the most inclusive clade containing *Baena arenosa* Leidy, 1870 but not *Pleurosternon bullocki* Owen, 1842, or any species of Recent turtle." The hypothesized content of this clade has not changed from the taxon list of Lyson and Joyce (2011), with the exception of the addition of taxa not included in their analysis, including *Neurankylus wyomingensis* Gilmore, 1919, *Neurankylus* sp. nov. A, *Neurankylus* sp. nov. B, the Milk River *Neurankylus* Larson et al., in press, *Neurankylus baueri* Gilmore, 1916, *Thescelus insiliens* Hay, 1908, *Thescelus hemispherica* Gilmore, 1935, *Thescelus rapiens* Hay, 1908, the new pig-nosed taxon (Chapter 1), *"Baena" hayi* Gilmore, 1916, *Goleremys mckennai* Hutchison, 2004, and *Baena hatcheri* Hay, 1901. Larson et al. (in press) suggest that *"Dorsetochelys" buzzops* and *Uluops uluops* may also be members of Baenidae; however, the phylogenetic placement of these taxa and other enigmatic basal paracryptodires is out of the scope of this study. The basal baenid *Arundelemys dardeni*

(Lyson and Joyce, 2011) is optimized as the sister taxon to the rest of Baenidae based on a convex frontal-nasal suture, with the frontals extending anteriorly, partially sub-dividing the nasals. Lipka et al. (2006) found this taxon to be sister to the rest of Paracryptodira. Larson et al. (in press) found *Arundelemys* to be the sister to *Neurankylus* spp. in their majority rule parsimony and greatest likelihood Bayesian analyses and in a basal baenid polytomy in their parsimony Bayesian congruent phylogeny.

UNNAMED CLADE (*Trinitichelys* + all other baenids)

This clade is diagnosed by three synapomorphies: the development of the lingual ridge is restricted to the anterior portion of lingual margin of the triturating surface, whereas it is developed along the entire length of this margin in *Glyptops plicatulus* and *A. dardeni*; the foramen prepalatinum being formed by the premaxillae and vomer, as opposed to being completely within the premaxillae; and a pentagonal basisphenoid, rather than the long, rectangular element in basal taxa. Prior to the phylogenetic analysis of Lyson and Joyce (2011), which found *A. dardeni* to be more closely related to *Baena arenosa* than to *Pleurosternon bullocki*, this clade was synonymous with Baenidae. The members of this clade are restricted to Laramidia and ranged from the Albian through the middle Eocene.

UNNAMED CLADE (*Neurankylus* + all other baenids)

This clade includes *Neurankylus* spp., *Thescelus* spp., and Baenodda, and it is diagnosed by a total of four synapomorphies: a wedge-shaped skull, differing from the oblong skull of *T. hiatti* and *G. plicatulus*; a larger external narial opening, of similar size

to or larger than the orbit; a distinct thickening of the plastron medial to the inguinal buttress; and a rugose or smooth cranial ornamentation, differing from the pustulose ornamentation of more basal taxa.

NEURANKYLUS

This analysis includes six described and one undescribed species of *Neurankylus*. Larson et al. (in press) reviews the history and current taxonomy of the genus. Gaffney (1972) synonymized all known species of this taxon at the time into a single species: *Neurankylus eximius*. Many more species of *Neurankylus* are now recognized (Larson et al., in press; see also Chapter II). The genus is united by the presence of an upturned lateral margin of the carapace (i.e., dorsolateral gutters, sensu Larson et al., in press). In the strict consensus, *Neurankylus wyomingensis* is recognized as the basal species within the genus, likely due to the presence of the pustulose carapace surface texture. This taxon is one of the oldest representatives of the genus, from the Coniacian Cody Shale of Wyoming (Dyman et al., 1997; Larson et al., in press).

UNNAMED CLADE (*N. eximius* + *N. baueri*)

This clade within the genus *Neurankylus* is united by the presence of a vermicular carapace surface texture with shallow, anastomosing pits and grooves. The interrelationships of the taxa form a polytomy of *Neurankylus* sp. nov. A, *Neurankylus* sp. nov. B, *N. eximius*, an unnamed species from the Hell Creek Formation, and a sub-clade of *N. baueri* and a new species from the Milk River formation. The positions of

Neurankylus sp. nov. B, *N. eximius*, and the Hell Creek *Neurankylus* vary throughout the various most parsimonious trees.

UNNAMED CLADE (*N. baueri* + Milk River *Neurankylus*)

N. baueri and a new species from the Milk River Formation of Alberta are united by intergular scutes with straight lateral margins and a broad contact with the humeral scutes. They both possess an anterior plastral lobe that has a truncated anterior margin, which is also observed in *N. eximius*. All other species of *Neurankylus* included in this phylogenetic analysis that preserve this part of the shell consistently possess a broadly rounded anterior plastron. In some trees, this clade is united by an asymmetrical, trapezoidal fourth marginal scute. All members of the genus except *Neurankylus* sp. nov. A and *N. eximius* possess this character, which may be a derived character state within *Neurankylus*.

UNNAMED CLADE (*Thescelus* + Baenodda)

Five synapomorphies diagnose this clade: intergular scutes that possess a smaller surface area than the gular scutes; medial contact of the gular scutes due to the reduction in size of the intergulars; a smooth carapace surface texture, as opposed to the pustulose texture of *G. plicatulus*, *T. hiatti*, and *N. wyomingensis* or the vermicular texture of all other species of *Neurankylus*; a wide vertical space between the posterior carapace and plastron; and inframarginals that are approximately equal in width to the ventral exposure of the marginal scutes.

THESCELUS

Thescelus spp., the clade including the most highly-nested non-baenodd members of Baenidae, is united by the presence of a deep nuchal emargination and an anterior plastron that extends well beyond the anterior margin of the carapace in dorsal view. Gaffney (1972) synonymized all specimens of this genus into one species, *T. insiliens*. However, differences in the morphology of the posterior carapace between *T. insiliens* and *T. hemispherica* suggest that these were likely different species (see Sullivan et al., in press). The holotype of *T. rapiens* is incomplete, and the autapomorphies described by Hay (1908) may be taphonomic (Sullivan et al., in press). However, this species is provisionally considered valid and included as a separate species in the analysis. In the strict consensus tree, the three species of *Thescelus* form a polytomy.

BAENODDA Gaffney and Meylan, 1988, converted clade name

Although Lyson and Joyce (2011) defined Baenidae and other paracryptodiran clades, they did not provide a formal phylogenetic definition for Baenodda. Previously, this clade has been diagnosed by the exposure of the fifth vertebral scute on the posterior margin of the carapace, scalloping on the posterior margin of the carapace, division of the pygal into an additional pair of peripherals, a triangular anterior lobe of the plastron, a reduced to absent dorsal prefrontal lappet, and nasals of reduced size (Brinkman, 2003; Lyson and Joyce, 2010). To best capture the previous usage and content of the group, I define Baenodda as follows:

Definition. The most inclusive clade containing *Baena arenosa* Leidy, 1870, but not *Thescelus insiliens* Hay, 1908, *Neurankylus eximius* Lambe, 1902, or any species of extant turtle.

Diagnosis. Baenodda is diagnosed by the following synapomorphies: at least lightly scalloped posterior margin of the carapace; exposure of the fifth vertebral scute along the posterior margin of the carapace; the presence of a pygal notch. In contrast to Brinkman (2003) and Lyson and Joyce (2010), my analysis does not find that the presence of a small exposure of the prefrontal on the dorsal skull roof or small nasals optimize as synapomorphies for this clade. This is likely because these characters are both absent in *H. latifrons* and small nasals are absent in the new Kaiparowits taxon.

UNNAMED CLADE (*Hayemys* + all other baenodds)

This clade consists of all baenodds except *"Denazinemys" ornata*. It is diagnosed by the synapomorphy of a triangular-shaped anterior lobe of the plastron. Originally, this morphology appeared to be restricted to members of the *Plesiobaena – Palatobaena* lineage, sensu Lyson and Joyce (2009a; 2009b). However, my analysis demonstrates that this hypothesized clade is likely paraphyletic; the addition of the cranially disparate pig-nosed taxon indicates that the *Plesiobaena* shell type actually represents a basal baenodd grade (see Chapter 1).

UNNAMED CLADE (*Hayemys* + pig-nosed taxon)

The pig nosed taxon and *H. latifrons* form a clade that is sister to all more nested baenodds. These two taxa share the synapomorphy of laterally expanded nasals. For a full comparison, see Chapter 1.

UNNAMED CLADE (*Peckemys* + all other baenodds)

This clade is diagnosed by five synapomorphies: a reduced dorsal exposure of the prefrontal; reduced frontal contribution to the postorbital skull roof; small exposure of the supraoccipital on the dorsal skull roof; extension of the premaxillae anterior to the overlying dorsal skull roof; and presence of a pointed snout. The most basal member of this clade, *Peckemys brinkman*, was thought to be part of a monophyletic clade including *Plesiobaena antiqua*, *Cedrobaena putorius*, *Gamerabaena sonsalla*, and *Palatobaena* spp. (Lyson and Joyce, 2009b). Prior to this, Gaffney (1972) classified *P. brinkman*, *P. antiqua*, and *C. putorius* all as members of the genus *Plesiobaena*, lumping the first two taxa into one species. My analysis indicates that the former *'Plesiobaena'* sensu Gaffney (1972) is actually paraphyletic, including three different lineages of baenodds.

UNNAMED CLADE (*Palatobaena* + all other baenodds)

All baenodds more highly-nested than *P. brinkman* are united by three synapomorphies: second vertebral scute square or rectangular in shape, as opposed to the hexagonal shape exhibited by basal baenids and baenodds; the presence of a small nuchal projection; and rostral constriction located near anterior end of the orbit, giving the animal anteriorly-facing orbits.

UNNAMED CLADE (*Cedrobaena* + *Gamerabaena* + *Palatobaena*)

C. putorius, *G. sonsalla*, and *Palatobaena* spp. form a monophyletic clade, as in previous phylogenetic analyses (Lyson and Joyce, 2009b; 2010). The members of this clade share five synapomorphies: dorsally oriented orbits; swollen maxillae, often associated with durophagy (Lyson and Joyce, 2009a; 2010); posterior end of the crista supraoccipitalis expanded and rounded, differing from the pointed crista of other baenids; posterior thickening of the parietals; and orbits inset into the maxilla due to the formation of a minor dorsolateral ridge on the maxilla.

UNNAMED CLADE (*Gamerabaena* + *Palatobaena*)

G. sonsalla and *Palatobaena* spp. are united by a strongly curved suture between the frontals and parietals and a distance between the orbit and cheek emargination that equals the diameter of the orbit.

PALATOBAENA

Palatobaena spp. is united by five synapomorphies: lingual ridge completely absent from the medial margin of the triturating surface; prefrontal does not contribute to dorsal skull roof; presence of a deep circumnarial sulcus; an obtuse angle between the maxillae; ventrally thickened jugal tubercle. The strict consensus tree places *P. cohen*, *P. bairdi*, and *P. gaffneyi* into a polytomy.

UNNAMED CLADE (*Plesiobaena* + all other baenodds)

P. antiqua, *"Baena" hayi*, *G. mckennai*, *S. estesi*, *C. undatum*, *B. arenosa*, *B. hatcheri*, *E. cephalica*, *D. nodosa*, and *Boremys* spp. are united by three characters: right and left triturating surfaces do not meet at the midline; frontal contribution to the orbits reduced to a small process; strongly z-shaped surangular-dentary suture.

UNNAMED CLADE (*"Baena" hayi* + all other baenodds)

This clade includes a basal polytomy of *"Baena" hayi*, *G. mckennai*, and a sub-clade including baenodds leading to *B. arenosa* + those leading to *Boremys* spp. It is diagnosed by a small external narial opening relative to the diameter of the eye, a state also observed in *Glyptops*. Among the 18 MPTs, *"Baena" hayi* most often more highly-nested than *G. mckennai*.

UNNAMED CLADE (*Baena* + *Boremys*)

A subclade of *B. arenosa*, *B. hatcheri*, *C. undatum*, *S. estesi* and a sub-clade of *Boremys* spp., *D. nodosa*, and *E. cephalica* make up this clade. Together, these two lineages are united by four synapomorphies: a variably shaped anterior plastron, ranging from subtriangular to subrectangular, with a broadly rounded anterior margin; a nuchal margin even with the first peripherals, with not emargination or projection; a posterior plastral lobe that tapers and then becomes subrectangular posteriorly; and an increased number of marginal scutes, from 12 pairs to 13.

UNNAMED CLADE (*Stygiochelys* + *Chisternon* + *Baena*)

S. estesi, *C. undatum*, *B. hatcheri*, and *B. arenosa*, share four synapomorphies: a posterodorsal notch in the margin of the orbit; contribution of the opisthotic to the stapedial foramen; presence of a nuchal scute; and a maximum combined width of the parietals is greater than their length.

UNNAMED CLADE (*Chisternon* + *Baena*)

Chisternon and *Baena* spp. are united by seven synapomorphies: no dorsal exposure of the prefrontal; large contribution of the jugal to the orbital margin; no dorsal expansion of the quadratojugal above the cavum tympanum; squamosal-parietal contact due to little upper temporal emargination; posterior thickening of the parietals; rectangular anterior plastral lobe with a broadly rounded anterior; and an upper temporal emargination that does not expose the otic capsules.

BAENA

B. arenosa and *B. hatcheri* are united by intergular and gular scutes that are similar in size. Lyson and Joyce (2010) did not find these taxa to represent a monophyletic clade; they found *B. hatcheri* belonged in a polytomy with *B. grandis*, *B. pulchra*, and *Eubaena*.

UNNAMED CLADE (*Eubaena* + *Denazinemys* + *Boremys*)

E. cephalica, *D. nodosa*, and *Boremys* spp. share four synapomorphies: a long preorbital snout; jugal excluded from the orbital margin; tubercle on dorsolateral dentary;

and a low coronoid process on the mandible. Although the only known skull for *D. nodosa* is missing a significant amount of the rostrum, the phylogenetic analysis optimized a long preorbital snout at this point because it is present in *E. cephalica* and *Boremys*. Although the snout of *D. nodosa* is broken (Chapter 2), it is consistent with a long preorbital skull.

UNNAMED CLADE (*Denazinemys* + *Boremys*)

D. nodosa and *Boremys* spp. are united by three synapomorphies: a strongly scalloped posterior carapace with distinct serrations; a weakly scalloped anterior margin of the carapace; and ornamentation on the carapace consisting of large, distinct, ovate to circular knobs. Lucas and Sullivan (2006) erected the genus *Denazinemys* for baenids with a prominent nodular texture, *"Baena" nodosa* and *"Baena" ornata*. Lyson and Joyce (2011), Lyson et al. (2011), and my analysis found this genus to be paraphyletic. Using TNT, I tested the suboptimality of constraining a topology with the clade of *Denazinemys nodosa* + *"Denazinemys" ornata*. This requires 6 additional steps, recovering 108 most parsimonious trees with a length of 266 steps.

BOREMYS

B. grandis and *B. pulchra* share five synapomorphies: the presence of a nuchal scute; the presence of a postpleural (posterior supernumerary pleural scute); the presence of supramarginal scutes; anal scute restricted to the xiphiplastra; and a widely scattered, subdued, nodular carapace ornamentation.

Discussion

Gaffney (1972) provided the first systematic review and phylogenetic analysis of Baenidae. Subsequent workers (Brinkman and Nicholls, 1991, 1993; Hutchison, 2004; Lipka et al., 2006; Joyce, 2007; Lyson and Joyce, 2009a, 2009b, 2010, 2011; Larson et al., in press) have also built on this work with taxonomic revision, new taxa, and expanded phylogenetic analyses. This study has the most comprehensive taxon and character sampling for baenids to date, including 32 ingroup taxa and 106 discrete characters.

Arundelemys dardeni was originally described by Lipka et al. (2006), who found it as sister taxon to Baenoidea (Baenidae + Pleurosternidae). Lyson and Joyce's (2011) analysis of paracryptodiran relationships recovered *A. dardeni* as the earliest-branching member of Baenidae. Larson et al. (in press) hypothesized, based on their majority-rule consensus and Bayesian a trees that *A. dardeni* is the sister taxon of *Neruankylus* spp. However, the strict consensus of their parsimony analysis showed a basal polytomy within Baenidae of *A. dardeni*, *Trinitichelys hiatti*, and *Neurankylus* spp. My phylogeny agrees with that of Lyson and Joyce (2011) in recovering *A. dardeni* as the basal-most baenid rather than in a clade with *Neurankylus*. Four additional steps are required for *A. dardeni* to be the sister taxon of *Neurankylus*, with a total tree length of 164 and 140 MPTs. Before the description of *A. dardeni*, Gaffney's (1972) phylogeny placed *T. hiatti* as the most basal baenid, whereas Lipka et al. (2006) and Joyce (2007) recovered *N. eximius* in this position. Lyson and Joyce (2009a, 2009b, 2010) place *T. hiatti* as sister taxon to *N. eximius*, a clade that is sister to all other baenids. This relationship requires five additional steps for a tree length of 165, with 112 MPTs. Again, this study agrees

with Lyson and Joyce (2011) and Lyson et al. (2011), finding *T. hiatti* as its own branch that is sister taxon to a clade including both *Neurankylus* and the rest of Baenidae.

In the past, phylogenetic analyses have included only one terminal taxon for the genus *Neurankylus*, *N. eximius*, (Brinkman and Nicholls, 1993; Lipka et al., 2006; Joyce, 2007; Lyson and Joyce, 2009a, 2009b, 2010, 2011). Larson et al. (in press) were the first to code separate terminal taxa for multiple species of *Neurankylus*, several of which were originally synonymized with *N. eximius* or considered nomena duibia by Gaffney (1972). They included *N. wyomingensis*, *N. eximius*, *N. baueri*, a new species from the Milk River Formation, and two unnamed specimens from the Lance (YPM 8239) and Fruitland (ROM 864) formations. Because most phylogenetically informative feature are not preserved in YPM 8239, it was not included in this study. My analysis included these four named taxa, an unnamed taxon from the Hell Creek Formation (e.g., UCMP V86075/132057), and two new species from the Kaiparowits Formation described in Chapter II. My study agrees with the results of Larson et al. (in press), who found that *N. wyomingensis* is the most basal member of the genus. Larson et al. (in press) found *N. eximius* to be more highly-nested than *N. wyomingensis*, but sister to all other members of the genus included in their study; this relationship was not resolved in my analysis, the strict consensus contains a polytomy of all other members of the genus, with only the Milk River *Neurankylus* and *N. baueri* forming a clade in all MPTs. Among the 18 MPTs, the phylogenetic positions of *Neurankylus* sp. nov A, *Neurankylus* sp. nov. B., *N. eximius*, and the Hell Creek *Neurankylus* vary greatly. The sister-taxon relationship of *N. baueri* and the Milk River *Neurankylus* in my analysis is consistent with the results of Larson et al. (in press) who recovered a clade formed by a polytomy of *N. baueri*, the

Milk River *Neurankylus*, ROM 864, and YPM 8239. Excluding the two unnamed

specimens not in my study, my analysis agrees with this topology.

As in other studies (Lyson and Joyce, 2010; Larson et al., in press), *Thescelus* is

found to be more highly-nested than *Neurankylus*. My analysis does not find a consistent

relationship between the three species of the genus, probably because of the large amount

of missing data for *T. rapiens*, including parts of the carapace and plastron. No skulls are

currently known from any of the identified species of *Thescelus*. *"Denazinemys" ornata*

is found to be the earliest-diverging individual lineage within Baenodda. Lyson and Joyce

(2011) were the first to test the phylogenetic position of this taxon, finding it to form a

basal baenodd polytomy with *H. latifrons* and two major baenodd clades. *H. latifrons* was

found by Gaffney (1972), Brinkman and Nicholls (1993), and Lyson and Joyce (2009a,

2009b) to be sister to all other baenodds, and forming a polytomy with Baenodda and *T.*

insiliens in the analysis of Lyson and Joyce (2010). This analysis finds *H. latifrons* to be

sister to the new pig-nosed taxon (see Chapter I), a taxon not in any previous analyses.

This clade is found to be more nested within Baenodda than *"Denazinemys" ornata*.

With the identification and addition of many new taxa, the relationships of

derived members of Baenodda have varied drastically since Gaffney's (1972) preliminary

analysis. Gaffney found *P. antiqua* to be sister to *E. cephalica* + *S. estesi*, whereas *P.*

bairdi was suggested to be linked to *B. arenosa* + *C. undatum*. Brinkman and Nicholls

(1991) found *Boremys* most closely related to *E. cephalica*, with *S. estesi* sister to this

clade. Hutchison (2004) included *Palatobaena* within the clade Eubaenina as the sister

taxon to *S. estesi*, with *G. mckennai* and the clade of *Boremys* + *E. cephalica* as

successive outgroups. Brinkman (2003) recognized that specimens referred to

Plesiobaena antiqua and *"Plesiobaena" putorius* actually comprise three disparate taxa, but did not test their relationships. Most recently, Lyson and Joyce (2009a, 2009b, 2010) found that these three taxa (*C. putorius, P. brinkman*, *P. antiqua*) form a paraphyletic clade, with each of these taxa as successive outgroups to *G. sonsalla + Palatobaena* spp. In contrast, Lyson and Joyce (2011) found *P. antiqua*, *P. brinkman*, and a clade of the rest of these taxa in a poorly supported polytomy. My analysis supports a clade formed by *C. putorius*, *G. sonsalla*, and *Palatobaena* spp. However, *P. antiqua* is found to be sister taxon to a clade similar to one reconstructed by Lyson and Joyce (2009a, 2009b, 2010, 2011) that includes *G. mckennai*, *S. estesi*, *C. undatum*, *B. arenosa*, *E. cephalica*, *D. nodosa*, and *Boremys* spp. In contrast, *P. brinkman* is the sister taxon to these two larger clades, basal to all baenodds except *"Denazinemys" ornata*, the new pig-nosed taxon and *H. latifrons*. Hutchison et al. (in press) originally assigned shells of the new Kaiparowits taxon to *Plesiobaena* sp. I tested the suboptimality of constraining the pig-nosed baenid and *P. antiqua* as sister taxa. This topology requires four additional steps, with 2,457 MPTs recovered with a length of 264 steps.

Within the clade more closely related to *B. arenosa* than to *P. bairdi*, there is a polytomy formed by *G. mckennai*, *"Baena" hayi*, and a clade of all other taxa. Although Hutchison (2004) found *G. mckennai* to be sister taxon to a clade of *S. estesi* and *Palatobaena*, Lyson and Joyce (2009a, 2009b) found this species to be sister to a clade including *S. estesi*, *C. undatum*, and *B. arenosa*. *Goleremys* was removed from subsequent analyses (Lyson and Joyce, 2010, 2011) because it acted as a wildcard taxon; in this analysis, removing *G. mckennai* does not affect the topology of the rest of the tree. Although *"Baena" hayi* was found to be the sister taxon to *P. antiqua*, *G. sonsalla*, and

Palatobaena spp. by Lyson and Joyce (2010) my analysis finds *"Baena" hayi* more closely related to *Boremys* spp. and *B. arenosa*. Inclusion of *"Baena" hayi* in a clade with *P. antiqua*, *G. sonsalla*, and *Palatobaena* spp. requires four additional steps, recovering 4,099 MPTs with a length of 264 steps. Testing the suboptimality of a clade of these taxa and *C. putorius* recovers 2,312 MPTs with a length of 262 steps.

The topology of *S. estesi* as the sister taxon to *C. undatum* + *Baena* spp. and *D. nodosa* and *E. cephalica* as successive outgroups to *Boremys* spp is shared by the present analysis and that of Lyson and Joyce (2011). The major difference between the findings of these studies and that of Lyson and Joyce (2010) is the placement of *Baena hatcheri*. While they find *"Baena" hatcheri* to form a polytomy with *Boremys* spp. and *E. cephalica*, by analysis finds that *B. hatcheri* is sister to *B. arenosa*. This extends the range of the genus *Baena* back across the Cretaceous-Paleogene boundary. A constraint analysis was performed to test the suboptimality of a clade including *B. hatcheri*, *Boremys* spp., and *E. cephalica*. This produced 36 MPTs and required sex additional steps. Lyson and Joyce (2010) proposed the potential synonymy of *B. hatcheri* (shell taxon) and *E. cephalica* (skull taxon) because they overlap temporally and had a close phylogenetic relationship. However, after examining shell material associated with cranial material (UCMP V73023/107617 and UCMP V88020/133929) from the earliest Paleocene Tullock Formation of Montana and unpublished shell material from the latest Cretaceous Hell Creek Formation of North Dakota (Lyson, pers. comm.), this synonymy appears unlikely. With the addition of shell scorings for *E. cephalica* and new character data from the newly described skull of *D. nodosa* (Chapter 2), these taxa remain in their respective phylogenetic positions relative to *Boremys* spp.

Paleobiogeographic Analysis

Cretaceous baenid distributions

The basal baenid *A. dardeni* was discovered in Maryland, whereas all other baenids are known from western North America. Few baenids are known from the Albian-Santonian; these include *Trinitichelys hiatti* from Texas, *Neurankylus wyomingensis* of Wyoming, and a new species of *Neurankylus* from the Milk River Formation of southern Alberta. Campanian baenids are much better represented, particularly from the late Campanian. The Dinosaur Park and Judith River formations of Alberta and Montana, respectively, each preserve three baenid species: *Plesiobaena antiqua*, *Boremys pulchra*, and *Neurankylus eximius*. The newly described baenid turtle assemblage of the correlative Kaiparowits Formation in southern Utah (Chapter 2) includes five species: three of which are restricted to the Kaiparowits Formation, two new species of *Neurankylus*, and a new pig-nosed taxon; and two of which are shared with the San Juan Basin in northern New Mexico, *Denazinemys nodosa*, and *Boremys grandis*. The slightly younger San Juan Basin also preserves *Neurankylus baueri*, *Thescelus hemispherica*, *Thescelus rapiens*, and *"Denazinemys" ornata*. In addition to Utah and New Mexico, *D. nodosa* is also known from the Aguja Formation of western Texas. Maastrichtian baenids are better known from northern Laramidia, particularly the Lance and Hell Creek formations of Wyoming, Montana, and the Dakotas. These baenids include *Neurankylus* sp., *Thescleus insiliens*, *Hayemys latifrons*, *Peckemys brinkman*, *Cedrobaena putorius*, *Gamerabaena sonsalla*, *Palatobaena cohen*, *"Baena" hayi*, *Stygiochelys estesi*, *Baena hatcheri*, and *Eubaena cephalica*. *P. brinkman* and *S. estesi* are also known from the Maastrichtian of the Denver Basin of Colorado (Hutchison and

Holroyd, 2003; Lyson and Joyce, 2009b). For a complete list of catalogue numbers of specimens observed for this study and their stratigraphic and geographic context, see Appendix A.

Methods

The new phylogeny described above forms the basis for the biogeographic analysis. Because the focus of this study is Late Cretaceous biogeography, the outgroup taxon from the Jurassic and all baenids found only in the Cenozoic were pruned from the phylogeny. The reasoning behind pruning taxa that post- or predate the target temporal range for the biogeographic analysis has been previously reviewed (Grande, 1985; Upchurch et al., 2002); Donoghue and Moore, 2003; Turner, 2004; Nesbitt et al., 2009). Because the focus of this study is on the paleobiogeographic history of Laramidia, pruning taxa that were restricted to the Jurassic and Cenozoic is critical because Laramidia was not isolated from the rest of North America prior to of following the Late Cretaceous. Pruned taxa include the Late Jurassic pleurosternid outgroup *G. plicatulus*, and the Paleogene baenids *P. bairdi*, *P. gaffneyi*, *G. mckennai*, *C. undatum*, and *B. arenosa*. Available phylogenetic biogeographic methods required fully bifurcating (i.e., fully-resolved) trees. Several approaches were taken to resolve the polytomies in the recovered trees. In the first approach, after pruning Paleogene taxa, the remaining polotomies in the strict consensus tree (*Neurankylus* spp. and *Thescelus* spp.) were resolved by collapsing the genus into a single terminal taxon. However, such an approach obscures finer-scale temporal and biogeographic patterns among these species, so to

assess the biogeographic patterns among the constituent species of these two genera, three of the 18 most parsimonious trees (MPTs) were randomly chosen for analysis.

The phylogeny was then temporally calibrated using available age data for each taxon. The ages for many baenids from the Upper Cretaceous, particularly those from the Campanian Kaiparowits Formation, are extremely well constrained temporally (Roberts et al., in press). For those baenids that were restricted to a particular portion of a geologic stage, numerical ages from the 2009 Geologic Timescale were used (Walker and Geissman, 2009). The temporal ranges and all references utilized to determine them can be found in Appendix D. Several of the Maastrichtian species are also present in the Paleocene and were retained in the analysis even if the midpoint for their temporal range was Cenozoic. The final age applied to each taxon in each tree was the midpoint of its cumulative stratigraphic range and geochronologic uncertainty. Two different types of branch length calculation were utilized to temporally calibrate the trees. The first of these was a strict temporal calibration, which assumes a minimal length for unconstrained ghost lineages (Nesbitt et al., 2009); these branches were set to 0.1 Ma. The second method utilized was a smoothed temporal calibration (Nesbitt et al., 2009). This assumes a minimal branch length for the oldest taxon in the analysis (*Arundelemys dardeni*) and spreads the ages of zero-length lineages evenly between this oldest constraint and an internal constraint higher on the tree.

The biogeographic areas in the analysis were defined at the depocenter/basin scale, as this clade of turtles is restricted to North America and, for the most part, Laramidia, with often basin-scale endemic species distributions. Appalachia was included because the basal-most baenid is from Maryland. The other geographic areas utilized

were Texas (Trinity Group, Aguja Formation), New Mexico (San Juan Basin), southern Utah (Kaiparowits Plateau), Montana/Wyoming/Dakotas, and southern Alberta (Milk River, Oldman, Dinosaur Park formations). The combination of Montana, Wyoming, and the Dakotas was included because most of the taxa from this area are from the late Maastrichtian (latest Cretaceous), where Hell Creek Formation spreads across several states and is coeval and in the same sedimentary basin as the Lance Formation. Baenid-bearing stratigraphic units in this area are from Montana (Judith River, Hell Creek formations), Wyoming (Cody Shale, Lance Formation), and the Dakotas (Hell Creek Formation).

The DEC method for biogeographic analyses (Ree et al., 2005; Ree and Smith, 2008) is a likelihood method that uses instantaneous rates of range modifications, i.e., dispersals and local extinctions, along phylogenetic branches to estimate the relative likelihood of various ancestral range scenarios at points of cladogenesis. By explicitly incorporating the temporal and geographic data for all terminal taxa in the phylogeny, this analysis calculates the ancestral ranges for all internal nodes. Dispersal constraints may be placed to limit ancestral ranges in two particular areas (e.g., two basins that are separated geographically by a significant distance and therefore would require a taxon to transit through a third area). Direct dispersal was not allowed directly between the following area pairs: Appalachia-Alberta; Texas-Montana; Texas-Alberta; New Mexico-Montana; New Mexico-Alberta; and Utah-Alberta. The New Mexico-Montana constraint was removed for the consensus trees because the genus *Thescelus* as a single taxon possesses this range. The possibility of dispersal from a certain area to another can be weighted relative to the likelihood of dispersal to other areas. However, because my

study is at the subcontinental scale, all possible dispersals were left unweighted to minimize possible assumptions. I limited the maximum number of potential areas in the reconstructed ancestral ranges based on the maximum number of observed areas inhabited by a single taxon in each analysis. For the strict consensus, this maximum was limited to five areas, because the genus *Neurankylus* is found in Texas, New Mexico, Utah, Montana, and Alberta, the most areas inhabited by any taxon on the strict consensus tree. For the analyses run on the randomly selected MPTs, the maximum was set at three because *D. nodosa* is found in the most areas of any taxon: Texas, New Mexico, and Utah.

Results

The biogeographic analyses of Cretaceous baenids, for the most part, exhibit similar results across all tree topologies and temporal calibrations (Figs. 3.4-3.11). The complete results, including relative probabilities for alternate ancestral range reconstructions at various nodes, are reported in Appendix E. In general, basal baenids exhibit a more cosmopolitan ancestral range. Following the complete isolation of Laramidia (approximately 100 Ma), the clade became more endemic, with an ancestral range in the Montana region; individual baenid lineages then disperse to southern Laramidia and Alberta.

The ancestral range for *Arundelemys* is consistently reconstructed as Appalachia in all analyses. Ancestral range reconstructions for the branch leading to the rest of Baenidae are not well-constrained; some analyses reconstruct this as a single area (i.e., Texas or Appalachia), whereas others (all smoothed calibrations) reconstruct a much
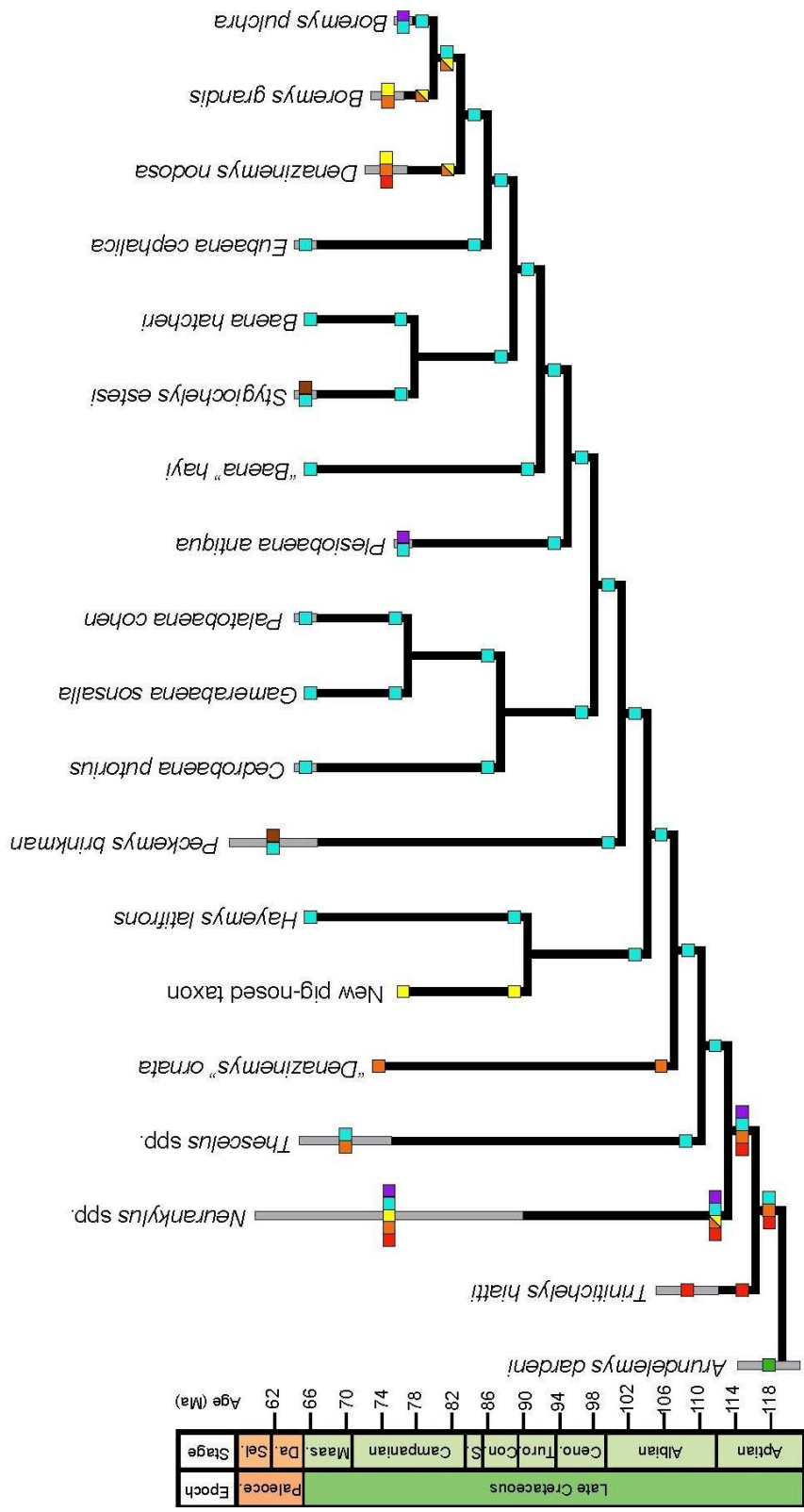
Figure 3.4. Biogeographic results for the smoothed temporal calibration of the strict consensus tree, including only Cretaceous taxa. Color boxes on branches represent ancestral states for clades/taxa, while those at the termination of branches represent the observed distribution of the respective taxa. Geographic key: Alberta, purple; Appalachia, green; Colorado, brown; Montana-Wyoming-Dakotas, light blue; New Mexico (San Juan Basin), orange; Texas, red; southern Utah (Kaiparowits Basin), yellow.
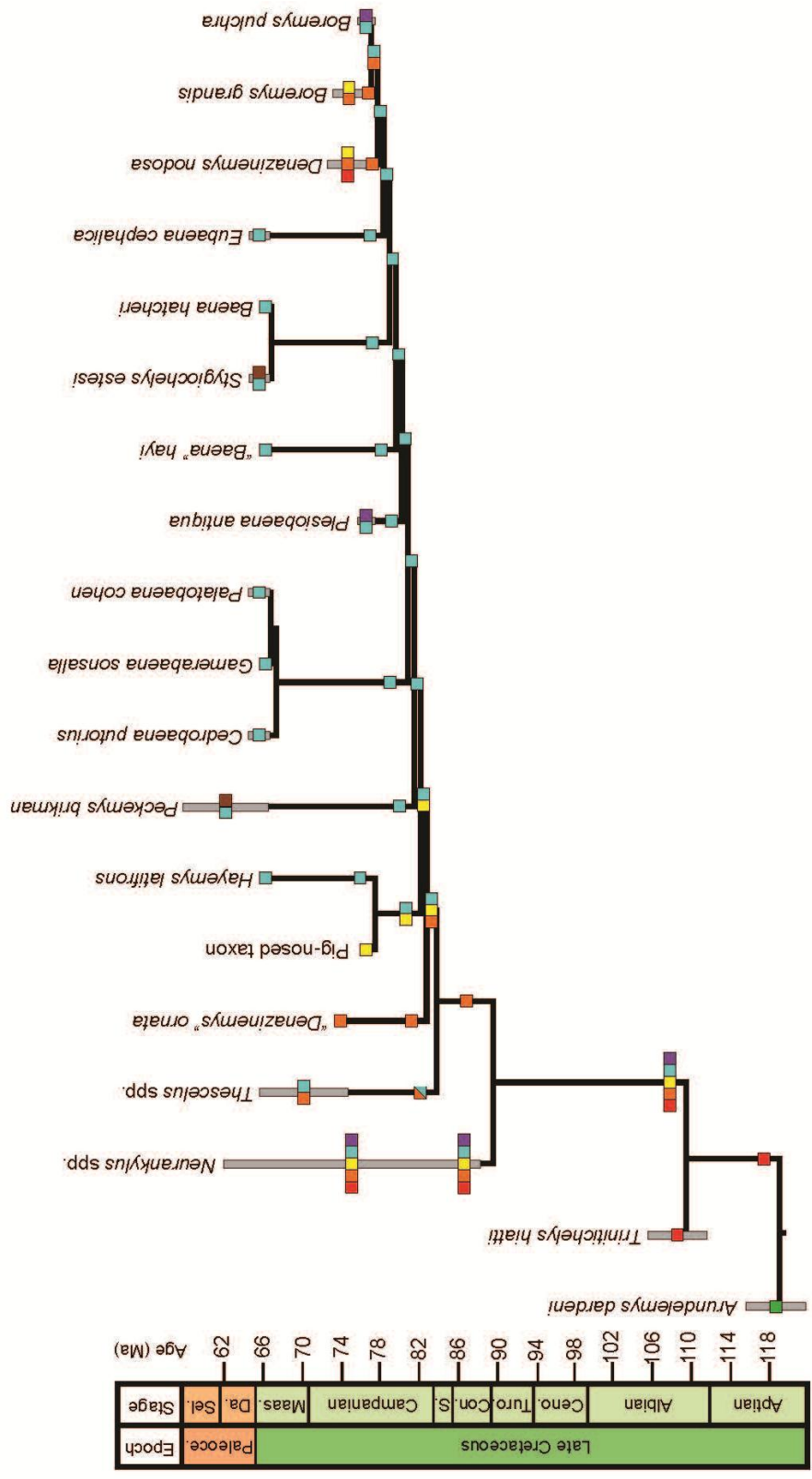
Figure 3.5. Biogeographic results for the strict temporal calibration of the strict consensus tree, including only Cretaceous taxa. Color boxes on branches represent ancestral states for clades/taxa, while those at the termination of branches represent the observed distribution of the respective taxa. Geographic key: Alberta, purple; Appalachia, green; Colorado, brown; Montana-Wyoming-Dakotas, light blue; New Mexico (San Juan Basin), orange; Texas, red; southern Utah (Kaiparowits Basin), yellow.
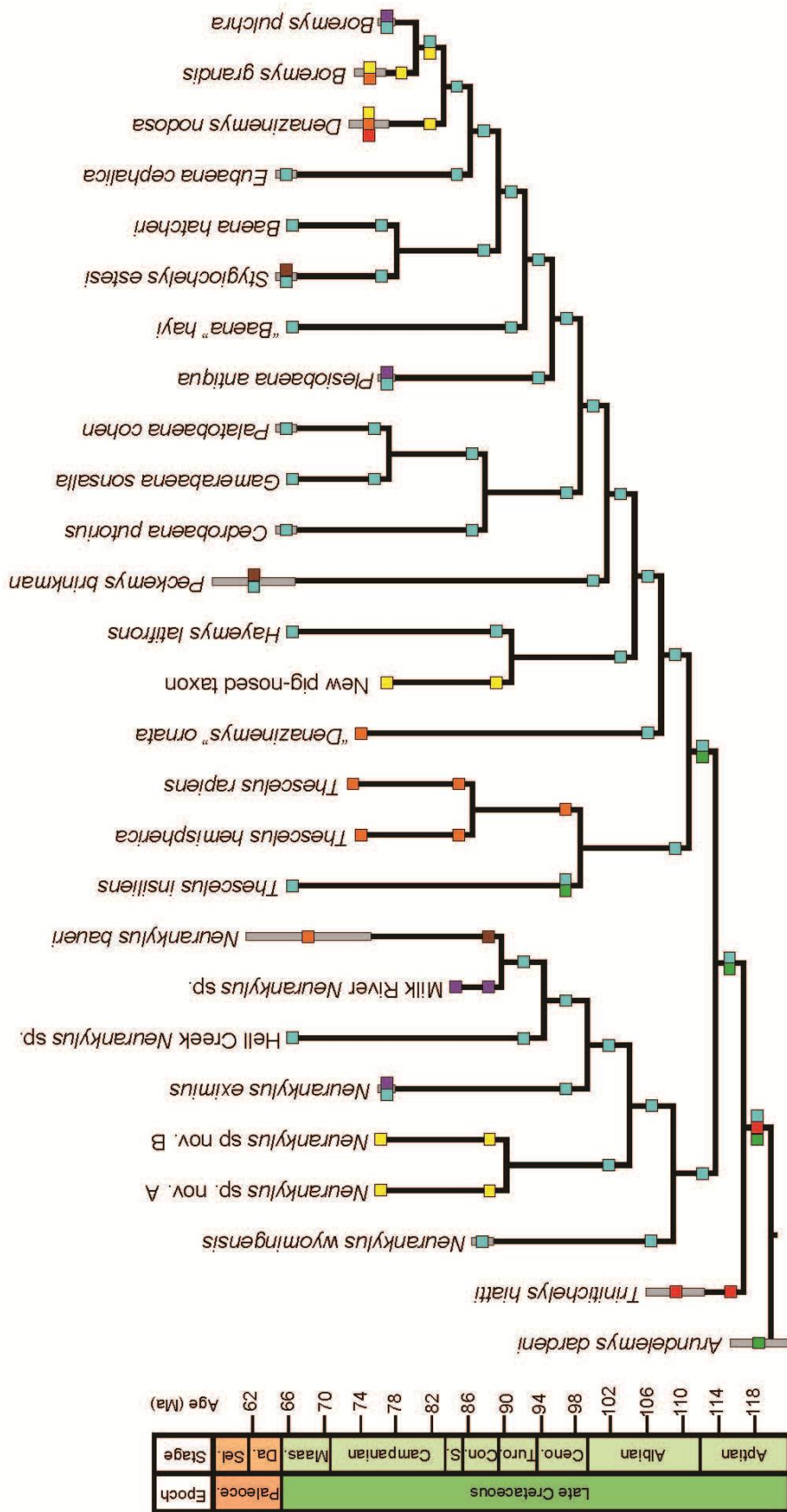
Figure 3.6. Biogeographic results for the smoothed temporal calibration of MPT #1. Color boxes on branches represent ancestral states for clades/taxa, while those at the termination of branches represent the observed distribution of the respective taxa. Geographic key: Alberta, purple; Appalachia, green; Colorado, brown; Montana-Wyoming-Dakotas, light blue; New Mexico (San Juan Basin), orange; Texas, red; southern Utah (Kaiparowits Basin), yellow.
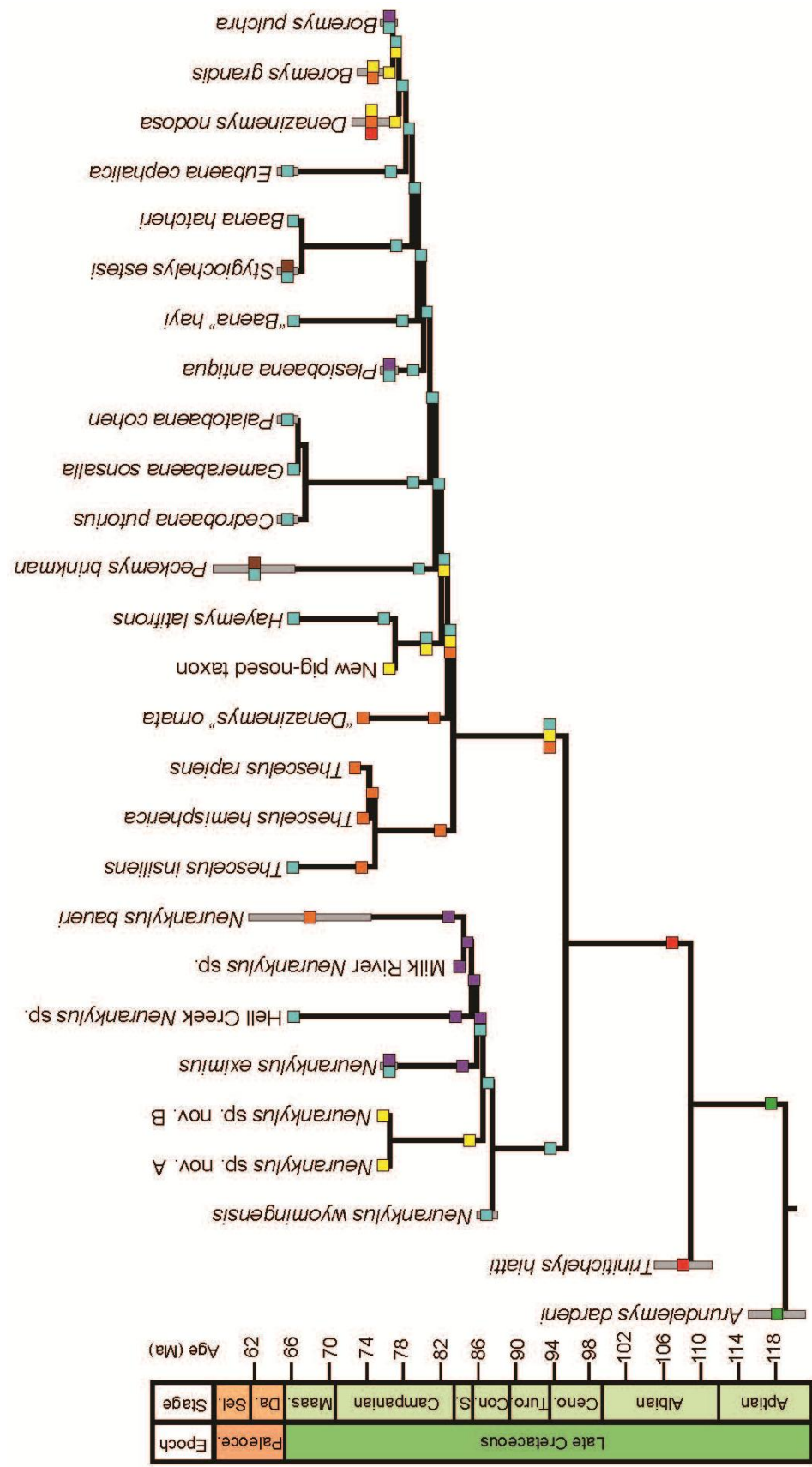
Figure 3.7. Biogeographic results for the strict temporal calibration of MPT #1. Color boxes on branches represent ancestral states for clades/taxa, while those at the termination of branches represent the observed distribution of the respective taxa. Geographic key: Alberta, purple; Appalachia, green; Colorado, brown; Montana-Wyoming-Dakotas, light blue; New Mexico (San Juan Basin), orange; Texas, red; southern Utah (Kaiparowits Basin), yellow.
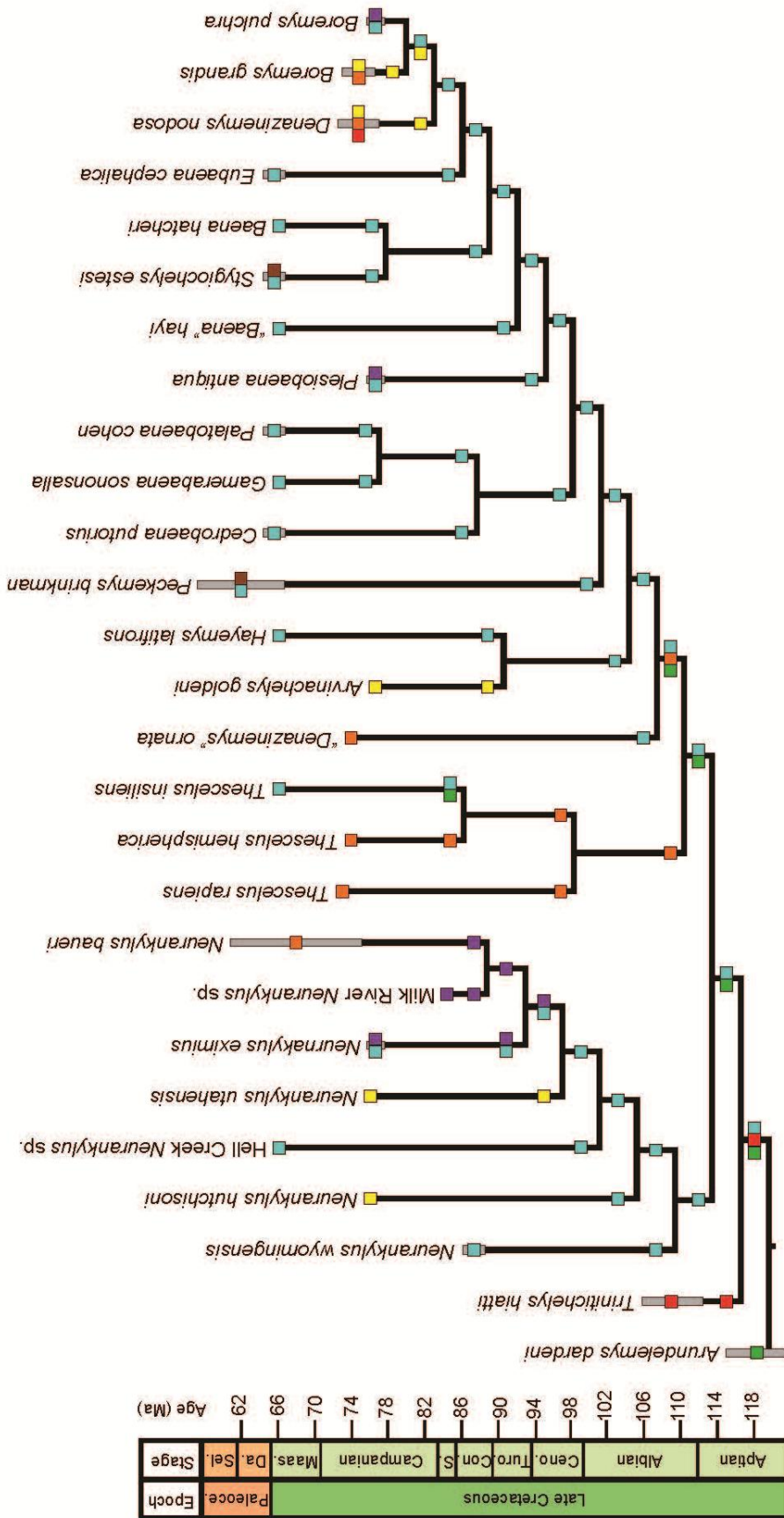
Figure 3.8. Biogeographic results for the smoothed temporal calibration of MPT #11. Color boxes on branches represent ancestral states for clades/taxa, while those at the termination of branches represent the observed distribution of the respective taxa. Geographic key: Alberta, purple; Appalachia, green; Colorado, brown; Montana-Wyoming-Dakotas, light blue; New Mexico (San Juan Basin), orange; Texas, red; southern Utah (Kaiparowits Basin), yellow.
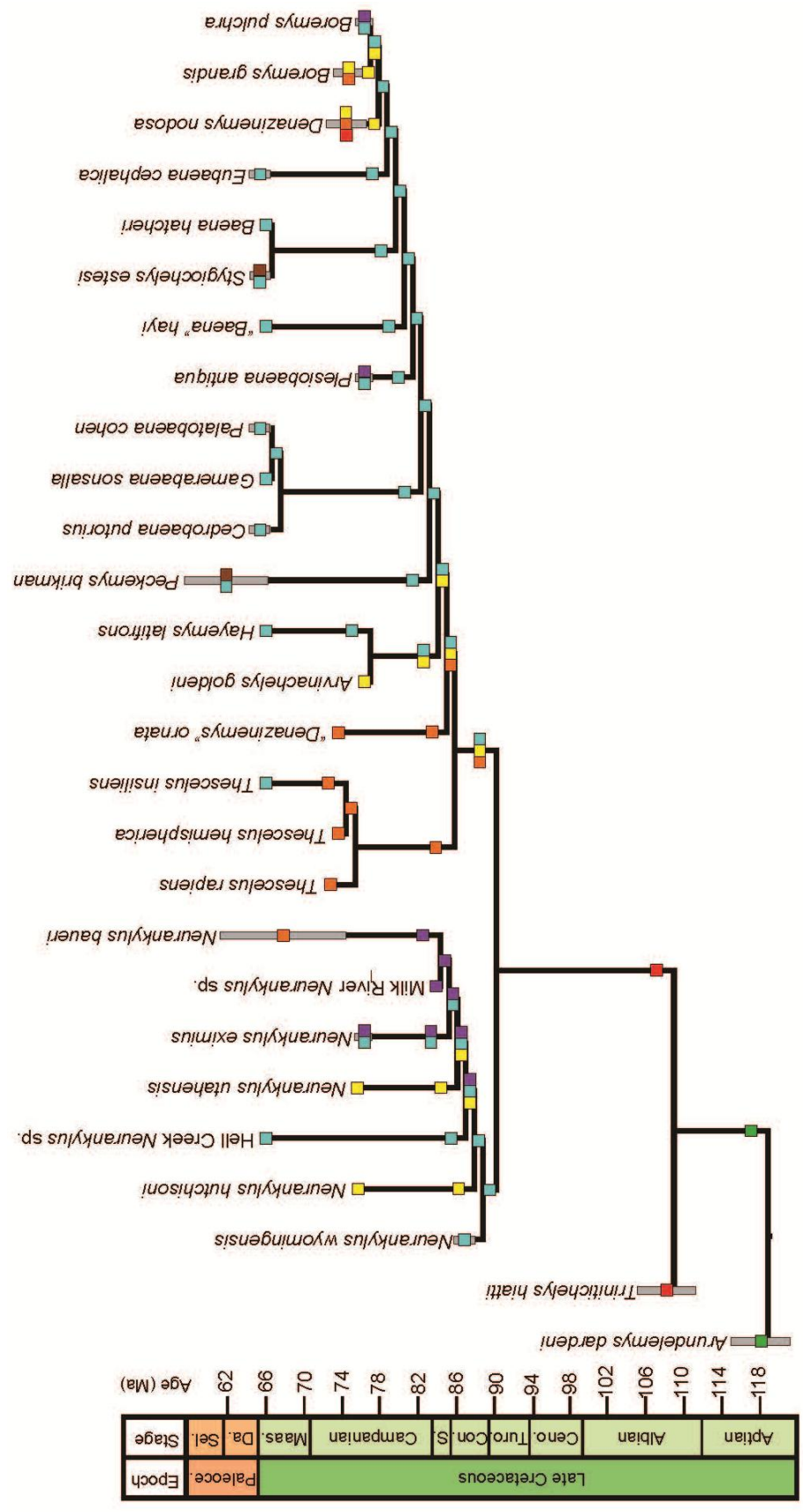
Figure 3.9. Biogeographic results for the strict temporal calibration of MPT #11. Color boxes on branches represent ancestral states for clades/taxa, while those at the termination of branches represent the observed distribution of the respective taxa. Geographic key: Alberta, purple; Appalachia, green; Colorado, brown; Montana-Wyoming-Dakotas, light blue; New Mexico (San Juan Basin), orange; Texas, red; southern Utah (Kaiparowits Basin), yellow.
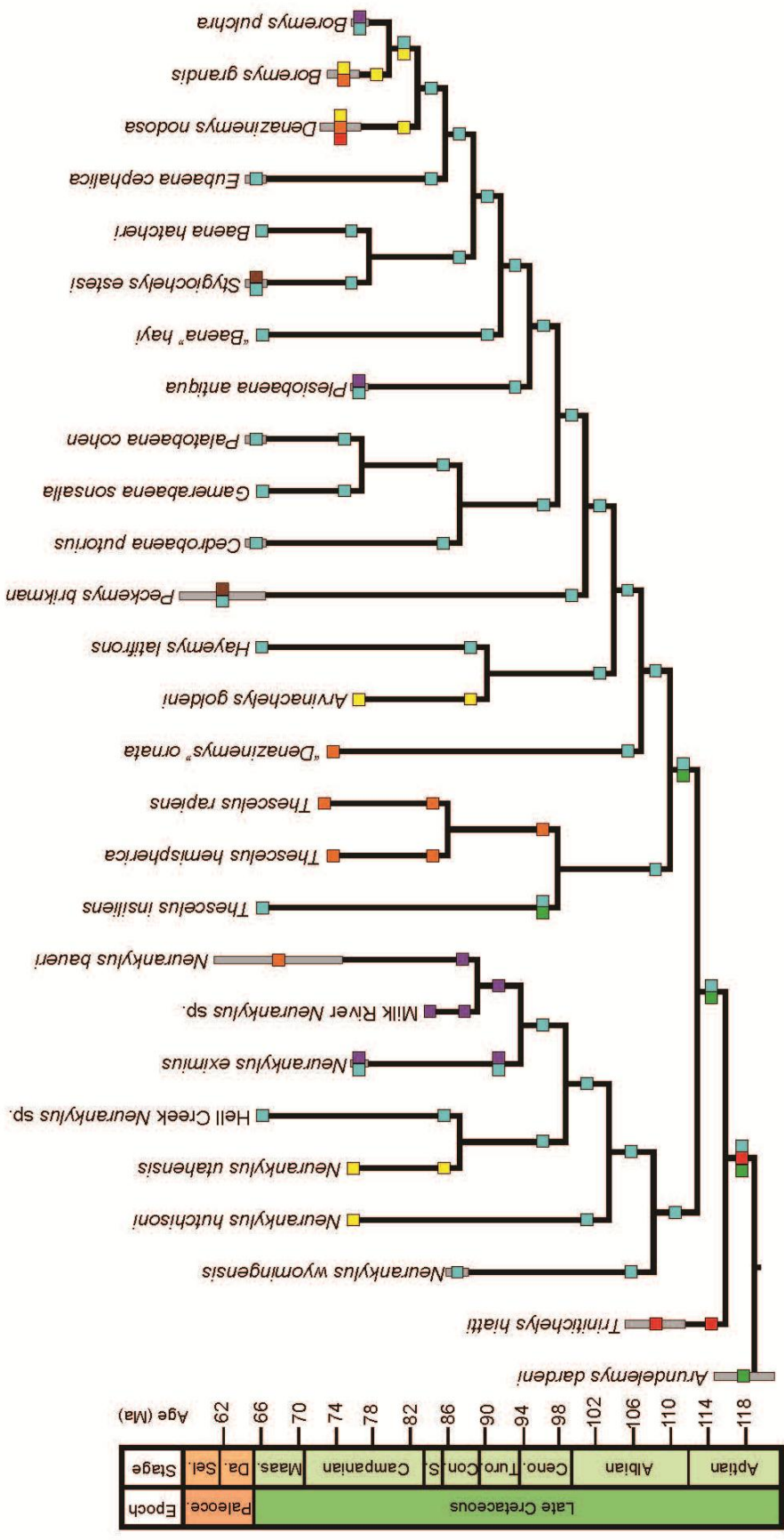
Figure 3.10. Biogeographic results for the smoothed temporal calibration of MPT #18. Color boxes on branches represent ancestral states for clades/taxa, while those at the termination of branches represent the observed distribution of the respective taxa. Geographic key: Alberta, purple; Appalachia, green; Colorado, brown; Montana-Wyoming-Dakotas, light blue; New Mexico (San Juan Basin), orange; Texas, red; southern Utah (Kaiparowits Basin), yellow.
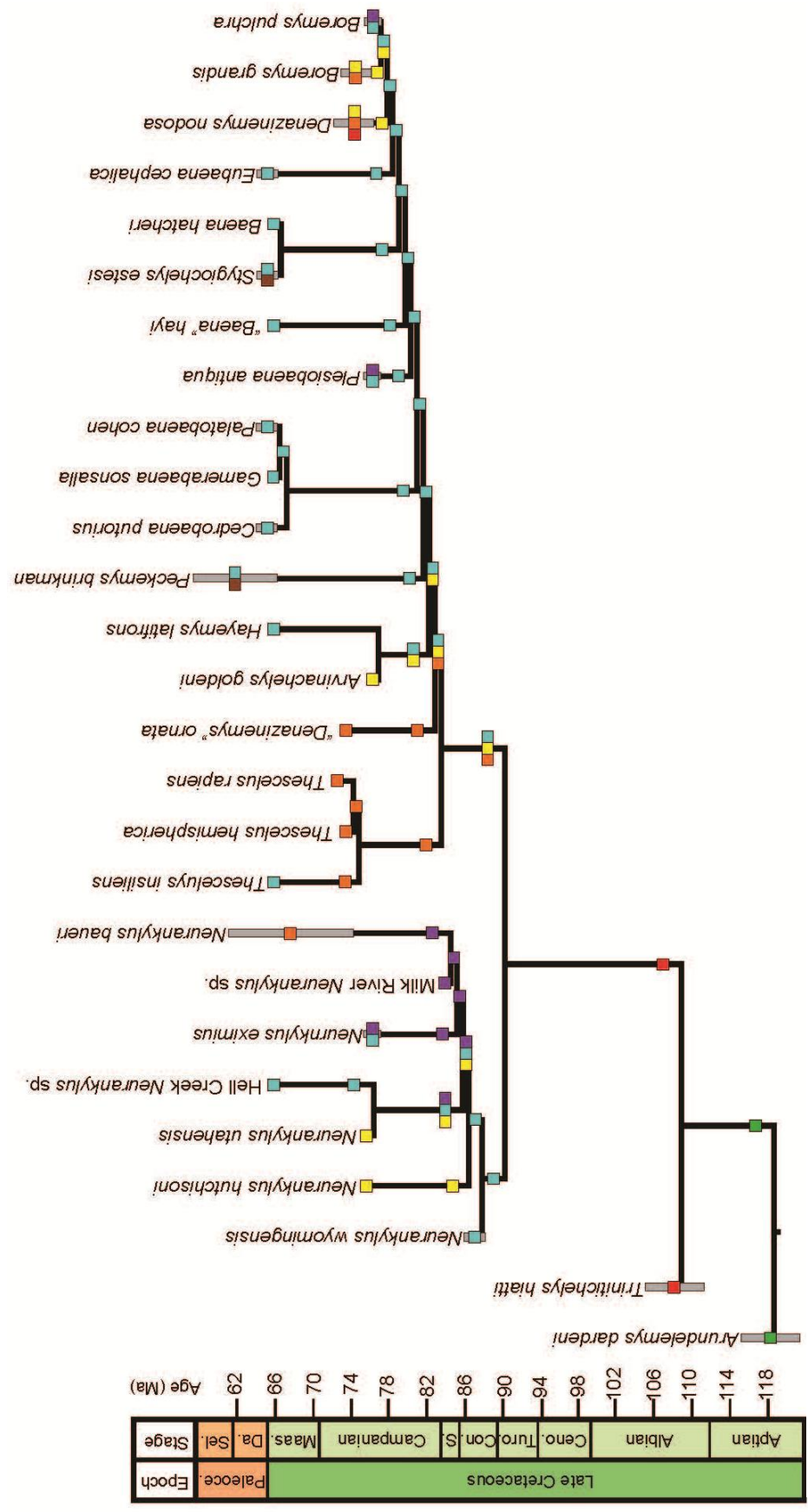
Figure 3.11. Biogeographic results for the strict temporal calibration of MPT #18. Color boxes on branches represent ancestral states for clades/taxa, while those at the termination of branches represent the observed distribution of the respective taxa. Geographic key: Alberta, purple; Appalachia, green; Colorado, brown; Montana-Wyoming-Dakotas, light blue; New Mexico (San Juan Basin), orange; Texas, red; southern Utah (Kaiparowits Basin), yellow.

more cosmopolitan ancestral range of Texas, New Mexico, and Montana or Appalachia, Texas, and Montana. On the consensus tree analysis, *Neurankylus* + the rest of Baenidae possesses a cosmopolitan ancestral range because all species of *Neurankylus* are collapsed into one terminal taxon, giving the genus a widespread range. Among analyses of the individual MPTs, the ancestral range of this clade is reconstructed as either Texas (strict calibrations) or Appalachia and Montana (smoothed calibrations).

When the genus *Neurankylus* is considered a single terminal taxon in the strict consensus analyses, it is reconstructed with a cosmopolitan distribution. However, when three random MPTs are analyzed, a different signal results. On all of the individual MPT analyses, both strict and smooth calibrated, the reconstructed ancestral range for the genus is the Montana region. This is to be expected, as the most basal taxon in all trees (*N. wyomingensis*) and two of the other taxa inhabit the region. Variation through the rest of the *Neurankylus* lineage is seen between the strict and smooth calibrated trees. For the smooth temporal calibrations of the individual MPTs, the spine of the *Neurankylus* lineage is reconstructed as having an ancestral range of the Montana region. Individual lineages then disperse to southern Utah and Alberta. Even when *Neurankylus* sp. nov. A and *Neurankylus* sp. nov. B are sister taxa (MPT 1), the ancestral range for this clade is reconstructed as Montana in the smoothed time calibration. This reconstruction suggests that each of these Utah lineages dispersed to the Kaiparowits Plateau individually. In contrast, for the strict calibrations, the ancestral range for the clade of these two taxa is reconstructed as southern Utah. This would suggest that a lineage of *Neurankylus* dispersed to the Kaiparowits Plateau and then speciated into two morphologically disparate taxa (Chapter 2). For the smoothed calibration for MPT 1, the Montana

ancestral range continues up the spine of the *Neurankylus* lineage, with the lineages leading to *N. eximius* and the Milk River *Neurankylus* dispersing to Alberta and dispersal of *N. baueri* to the San Juan Basin via the Denver Basin. The strict calibration for MPT 1 suggests dispersal to Alberta for the branch leading to more derived *Neurankylus*. Alberta is then considered the ancestral range for the rest of the lineage, with individual dispersals to Montana and New Mexico by two of the species. For the smoothed temporal calibrations of MPTs 11 and 18, all species within *Neurankylus* possess an ancestral range in the Montana region, with the exception of clade 4, whose ancestors had dispersed to Alberta. Three separate lineages (*Neurankylus* sp. nov. A, *Neurankylus* sp. nov. B, and *N. baueri*) then disperse to southern Laramidia. The strict temporal calibrations for these two MPTs differ in that the lineage of all *Neurankylus* more derived than *Neurankylus* sp. nov. A possesses a more cosmopolitan distribution of Utah, Montana, and Alberta. Following the divergence of *Neurankylus* sp. nov. B, this ancestral range is then restricted to Montana and Alberta (MPT 11) or Alberta (MPT 18).

The lineage leading to *Thescelus* spp. + Baenodda shows some variation across various analyses. This ancestral range is reconstructed as New Mexico in the strict calibration of the strict consensus tree and Montana in the smoothed calibration of the same tree. For all analyses of strict temporal calibration of individual MPTs, this ancestral range is reconstructed as relatively cosmopolitan, whereas the smoothed calibration analyses reconstruct this ancestral range as Appalachia and Montana. The lineage leading to *Thescelus* spp. is reconstructed as having an ancestral range of New Mexico; when *T. insiliens* is reconstructed as the basal taxon of the genus in some MPTs and analyzed using a smoothed temporal calibration, the ancestral range is reconstructed

as the Montana area. Baenodda exhibits a relatively cosmopolitan ancestral range of New Mexico, Utah, and Montana in all strict temporally calibrated trees. Most smooth calibration analyses of the individual MPTs reconstruct this ancestral range restricted to Montana, with the exception of MPT 11, which also has a cosmopolitan distribution (Appalachia, New Mexico, and Montana).

The basal-most baenodd, *"Denazinemys" ornata*, is reconstructed with an ancestral range of New Mexico in all analyses using a strict temporal calibration; conversely, smoothed calibrations yield an ancestral range of Montana and then disperses south. The clade of the pig-nosed taxon and *H. latifrons* possesses an ancestral range of Utah and Montana in strict calibrations and a Montana-only range in smoothed calibrated trees, with the lineage leading to the new Kaiparowits taxon dispersing to Utah.

For the remainder of Baenodda, the ancestral ranges reconstructed for all analyses are consistently in the Montana-Wyoming-Dakotas region. Individual lineages typically show dispersal to other regions of Laramidia. *P. brinkman* and *S. estesi* both have ancestral and observed ranges in Montana, with additional dispersal into the Denver Basin of Colorado. *P. antiqua* also possesses a Montana ancestral range that dispersed into south-central Alberta. The lineage leading to *D. nodosa* and *Boremys* in all analyses has a Montana ancestral range, indicated that the southern Laramidian occurrences of *D. nodosa* and *Boremys* represent separate dispersal events. The ancestral lineage of *Boremys* is reconstructed as a widespread ancestral range that is some combination of Montana and one or more southern Laramidian areas. These data imply that the presence of *B. grandis* in the south and *B. pulchra* in Montana represent an allopatric speciation

event, with later dispersal of *B. grandis* into additional southern areas and dispersal of *B. pulchra* into Alberta.

Many differences between the results for strict and smoothed time calibrated trees result from differences in branch length, and, thus, more or less time for the animals to disperse to new geographic regions. For example, on MPT 1, where *Neurankylus* sp. nov. A and *Neurankylus* sp. nov. B are found to be sister taxa and this speciation event is inferred to occur only 0.1 Ma prior to the species' temporal ranges in the strict calibration, it would be much more likely that the dispersal event occurred prior to speciation. However, when given 13.49 Ma since divergence in the smoothed calibration, it is possible that the animals diverged in the ancestral range of Montana and then individually dispersed to southern Utah.

Discussion

The Kaiparowits Formation of Utah is correlative with the fossil-bearing strata of the Dinosaur Park and Judith River formations (Roberts et al., in press). Therefore, the hypothesis of two biogeographic provinces during the middle to late Campanian of Laramidia (e.g., Lehman et al., 1997, 2001) is supported by my data, based on the observed distribution of baenid taxa. Three taxa are shared between Dinosaur Park and Judith River assemblages; none of these species are found in southern basins. The hypothesis of basin-scale endemism (e.g., Sampson et al., 2010) is also supported; of the five baenid species recognized in the Kaiparowits Formation of southern Utah, three are restricted only to this basin. Of the remaining two species, *B. grandis* is also found in the slightly younger Kirtland Formation of New Mexico, whereas *D. nodosa* is known from

the San Juan Basin and Aguja Formation of Texas. Conversely, four baenid species –
Neurankylus baueri, *Thescelus hemispherica*, *Thescelus rapiens* and *"Denazinemys"*
ornata – from the Kirtland Formation are absent from the Kaiparowits Formation.

Sullivan and Lucas (2006) proposed the 'Kirtlandian' land vertebrate age based
on differences between the vertebrates of the San Juan Basin (Kirtland and Fruitland
formations) and older strata they assigned to the Judithian land mammal age. These
authors attributed these faunal differences to different geological ages of fossil
assemblages rather than latitude or other biogeographic explanations. However, with the
new data from the Kaiparowits Formation, this argument is now moot. With the aid of
radiometric dates for ash beds within the Kaiparowits Formation, it is clear that the
formation is Judithian in age (Roberts et al., in press). In addition, the presence of baenids
suggestive of the Kirtlandian within the Judithian Kaiparowits Formation calls to
question the validity of this land vertebrate age. Given the pervasiveness of endemic taxa
during the late Campanian, it is very easy to confuse penecontemporaneous endemic
assemblages for different biostratigraphic assemblages. The only way the validity of the
Kirtlandian can be directly tested would be the identification of of Kirtlandian vertebrates
in correlative strata (~74-72 Ma) from northern Laramidian basins.

Baenid turtles do exhibit evidence for latitudinal differences in distribution during
the Campanian, with two clear biogeographic provinces. Unfortunately, the exact nature
of the boundaries between these provinces cannot be determined with the current data.
Gates et al. (2010) give four alternate hypotheses for vertebrate distribution across
Laramidia: a cosmopolitan distribution, two provinces with a sharp boundary, two
provinces with a central faunal mixing zone, or a continuous latitudinal gradient. Using

available data on baenid distribution, only the cosmopolitan hypothesis can be ruled out,

although the continuous gradient hypothesis appears unlikely, as no northern taxa make it

into southern Utah. Lehman (1991, 2001) placed the boundary between these proposed

biogeographic provinces somewhere in northern Utah and/or Colorado. Testing the

nature of the biogeographic boundary would be possible with better data from the

Mesaverde Group of the Book Cliffs region of central Utah and western Colorado, which

has yet to be systematically prospected for vertebrate fossils..

Considering the results of the biogeographic analyses on all consensus and MPTs,

several key conclusions can be made: 1) basal baenids likely possessed a cosmopolitan

distribution; 2) early on, within the lineages leading to derived species of *Neurankylus*

and derived members of Baenodda, an ancestral range of northern Laramidia, particularly

within the Montana and Wyoming area, was established; 3) southern Laramidian taxa

from the Campanian are nested within clades with ancestral ranges in northern

Laramidia. Overall, this provides a different signal than that of Sampson et al. (2010),

which suggested that northern Maastrichtian chasmosaurines were nested among clades

of southern Campanian taxa.

Sampson et al. (2010) proposed a sequence of events to explain the distribution of

chasmosaurines through the Late Cretaceous, which included the emplacement of a

barrier around 77.0 Ma that prevented north-south dispersal of vertebrates across

Laramidia until approximately 75.7 Ma, when several lineages of chasmosaurines were

allowed to disperse across the continent. Candidates for this barrier included an east-west

trending mountain range (e.g., the Uinta Mountains of Utah), transgression in central

Utah of the Western Interior Seaway, or a large river system in the area (Sampson et al.,

2010). An alternative is latitudinally-forced differing climatic regimes, which would corroborate the disparate northern and southern palynomorphs derived from the Campanian of western North America (Lehman, 1997).

Depending on whether the strict or smoothed temporal calibration is the preferred model, the cladogenetic events that lead to most southern Laramidian taxa nearly all occur prior to the hypothesized 77.0 Ma. For instance, depending on the calibration, the speciation event leading to *Boremys grandis* and *B. pulchra* may have occurred between 79.38 and 76.5 Ma. The *D. nodosa* lineage extends back somewhere between 82.36 and 76.6 Ma, although the discovery of *Denazinemys* (UMNH VP 8062) from near the base of the Wahweap Formation (Lively, unpubl. data) of southern Utah means the origin of this lineage is likely older than 80 Ma (Jinnah et al., 2009). The calculated branch lengths for all other baenids from southern Laramidia place cladogenetic events well before the hypothesized 77.0 Ma boundary emplacement.

Conclusions

My new phylogenetic analysis demonstrates that 1) *Arundelemys dardeni* from the Aptian of Maryland is the basal-most baenid; 2) *Neurankylus* represents a diverse basal radiation of Baenidae with at least seven distinct species present during the Late Cretaceous – four of which are Campanian in age; 3) *"Denazinemys"*, sensu Lucas and Sullivan (2006) is polyphyletic, with *"Denazinemys" ornata* as the earliest diverging lineage of the subclade Baenodda; 4) taxa previously referred to the genus *Plesiobaena* belong to different lineages, in contrast to the previous results of Lyson and Joyce

(2009b, 2011), who found them to form a monophyletic clade with *Gamerabaena sonsalla* and *Palatobaena* spp.

The distribution of baenids during the Campanian supports the hypothesis that at least two distinct biogeographic provinces were present during this stage. However, more data from regions such as central Utah are needed to fully understand the nature of the boundary between the two provinces. A phylogenetic biogeographic analysis of the clade suggests that, unlike dinosaur clades, baenids possessed ancestral ranges in northern Laramidia and individual lineages dispersed to southern Laramidia during the Campanian. Because many baenid cladogenic events appear to be near or well before the hypothesized climatic boundary emplacement at ~77 Ma (Sampson et al., 2010), this pattern in baenids does not refute the hypothesis that some vertebrate groups exhibited a similar pattern to chasmosaurine ceratopsians (Sampson et al., 2010).

APPENDIX A

LIST OF SPECIMENS USED

Taxon	Formation	Locality
Glyptops plicatulus		
AMNH 6099*	Morrison Fm	Colorado
AMNH 336	Morrison Fm	Wyoming
YPM 1784	Morrison Fm	Wyoming
YPM 4717	Morrison Fm	Wyoming
Arundelemys dardeni		
USNM 497740*	Arundel Clay Facies, Patuxent Fm	Maryland
Trinitichelys hiatti		
MCZ 4070*	Trinity Gp	Texas
Neurankylus wyomingensis		
USNM 7581*	Colorado Shale	Wyoming
Neurankylus eximius		
TMP 2003.012.0171	Dinosaur Park Fm	Alberta
Neurankylus baueri		
USNM 8344*	Hunter Wash Mbr, Kirtland Fm	New Mexico
USNM 8531	Hunter Wash Mbr, Kirtland Fm	New Mexico
USNM 13228	Hunter Wash Mbr, Kirtland Fm	New Mexico
NMMNH P-57874	Ojo Encino Mbr, Nacimiento Fm	New Mexico
Milk River *Neurankylus*		
TMP 2007.035.0045*	Milk River Fm	Alberta
Hell Creek *Neurankylus*		
UCMP V84010/129724	Hell Creek Fm	Montana
UCMP V8318/130137	Hell Creek Fm	Montana

UCMP V84043/131700	Hell Creek Fm	Montana
UCMP V86075/132057	Hell Creek Fm	North Dakota
UCMP V86048/177966	Hell Creek Fm	North Dakota

Kaiparowits *Neurankylus* sp. nov. A

UCMP V93118/154450*	Kaiparowits Fm	Utah

Kaiparowits *Neurankylus* sp. nov. B

BYU 9411	Kaiparowits Fm	Utah
BYU 12001	Kaiparowits Fm	Utah

Thescelus insiliens

AMNH 1108*	Lance Fm	Wyoming

Thescelus hemispherica

USNM 12818*	Hunter Wash Mbr, Kirtland Fm	New Mexico

Thescelus rapiens

AMNH 6066*	De-na-zin Mbr, Kirtland Fm	New Mexico

"Denazinemys" ornata

USNM 13229*	Hunter Wash Mbr, Kirtland Fm	New Mexico
USNM 12821	Hunter Wash Mbr, Kirtland Fm	New Mexico
USNM 11083	De-na-zin Mbr, Kirtland Fm	New Mexico

Hayemys latifrons

AMNH 6139*	Lance Fm	Wyoming

New Kaiparowits Taxon

UMNH VP 21151*	Kaiparowits Fm	Utah
UMNH VP 20451	Kaiparowits Fm	Utah
UMNH VP 20183	Kaiparowits Fm	Utah

Plesiobaena antiqua

AMNH 9046	Dinosaur Park Fm	Alberta
AMNH 5241	Dinosaur Park Fm	Alberta
TMP 1986.036.0681	Dinosaur Park Fm	Alberta
TMP 1992.036.0681	Dinosaur Park Fm	Alberta
TMP 1994.012.0273	Dinosaur Park Fm	Alberta
TMP 1999.055.0145	Dinosaur Park Fm	Alberta
TMP 1993.019.0002	Dinosaur Park Fm	Alberta
TMP 1981.041.0103	Dinosaur Park Fm	Alberta
TMP 1990.119.0001	Dinosaur Park Fm	Alberta
TMP 1995.012.0122	Dinosaur Park Fm	Alberta
TMP 1992.040.0033	Dinosaur Park Fm	Alberta
TMP 1980.016.1693	Dinosaur Park Fm	Alberta

TMP 1990.036.0160	Dinosaur Park Fm	Alberta
TMP 2007.012.0001	Dinosaur Park Fm	Alberta
TMP 1985.058.0045	Dinosaur Park Fm	Alberta

Peckemys brinkman

UMMP 20490*†	Hell Creek Fm	Montana
MRF 239	Hell Creek Fm	North Dakota
UCMP V73023/113318	Hell Creek Fm	Montana
UCMP V5620/49759	Lance Fm	Wyoming

Cedrobaena putorius

YPM-PU 14984*	Fort Union Fm	Wyoming
YPM-PU 20600	Fort Union Fm	Wyoming
MRF 239	Hell Creek Fm	North Dakota

Gamerabaena sonsalla

ND 06-14.1*‡	Hell Creek Fm	North Dakota

Palatobaena bairdi

YPM-PU 16839*	Fort Union Fm	Wyoming
YPM 17108	Fort Union Fm	Wyoming

Palatobaena cohen

YPM 57498*	Hell Creek Fm	North Dakota
UCMP V75180/114539	Hell Creek Fm	Wyoming

Palatobaena gaffneyi

UCMP V71238/114529*	Wasatch Fm	Wyoming

Goleremys mckennai

UCMP V99042/179519*	Goler Fm	California

Stygiochelys estesi

AMNH 2601*	Hell Creek Fm	Montana
UCMP V73023/113316	Hell Creek Fm	Montana

Chisternon undatum

AMNH 5904	Bridger Fm	Wyoming
AMNH 5961	Black's Fork Mbr, Bridger Fm	Wyoming
AMNH 5962	Black's Fork Mbr, Bridger Fm	Wyoming
AMNH 25554	Bridger Fm	Wyoming
USNM 12839	Bridger Fm	Wyoming
USNM 16781	Bridger Fm	Wyoming

Baena arenosa

USNM 103*	Bridger Fm	Wyoming
AMNH 5970	Black's Fork Mbr, Bridger Fm	Wyoming

AMNH 5971	Bridger Fm	Wyoming
AMNH 5973	Black's Fork Mbr, Bridger Fm	Wyoming
AMNH 5977	Black's Fork Mbr, Bridger Fm	Wyoming
USNM 18102	Bridger Fm	Wyoming

Baena hatcheri
| AMNH 106 | Lance Fm | Wyoming |

Eubaena cephalica
AMNH 4948	Hell Creek Fm	Montana
MRF 571	Hell Creek Fm	North Dakota
MRF 572	Hell Creek Fm	North Dakota
MRF 598	Hell Creek Fm	North Dakota
MRF 599	Hell Creek Fm	North Dakota
MRF 642	Hell Creek Fm	North Dakota
MRF 643	Hell Creek Fm	North Dakota
MRF 697	Hell Creek Fm	North Dakota
MRF 698	Hell Creek Fm	North Dakota
MRF 765	Hell Creek Fm	North Dakota
MRF 766	Hell Creek Fm	North Dakota
MRF 798	Hell Creek Fm	North Dakota
MRF 906	Hell Creek Fm	North Dakota
UCMP V73023/107617	Hell Creek Fm	Montana
UCMP V73023/117242	Hell Creek Fm	Montana
UCMP V84027/130142	Hell Creek Fm	Montana
UCMP V88020/133929	Tullock Fm	Montan

Denazinemys nodosa
USNM 83445*	De-na-zin Mbr, Kirtland Sh	New Mexico
BYU 19123	Kaiparowits Fm	Utah
NMMNH P-41229	Hunter Wash Mbr, Kirtland Fm	New Mexico
NMMNH P-49945	Fossil Forest Mbr, Fruitland Fm	New Mexico
TMM 42534-4	Aguja Fm	Texas
TMM 43251-1	Aguja Fm	Texas
UCMP 99441/159399	Kaiparowits Fm	Utah
UCMP 95087/159703	Kaiparowits Fm	Utah
UCMP V95083/194125	Kaiparowits Fm	Utah
UCMP V93070/194207	Kaiparowits Fm	Utah
UCMP 93084/194248	Kaiparowits Fm	Utah
UCMP V93096/194271	Kaiparowits Fm	Utah
UCMP V94028/194335	Kaiparowits Fm	Utah
UCMP 94039/194342	Kaiparowits Fm	Utah
UMNH VP 9545	Kaiparowits Fm	Utah
UMNH VP 12501	Kaiparowits Fm	Utah
UMNH VP 12647	Kaiparowits Fm	Utah
UMNH VP 13906	Kaiparowits Fm	Utah

UMNH VP 16113	Kaiparowits Fm	Utah
UMNH VP 16872	Kaiparowits Fm	Utah
UMNH VP 20446	Kaiparowits Fm	Utah
UMNH VP 20447	Kaiparowits Fm	Utah
USNM 11327	Fruitland Fm	New Mexico
USNM 12819	Hunter Wash Mbr, Kirtland Sh	New Mexico

Boremys pulchra

UCMP V82222/1301155	Judith River Rm	Montana
TMP 1979.014.1053	Dinosaur Park Fm	Alberta
TMP 1980.016.0001	Dinosaur Park Fm	Alberta
TMP 1981.028.0001	Dinosaur Park Fm	Alberta
TMP 1987.046.0060	Dinosaur Park Fm	Alberta
TMP 1988.002.0010	Dinosaur Park Fm	Alberta
TMP 1990.119.0006	Dinosaur Park Fm	Alberta
TMP 1999.055.0223	Dinosaur Park Fm	Alberta
TMP 2001.012.0036	Dinosaur Park Fm	Alberta
USNM 8803	Dinosaur Park Fm	Alberta

Boremys grandis

USNM 12979*	De-na-zin Mbr, Kirtland Sh	New Mexico
UCMP V94009/151773	Kaiparowits Fm	Utah
UCMP V97098/156997	Kaiparowits Fm	Utah
UMNH VP 18628	Kaiparowits Fm	Utah
USNM 12978	Kirtland Sh	New Mexico

"Baena" hayi

USNM 6728*	Lance Fm	Wyoming

*Holotype
† Scorings based on figures of Lyson and Joyce, 2009b
‡ Scorings based on figures of Lyson and Joyce, 2010

APPENDIX B

LIST OF CHARACTERS USED IN PHYLOGENETIC ANALYSIS

Changes to previously published characters in **bold**.

1) Skull shape in dorsal view (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C3.1): 0 = oblong and rounded anteriorly; 1 = wedge-shaped, skull tapers towards the anterior tip; 2 = short and rounded.

2) Interorbital width (Lyson and Joyce, 2009a): 0 = wide; 1 = narrow.
Comments: To test the validity of this character, a scatter plot of skull lengths vs. interorbital widths was generated. This demonstrated that there are outliers with a wide dorsal space between the orbits compared to other baenid taxa.

3) Preorbital skull length (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 11): 0 = short, snout shorter than **or subequal to** orbit diameter; 1 = long, snout longer than orbit diameter.

4) Orbit shape (Lyson and Joyce, 2009a): 0 = circular to oval; 1 = generally circular, but with a distinct posterodorsal notch.

5) Orbit height relative to maxillary height (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 19): 0 = orbit larger than **or subequal to** maxillary height below orbit; 1 = orbit smaller than maxillary height below orbit.

6) Orientation of orbit (Lyson and Joyce, 2009a): 0 = orbits mostly oriented laterally; 1 = orbits mostly oriented dorsally.

7) Development of the lingual ridge (Lyson and Joyce, 2009a; in part Gaffney and Meylan, 1988, C2.3, C7.1): 0 = lingual ridge developed along the entire lingual margin of palate; 1 = lingual ridge only developed along the anterior half of the lingual margin of the palate; 2 = lingual ridge absent.
Comment: These character states form a morphocline and can be run ordered in an analysis.

8) Shape of triturating surface (Lyson and Joyce, 2009a; in part Gaffney and Meylan, 1988, C2.3, C7.1; Brinkman and Nicholls, 1991, 1): 0 = lingual and labial margins more or less parallel; 1 = lingual and labial margins diverge posteriorly, triturating surface expanded posteriorly.

9) Intermaxillary arch/tongue groove (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C8.1): 0 = right and left triturating surfaces do not meet along midline; tongue groove, if present, narrow; 1 = right and left triturating surface contact one another along the midline along a rounded bridge, the intermaxillary arch; tongue groove wide.

10) Palatine contribution to triturating surface (Lyson and Joyce, 2009a): 0 = absent, the palatine sits below triturating surface, or contributes to it only very lightly; 1 = present, palatine clearly contributes to triturating surface.

11) Swollen maxillae (Lyson and Joyce, 2009a): 0 = absent, labial ridge of maxillae gracile; 1 = present, labial margins of maxillae greatly thickened.

12) Nasal size (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C.1; in part Brinkman and Nicholls, 1991, 10): 0 = large, forms most of the preorbital skull surface; 1 = reduced, form only small portion of preorbital skull surface.

13) Frontal contribution to external nares (Lyson and Joyce, 2009a; in part Brinkman and Nicholls, 1991, 10): 0 = absent; 1 = present, frontals contribute to external nares by sending processes between nasals and maxillae; 2 = present, frontals contribute to external nares by sending processes along the midline between the nasals.
Comments: This character is left unordered because the character states are not homologous with one another and do not form a morphocline.

14) Prefrontal exposure on skull roof (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C2.1): = prefrontals contribute significantly to the dorsal skull roof; 1 = prefrontal contribution to the skull roof greatly reduced to a small sliver; 2 = prefrontal contribution to skull roof completely absent.
Comments: These character states form a morphocline and can be run ordered in an analysis.

15) Contribution of frontal to the postorbital portion of the skull roof (Lyson and Joyce, 2009a): 0 = frontals contribution to postorbital portion of skull similar to orbital portion of skull; 1 = frontal contribution to postorbital portion of skull greatly reduced relative to orbital portion.

16) Frontal contribution to orbits (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 20): 0 = large; 1 = reduced to a small process; 2 = absent.

Comments: These character states form a morphocline and can be run ordered in an analysis.

17) Frontal contact with maxilla (Lyson and Joyce, 2009a): 0 = absent, frontals and maxillae separated by prefrontals and/or nasals; 1 = present, frontals and maxillae contact between prefrontals and nasals.

18) Jugal contribution to orbit in adult individuals (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C6.4; Brinkman and Nicholls, 1991, 13): 0 = absent; 1 = reduced; 2 = large.
    Comments: Lyson and Joyce (2009a) note that this can change throughout ontogeny, but a clear phylogenetic signal is noted when scored in adult individuals. The character states form a morphocline and can be run ordered in an analysis.

19) Jugal contribution to labial ridge (Lyson and Joyce, 2009a): 0 = absent; 1 = present, jugal sends a narrow process ventrally that forms the most posterior portion of the labial ridge, just behind the maxilla.

20) Posterodorsal extension of quadratojugal above cavum tympani (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C6.5): 0 = present; 1 = absent.

21) Squamosal contact with parietal (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C6.3): 0 = present, upper temporal emargination shallow; 1 = absent, upper temporal emargination deep.

22) Posterior end of crista supraoccipitalis (Lyson and Joyce, 2009a): 0 = crista supraoccipitalis ends in a point; 1 = crista supraoccipitalis expanded posteriorly and rounded.

23) Posterior thickening of parietal (Lyson and Joyce, 2009a): 0 = absent, parietals thin out toward their posterior edge; 1 = present, parietals greatly thickened at their posterior edge.

24) Posterior extension of the crista supraoccipitalis (Lyson and Joyce, 2009a): 0 = crista extends posterior to occipital condyle; 1 = crista reduced and does not extend posterior to occipital condyle.

25) Foramen prepalatinum (Lyson and Joyce, 2009a): 0 = located within premaxillae; 1 = located within contact of premaxillae and vomer.

26) Posterior edge of vomer (Lyson and Joyce, 2009a): 0 = posterior suture with pterygoids straight or concave; 1 = posterior suture with pterygoids pointed posteriorly or convex.

27) Foramen palatinum posterius (Lyson and Joyce, 2009a): 0 = formed by pterygoid and palatine; 1 = formed entirely by palatine.

28) Midline contact of pterygoids (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C1.1; Brinkman and Nicholls, 1991, 9): 0 = absent; 1 = present, but small; 2 = present and large.
Comments: These character states form a morphocline and can be run ordered in an analysis.

29) Pterygoid contact with basioccipital (Lyson and Joyce, 2009a: 0 = poorly developed; 1 = well developed.

30) Epipterygoid (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C4.2): 0 = present; 1 = absent, or at least not apparent as separate ossification.

31) Basisphenoid size and shape (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 14): 0 = rectangular and long; 1 = pentagonal; 2 = triangular.

32) Contribution of opisthotic to stapedial foramen (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 8); 0 = opisthotic excluded from stapedial foramen; 1 = opisthotic enters stapedial foramen.

33) Splenial (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C6.1): 0 = present and large; 1 = reduced in size; 2 = absent.
Comments: The three character states form a morphocline and can be run ordered in an analysis.

34) Tubercle on posterolateral edge of dentary (Lyson and Joyce, 2009a): 0 = absent; 1 = present.
Comments: Lyson and Joyce (2009a) acknowledge that the formation of this tubercle, which is likely a muscle attachment site, may be age-dependent in regards to size. However, they see that this tuber is taxon specific. I confirm this based on a juvenile mandible fragment from the Mesa Verde Group of Wyoming which possesses a prominent posterodorsal dentary tubercle.

35) Shape of the suture between the dentary and surangular (Lyson and Joyce, 2009a): 0 = strongly Z-shaped; 1 = straight or mostly straight.

36) Scalloping of posterior rim of carapace (Lyson and Joyce, 2009a) 0 = absent, posterior margin of carapace smooth; 1 = present, but light; 2 = present and very distinct.
Comments: These character states form a morphocline and can be run ordered in an analysis.

37) Fifth vertebral scute contributes to posterior margin of carapace (Lyson and Joyce, 2009a): 0 = absent, only the marginals are exposed on the posterior

margin of the carapace; 1 = present.

38) Posterior margin of the carapace **beyond the inguinal buttress** (in part Lyson and Joyce, 2009a): 0 = posterior margin rounded **or flattened**; 1 = **posterior margin subtriangular**.
Comments: This character was amended from that of Lyson and Joyce (2009a) to capture the similarity between *Plesiobaena antiqua* and a similar taxon from the Kaiparowits Formation and the difference between these taxa and baenids with rounded or flat posteriors such as *Denazinemys nodosa*.

39) Presence of carapacial fontanelles in fused or otherwise clearly adult shells (Lyson and Joyce, 2009a): 0 = fenestrae are absent; 1 = fenestrae present between the costals and peripherals.

40) Preneural, supernumerary bone anterior to the first neural (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 1): 0 = absent; 1 = present.

41) Number of peripherals (Lyson and Joyce, 2009a; in part Gaffney and Meylan, 1988, C4.3): 0 = eleven pairs; 1 = twelve pairs.

42) Mesoplastra (Lyson and Joyce, 2009a): 0 = present, in midline contact; 1 = present but midline contact absent.

43) Cervical scutes (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C5.2; Brinkman and Nicholls, 1991, 6): 0 = always single; 1 = sometimes or always divided.
Comments: A subdivided cervical scute is identified when all of the hypothesized subdivisions are located on the nuchal bone (Brinkman, pers. comm.).

44) Vertebral shape (Lyson and Joyce, 2009a): 0 = vertebrals wider than long; 1 = vertebrals longer than wide.

45) Nuchal scute, a supernumerary scute anterior to the first vertebral residing on the nuchal bone (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 7): 0 = absent; 1 = present.

46) Prepleural scute, a supernumerary scute anterior to the first pleural (Lyson and Joyce, 2009a; Gaffney and Meylan, 1988, C5.3; Brinkman and Nicholls, 1991, 3): 0 = absent; 1 = present.

47) Postpleural, a supernumerary scute posterior to the fourth pleural (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 18): 0 = absent; 1 = present.

48) Supramarginal scutes, supernumerary scutes lateral to the pleural series (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 16): 0 = absent; 1 = present.

49) Position of marginal I (Lyson and Joyce, 2009a): **0 = 1/3 or more of marginal I is located on the nuchal bone**; 1 = more than ¾ is positioned on peripheral I. Comments: The first character state was edited because the first marginal of most taxa scored for having a marginal I "placed symmetrically over nuchal/peripheral I suture" was actually positioned more on the first peripheral, but not more than ¾ on it.

50) Anterior plastral lobe (Lyson and Joyce, 2009a; Brinkman and Nicholls, 1991, 4) overall rectangular in outline, anterior rim broadly rounded; 1 = overall triangular, anterior rim tapered to a blunt point; **2 = relatively long, sub-rectangular to sub-triangular in shape, anterior tip rounded**. **Comments: The last character state was added to acknowledge that some specimens of taxa scored as having a rectangular anterior plastral lobe actually possess a sub-triangular anterior plastron. However, this morphology is different than those previously scored as having a sub-triangular anterior plastron in being relatively long and not possessing a blunt tip. These character states do not form a morphocline and are, thus, left unordered.**

51) Epiplastral processes or cleithra (Lyson and Joyce, 2009a): 0 = reduced put present; 1 = absent.

52) Intergular scutes ((Lyson and Joyce, 2009a; in part Brinkman and Nicholls, 1991, 5): 0 = intergulars as large as gulars (by surface area0; 1 = gulars significantly smaller than extragulars or even absent.

53) Medial contact of extragulars (Lyson and Joyce, 2009a; in part Brinkman and Nicholls, 1991, 5) 0 = absent; 1 = present, posterior to the gulars.

54) Placement of anal scute (Lyson and Joyce, 2009a): 0 = anal on xiphiplastron only; 1 = anal scute crosses hypo/xiphiplastral suture.

55) Shape of vertebral scute I (Lyson and Joyce, 2010): 0 = hexagonal, anterior margin as wide as **or wider than** posterior margin; 1 = hexagonal, anterior margin significantly narrower than posterior margin.

56) Shape of xiphiplastron-hypoplastron suture in ventral view (Lyson and Joyce, 2010): 0 = straight; 1 = Z-shaped.

57) Pygal notch (Lyson and Joyce, 2010): 0 = absent; 1 = present.

58) Anterior scallops on carapace (Lyson and Joyce, 2010): 0 = absent; 1 = weakly scalloped anterior quarter of carapace.

59) Shape of vertebral scute II (Lyson and Joyce, 2010): 0 = hexagonal; 1 = square or rectangular.

60) Deep circumnarial sulcus (Lyson and Joyce, 2010, 61): 0 = absent; 1 = present.

61) Shape of processus externus pterygoideus (Lyson and Joyce, 2010, 62): 0 = curved flange that comes to a point laterally; 1 = greatly reduced, rounded.

62) Angle between maxillae (Lyson and Joyce, 2010, 63): 0 = acute angle; 1 = obtuse angle.

63) Jugal thickening or tubercle (Lyson and Joyce, 2010, 64): 0 = jugal thins ventrally; 1 = jugal thickens or has rounded tubercle.

64) Vertical indentation in maxilla anterior to orbit (Lyson and Joyce, 2010, 65): 0 = absent; 1 = present.

65) Shape of posterior portion of basioccipital tubercles in posterior view (Lyson and Joyce, 2010, 66): 0 = blocky; 1 = sagittally horizontal tubercles present.

66) Distance between posterior margin of orbit and anterior portion of cheek emargination (Lyson and Joyce, 2010, 67): 0 = **less than the** diameter of the orbit; 1 = equal to the diameter of the orbit.

67) Shape of the parietal and frontal suture (Lyson and Joyce, 2010, 68): 0 = slightly curved or straight; 1 = greatly curved or notched.

68) Size of mandibular condyle (Lyson and Joyce, 2010, 69); 0 = small; 1 = large. **Comments: To test whether or not this was a valid character, a scatter plot was generated comparing the length of the skull of individual specimens to the area of the mandibular condyle (i.e., the length multiplied by the width of the condyle). This shows that several taxa do plot with a larger mandibular condyle relative to the size of the skull. However, this character was scored differently for *Palatobaena gaffneyi*.**

69) Supraoccipital exposure on the skull roof (Lyson and Joyce, 2010, 70): 0 = absent; 1 = small exposure; 2 = large exposure.
Comments: These character states form a morphocline and can be run ordered in an analysis.

70) Orbit inset into maxilla (Lyson and Joyce, 2010, 71): 0 = absent, floor of orbit flat; 1 = present, orbit appears 'sunk' into dorsal portion of maxilla due to

formation of narrow ridge formed by maxilla along the ventral rim of the orbit.

71) Lateral expansion of parietal (Lyson and Joyce, 2009b, 72; Gaffney, 1982): 0 = combined width of parietals is less than length; 1 = maximum combined width of parietals is greater than length

72) Cheek emargination (Lyson and Joyce, 2011b, 75): 0 = little to no emargination; 1 = deeply emarginated, reaching at least to ventral margin of orbit.

73) Nasal and frontal suture shape (Lyson and Joyce, 2011b, 77): 0 = relatively straight; 1 = convex anteriorly with frontals extending in between nasals.

74) Anterior dorsal skull roof and underlying premaxillae relationship (Lyson and Joyce, 2011b, 78): 0 = dorsal skull roof extends anteriorly as far as **or beyond** the underlying premaxillae; 1 = dorsal skull roof does not reach anterior edge of premaxillae.

75) Hooked mandible (Lyson and Joyce, 2011b, 79): 0 = absent; 1 = present.

76) Shape of anterior portion of skull (Lyson and Joyce, 2011b, 81): 0 = rectangular snout; 1 = pointed snout; **2 = rounded snout**.

77) Size of cavum tympanum (Lyson and Joyce, 2011b, 83): 0 = small, significantly smaller than the orbit; 1 = large, approximately the same size as the orbit.

78) Size of the external narial opening(s) (Lyson and Joyce, 2011b, 84): 0 = small, significantly smaller than the orbit; 1 = large, approximately the same size as **or large than** the orbit.

79) Articular surfaces on cervical vertebrae (Lyson and Joyce, 2011b, 87): 0 = no, all **acoelous**; 1 = yes, some vertebrae are procoelous, opisthocoelous, or biconvex.

80) Shell sculpturing (Lyson and Joyce, 2011b, 90): 0 = smooth to slightly sculptured; 1 = distinct tubercles for sculpturing, "Glyptops-like" sculpturing; 2 = large, distinct knobs; **3 = vermicular texture with anastomosing pits, "Neurankylus-type" sculpturing**.

81) Distinct thickening of plastron medial to axillary buttress (Lyson and Joyce, 2011b, 95): 0 = absent; 1 = present.

82) Development of axillary buttress (Lyson and Joyce, 2011b, 96): 0 = poorly developed with the buttress only weakly extending onto the costals; 1 = well developed with the buttress extending onto the costals, **articulating with the first dorsal rib** (forming a distinct neck shield).

83) Extent of inguinal buttress (Lyson and Joyce, 2011b, 97): 0 = poorly developed with the buttress not extending onto the middle of the costals (ends on the distal portion of costal); 1 = well developed with the buttress reaching the middle of the costals.

84) Plastral lobe dimensions (Lyson and Joyce, 2011b, 101): 0 = posterior lobe larger than anterior lobe; 1 = anterior lobe larger than posterior lobe.

85) Posterior portion of carapace (Lyson and Joyce, 2011b, 105): 0 = wide space between carapace and plastron; 1 = extends ventrally to approximately the level of the plastron.

86) Temporal emargination (Larson et al., in press, 71): 0 = does not expose otic capsule; 1 = stapedial foramen exposed in dorsal view; 2 = anterior to anterior margin of otic capsule.
Comments: These character states form a morphocline and can be run ordered in an analysis.

87) Nuchal morphology (in part Larson et al., in press, 73, 88): 0 = small nuchal projection present; 1 = nuchal margin even with first peripherals; 2 = nuchal slightly recessed; 3 = nuchal deeply emarginated.
Comments: these character states form a morphocline and can be run ordered in an analysis.

88) Skull ornamentation (in part Lyson and Joyce, 2011b, 89; in part Larson et al., in press, 74): 0 = pustulose, "Glyptops-like"; 1 = no sculpturing or rugose.

89) Cervical scute shape, if a single scale is present (in part Larson et al., in press, 87): 0 = wider than long; 1 = longer than wide.
Rectangular anterior plastral lobe (if this character state is present for character 50): 0 = rounded anterior margin; 1 = truncated anterior margin.

90) Rectangular anterior plastral lobe (if this character state is present for character 50): 0 = rounded anterior margin; 1 = truncated anterior margin.

91) Plastron extends beyond anterior margin of carapace in dorsal view: 0 = absent; 1 = present.

92) Shape of posterior lobe of plastron: 0 = sub-rectangular; 1 = plastron sub-triangular, tapering posteriorly anterior to femoral-anal sulcus, rectangular in shape posterior to this sulcus.

93) Mid-dorsal keel on carapace: 0 = absent; 1 = present only posteriorly; 2 = present along entire length of carapace.

94) Nodular texture (if this state is present for character 80): 0 = tightly packed and prominent; 1 = widely scattered and subdued.

95) Number of marginal scute pairs: 0 = twelve; 1 = thirteen.

96) Rostral constriction: 0 = absent, skull somewhat oblong in shape; 1 = near middle of dorsal orbit; 2 = near anterior margin of orbit.
Comments: The rostral constriction is defined as the point where the skull roof in a wedge-shaped skull ceases to taper and deflects anteriorly. The placement of the rostral constriction further forward on the skull allows the orbits to face forward.

97) Lateral expansion of the nasals: 0 = absent; 1 = present.

98) Cavum tympanum: 0 = circular; 1 = oval, taller than wide.

99) Height of coronoid process: 0 = low, not significantly taller than ramus of dentary; 1 = significantly taller than ramus of dentary, robust.

100) Fifth costal narrows distally: 0 = absent; 1 = present.

101) Lateral margin of carapace rounded and upturned (dorsolateral gutters, sensu Larson et al., in press, 86): 0 = absent; 1 = present.

102) Second and third vertebrals (Larson et al., in press, 90): 0 = do not narrow anteriorly; 1 = narrow anteriorly.

103) Fourth marginal resembling asymmetrical trapezoid, with widest point positioned posteriorly (Larson et al., in press, 92): 0 = absent; 1 = present.

104) Intergular shape (Larson et al., in press, 100): 0 = rectangular with large intergular-humeral sulcus; 1 = heart-shaped with little or no intergular-humeral sulcus; 2 = semicircular, no humeral contact.

105) Intergular-gular sulci (Larson et al., in press, 102): 0 = straight; 1 = curved.

106) Inframarginals (Larson et al., in press, 103): 0 = narrower; 1 = roughly equal to; 2 = wider than ventral exposure of marginals.
Comments: The character states form a logical morphocline and may be run ordered in an analysis.

APPENDIX C

CHARACTER-TAXON MATRIX

	1	2	3	4	5	6	7	8	9	10
Glyptops plicatulus	0	1	0	0	0	0	0	0	?	0
Arundelemys dardeni	0	1	0	0	0	0	0	0	1	0
Neurankylus wyomingensis	?	?	?	?	?	?	?	?	?	?
Neurankylus eximius	?	?	?	?	?	?	?	?	?	?
Neurankylus baueri	1	0	0	0	0	0	?	?	?	?
Milk River *Neurankylus*	?	?	?	?	?	?	?	?	?	?
Neurankylus **sp. nov. A**	?	?	?	?	?	?	?	?	?	?
Neurankylus **sp. nov. B**	?	?	?	?	?	?	?	?	?	?
Hell Creek *Neurankylus*	?	0	0	0	?	0	?	?	?	?
Trinitichelys hiatti	0	1	0	0	0	0	1	0	0	0
Thescelus insiliens	?	?	?	?	?	?	?	?	?	?
Thescelus rapiens	?	?	?	?	?	?	?	?	?	?
Thescelus hemispherica	?	?	?	?	?	?	?	?	?	?
Hayemys latifrons	1	0	0	0	0	0	?	?	?	?
Plesiobaena antiqua	1	1	0	0	0	0	1	1	0	1
Peckemys brinkman	1	1	0	0	0	0	1	1	1	1
Cedrobaena putorius	1	1	0	0	0	1	1	1	1	1
Gamerabaena sonsalla	?	0	0	0	0	1	1	1	1	0
Palatobaena cohen	2	0	0	0	0	1	2	1	1	1
Palatobaena bairdi	2	0	0	0	0	1	2	1	1	1
Palatobaena gaffneyi	2	1	0	0	1	1	2	1	1	1
"Denazinemys" ornata	?	?	?	?	?	?	?	?	?	?
Denazinemys nodosa	1	1	?	0	?	0	?	?	?	0
Boremys pulchra	1	1	1	0	0	0	?	?	?	?
Boremys grandis	?	?	?	?	?	?	?	?	?	?
Eubaena cephalica	1	1	1	0	0	1	2	1	0	0
Stygiochelys estesi	1	1	0	1	0	0	1	1	?	0
Chisternon undatum	1	1	0	1	0	0	1	1	?	0
Baena arenosa	1	1	0	1	0	0	1	1	0	0
Goleremys mckennai	1	1	0	0	1	0	1	1	0	1

"Baena" hatcheri	?	?	?	?	?	?	?	?	?	?
"Baena" hayi	?	?	?	?	?	?	?	?	?	?
Pig-nosed taxon	1	1	0	0	0	1	1	1	?	1

	11	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Glyptops plicatulus	0	0	0	0	?	0	0	0	0	0
Arundelemys dardeni	0	0	0	0	1	1	0	0	0	?
Neurankylus wyomingensis	?	?	?	?	?	?	?	?	?	?
Neurankylus eximius	?	?	?	0	?	?	?	?	?	?
Neurankylus baueri	0	0	0	0	0	1	0	?	?	?
Milk River *Neurankylus*	?	?	?	?	?	?	?	?	?	?
Neurankylus **sp. nov. A**	?	?	?	?	?	?	?	?	?	?
Neurankylus **sp. nov. B**	?	?	?	?	?	?	?	?	?	?
Hell Creek *Neurankylus*	?	?	?	0	0	1	?	?	?	?
Trinitichelys hiatti	0	0	0	1	0	0	0	0	0	0
Thescelus insiliens	?	?	?	?	?	?	?	?	?	?
Thescelus rapiens	?	?	?	?	?	?	?	?	?	?
Thescelus hemispherica	?	?	?	?	?	?	?	?	?	?
Hayemys latifrons	0	0	0	0	0	2	1	1	?	0
Plesiobaena antiqua	0	1	0&2	1	1	0	1	0	1	0
Peckemys brinkman	0	?	?	1	1	1	1	1	1	0
Cedrobaena putorius	1	?	?	1	1	1	1	1	0	0
Gamerabaena sonsalla	1	1	1	1	0	2	1	0	1	?
Palatobaena cohen	1	1	2	2	0	1	1	1	1	0
Palatobaena bairdi	1	1	2	2	1	1	1	2	1	0
Palatobaena gaffneyi	1	1	2	2	1	1	1	1	1	0
"Denazinemys" ornata	?	?	?	?	?	?	?	?	?	?
Denazinemys nodosa	?	?	?	1	1	0	1	0	0	0
Boremys pulchra	0	1	0	1	1	0	1	0	0	0
Boremys grandis	?	?	?	?	?	?	?	?	?	?
Eubaena cephalica	0	1	0	1	1	0	1	0	0	0
Stygiochelys estesi	1	1	?	1	1	0	1	1	0	0
Chisternon undatum	0	1	1	2	1	0	1	2	0	1
Baena arenosa	0	1	?	2	1	0	1	2	0	1
Goleremys mckennai	1	1	0	2	1	0	1	2	0	0
"Baena" hatcheri	?	?	?	?	?	?	?	?	?	?
"Baena" hayi	?	?	?	?	?	?	?	?	?	?
Pig-nosed taxon	0	0	0	?	?	?	?	?	?	0

	21	22	23	24	25	26	27	28	29	30
Glyptops plicatulus	?	?	0	?	0	0	0	0	0	0
Arundelemys dardeni	?	?	0	?	0	0	0	2	1	0
Neurankylus wyomingensis	?	?	?	?	?	?	?	?	?	?
Neurankylus eximius	?	?	?	?	?	?	?	?	?	?
Neurankylus baueri	0	1	0	0	?	?	?	2	1	?
Milk River *Neurankylus*	?	?	?	?	?	?	?	?	?	?
Neurankylus **sp. nov. A**	?	?	?	?	?	?	?	?	?	?
Neurankylus **sp. nov. B**	?	?	?	?	?	?	?	?	?	?
Hell Creek *Neurankylus*	?	?	?	?	?	?	?	?	1	?
Trinitichelys hiatti	0	0	0	0	1	0	0	2	1	?
Thescelus insiliens	?	?	?	?	?	?	?	?	?	?
Thescelus rapiens	?	?	?	?	?	?	?	?	?	?
Thescelus hemispherica	?	?	?	?	?	?	?	?	?	?
Hayemys latifrons	1	?	0	?	?	?	1	2	1	?
Plesiobaena antiqua	1	0	0	0	1	1	0	2	1	1
Peckemys brinkman	1	0	0	0	1	1	0	2	1	?
Cedrobaena putorius	1	1	1	0	1	0	0	2	1	?
Gamerabaena sonsalla	?	?	1	?	?	1	0	2	1	1
Palatobaena cohen	1	1	0	0	1	1	0	2	1	?
Palatobaena bairdi	1	1	1	0	1	1	0	2	1	1
Palatobaena gaffneyi	1	1	1	0	1	1	0	1	1	1
"Denazinemys" ornata	?	?	?	?	?	?	?	?	?	?
Denazinemys nodosa	1	0	0	0	?	0	1	1	1	?
Boremys pulchra	1	0	0	0	?	?	0	2	1	1
Boremys grandis	?	?	?	?	?	?	?	?	?	?
Eubaena cephalica	1	0	0	0	0	0	0	1&2	1	1
Stygiochelys estesi	1	0	0	?	0	1	1	1	1	1
Chisternon undatum	0	0	1	1	0	0	0&1	1	1	1
Baena arenosa	0	1	1	1	?	1	0	1	1	1
Goleremys mckennai	1	0	0	0	1	0	0	2	1	1
"Baena" hatcheri	?	?	?	?	?	?	?	?	?	?
"Baena" hayi	?	?	?	?	?	?	?	?	?	?
Pig-nosed taxon	1	0	0	1	1	?	?	2	1	?

	31	32	33	34	35	36	37	38	39	40
Glyptops plicatulus	0	0	0	0	?	0	0	0	0	0
Arundelemys dardeni	0	1	?	?	?	?	?	?	?	?
Neurankylus wyomingensis	?	?	?	?	?	0	0	0	0	?
Neurankylus eximius	2	1	?	?	?	0	0	0	0	0
Neurankylus baueri	2	?	2	0	?	1	0	0	0	0
Milk River *Neurankylus*	?	1	?	?	?	0	?	?	0	?
Neurankylus **sp. nov. A**	?	?	?	?	?	0	0	0	0	?
Neurankylus **sp. nov. B**	?	?	?	?	?	0	0	0	0	?
Hell Creek *Neurankylus*	2	1	?	?	?	0	0	0	0	?
Trinitichelys hiatti	1	1	?	?	?	?	?	?	0	?
Thescelus insiliens	?	?	?	?	?	0	0	0	0	?
Thescelus rapiens	?	?	?	?	?	?	?	?	0	?
Thescelus hemispherica	?	?	?	?	?	0	0	0	0	?
Hayemys latifrons	1	0	?	?	?	?	?	?	?	?
Plesiobaena antiqua	1	0	0	1	0	0&1	1	1	1	0
Peckemys brinkman	1	0	0	1	1	1	?	?	?	0
Cedrobaena putorius	1	0	?	?	?	?	?	?	?	?
Gamerabaena sonsalla	1	0	?	?	?	?	?	?	?	?
Palatobaena cohen	1	0	0	1	1	0	?	?	?	0
Palatobaena bairdi	1	0	0	1	1	?	?	?	?	?
Palatobaena gaffneyi	1	?	?	1	?	?	?	?	?	?
"Denazinemys" ornata	?	?	?	?	?	1	1	0	0	?
Denazinemys nodosa	1	0	?	0	?	2	1	0	0	1
Boremys pulchra	1	0	1	0	0	2	1	0	0	1
Boremys grandis	?	?	?	?	?	2	1		0	1
Eubaena cephalica	1&2	0	2	0	0	1	1	0	0	?
Stygiochelys estesi	1	1	?	1	0	?	?	?	0	?
Chisternon undatum	1	1	2	0	0	1	1	?	0	0
Baena arenosa	1	1	2	1	0	1	1	0	0	0
Goleremys mckennai	1	?	?	?	?	?	?	?	0	?
"Baena" hatcheri	?	?	?	?	?	?	?	?	0	0
"Baena" hayi	?	?	?	?	?	1	1	0	0	?
Pig-nosed taxon	1	?	?	1	?	2	1	1	0	?

	41	42	43	44	45	46	47	48	49	50
Glyptops plicatulus	0	0	0	0	0	0	0	0	0	0
Arundelemys dardeni	?	?	?	?	?	?	?	?	?	?
Neurankylus wyomingensis	?	?	?	0	?	?	0	0	?	?
Neurankylus eximius	0	0	0	0	0	0	0	0	0	0
Neurankylus baueri	?	0	0	0	0	0	0	0	0	0
Milk River *Neurankylus*	?	?	0	0	0	0	0	0	?	0
Neurankylus **sp. nov. A**	?	?	0	0	0	0	0	0	?	0
Neurankylus **sp. nov. B**	?	?	0	0	0	0	0	0	?	0
Hell Creek *Neurankylus*	?	?	0	0	0	0	0	0	?	0
Trinitichelys hiatti	?	?	0	0	0	0	?	0	0	0
Thescelus insiliens	?	?	0	0	0	0	0	0	?	0
Thescelus rapiens	?	?	?	0	0	0	?	0	?	?
Thescelus hemispherica	?	?	0	0	0	0	0	0	?	0
Hayemys latifrons	?	?	?	?	?	?	?	?	?	?
Plesiobaena antiqua	1	0	0	0	0	0	0	0	1	1
Peckemys brinkman	1	0	0	0	0	0	0	0	0	1
Cedrobaena putorius	?	?	?	?	?	?	?	?	?	?
Gamerabaena sonsalla	?	?	?	?	?	?	?	?	?	?
Palatobaena cohen	?	0	0	0	0	0	0	0	1	1
Palatobaena bairdi	?	?	?	?	?	?	?	?	?	?
Palatobaena gaffneyi	?	?	?	?	?	?	?	?	?	?
"Denazinemys" ornata	?	?	0	0	0	0	0	0	?	0
Denazinemys nodosa	?	0	1	1	0	1	0	0	0	2
Boremys pulchra	1	0	0&1	0&1	1	1	1	1	0	2
Boremys grandis	1	0	1	1	1	1	1	1	0	0
Eubaena cephalica	?	?	0	0	0	0	0	0	?	?
Stygiochelys estesi	?	?	1	1	1	1	?	0	?	2
Chisternon undatum	1	0	1	1	1	1	0	0	0	0
Baena arenosa	1	1	1	1	0	1	0	0	0	0
Goleremys mckennai	?	?	?	?	?	?	?	?	?	?
"Baena" hatcheri	?	0	1	0	1	1	?	0	?	0
"Baena" hayi	?	?	1	0	0	0	0	0	?	1
Pig-nosed taxon	?	?	0	0	0	0	0	0	?	1

	51	52	53	54	55	56	57	58	59	60
Glyptops plicatulus	0	?	0	?	0	0	0	0	0	0
Arundelemys dardeni	?	?	?	?	?	?	?	?	?	0
Neurankylus wyomingensis	?	?	?	?	?	?	0	?	?	?
Neurankylus eximius	1	0	0	0	0	?	0	0	0	?
Neurankylus baueri	1	0	0	0	0	0	0	0	0	0
Milk River *Neurankylus*	1	0	0	?	0	?	0	0	0	?
Neurankylus **sp. nov. A**	1	0	0	?	0	?	0	0	0	?
Neurankylus **sp. nov. B**	1	0	0	?	0	?	0	0	0	?
Hell Creek *Neurankylus*	1	0	0	?	0	?	0	0	0	?
Trinitichelys hiatti	1	0	0	0	0	?	?	0	0	0
Thescelus insiliens	1	?	?	?	0	?	0	0	0	?
Thescelus rapiens	?	?	?	?	0	?	?	0	0	?
Thescelus hemispherica	1	1	1	?	0	?	0	0	0	?
Hayemys latifrons	?	?	?	?	?	?	?	?	?	0
Plesiobaena antiqua	1	1	1	1	0	1	1	0	1	0
Peckemys brinkman	1	1	1	?	0	?	?	0	0	0
Cedrobaena putorius	?	?	?	?	?	?	?	?	?	0
Gamerabaena sonsalla	?	?	?	?	?	?	?	?	?	0
Palatobaena cohen	1	1	1	1	1	1	?	0	1	1
Palatobaena bairdi	?	?	?	?	?	?	?	?	?	1
Palatobaena gaffneyi	?	?	?	?	?	?	?	?	?	1
"Denazinemys" ornata	1	1	1	?	0	?	1	0	0	?
Denazinemys nodosa	1	0	1	1	1	1	1	1	1	0
Boremys pulchra	1	0	1	0	1	1	1	1	1	0
Boremys grandis	1	1	1	0	1	1	1	1	1	?
Eubaena cephalica	?	1	1	?	0	?	1	0	?	0
Stygiochelys estesi	?	1	1	?	1	?	?	0	1	0
Chisternon undatum	1	1	1	1	1	1	1	0	1	0
Baena arenosa	1	0	1	1	1	1	1	0	1	0
Goleremys mckennai	?	?	?	?	?	?	?	?	?	0
"Baena" hatcheri	1	0	0	1	1	1	?	?	1	?
"Baena" hayi	1	1	1	?	1	?	1	0	1	?
Pig-nosed taxon	1	1	1	1	0	1	1	0	0	0

	61	62	63	64	65	66	67	68	69	70
Glyptops plicatulus	0	0	0	0	0	-	?	0	0	0
Arundelemys dardeni	0	0	0	0	0	?	1	0	0	0
Neurankylus wyomingensis	?	?	?	?	?	?	?	?	?	?
Neurankylus eximius	?	?	?	?	?	?	?	?	?	?
Neurankylus baueri	?	0	0	0	0	?	0	1	0	0
Milk River *Neurankylus*	?	?	?	?	?	?	?	?	?	?
Neurankylus **sp. nov. A**	?	?	?	?	?	?	?	?	?	?
Neurankylus **sp. nov. B**	?	?	?	?	?	?	?	?	?	?
Hell Creek *Neurankylus*	?	?	?	?	?	?	?	?	?	?
Trinitichelys hiatti	0	0	0	0	0	0	0	0	?	0
Thescelus insiliens	?	?	?	?	?	?	?	?	?	?
Thescelus rapiens	?	?	?	?	?	?	?	?	?	?
Thescelus hemispherica	?	?	?	?	?	?	?	?	?	?
Hayemys latifrons	?	0	0	0	0	?	0	0	?	0
Plesiobaena antiqua	0	0	0	0	0	0	0	0	1	0
Peckemys brinkman	0	0	0	0	0	0	0	0	1	0
Cedrobaena putorius	0	0	0	0	0	0	0	0	0	1
Gamerabaena sonsalla	?	0	0	1	?	1	1	?	?	1
Palatobaena cohen	1	1	1	0	1	1	1	1	1	1
Palatobaena bairdi	1	1	1	0	1	1	1	1	2	1
Palatobaena gaffneyi	1	1	1	0	?	1	1	0	2	1
"Denazinemys" ornata	?	?	?	?	?	?	?	?	?	?
Denazinemys nodosa	0	0	0	0	0	0	1	0	1	0
Boremys pulchra	?	0	0	0	0	0	0	?	1	0
Boremys grandis	?	?	?	?	?	?	?	?	?	?
Eubaena cephalica	0	0	0	0	0	1	1	0	1	0
Stygiochelys estesi	?	0	0	0	0	1	0	0	1	0
Chisternon undatum	0	0	0	0	0	0	1	0	1	0
Baena arenosa	0	0	0	0	0	0	0	0	1	0
Goleremys mckennai	1	0	0	0	0	1	0	1	?	0
"Baena" hatcheri	?	?	?	?	?	?	?	?	?	?
"Baena" hayi	?	?	?	?	?	?	?	?	?	?
Pig-nosed taxon	0	0	?	0	1	0	?	0	0	1

	71	72	73	74	75	76	77	78	79	80
Glyptops plicatulus	0	0	0	0	0	1	0	0	0	1
Arundelemys dardeni	?	?	1	0	?	0	?	0	?	?
Neurankylus wyomingensis	?	?	?	?	?	?	?	?	?	1
Neurankylus eximius	?	?	?	?	?	?	?	1	?	3
Neurankylus baueri	1	?	0	0	1	0	?	?	?	3
Milk River *Neurankylus*	?	?	?	?	?	?	?	?	?	3
Neurankylus **sp. nov. A**	?	?	?	?	?	?	?	?	?	3
Neurankylus **sp. nov. B**	?	?	?	?	?	?	?	?	?	3
Hell Creek *Neurankylus*	?	?	?	?	?	?	?	?	?	3
Trinitichelys hiatti	0	0	0	0	?	0	0	0	?	1
Thescelus insiliens	?	?	?	?	?	?	?	?	?	0
Thescelus rapiens	?	?	?	?	?	?	?	?	?	0
Thescelus hemispherica	?	?	?	?	?	?	?	?	?	0
Hayemys latifrons	0	1	0	0	?	0	1	1	?	?
Plesiobaena antiqua	0	1	0	1	0	1	1	1	1	0
Peckemys brinkman	0	1	?	1	?	1	1	1	?	?
Cedrobaena putorius	0	1	?	1	?	1	1	0	?	?
Gamerabaena sonsalla	?	?	0	?	?	?	?	1	?	?
Palatobaena cohen	1	1	1	1	0	2	1	1	?	0
Palatobaena bairdi	0	1	1	1	0	2	1	1	?	?
Palatobaena gaffneyi	0	1	?	1	?	2	1	1	?	?
"Denazinemys" ornata	?	?	?	?	?	?	?	?	?	2
Denazinemys nodosa	0	1	?	?	?	?	1	?	?	2
Boremys pulchra	0	1	0	?	0	1	1	0	0	2
Boremys grandis	?	?	?	?	?	?	?	?	?	2
Eubaena cephalica	0	1	1	1	0	1	1	0	?	0
Stygiochelys estesi	1	1	?	1	?	1	1	0	?	0
Chisternon undatum	1	1	0	1	0	1	1	0&1	1	0
Baena arenosa	1	1	?	1	0	1	1	1	1	0&2
Goleremys mckennai	0	1	0	1	?	1	1	0	?	?
"Baena" hatcheri	?	?	?	?	?	?	?	?	?	0
"Baena" hayi	?	?	?	?	?	?	?	?	?	0
Pig-nosed taxon	?	1	0	0	1	0	1	1	?	0

	81	82	83	84	85	86	87	88	89	90
Glyptops plicatulus	0	0	0	1	1	?	1	0	0	0
Arundelemys dardeni	?	?	?	?	?	?	?	0	?	?
Neurankylus wyomingensis	?	?	?	?	?	?	?	?	?	?
Neurankylus eximius	?	?	?	0	1	?	2	1	1	1
Neurankylus baueri	1	1	1	0	1	0	2	1	1	1
Milk River *Neurankylus*	?	?	?	0	?	?	2	?	?	1
Neurankylus **sp. nov. A**	1	1	1	1	1	?	2	?	1	0
Neurankylus **sp. nov. B**	?	1	1	1	1	?	?	?	1	0
Hell Creek *Neurankylus*	1	1	1	?	1	?	2	1	0	0
Trinitichelys hiatti	0	1	1	?	?	1	2	0	0	0
Thescelus insiliens	?	1	?	0	0	?	3	?	0	?
Thescelus rapiens	?	?	?	?	?	?	3	?	?	?
Thescelus hemispherica	?	1	1	?	0	?	3	?	0	1
Hayemys latifrons	?	?	?	?	?	2	?	1	?	?
Plesiobaena antiqua	1	1	1	0	0	2	0	1	0	-
Peckemys brinkman	1	1	1	0	0	2	1	1	0	-
Cedrobaena putorius	?	?	?	?	?	2	?	1	?	?
Gamerabaena sonsalla	?	?	?	?	?	?	?	1	?	?
Palatobaena cohen	1	1	1	0	0	2	0	1	0	-
Palatobaena bairdi	?	?	?	?	?	?	?	1	?	?
Palatobaena gaffneyi	?	?	?	?	?	?	?	1	?	?
"Denazinemys" ornata	1	?	?	0	0	?	1	?	0	0
Denazinemys nodosa	1	1	1	0	0	2	1	1	-	-
Boremys pulchra	1	1	1	0	0	2	1	1	0	-
Boremys grandis	1	1	1	?	0	?	1	?	-	0
Eubaena cephalica	?	1	?	?	?	2	2	1	0	0
Stygiochelys estesi	?	?	?	?	?	2	1	1	-	0
Chisternon undatum	1	1	1	0	?	0	1	1	-	0
Baena arenosa	1	1	1	0	0	0	1	1	-	0
Goleremys mckennai	?	?	?	?	?	?	?	1	?	?
"Baena" hatcheri	1	1	1	0	?	?	1	?	-	0
"Baena" hayi	1	1	1	0	0	?	0	?	-	-
Pig-nosed taxon	1	1	1	0	0	2	1	1	0	-

	91	92	93	94	95	96	97	98	99	100
Glyptops plicatulus	0	0	0	-	0	0	0	?	0	0
Arundelemys dardeni	?	?	?	?	?	0	0	?	?	?
Neurankylus wyomingensis	?	0	?	-	?	?	?	?	?	?
Neurankylus eximius	0	0	1	-	0	?	?	?	?	0
Neurankylus baueri	0	0	2	-	0	1	0	?	1	0
Milk River *Neurankylus*	0	0	?	-	?	?	?	?	?	?
Neurankylus **sp. nov. A**	0	0	1	-	1	?	?	?	?	?
Neurankylus **sp. nov. B**	0	0	1	-	0	?	?	?	?	?
Hell Creek *Neurankylus*	0	0	2	-	?	?	?	?	?	?
Trinitichelys hiatti	0	?	?	-	?	0	0	0	?	?
Thescelus insiliens	1	?	?	-	?	?	?	?	?	?
Thescelus rapiens	1	?	?	-	?	?	?	?	?	?
Thescelus hemispherica	1	?	1	-	?	?	?	?	?	?
Hayemys latifrons	?	?	?	?	?	1	1	0	?	?
Plesiobaena antiqua	0	0	2	-	0	2	0	0	1	0
Peckemys brinkman	0	0	?	-	?	1	?	1	1	?
Cedrobaena putorius	?	?	?	?	?	2	?	0	?	?
Gamerabaena sonsalla	?	?	?	?	?	?	0	?	?	?
Palatobaena cohen	0	0	?	-	?	-	0	0	1	0
Palatobaena bairdi	?	?	?	?	?	-	0	?	1	?
Palatobaena gaffneyi	?	?	?	?	?	-	0	?	1	?
"Denazinemys" ornata	0	?	1	0	1	?	?	?	?	?
Denazinemys nodosa	0	1	2	0	1	2	?	0	0	1
Boremys pulchra	0	1	2	1	?	2	0	?	0	1
Boremys grandis	0	1	0	1	?	?	?	?	?	?
Eubaena cephalica	0	1	0	-	?	1	0	0	0	?
Stygiochelys estesi	0	?	?	-	?	2	?	0	?	?
Chisternon undatum	0	1	0	-	?	2	0	0	1	0
Baena arenosa	0	0	0	-	?	2	0	1	1	0
Goleremys mckennai	?	?	?	?	?	2	?	1	?	?
"Baena" hatcheri	0	1	0	-	1	?	?	?	?	?
"Baena" hayi	0	0	1	-	0	?	?	?	?	?
Pig-nosed taxon	0	0	2	-	?	1	1	0	1	0

	101	102	103	104	105	106
Glyptops plicatulus	0	0	?	0	0	0
Arundelemys dardeni	?	?	?	?	?	?
Neurankylus wyomingensis	1	1	?	?	?	0
Neurankylus eximius	1	1	0	1	1	1
Neurankylus baueri	1	1	1	0	0	0
Milk River *Neurankylus*	1	1	1	0	0	0
Neurankylus **sp. nov. A**	?	1	0	?	?	0
Neurankylus **sp. nov. B**	1	1	1	0	1	0
Hell Creek *Neurankylus*	1	1	1	1	1	?
Trinitichelys hiatti	0	1	0	0	0	0
Thescelus insiliens	0	1	?	?	?	?
Thescelus rapiens	0	1	1	?	?	?
Thescelus hemispherica	0	1	1	?	?	1
Hayemys latifrons	?	?	?	?	?	?
Plesiobaena antiqua	0	0	0	-	-	2
Peckemys brinkman	0	0	0	-	-	2
Cedrobaena putorius	?	?	?	?	?	?
Gamerabaena sonsalla	?	?	?	?	?	?
Palatobaena cohen	0	0	0	-	-	?
Palatobaena bairdi	?	?	?	?	?	?
Palatobaena gaffneyi	?	?	?	?	?	?
"Denazinemys" ornata	?	?	?	?	?	?
Denazinemys nodosa	0	0	0	2	1	2
Boremys pulchra	0	0	0	2	1	?
Boremys grandis	0	0	?	2	1	1
Eubaena cephalica	?	0	?	2	1	?
Stygiochelys estesi	0	0	?	2	1	1
Chisternon undatum	0	0	0	2	1	?
Baena arenosa	0	0	0	2	2	2
Goleremys mckennai	?	?	?	?	?	?
"Baena" hatcheri	?	0	?	0	0	?
"Baena" hayi	0	0	?	-	-	0
Pig-nosed taxon	0	0	0	-	-	1

Question marks (?) represent missing data.

Dashes (-) represent characters that do not apply to a taxon.

APPENDIX D

TEMPORAL AND GEOGRAPHIC RANGES

Taxon	Lower*	Upper*	Median*	Ranges**
Glyptops plicatulus	Jurassic	Jurassic	Jurassic	-
Arundelemys dardeni	115	121	118.0	Appalachia
Neurankylus wyomingensis	87.88	85.85	86.9	MT
Neurankylus eximius	77.24	75.55	76.4	MT,AB
Neurankylus baueri	74.17	61.7	67.9	NM
Milk River *Neurankylus*	84.5	83.5	84.0	AB
Neurankylus sp. nov. A	76.24	75.36	75.8	UT
Neurankylus sp. nov. B	76.24	75.36	75.8	UT
Hell Creek *Neurankylus*	66.71	65.5	66.1	MT
Neurankylus spp.	87.88	61.7	74.8	NM,UT,MT,AB
Trinitichelys hiatti	111	105	108.0	TX
Thescelus insiliens	66.71	65.5	66.1	MT
Thescelus rapiens	73.16	72.4	72.8	NM
Thescelus hemispherica	74.3	73.1	73.7	NM
Thescelus spp.	74.3	65.5	69.9	-
Hayemys latifrons	66.71	65.5	66.1	MT
Plesiobaena antiqua	77.24	75.55	76.4	MT,AB
Peckemys brinkman	66.71	57.2	62.0	MT,CO
Cedrobaena putorius	66.71	64.2	65.5	MT
Gamerabaena sonsalla	66.71	65.5	66.1	MT
Palatobaena cohen	66.71	64.2	65.5	MT
Palatobaena bairdi	Cenozoic	Cenozoic	Cenozoic	MT
Palatobaena gaffneyi	Cenozoic	Cenozoic	Cenozoic	-
"Denazinemys" ornata	74.3	73.1	73.7	NM
Denazinemys nodosa	76.6	72.4	74.5	TX,NM,UT
Boremys pulchra	77.24	75.55	76.4	MT,AB
Boremys grandis	76.24	73.1	74.7	NM,UT
Eubaena cephalica	66.71	64.2	65.5	MT
Stygiochelys estesi	66.71	64.2	65.5	MT,CO
Chisternon undatum	Cenozoic	Cenozoic	Cenozoic	-

Baena arenosa	Cenozoic	Cenozoic	Cenozoic	-
Goleremys mckennai	Cenozoic	Cenozoic	Cenozoic	-
Baena hatcheri	66.71	65.5	66.1	MT
"Baena" hayi	66.71	65.5	66.1	MT
Pig-nosed taxon	76.6	76.14	76.4	UT

*Lower, upper, and median ages in Ma.

**Geographic ranges include Appalachia, Texas (TX), New Mexico (NM), Utah (UT), Montana/Wyoming/Dakotas (MT), and Alberta (AB).

APPENDIX E

GEOGRAPHIC DISPERSAL CONSTRAINTS

Appalachia	E
Texas	T
San Juan Basin, New Mexico	N
Kaiparowits Basin, Utah	K
Denver Basin, Colorado	C
MT-WY-SD-ND	M
Southern Alberta	A

For strict consensus trees, where the genera *Neurankylus* and *Thescelus* are collapsed into single terminal taxa:

	E	T	N	K	C	M	A
E	-	+	+	+	+	+	X
T	+	-	+	+	+	X	X
N	+	+	-	+	+	+	X
K	+	+	+	-	+	+	X
C	+	+	+	+	-	+	+
M	+	X	+	+	+	-	+
A	X	X	X	X	+	+	-

Maximum number of ranges: 5.

For all most parsimonious trees, where all terminal taxa are species:

	E	T	N	K	C	M	A
E	-	+	+	+	+	+	X
T	+	-	+	+	+	X	X
N	+	+	-	+	+	X	X
K	+	+	+	-	+	+	X
C	+	+	+	+	-	+	+
M	+	X	X	+	+	-	+
A	X	X	X	X	+	+	-

Maximum number of ranges: 3.

APPENDIX F

DISPERAL-EXTINCTION-CLADOGENESIS ANALYSIS RESULTS

Arundelemys dardeni + Boremys pulchra

Analysis	*Arundelemys* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Appalachia	TX+NM+MT	-56.64	0.2157
	Appalachia	TX+NM+MT+AB	-56.74	0.1941
	Appalachia	TX+NM+UT+MT	-57.03	0.1454
	Appalachia	TX+UT+MT+AB	-57.22	0.1198
	Appalachia	TX+UT+MT	-57.48	0.09286
Strict Consensus Strict Temporal Calibration	Appalachia	TX	-63.03	0.1427
	Appalachia	TX+NM+MT+AB	-63.52	0.0878
	Appalachia	TX+UT+MT+AB	-63.52	0.08768
	Appalachia	TX+NM+UT+AB	-63.67	0.07563
	Appalachia	NM+UT+MT+AB	-63.71	0.07231
MPT #1 Smoothed Temporal Calibration	Appalachia	Appalachia+TX+MT	-85.55	0.4807
	Appalachia	TX+UT	-86.71	0.1515
	Appalachia	Appalachia+TX	-87.53	0.0666
MPT #1 Strict Temporal Calibration	Appalachia	Appalachia	-87.52	0.1379
	Appalachia	TX	-87.75	0.1097
	Appalachia	Appalachia+TX	-88.04	0.08205
	Appalachia	TX+UT	-88.25	0.06686
MPT #11 Smoothed Temporal Calibration	Appalachia	Appalachia+TX+MT	-90.47	0.4011
	Appalachia	TX+UT	-94.22	0.1892
MPT #11 Strict Temporal Calibration	Appalachia	Appalachia	-93.18	0.1243
	Appalachia	TX	-93.24	0.1173
	Appalachia	Appalachia+TX	-93.59	0.08286
	Appalachia	TX+UT	-93.65	0.07825
	Appalachia	Appalachia+TX+MT	-94.03	0.05311

	Appalachia	Appalachia+TX+UT	-94.03	0.05304
MPT#18 Smoothed Temporal Calibration	Appalachia	Appalachia+TX+MT	-87.9	0.4544
	Appalachia	TX+UT	-88.9	0.1672
MPT #18 Strict Temporal Calibration	Appalachia	Appalachia	-89.89	0.134
	Appalachia	TX	-90.13	0.1127
	Appalachia	Appalachia+TX	-90.46	0.08147
	Appalachia	TX+UT	-90.58	0.07184
	Appalachia	Appalachia+TX+MT	-90.9	0.05235
	Appalachia	Appalachia+TX+UT	-90.94	0.05051

Trinitichelys hiatti + Boremys pulchra

Analysis	*Trinitichelys* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Texas	TX+NM+MT+AB	-57.18	0.1251
	Texas	NM+MT	-57.22	0.1202
	Texas	TX+NM+MT	-57.45	0.09579
	Texas	TX+NM+UT+MT	-57.47	0.09374
Strict Consensus Strict Temporal Calibration	Texas	TX+NM+UT+MT+AB	-62.02	0.3906
	Texas	NM+UT+MT+AB	-63.12	0.1309
	Texas	Texas	-63.32	0.1071
MPT #1 Smoothed Temporal Calibration	Texas	Appalachia+MT	-85.69	0.4204
	Texas	Utah	-87.25	0.08818
	Texas	UT+MT	-87.34	0.08009
MPT #1 Strict Temporal Calibration	Texas	Texas	-87.42	0.1534
	Texas	Appalachia+MT	-88.09	0.07803
	Texas	UT+MT	-88.34	0.06116
MPT #11 Smoothed Temporal Calibration	Texas	Appalachia+MT	-90.52	0.3808
	Texas	Utah	-91.69	0.1175
	Texas	UT+MT	-91.98	0.08812
MPT #11 Strict Temporal Calibration	Texas	Texas	-92.99	0.1501
	Texas	Appalachia+MT	-93.63	0.07928
	Texas	UT+MT	-93.75	0.07027
	Texas	Utah	-93.87	0.06235
MPT#18 Smoothed Temporal Calibration	Texas	Appalachia+MT	-88.05	0.3915
	Texas	UT	-89.39	0.1024

MPT #18 Strict	Texas	Texas	-89.88	0.1448
Temporal	Texas	Appalachia+MT	-90.47	0.08086
Calibration	Texas	UT+MT	-90.63	0.0684

Neurankylus spp. + *Boremys pulchra*

Analysis	*Neurankylus* branch	*Boremys* branch	Log Likeli-hood	Relative Probability
Strict	TX+UT+MT+AB	Montana	-57.85	0.06422
Consensus	TX+NM+MT+AB	Montana	-57.85	0.06422
Smoothed	TX+NM+UT+MT+AB	Montana	-57.99	0.05553
Temporal	TX+NM+MT+AB	New Mexico	-58.02	0.05433
Calibration				
Strict	TX+NM+UT+MT+AB	New Mexico	-62.29	0.2982
Consensus	TX+NM+UT+MT+AB	Montana	-62.33	0.2878
Strict	TX+NM+UT+MT+AB	Utah	-63.06	0.1384
Temporal				
Calibration				
MPT #1	Montana	Appalachia+MT	-85.98	0.3117
Smoothed	Montana	Montana	-87.04	0.1087
Temporal	Montana	Appalachia+NM+MT	-87.19	0.09337
Calibration				
MPT #1	Montana	NM+UT+MT	-86.84	0.2725
Strict	Montana	Montana	-87.94	0.09109
Temporal	Montana	UT+MT	-88.04	0.08263
Calibration	Montana	NM+UT	-88.17	0.07212
MPT #11	Montana	Appalachia+MT	-90.89	0.2627
Smoothed	Montana	Appalachia+NM+MT	-91.46	0.1491
Temporal	Utah	Utah	-91.95	0.09045
Calibration				
MPT #11	Montana	NM+UT+MT	-92.35	0.2861
Strict	Montana	UT+MT	-93.56	0.0852
Temporal	Montana	Montana	-93.62	0.08049
Calibration	UT+MT+AB	Utah	-93.72	0.07283
	Montana	NM+UT	-93.74	0.07093
MPT#18	Montana	Appalachia+MT	-88.36	0.2856
Smoothed	Montana	Montana	-89.29	0.1129
Temporal	Montana	Appalachia+NM+MT	-89.56	0.08639
Calibration	Utah	Utah	-89.61	0.08218
MPT #18	Montana	NM+UT+MT	-89.25	0.2717
Strict	Montana	Montana	-90.49	0.07922
Temporal	Montana	UT+MT	-90.51	0.0776
Calibration	UT+MT+AB	Utah	-90.57	0.07308
	Montana	NM+UT	-90.6	0.07063

Neurankylus wyomingensis + Neurankylus baueri

Analysis	*N. wyomingensis* branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-85.14	0.7282
	Montana	UT+MT	-86.74	0.1458
MPT #1 Strict Temporal Calibration	Montana	Montana	-85.82	0.7545
	Montana	UT+MT+AB	-87.99	0.08628
	Montana	UT+MT+AB	-88.34	0.06084
	Montana	UT+MT	-88.7	0.04263
	Montana	Alberta	-90.51	0.006992
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-89.93	0.6866
	Montana	UT+MT	-91.47	0.1472
	Utah	Utah	-92.56	0.04918
	Montana	Utah	-92.97	0.03267
MPT #11 Strict Temporal Calibration	Montana	Montana	-91.43	0.7161
	Montana	UT+MT+AB	-93.25	0.1163
	Montana	UT+MT	-93.5	0.09095
	Montana	MT+AB	-94.51	0.03281
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-87.5	0.679
	Montana	UT+MT	-89.13	0.1328
	Utah	Utah	-90.42	0.03636
	Montana	Utah	-90.62	0.02999
	Montana	UT+MT+AB	-90.93	0.02183
MPT #18 Strict Temporal Calibration	Montana	Montana	-88.29	0.7121
	Montana	UT+MT+AB	-90.08	0.1188
	Montana	UT+MT	-90.47	0.08068
	Montana	MT+AB	-91.11	0.04231

Neurankylus **spp. nov. +** *Neurankylus baueri* **(MTP #1 only)**

Analysis	*Neurankylus* sp. nov. branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-85.79	0.3777
	Utah	Montana	-86.11	0.2751
	Utah	UT+MT	-87.39	0.07647
	Utah	MT+AB	-87.39	0.07617
MPT #1 Strict Temporal Calibration	Utah	MT+AB	-86.73	0.3048
	Utah	UT+MT+AB	-87.71	0.1143
	Montana	Montana	-87.89	0.09547
	Montana	MT+AB	-87.91	0.09397

| | Montana | Alberta | -87.95 | 0.09026 |
| | UT+MT | Alberta | -88.09 | 0.0784 |

Neurankylus sp. nov. A + *Neurankylus* sp. nov. B (MPT #1 only)

Analysis	*Neurankylus* sp. nov. A branch	*Neurankylus* sp. nov. B branch	Log likeli-hood	Relative probability
MPT #1 Smoothed Temporal Calibration	Utah	Utah	-85.02	81.96
	UT+MT	Utah	-87.56	0.0643
	Utah	UT+MT	-87.56	0.0643
	Appalachia+UT	Utah	-90.26	0.004335
MPT #1 Strict Temporal Calibration	Utah	Utah	-85.55	0.9944

Neurankylus eximius + *Neurankylus baueri* (MPT #1 only)

Analysis	*N. eximius* branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-85.34	0.5927
	Alberta	MT+AB	-87.64	0.05932
	Montana	MT+AB	-87.78	0.05169
MPT #1 Strict Temporal Calibration	Alberta	Alberta	-86.87	0.2664
	MT+AB	Alberta	-87.23	0.1855
	Alberta	MT+AB	-87.69	0.1162
	Montana	Montana	-87.78	0.1067
	Montana	MT+AB	-87.9	0.09507

Hell Creek Fm *Neurankylus* sp. + *Neurankylus baueri* (MPT #1 only)

Analysis	Hell Creek *Neurankylus* sp. branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-85.87	0.3501
	Montana	Alberta	-86.88	0.1272
	Montana	CO+AB	-87.15	0.09697
	Montana	MT+AB	-87.34	0.0806
MPT #1 Strict Temporal Calibration	Alberta	Alberta	-86.08	0.5844
	Alberta	Alberta	-87.83	0.1019
	MT+AB	Alberta	-88.14	0.0743
	Montana	Montana	-88.23	0.06794
	Montana	MT+AB	-88.28	0.06458

Neurankylus **sp. nov. A +** *Neurankylus baueri* **(MPT #11 & #18)**

Analysis	*Neurankylus* sp. nov. branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-90.52	0.3789
	Utah	UT+MT	-90.88	0.2662
	Utah	Montana	-91.87	0.09849
	Utah	Utah	-92.07	0.08035
MPT #11 Strict Temporal Calibration	Utah	UT+MT+AB	-91.74	0.5252
	Montana	Montana	-93.17	0.1253
	Utah	UT+MT	-93.38	0.1019
	Utah	MT+AB	-93.53	0.08797
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-88.15	0.3549
	Utah	UT+MT	-88.7	0.2042
	Utah	Montana	-89.4	0.1011
	Utah	UT+MT+AB	-89.44	0.09776
MPT #18 Strict Temporal Calibration	Utah	UT+MT+AB	-88.79	0.4327
	Utah	MT+AB	-89.38	0.2391
	Montana	MT+AB	-90.63	0.06847
	Montana	Montana	-90.76	0.05998

Hell Creek Fm *Neurankylus* **sp. +** *Neurankylus baueri* **(MPT #11 only)**

Analysis	Hell Creek *Neurankylus* branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-90.36	0.4448
	Montana	UT+MT	-91.02	0.2312
	Montana	UT+MT+AB	-91.63	0.1249
MPT #11 Strict Temporal Calibration	Montana	UT+MT+AB	-91.96	0.4221
	Montana	Montana	-92.84	0.1748
	Montana	MT+AB	-93.53	0.08756
	Alberta	UT+MT+AB	-93.54	0.08676
	Montana	UT+MT	-93.73	0.07212

Neurankylus **sp. nov. B +** *Neurankylus baueri* **(MPT #11 only)**

Analysis	*Neurankylus* sp. nov. B branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #11	Utah	MT+AB	-91.1	0.2129

Smoothed Temporal Calibration	Montana	Montana	-91.21	0.1898
	Utah	Montana	-91.57	0.1334
	Utah	UT+MT	-91.89	0.09654
	Utah	UT+MT+AB	-91.95	0.0919
MPT #11 Strict Temporal Calibration	Utah	MT+AB	-92.21	0.3281
	Utah	UT+MT+AB	-92.99	0.1505
	Montana	Montana	-93.08	0.1376
	UT+MT	Alberta	-93.45	0.09476

Neurankylus **sp. nov. B +** *Neurankylus baueri* **(MPT #18 only)**

Analysis	*Neurankylus* sp. nov. B branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-88.11	0.3681
	UT+MT	Alberta	-89.23	0.1197
	UT+MT	Montana	-89.47	0.09422
MPT #18 Strict Temporal Calibration	UT+MT+AB	Alberta	-89.57	0.198
	UT+MT	Alberta	-89.83	0.1522
	MT+AB	Alberta	-90.01	0.1275
	Montana	Alberta	-90.09	0.1178

Neurankylus **sp. nov. B + Hell Creek Fm** *Neurankylus* **sp. (MPT #18 only)**

Analysis	*Neurankylus* sp. nov. B branch	Hell Creek *Neurankylus* branch	Log likeli-hood	Relative probability
MPT #11 Smoothed Temporal Calibration	Utah	Montana	-87.79	0.5091
	Montana	Montana	-89.09	0.1378
	Utah	UT+MT	-89.59	0.08377
MPT #11 Strict Temporal Calibration	Utah	Montana	-88.92	0.3779
	Utah	MT+AB	-89.54	0.2046
	Utah	UT+MT+AB	-90.18	0.1075
	Utah	UT+MT	-90.34	0.09131
	Utah	Utah	-90.54	0.07502

Neurankylus eximius **+** *Neurankylus baueri* **(MPT #11 & #18)**

Analysis	*N. eximius* branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #11 Smoothed Temporal Calibration	MT+AB	Alberta	-90.69	0.3215
	Montana	Montana	-91.92	0.09331

	Alberta	Alberta	-92.34	0.06183
MPT #11 Strict Temporal Calibration	MT+AB	Alberta	-92.33	0.2906
	Alberta	Alberta	-92.5	0.2466
	Montana	Alberta	-93.61	0.08123
	UT+MT+AB	Alberta	-93.69	0.07485
MPT#18 Smoothed Temporal Calibration	MT+AB	Alberta	-88.48	0.2543
	Alberta	Alberta	-88.6	0.2264
	Montana	Montana	-89.05	0.1434
MPT #18 Strict Temporal Calibration	Alberta	Alberta	-88.35	0.67.11
	MT+AB	Alberta	-90.02	0.1261

Milk River Fm *Neurankylus* sp. + *Neurankylus baueri*

Analysis	*N. wyomingensis* branch	*N. baueri* branch	Log likeli-hood	Relative probability
MPT #1 Smoothed Temporal Calibration	Alberta	Colorado	-86.73	0.1484
	Alberta	Montana	-86.74	0.1462
	Alberta	Alberta	-86.92	0.1224
	Alberta	UT+MT	-87.03	0.11
MPT #1 Strict Temporal Calibration	Alberta	Alberta	-85.78	0.7894
	Alberta	Montana	-87.88	0.09629
	Alberta	MT+AB	-88.49	0.05254
	Alberta	UT+MT	-89.26	0.024.7
MPT #11 Smoothed Temporal Calibration	Alberta	Alberta	-90.83	0.2776
	Alberta	Colorado	-91.19	0.1942
	Alberta	UT+MT	-91.62	0.1261
	Alberta	NM+CO	-92.06	0.0816
	Alberta	Montana	-92.3	0.06405
MPT #11 Strict Temporal Calibration	Alberta	Alberta	-91.45	0.7057
	Alberta	Montana	-93.22	0.1193
	Alberta	UT_MT	-93.76	0.07006
	Alberta	MT+AB	-93.92	0.05943
MPT#18 Smoothed Temporal Calibration	Alberta	Alberta	-88.29	0.3079
	Alberta	Colorado	-88.74	0.1967
	Alberta	NM+CO	-89.57	0.08549
	Alberta	Montana	-89.72	0.07343
	Alberta	UT+MT	-89.91	0.06073
MPT #18 Strict Temporal Calibration	Alberta	Alberta	-88.1	0.8628
	Alberta	Montana	-90.82	0.05684
	Alberta	MT+AB	-91.49	0.02916
	Alberta	UT+MT	-91.77	0.02204

Thescelus **spp.** + *Boremys pulchra*

Analysis	*Thescelus* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict	Montana	Montana	-56.07	0.3817
Consensus	New Mexico	New Mexico	-56.32	0.297
Smoothed	New Mexico	NM+MT	-57.13	0.1318
Temporal	Montana	NM+MT	-57.13	0.1317
Calibration	New Mexico	NM+UT+MT	-59.65	0.01062
Strict	New Mexico	NM+UT+MT	-62.38	0.2737
Consensus	Montana	NM+UT+MT	-62.38	0.2737
Strict Temporal	New Mexico	NM+MT	-62.68	0.2019
Calibration	Montana	NM+MT	-62.68	0.2019
	Montana	Montana	-86.79	0.1391
MPT #1	Appalachia+MT	Montana	-87.22	0.09057
Smoothed	Utah	Utah	-87.44	0.07257
Temporal	Appalachia	Appalachia+MT	-87.6	0.06207
Calibration	Montana	Appalachia+MT	-87.68	0.05748
	New Mexico	Appalachia+NM+MT	-87.68	0.0573
MPT #1 Strict	New Mexico	NM+UT+MT	-86.09	0.581
Temporal	Utah	NM+UT+MT	-87.4	0.1557
Calibration	Montana	NM+UT+MT	-87.74	0.1106
	New Mexico	Appalachia+NM+MT	-91.31	0.1724
MPT #11	New Mexico	NM+UT+MT	-91.37	0.08942
Smoothed	Utah	Utah	-92.11	0.07771
Temporal	Montana	Montana	-92.34	0.06419
Calibration	Appalachia+MT	Montana	-92.52	0.05164
	Appalachia	Appalchia+MT	-92.54	0.05015
MPT #11 Strict	New Mexico	NM+UT+MT	-91.32	0.7977
Temporal	Utah	NM+UT+MT	-93.86	0.06292
Calibration				
MPT#18	Montana	Montana	-89.02	0.1482
Smoothed	Utah	Utah	-89.54	0.08817
Temporal	Appalachia+MT	Montana	-89.59	0.09377
Calibration				
MPT #18 Strict	New Mexico	NM+UT+MT	-88.49	0.5839
Temporal	Utah	NM+UT+MT	-89.79	0.1596
Calibration	Montana	NM+UT+MT	-90.12	0.1147

Thescelus insiliens + Thescelus rapiens (**MPT #1 & #18**)

Analysis	*T. insiliens* branch	*T. rapiens* branch	Log likeli-hood	Relative probability
MPT #1 Smoothed Temporal Calibration	Appalachia+MT	New Mexico	-86.8	0.1381
	Montana	Appalachia+NM	-87.19	0.09295
	UT+MT	New Mexico	-87.44	0.07287
MPT #1 Strict Temporal Calibration	New Mexico	New Mexico	-86.84	0.2742
	UT+NM	New Mexico	-87.6	0.1273
	Utah	New Mexico	-87.77	0.108
MPT#18 Smoothed Temporal Calibration	Appalachia+MT	New Mexico	-89.16	0.1284
	Montana	Appalachia+NM	-89.56	0.08643
	UT+MT	New Mexico	-89.71	0.07429
MPT #18 Strict Temporal Calibration	New Mexico	New Mexico	-89.28	0.2642
	UT+NM	New Mexico	-89.97	0.1326
	Utah	New Mexico	-90.13	0.1127

Thescelus hemispherica + Thescelus rapiens (**MPT #1 & #18**)

Analysis	*T. hemispherica* branch	*T. rapiens* branch	Log likeli-hood	Relative probability
MPT #1 Smoothed Temporal Calibration	New Mexico	New Mexico	-84.99	0.8398
	New Mexico	Appalachia+NM	-88.36	0.02896
	Appalachia+NM	New Mexico	-88.42	0.02729
MPT #1 Strict Temporal Calibration	New Mexico	New Mexico	-85.56	0.9856
MPT#18 Smoothed Temporal Calibration	New Mexico	New Mexico	-87.29	0.826
	New Mexico	Appalachia+NM	-90.68	0.02804
	Appalachia+NM	New Mexico	-90.74	0.02643
MPT #18 Strict Temporal Calibration	New Mexico	New Mexico	-87.97	0.9854

Thescelus rapiens + Thescelus insiliens (**MPT #11 only**)

Analysis	*T. rapiens* branch	*T. insiliens* branch	Log likeli-hood	Relative probability
MPT #11 Smoothed Temporal Calibration	New Mexico	New Mexico	-90.61	0.348
	New Mexico	Appalachia+NM+MT	-91.38	0.1614
	New Mexico	NM+UT+MT	-91.92	0.09349
	New Mexico	Appalachia+NM	-92.05	0.08211
	New Mexico	NM+UT	-92.14	0.07509

| | New Mexico | New Mexico | -91.41 | 0.7311 |
| MPT #11 Strict Temporal Calibration | New Mexico | NM+UT | -93.7 | 0.07395 |

Thescelus hemispherica + Thescelus insiliens (**MPT #11 only**)

Analysis	*T. rapiens* branch	*T. insiliens* branch	Log likeli-hood	Relative probability
MPT #11 Smoothed Temporal Calibration	New Mexico	Appalachia+MT	-91.39	0.1591
	Appalachia+NM	Montana	-91.67	0.1198
	New Mexico	UT+MT	-91.7	0.1161
MPT #11 Strict Temporal Calibration	New Mexico	New Mexico	-91.44	0.7093
	New Mexico	Utah	-93.91	0.06021

"Denazinemys" ornata + Boremys pulchra

Analysis	*"Denazinemys" ornata* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	New Mexico	Montana	-55.31	0.8132
	Montana	Montana	-57.47	0.09352
	New Mexico	UT+MT	-58.05	0.05257
Strict Consensus Strict Temporal Calibration	New Mexico	UT+MT	-61.65	0.5668
	New Mexico	Montana	-61.96	0.4166
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-86.16	0.261
	Appalachia	Montana	-87.09	0.103
	Appalachia +NM	Montana	-87.4	0.07596
	New Mexico	UT+Montana	-87.6	0.06196
	Utah	Utah	-87.64	0.0598
MPT #1 Strict Temporal Calibration	New Mexico	UT+MT	-85.79	0.7829
	New Mexico	NM+UT+MT	-88.29	0.06388
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-91.48	0.1451
	Appalachia+NM	Montana	-91.6	0.1292
	New Mexico	UT+MT	-91.8	0.1053
	Appalachia	Montana	-92.06	0.0816
	New Mexico	Appalachia+MT	-92.19	0.07113
	Utah	Utah	-92.35	0.06111
MPT #11 Strict Temporal Calibration	New Mexico	UT+MT	-91.28	0.835
	New Mexico	NM+UT+MT	-93.98	0.05629
MPT#18	Montana	Montana	-88.43	0.2664

Smoothed Temporal Calibration	Appalachia	Montana	-89.46	0.09495
MPT #18 Strict Temporal Calibration	New Mexico New Mexico	UT+MT NM+UT+MT	-88.17 -90.79	0.8001 0.05862

Hayemys latifrons + Boremys pulchra

Analysis	*Hayemys* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana UT+MT	Montana Montana	-55.22 -57.54	0.8882 0.08729
Strict Consensus Strict Temporal Calibration	UT+MT Montana	Montana Montana	-61.64 -61.98	0.573 0.4082
MPT #1 Smoothed Temporal Calibration	Montana UT+MT	Montana Montana	-85.26 -86.72	0.6416 0.1493
MPT #1 Strict Temporal Calibration	UT+MT Utah Montana	Montana Montana Montana	-86.06 -87.2 -88.3	0.5988 0.1901 0.06335
MPT #11 Smoothed Temporal Calibration	Montana UT+MT	Montana Montana	-90.14 -91.25	0.5564 0.1821
MPT #11 Strict Temporal Calibration	UT+MT Utah	Montana Montana	-91.51 -92.88	0.6616 0.1685
MPT#18 Smoothed Temporal Calibration	Montana UT+MT	Montana Montana	-87.57 -89.01	0.6339 0.1493
MPT #18 Strict Temporal Calibration	UT+MT Utah	Montana Montana	-88.42 -89.95	0.6249 0.182

Pig-nosed taxon + *Hayemys latifrons*

Analysis	Pig-nosed taxon branch	*Hayemys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Utah	Montana	-55.14	0.965
Strict Consensus Strict Temporal Calibration	Utah	Montana	-61.08	1
MPT #1 Smoothed Temporal Calibration	Utah	Montana	-85.56	0.4781
	Montana	Montana	-86.49	0.1886
	Utah	UT+MT	-87.33	0.08128
MPT #1 Strict Temporal Calibration	Utah	Montana	-86.17	0.5338
	Utah	Utah	-87.05	0.2219
	Utah	UT+MT	-87.45	0.1483
MPT #11 Smoothed Temporal Calibration	Utah	Montana	-90.28	0.4807
	Montana	Montana	-91.35	0.1659
MPT #11 Strict Temporal Calibration	Utah	Montana	-91.63	0.5862
	Utah	Utah	-92.76	0.1894
	Utah	UT+MT	-93.02	0.1468
MPT#18 Smoothed Temporal Calibration	Utah	Montana	-87.89	0.4576
	Montana	Montana	-88.76	0.193
	Utah	UT+MT	-89.61	0.08237
	UT+MT	Montana	-89.96	0.05784
MPT #18 Strict Temporal Calibration	Utah	Montana	-88.53	0.5617
	Utah	Utah	-89.52	0.2078
	Utah	UT+MT	-89.9	0.1431

Peckemys brinkman + Boremys pulchra

Analysis	*Peckemys* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana	Montana	-55.12	0.9833
Strict Consensus Strict Temporal Calibration	Montana	Montana	-61.09	0.9883
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-84.89	0.93.06
	CO+MT	Montana	-88.98	0.01554
	UT+MT	Montana	-89.23	0.01212
MPT #1 Strict Temporal Calibration	Montana	Montana	-85.61	0.9311
	UT+MT	Montana	-89.29	0.02368
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-89.63	0.9218
	CO+MT	Montana	-93.69	0.01602
	UT+MT	Montana	-93.81	0.01416

MPT #11 Strict Temporal Calibration	Montana UT+MT	Montana Montana	-91.15 -95.05	0.9453 0.01927
MPT#18 Smoothed Temporal Calibration	Montana CO+MT UT+MT	Montana Montana Montana	-87.19 -91.28 -91.37	0.9258 0.01552 0.01416
MPT #18 Strict Temporal Calibration	Montana UT+MT	Montana Montana	-88.02 -91.78	0.9371 0.0217

Palatobaena cohen + Boremys pulchra

Analysis	*Palatobaena* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana	Montana	-55.11	0.9941
Strict Consensus Strict Temporal Calibration	Montana	Montana	-61.09	0.9886
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-84.83	0.9879
MPT #1 Strict Temporal Calibration	Montana	Montana	-85.56	0.9842
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-89.56	0.9875
MPT #11 Strict Temporal Calibration	Montana	Montana	-91.11	0.9866
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-87.12	0.987
MPT #18 Strict Temporal Calibration	Montana	Montana	-87.97	0.9853

Cedrobaena putorius + Palatobaena cohen

Analysis	*Cedrobaena* branch	*Palatobaena* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana	Montana	-55.1	0.9995
Strict Consensus Strict Temporal Calibration	Montana	Montana	-61.08	1
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-84.83	0.9855
MPT #1 Strict Temporal Calibration	Montana	Montana	-85.55	0.9929

MPT #11 Smoothed Temporal Calibration	Montana	Montana	-89.57	0.9875
MPT #11 Strict Temporal Calibration	Montana	Montana	-91.1	0.9945
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-87.13	0.987
MPT #18 Strict Temporal Calibration	Montana	Montana	-87.96	0.9936

Gamerabaena sonsalla + Palatobaena cohen

Analysis	*Gamera-baena* branch	*Palatobaena* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana	Montana	-55.1	0.9996
Strict Consensus Strict Temporal Calibration	Montana	Montana	-61.08	1
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-84.83	0.99
MPT #1 Strict Temporal Calibration	Montana	Montana	-85.54	0.999
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-89.56	0.9902
MPT #11 Strict Temporal Calibration	Montana	Montana	-91.1	0.9992
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-87.12	0.989
MPT #18 Strict Temporal Calibration	Montana	Montana	-87.95	0.9991

Plesiobaena antiqua + Boremys pulchra

Analysis	*Plesiobaena* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana	Montana	-55.14	0.9673
Strict Consensus Strict Temporal Calibration	Montana	Montana	-61.12	0.9607
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-84.86	0.9614
MPT #1 Strict Temporal Calibration	Montana	Montana	-85.58	0.961

	Montana	Montana	-89.59	0.9612
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-89.59	0.9612
MPT #11 Strict Temporal Calibration	Montana	Montana	-91.14	0.9621
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-87.15	0.9606
MPT #18 Strict Temporal Calibration	Montana	Montana	-87.99	0.9615

"Baena" hayi + Boremys pulchra

Analysis	_"Baena" hayi_ branch	_Boremys_ branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana	Montana	-55.11	0.9912
Strict Consensus Strict Temporal Calibration	Montana	Montana	-61.09	0.9905
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-84.83	0.9858
MPT #1 Strict Temporal Calibration	Montana	Montana	-95.56	0.9846
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-89.57	0.9858
MPT #11 Strict Temporal Calibration	Montana	Montana	-91.11	0.9859
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-87.13	0.9852
MPT #18 Strict Temporal Calibration	Montana	Montana	-87.97	0.9852

Stygiochelys estesi + Boremys pulchra

Analysis	_Stygiochelys_ branch	_Boremys_ branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana	Montana	-55.15	0.9521
Strict Consensus Strict Temporal Calibration	Montana	Montana	-61.13	0.9547
MPT #1 Smoothed Temporal Calibration	Montana Montana	Montana UT+MT	-84.87 -88.28	0.9461 0.0314
MPT #1 Strict Temporal Calibration	Montana Montana	Montana UT+MT	-85.6 -88.97	0.9428 0.03232

MPT #11 Smoothed Temporal Calibration	Montana Montana	Montana UT+MT	-89.61 -93.01	0.9461 0.03146
MPT #11 Strict Temporal Calibration	Montana Montana	Montana UT+MT	-89.61 -93.01	0.9461 0.03146
MPT#18 Smoothed Temporal Calibration	Montana Montana	Montana UT+MT	-87.17 -90.57	0.9456 0.0313
MPT #18 Strict Temporal Calibration	Montana Montana	Montana UT+MT	-88.01 -91.39	0.9439 0.03218

Stygiochelys estesi + Baena hatcheri

Analysis	*Stygiochelys* branch	*Baena* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana CO+MT	Montana Montana	-55.23 -57.34	0.8848 0.1069
Strict Consensus Strict Temporal Calibration	CO+MT Montana	Montana Montana	-61.58 -62.03	0.606 0.3861
MPT #1 Smoothed Temporal Calibration	Montana CO+MT	Montana Montana	-84.94 -87.32	0.8883 0.08242
MPT #1 Strict Temporal Calibration	CO+MT Montana Colorado	Montana Montana Montana	-86.21 -86.39 -89.9	0.5155 0.4278 0.01283
MPT #11 Smoothed Temporal Calibration	Montana CO+MT	Montana Montana	-89.67 -92.05	0.8886 0.08239
MPT #11 Strict Temporal Calibration	CO+MT Montana	Montana Montana	-91.73 -91.95	0.5288 0.4259
MPT#18 Smoothed Temporal Calibration	Montana CO+MT	Montana Montana	-87.23 -89.63	0.8877 0.0843
MPT #18 Strict Temporal Calibration	CO+MT Montana Colorado	Montana Montana Montana	-88.61 -88.8 -92.33	0.5181 0.4288 0.01254

Eubaena cephalica + Boremys pulchra

Analysis	*Eubaena* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	Montana Montana Montana Montana	Montana NM+MT UT+MT MT+AB	-55.37 -57.65 -57.66 -58.7	0.7689 0.07799 0.07785 0.02749
Strict Consensus Strict Temporal Calibration	Montana Montana	Montana NM+MT	-61.34 -63.63	0.7747 0.078

	Montana	UT+MT	-63.64	0.07771
	Montana	MT+AB	-64.37	0.03742
MPT #1 Smoothed Temporal Calibration	Montana	Montana	-85.1	0.7542
	Montana	UT+MT	-86.74	0.1461
	Montana	MT+AB	-88.39	0.02815
	Montana	UT+MT+AB	-88.55	0.02385
MPT #1 Strict Temporal Calibration	Montana	Montana	-85.82	0.7594
	Montana	UT+MT	-87.44	0.1505
	Montana	MT+AB	-88.88	0.03544
	Montana	UT+MT+AB	-89.05	0.02982
MPT #11 Smoothed Temporal Calibration	Montana	Montana	-89.83	0.754
	Montana	UT+MT	-91.47	0.1762
	Montana	MT+AB	-93.12	0.02833
	Montana	UT+MT+AB	-93.28	0.02394
MPT #11 Strict Temporal Calibration	Montana	Montana	-91.37	0.7626
	Montana	UT+MT	-92.98	0.1521
	Montana	MT+AB	-94.43	0.03572
MPT#18 Smoothed Temporal Calibration	Montana	Montana	-87.39	0.7531
	Montana	UT+MT	-89.04	0.1449
	Montana	MT+AB	-90.68	0.02813
	Montana	UT+MT+AB	-90.84	0.02392
MPT #18 Strict Temporal Calibration	Montana	Montana	-88.22	0.7606
	Montana	UT+MT	-89.84	0.1512
	Montana	MT+AB	-91.28	0.03568
	Montana	UT+MT+AB	-91.46	0.02988

Denazinemys nodosa + Boremys pulchra

Analysis	*Denazinemys* branch	*Boremys* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	New Mexico	NM+MT	-56.26	0.3149
	Utah	UT+MT	-56.26	0.3148
	New Mexico	NM+MT+AB	-57.43	0.09725
	Utah	UT+MT+AB	-57.43	0.09719
Strict Consensus Strict Temporal Calibration	New Mexico	NM+MT	-62.14	0.3465
	Utah	UT+MT	-62.14	0.3463
	New Mexico	NM+MT+AB	-63.03	0.143
	Utah	UT+MT+AB	-63.03	0.1428
MPT #1 Smoothed Temporal Calibration	Utah	UT+MT	-85.39	0.5672
	Utah	UT+MT+AB	-86.36	0.2141
	New Mexico	NM+UT+MT	-87.5	0.06847
	Utah	NM+UT+MT	-87.54	0.06601
MPT #1 Strict Temporal Calibration	Utah	UT+MT	-85.95	0.6631
	Utah	UT+MT+AB	-86.82	0.278

	Montana	Montana	-89.4	0.02111
MPT #11 Smoothed Temporal Calibration	Utah	UT+MT	-90.12	0.5667
	Utah	UT+MT+AB	-91.09	0.2145
	New Mexico	NM+UT+MT	-92.23	0.06858
	Utah	NM+UT+MT	-92.27	0.0661
MPT #11 Strict Temporal Calibration	Utah	UT+MT	-91.5	0.6717
	Utah	UT+MT+AB	-92.37	0.2795
MPT#18 Smoothed Temporal Calibration	Utah	UT+MT	-87.69	0.5626
	Utah	UT+MT+AB	-88.65	0.2139
	New Mexico	NM+UT+MT	-89.79	0.06844
	Utah	NM+UT+MT	-89.83	0.06588
MPT #18 Strict Temporal Calibration	Utah	UT+MT	-88.36	0.6664
	Utah	UT+MT+AB	-89.23	0.2764
	Montana	Montana	-91.97	0.01797

Boremys grandis + Boremys pulchra

Analysis	*B. grandis* branch	*B. pulchra* branch	Log likeli-hood	Relative probability
Strict Consensus Smoothed Temporal Calibration	New Mexico	MT+AB	-56.47	0.2552
	Utah	MT+AB	-56.47	0.2551
	NM+UT	Montana	-56.56	0.234
	New Mexico	Montana	-57.17	0.1266
	Utah	Montana	-57.17	0.1266
Strict Consensus Strict Temporal Calibration	New Mexico	MT+AB	-62.19	0.3312
	Utah	MT+AB	-62.19	0.3308
	New Mexico	Montana	-62.94	0.1557
	Utah	Montana	-62.94	0.1556
MPT #1 Smoothed Temporal Calibration	Utah	MT+AB	-85.6	0.4588
	NM+UT	Montana	-86.1	0.2773
	Utah	Montana	-86.46	0.1943
	NM+UT+MT	Montana	-88.87	0.01739
	Utah	UT+MT+AB	-88.89	0.01708
MPT #1 Strict Temporal Calibration	Utah	MT+AB	-86.02	0.6186
	Utah	Montana	-86.81	0.2804
	UT+MT	Montana	-88.84	0.03691
	NM+UT	Montana	-89.03	0.03051
MPT #11 Smoothed Temporal Calibration	Utah	MT+AB	-90.33	0.4598
	NM+UT	Montana	-90.83	0.2779
	Utah	Montana	-91.19	0.1944
	NM+UT+MT	Montana	-93.63	0.01698
	Utah	UT+MT+AB	-93.65	0.01666
MPT #11 Strict Temporal Calibration	Utah	MT+AB	-91.57	0.6247
	Utah	Montana	-92.35	0.2848

	UT+MT	Montana	-94.5	0.03339
	NM+UT	Montana	-94.56	0.03132
MPT#18 Smoothed Temporal Calibration	Utah	MT+AB	-87.89	0.4567
	NM+UT	Montana	-88.4	0.2753
	Utah	Montana	-88.76	0.1929
	NM+UT+MT	Montana	-91.09	0.01865
MPT #18 Strict Temporal Calibration	Utah	MT+AB	-88.42	0.6227
	Utah	Montana	-89.21	0.2827
	UT+MT	Montana	-91.32	0.0343
	NM+UT	Montana	-91.43	0.03088

APPENDIX G

MEASUREMENTS

Size of the mandibular condyle

Taxon	Specimen #	Skull Length (cm)	Mandibular Condyle Area (cm^2)
Pig-nosed taxon	UMNH VP 21151	4.954	0.352
Peckemys brinkman	UCMP 49759	5.8	0.84
Palatobaena gaffneyi	UCMP 114529	5.9	0.78
Palatobaena cohen	YPM 57498	7.2	1.4
Goleremys mckennai	UCMP 179519	6.9	1.5
Plesiobaena antiqua	TMP 1986.36.49	5.7	0.5
Plesiobaena antiqua	TMP 1994.12.273	4.35	0.29775
Baena arenosa	USNM 18102	7.5	0.6
Chisternon undatum	USNM 12839	8.8	0.77
Arundelemys dardeni	USNM 497740	5.8	0.4
Denazinemys nodosa	BYU 19123	4.8	0.54
Hayemys latifrons	AMNH 6139	7.032	0.78771
Stygiochelys estesi	AMNH 2601	6.077	0.835944
Eubaena cephalica	AMNH 4948	6.406	0.601592
Baena arenosa	AMNH 5971	6.406	0.678014
Neurankylus baueri	NMMNH P-57874	9.546	1.246293
Glyptops plicatulus	YPM 1784	5.366	0.23584
Palatobaena bairdi	YPM-PU 16839	5	1.2795
Glyptops plicatulus	AMNH 336	6.596	0.289506
Cedrobaena putorius	YPM-PU 14984	7.885	0.873852
Cedrobaena putorius	MRF 239	6.028	0.560328
Peckemys brinkman	MRF 231	4.498	0.3168
Eubaena cephalica	MRF 571	6.865	0.768208
Trinitichelys hiatti	MCZ 4070	5.653	0.377508

Size of Mandibular Condyle

Mandibular Condyle Area (cm²)

Skull Length (cm)

N. baueri

G. mckennai

P. cohen

P. bairdi

C. putorius

H. latifrons

E. cephalica

C. undatum

B. arenosa

S. estesi

P. brinkman

P. gaffneyi

B. arenosa

E. cephalica

C. putorius

P. antiqua

A. dardeni

T. hiatti

G. plicatulus

G. plicatulus

D. nodosa⁺

Pig nosed taxon

P. brinkman

P. antiqua
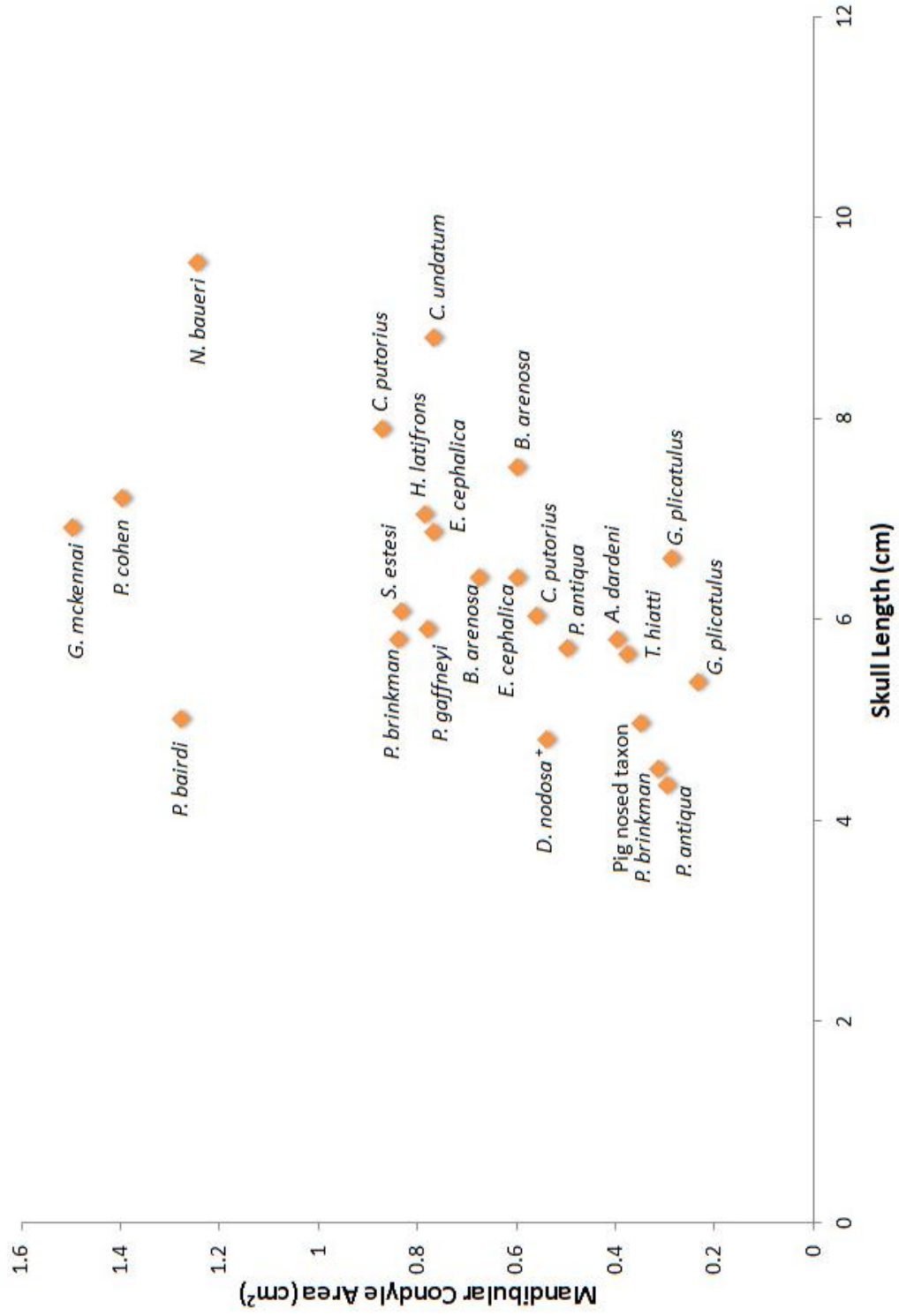
Interorbital width

Taxon	Specimen #	Skull Length (cm)	Interorbital Width (cm)
Pig-nosed taxon	UMNH VP 21151	4.954	2.18
Peckemys brinkman	UCMP 49759	5.8	2.1
Palatobaena gaffneyi	UCMP 114529	5.9	2.3
Palatobaena cohen	UCMP 131953	6.4	3.4
Palatobaena cohen	YPM 57498	7.2	3.4
Trinitichelys hiatti	MCZ 4070	5.653	1.411
Goleremys mckennai	UCMP 179519	6.9	2.1
Plesiobaena antiqua	TMP 1994.12.273	4.35	1.6
Plesiobaena antiqua	TMP 1999.55.145	5.5	1.8
Baena arenosa	USNM 18102	7.5	2.3
Chisternon undatum	USNM 12839	8.8	2.2
Arundelemys dardeni	USNM 497740	5.8	1.6
Denazinemys nodosa	BYU 19123	4.8	1.3
Hayemys latifrons	AMNH 6139	7.032	3.305
Stygiochelys estesi	AMNH 2601	6.077	1.743
Baena arenosa	AMNH 5971	6.406	2.643
Neurankylus baueri	NMMNH P-57874	9.546	3.621
Glyptops plicatulus	YPM 1784	5.366	0.874
Palatobaena bairdi	YPM-PU 16839	5.0	3.374
Glyptops plicatulus	AMNH 336	6.596	0.827
Cedrobaena putorius	MRF 239	6.028	1.841
Peckemys brinkman	MRF 231	4.498	1.456
Eubaena cephalica	MRF 571	6.865	1.632

Interorbital Wdith vs Skull Length

Skull Length (cm)

Interorbital Wdith (cm)

N. baueri

P. cohen

H. latifrons

C. undatum

B. arenosa

G. mckennai

P. cohen

B. arenosa

P. brinkman

E. cephalica

P. gaffneyi

S. estesi

P. bairdi

Pig nosed taxon

C. putorius

P. antiqua

A. dardeni

T. hiatti

P. antiqua

P. brinkman

G. plicatulus

D. nodosa

G. plicatulus

G. plicatulus
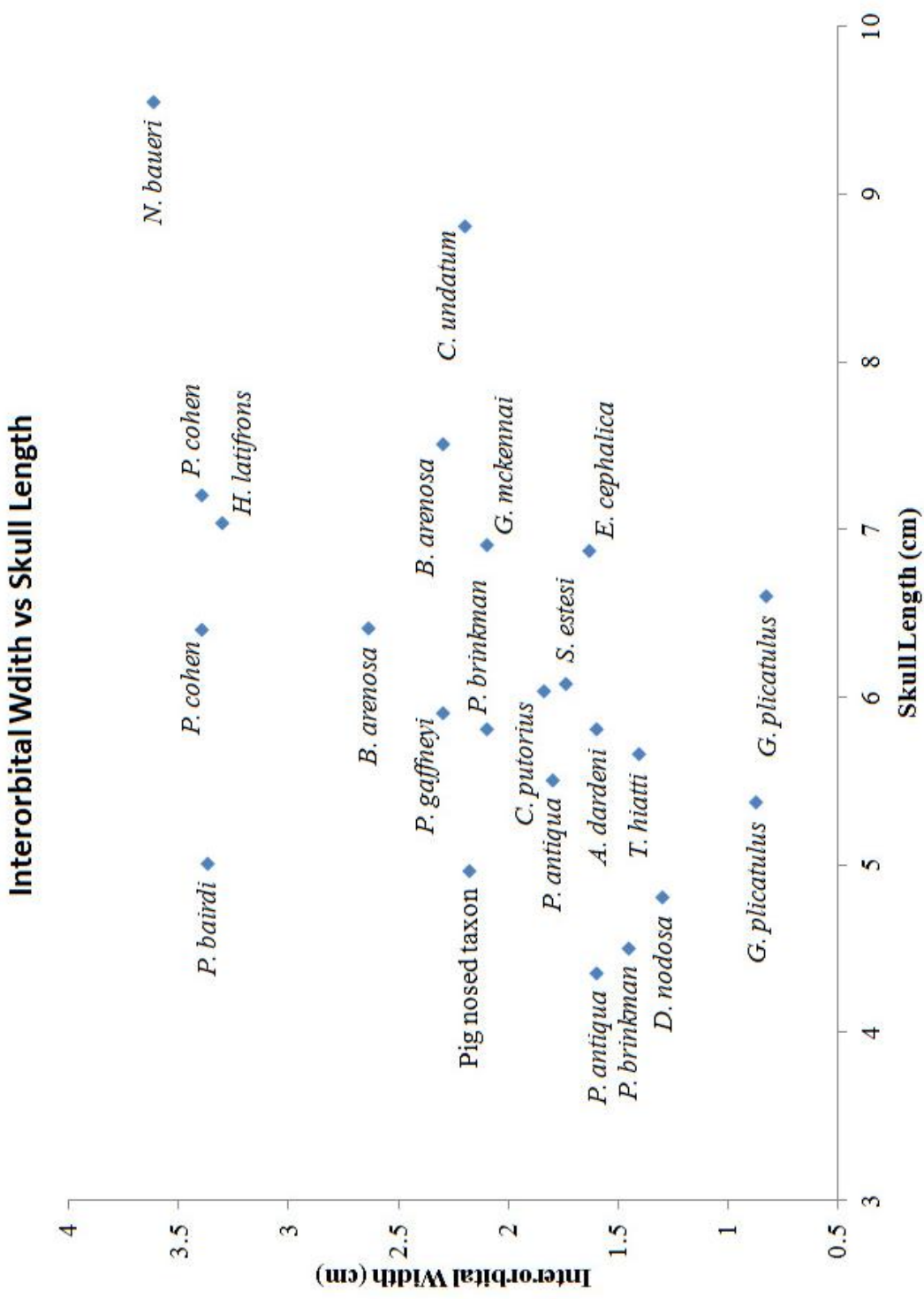
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