A NEW SPECIES OF BAENID TURTLE FROM THE KAIPAROWITS FORMATION (UPPER CRETACEOUS, CAMPANIAN) OF SOUTHERN UTAH

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ABSTRACT—Newly discovered baenid turtle specimens from the middle Campanian Kaiparowits Formation of southern Utah are described herein as a new taxon, Arvinachelys goldeni, gen. et sp. nov. The holotype consists of a nearly complete articulated skeleton and shell. 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 almost completely separated by a dorsal projection of the premaxillae and a ventral extension of the nasals, an autapomorphic feature among known baenid taxa. The skull is wedge-shaped with a broad rostrum and laterally expanded nasals. The importance of skull/shell associations is exemplified by Arvinachelys goldeni, because isolated shells attributable to this taxon had previously been assigned to the genus Plesiobaena, whereas phylogenetic analysis of more complete material supports a sister relationship with the Maastrichtian taxon Hayemys latifrons. These taxa are relatively basal within the Baenodda, a nested clade within Baenidae. The general shell morphology exhibited by Plesiobaena antiqua, Peckemys brinkmanii, and Palatobaena coheni was previously hypothesized to support a monophyletic clade that included those three taxa, along with Cedrobaena putorius, Gamerabaena sonsalla, Palatobaena bairdi, and Palatobaena gaffneyi. However, the inclusion of Arvinachelys goldeni, gen. et sp. nov., in a phylogenetic analysis of Baenidae indicates that the character states exhibited by those taxa are representative of plesiomorphic states within Baenodda, and the phylogenetic relationships within this clade are in need of reevaluation.

http://zoobank.org/urn:lsid:zoobank.org:pub:A5C5717C-4962-4056-8563-2C90C3276FDF

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

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INTRODUCTION

Baenidae is an extinct clade of freshwater turtles, the remains of which are restricted to Cretaceous–Eocene strata of North America (e.g., Gaffney, 1972; Hutchison, 1984; Holroyd and Hutchison, 2002; Brinkman, 2003). Along with Pleurosternidae, Dinochelys whitleyi Gaffney, 1979, Compsemys victa Leidy, 1856, and Uliops uluops Bakker, 1990, baenids are members of the extant clade Paracryptodira (Joyce, 2007; Lyon and Joyce, 2011). The oldest-known and most basal baenid, Arundelemys dardeni Lipka et al., 2006, was recovered from the Potomac Formation of Maryland (Lipka et al., 2006; Lyon 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 clades of freshwater turtles in Laramidia (Lyon and Joyce, 2010). The clade survived the Cretaceous–Paleocene extinction event and ultimately went extinct during the Eocene (Gaffney, 1972). The first comprehensive review and revision of the taxonomy and systematics of Baenidae was provided by Gaffney (1972). Several synonymies from that work were reassessed by Brinkman and Nicholls (1991), Lyon and Joyce (2009a, 2009b, 2010, 2011), Larson et al. (2012), and Sullivan et al. (2012). Three new taxa and additional taxonomic revisions were proposed by Lyson and Joyce (2009a, 2009b, 2010, 2011). However, their efforts focused on the baenids of the Maastrichtian–Paleocene Hell Creek Formation of northern Laramidia. Limited attention has been given 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 in New Mexico (e.g., Lucas and Sullivan, 2006; Sullivan et al., 2012).

Research performed over the past decade investigating the vertebrate assemblage of the Campanian Kaiparowits Formation in Grand Staircase-Escalante National Monument (southern Utah) has greatly increased our understanding of southern Laramidian Late Cretaceous non-marine ecosystems. Although faunal lists were published by Eaton et al. (1999), the first description of the turtle assemblage of the Kaiparowits Formation was provided by Hutchison et al. (2013). Among baenids, they recognized Denazinemys nodosa (Gilmore, 1916b), Boremys grandis Gilmore, 1935, Plesiobaena sp., and two distinct but unnamed species of Neurankylus. The genus Plesiobaena originally included Plesiobaena antiqua (Lambe, 1902) from the Campanian of Montana and Alberta and Plesiobaena putorius Gaffney, 1972, from the Maastrichtian of North and South Dakota and the Paleocene of Wyoming (Gaffney, 1972; Lyon and Joyce, 2009b). Clear differences between Campanian (Alberta) and Maastrichtian (Montana, Colorado, Wyoming) specimens ascribed to Plesiobaena antiqua were noted by Brinkman (2003), but taxonomic distinction was not proposed. Plesiobaena was revised and found to be paraphyletic by Lyson and Joyce (2009b). Thus, the genus was restricted to Plesiobaena

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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 Lyson and Joyce, 2009b, whereas specimens of ‘Plesiobaena’ putorius Gaffney, 1972, 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 Peckemys brinkman and none are known for Cedrobaena putorius (Gaffney, 1972). Because of similarities between Plesiobaena antiqua, Peckemys brinkman, and Palatobaena cohen Lyson and Joyce, 2009a, it was concluded that although it is possible to identify Plesiobaena antiqua within Campanian strata, distinguishing Maastrichtian taxa using only shells was not possible (Lyson and Joyce, 2009a, 2009b).

Plesiobaena sp. was identified from the Kaiparowits Formation based on two shell specimens preserving only the carapace and plastron, with no cranial material (Hutchison et al., 2013). A third, nearly complete articulated specimen was recently discovered in the Kaiparowits Formation. It includes a skull, shell, and numerous postcranial elements. An isolated skull also was discovered recently and assigned to the same taxon. I describe these new specimens and analyze them within a phylogenetic framework to determine their relationships within Baenidae.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York; BYU, Brigham Young University Museum of Paleontology, Provo, Utah; DMNH, Denver Museum of Nature and Science, Denver, Colorado; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MRF, Marmarth Research Foundation, Marmarth, North Dakota; ND, North Dakota Heritage Center, Bismarck, North Dakota; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; NM, Natural History Museum of Utah, Salt Lake City, Utah; USNM, National Museum of Natural History, Washington, D. C.; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut.

METHODS

The specimens described herein were collected, prepared, and curated using standard paleontological techniques. The skull and lower jaw are articulated in the holotype skull (UMNH VP 21151; Fig. 1), obscuring the palate and many features of the mandible. 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 (Fig. 2). 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 µA of current. A 1.5-mm lead filter was used to better image the interior of the specimen. That scan produced a total of 357, 587, and 538 slices in the coronal, frontal, and sagittal planes, respectively. I digitally segmented and reconstructed the specimen using Siem- ens Inveon Research Workspace version 3.0 software. Segmentation and three-dimensional (3-D) reconstruction 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, basioccipital, palate, and otic capsule.

I performed a phylogenetic analysis incorporating nearly all valid baenid taxa to determine the phylogenetic relationships of Arvinachelys goldeni, gen. et sp. nov. Thirty-three species were included in the analysis, including one outgroup taxon, the para- cryptodire Glyptops plicatulus (Cope, 1877). 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 Theseclus, sensu Sullivan et al. (2012), also were included. A total of 106 characters were used in the analysis, incorporating those from 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 complete character list is provided in Supplementary Data, Appendix S1. The complete character list is provided in Supplementary Data, Appendix S2. Characters 7, 14, 16, 18, 28, 33, 36, 69, and 106 form morphlines and were ordered in the analysis. All other characters were left unordered, and all characters were weighted equally. The complete character matrix is provided in Supplementary Data, Appendix S3. A maximum parsimony analysis was performed on the dataset using a traditional heuristic search with tree bisection-reconnection and 1000 random addition search replicates in the program Tree analysis using New Technology (TNT) version 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. Constraint analyses were
performed using TNT to determine the number of extra steps required for alternative phylogenetic hypotheses. These analyses were executed by amending the end of the .tnt file to include the script found at the end of Appendix S2. The number of steps required for the resultant tree from each constraint analysis was then compared with the number of steps of the original strict consensus tree.

**SYSTEMATIC PALEONTOLOGY**

**TESTUDINES** Batsch, 1788, 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

*Arvinachelys goldeni* gen. et sp. nov.

**Holotype**—UMNH VP 21151, a partial skull and mandible, nearly complete carapace, complete plastron, nearly complete right forelimb, partial right hind limb, 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 76.46 ± 0.14 and 75.97 ± 0.14 Ma. The specimen was discovered at UMNH VP locality 951 (Horse Mountain Gryposaur Quarry) in Grand Staircase-Escalante National Monument, Kane County, Utah, U.S.A.

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

**Diagnosis**—The new taxon is diagnosed by the following autapomorphies (indicated by an asterisk) and unique combination of characters: two distinct external nares formed by a dorsal projection of the premaxillae and a ventral midline expansion of the nasals*; narrow triturating surface on the mandible with a small or absent lingual ridge*; broad rostrum, as in *Hayemys latifrons* (Hay, 1908), differing from the tapered rostrum of all other members of Baenodda; lingual ridge developed only anteriorly on the maxillae; sagittally horizontal tubercula basioccipitale as in *Palatobaena cohen* and *Palatobaena bairdi* Gaffney, 1972, 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* Gilmore, 1916b, *Scabremys ornata* Gilmore, 1935, *‘Baena’ hayi* Gilmore, 1916a, *Chisternon undatum* (Leidy, 1916).
FIGURE 2. Three-dimensional reconstruction of the cranium of the holotype of *Arvinachelys goldeni* (UMNH VP 21151) based on µCT scanning: A, right lateral; B, dorsal; C, anterior; D, posterior; and E, ventral views. **Abbreviations**: *en*, external naris; *fm*, foramen magnum; *fpp*, posterior palatine foramen; *fst*, stapedial foramen; *tb*, tuburculae basioccipitale. White dashed lines represent inferred sutures. Scale bar equals 1 cm.
1872), *Baena arenosa* Leidy, 1870, and the unscalloped posterior of all other baenids; and a subtriangular anterior plastron with a blunt tip in some specimens, as in *Plesiobaena antiqua*, *Peckemys brinkman*, and *Palatobaena cohen*, differing from the more rectangular anterior plastral lobe of other baenids.

**Referred Specimens**—UMNH VP 21300, a nearly complete cranium missing only the left squamosal, portions of both palatines, and the left pterygoid; 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, U.S.A.

**DESCRIPTION**

The holotype preserves a nearly complete skull, nearly complete shell, cervical and caudal vertebrae, right scapula and coracoid, complete right distal forelimb, pelvic girdle, both femora, and partial distal hind limb. Most of the elements were found articulated. After preparation, the skull is still articulated with the mandible, the first two cervical vertebrae, and partial hyoid (Fig. 1). The cranium 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 also is preserved, along with a partial right pes. Four caudal vertebrae also are preserved in articulation.

A skull from slightly lower in section in the Kaiparowits Formation is referred to *Arvinachelys goldeni*, gen. et sp. nov., based on the presence of the unique combination of characters described above. That skull possesses open sutures and is missing only the left squamosal and portions of the palatines and pterygoids. The specimen is slightly crushed dorsoventrally anterior to the parietals.

**Skull**

The skull of UMNH VP 21151 is approximately 5.2 cm wide at its greatest extent (just anterior to the cavum tympanum) and is just under 5 cm (4.96 cm) long from snout to occipital condyle. UMNH VP 21300 is 5.8 cm wide and 5.4 cm long. 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. 1C), as in *Hayemys latifrons* (AMNH 6139). Unlike all other baenids, which have a single external narial opening, *Arvinachelys goldeni* possesses two
The external nares are oriented slightly laterally and are subequal in size with the orbits. It is possible that a similar morphology was present in *Hayemys 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 dorsal projection of the premaxillae, is not preserved in *Hayemys latifrons*. It is evident that *Hayemys latifrons* and *Arvinachelys goldeni* 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 postmortem ventromedial rotation of the maxilla of UMNH VP 21151 is taken into consideration, the orbit was most likely oriented slightly dorsally. A dorsal orientation of the orbits is only possible if the premolars are crushed and therefore the orientation and shape of the external narial opening(s) cannot be assessed. The most important of these features, the dorsal projection of the premaxillae, is not preserved in *Hayemys latifrons*. It is evident that *Hayemys latifrons* and *Arvinachelys goldeni* possessed the largest external narial opening(s) relative to the size of the skull of any baenid.

**FIGURE 4.** Three-dimensional reconstruction of the mandible of the holotype of *Arvinachelys goldeni* (UMNH VP 21151) based on μCT scanning: A, dorsal; B, left lateral; and C, posterodorsal view. The latter view is a surface rendering and best displays the large, lateral fossa on the mandible. **Abbreviations**: cp, coronoid process; fossa, hypothesized insertion site for adductor musculature; pra?, prearticular; sym, symphysis hook; tub, doral tubercle on dentary. Scale bar equals 1 cm.

distinct external nares separated by a bony septum formed by the contact between the premaxillae and nasals along the midline (Figs. 1B, 2C). The external nares are oriented slightly laterally and are subequal in size with the orbits. It is possible that a similar morphology was present in *Hayemys 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 dorsal projection of the premaxillae, is not preserved in *Hayemys latifrons*. It is evident that *Hayemys latifrons* and *Arvinachelys goldeni* possessed the largest external narial opening(s) relative to the size of the skull of any baenid.

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and prootic ventrally. Contact with the squamosal is prevented by a deep upper temporal emargination and wide exposure of the postorbital along this margin. The temporal emargination is deep enough to expose the anterior margin of the otic capsule in dorsal view.

The maxillae are separated by an approximately 88° angle in the coronal plane (visible ventrally). This angle is greater than that of most baenids, but less than that of *Palatobaena* spp., which have maxillae separated by greater than 90° in the coronal plane. A low lingual ridge appears to be present only anteriorly, and the triturating surface expands posteriorly. The labial ridges of the maxillae are gracile compared with the more robust labial ridge of *Palatobaena* spp. Therefore, it is unlikely that this animal would have been as specialized for durophagy as suggested for *Palatobaena* spp. (Lyson and Joyce, 2009a).

The prepalatine foramina are found at the suture between the premaxillae and vomer as in all baenids except *Eubaena cephalica, Stygiochelys estesi*, and *Chisternon undatum*. The posterior portion of the vomer is posteriorly convex, coming to a point where the element meets the pterygoids. The posterior palatine foramen is contained entirely within the palatine, as in *Hayemys latifrons, Stygiochelys estesi, Denazinemys nodosa*, and some specimens of *Chisternon undatum*. The external pterygoid process is a pointed, posterolaterally curved flange (Fig. 2E). This differs from the condition seen in *Palatobaena* spp., which have reduced external pterygoid processes. The interpterygoid suture is not preserved in UMNH VP 21300. However, based on the size of the basisphenoid and the placement of the posterior edge of the vomer, it is likely that *Arvinachelys goldeni* had a relatively narrow interpterygoid suture, comparable to that of *Denazinemys nodosa* (BYU 19123), *Stygiochelys estesi* (AMNH 2601; UCMP V73023/113316), and *Chisternon undatum* (AMNH 5961; AMNH 25554; USNM 12839). The basisphenoid is a large pentagonal element that contacts the pterygoids anteriorly and laterally and the basioccipital posteriorly. Unlike other baenids with a narrow interpterygoid suture, the basisphenoid does not possess a long tapered anterior projection; instead, the posterior portion of the basisphenoid is large with parallel margins. As in other baenids, the posterior internal carotid foramen is approximately halfway along the suture between the basisphenoid and pterygoid. The pterygoids contact each other anteromedially and

**FIGURE 5.** Carapace photographs (top) and line drawings (bottom) of *Arvinachelys goldeni* specimens: A, UMNH VP 21151; B, UMNH VP 20183; C, UMNH VP 20145. Black lines represent bones and the edge of the specimen; gray lines represent scale sulci. Abbreviations: ce, cervical scute; co, costal; fem, femur; hu, humerus; ma, marginal scute; pel, pelvis; pl, pleural scute; ve, vertebral scute. Scale bar equals 5 cm.
the basisphenoid posteromedially, the palatines and vomer ante-
riorly, the quadrates dorsolaterally, and possess a broad suture
with the basioccipital posteriorly. The pterygoid forms the ante-
rior and ventral rims of the trigeminal foramen. An epipterygoid
is not visible.

The lateral portion of the skull (Fig. 3C, D) is made up of the
maxilla, postorbital, jugal, and quadratojugal. The cheek emargi-
nation is deep, extending to a point dorsal to the ventral margin
of the orbit, as in Peckemys brinkman. The postorbital bar is
approximately half the width of the orbit. The jugal is a small ele-
ment on this bar that contacts the maxilla anteriorly, the postor-
bital dorsally, and the quadratojugal posteriorly. A narrow
suture between the maxilla and the postorbital excludes the jugal
from the margin of the orbit as in Arundelemys dardeni,
Trinitichelys hiatti, Plesiobaena antiqua, Gamerabaena sonsalla,
Eubaea cephalica, Denazinemys nodosa (BYU 19123), and
Boremys pulchra (Lambe, 1906) (TMP 1988.2.10). The postorbital
has a broad exposure on the lateral surface of the orbit, contact-
ing the squamosal posteriorly, the quadratojugal postolaterally,
the jugal ventrally, the postorbital anteromedially, and the frontal and parietal dorsomedially. The quadrato-
jugal is a mediolaterally 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
quadratojugal has an anterior expansion that forms the posterior
dorsal margins of the cheek emargination. This element con-
tacts the jugal anteriorly, the postorbital anterodorsally, the
squamosal posterodorsally, and the quadrate medially. The
cavum tympanum, which is rimmed anteriorly by the quadrateju-
gal and dorsally by the quadratojugal and squamosal, is circular
in shape and larger than the orbit. The squamosal forms the pos-
terolateral dorsal corner of the skull, contacting the quadrate
and opisthotic ventrally, the postorbital anteriorly, and the quad-
ratejugal anterodorsally. 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, the squamosal caps an expansion of the cavum
tympanum known as the antrum postoticum. The posterior mar-
gin of the squamosal extends beyond the occipital condyle.

The otic capsules are oriented mediolaterally in Arvinachelys
goldeni, especially compared with those of baenids such as Pale-
tobaena cohen and Denazinemys nodosa, which are slanted

FIGURE 6. Plastron photographs (top) and line drawings (bottom) of Arvinachelys goldeni specimens: A, UMNH VP 21151; B, UMNH VP 20183; C, UMNH VP 20145. Black lines represent bones; gray lines represent scale sulci. Abbreviations: an, anal scutes; en, entoplastron; fe, femoral scutes; gu, gular scutes; hs, humeral scutes; im, inframarginal scutes; ma, marginal scute; xi, xiphiplastra. Scale bar equals 5 cm.
postrolaterally. The nature of the contacts between individual elements of the otic capsule is difficult to determine because sutures are closed in this portion of the skull of the holotype and the region is riddled with cracks in UMHN VP 21300. The region of the skull in baenids comprises the quadrates, opisthotics, prootics, and supraoccipital (Gaffney, 1982). The opisthotic does appear to form part of the margin of the foramen stapedio-temporale in UMHN VP 21300. The ventral articular process of the quadrates bears the mandibular condyle, which serves as the articular surface for the lower jaw. The relative size of the mandibular condyle is smaller than that of most baenids. The ratio of the size (length x width) of the condyle to skull length is similar to that of Plesiobaena antiqua (TMP 1986.36.49; TMP 1994.12.273), Peckemys brinkmanii (MRF 231), Trinitichelys hiatti (MCZ 4070), Arundelemys dardeni (USNM 497740), and the paracryptodire Glyptops plicatus (AMNH 336), being 0.352±0.4954 and 0.4743±5.411 for Arvinachelys goldeni. This is significantly smaller than the same ratio for Palatobaena cohen (YPM 57498), which is scored as exhibiting a large mandibular condyle (character 68). As a whole, the otic capsule contacts the squamosal dorsolaterally, the quadratojugal laterally, the parieto-antodorsally, the basicranium ventrally, and the pterygoid anterotransversally.

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 basicranium, is conical in shape. The stapes becomes more rod-like laterally and eventually posteriorly compressed at its lateral-most extent. The stapes does not appear to differ from that of other pan-cryptodire Testudines.

The exoccipital contacts the opisthotic dorsolaterally and the basioccipital ventrally. Dorsal contact with the supraoccipital cannot be determined. A single, large foramen, the hypoglossal foramen, is formed entirely within the exoccipital. The basicranial tubercles exhibit a similar morphology to those of Palatobaena cohen in possessing a flat, horizontal flange posteriorly (sagitaly horizontal basioccipital tubercles, sensu Lyson and Joyce, 2010, character 66). The occipital condyle is short and rounded. It differs from that of Hayemys latifrons (AMNH 6139), which is extended more posteriorly and has a distinct neck. As in all other baenids, the basioccipital has broad contacts with the pterygoids anterotransversally and the basiphenoid anterolaterally.

The anterior horns of the hyoid apparatus are preserved in position 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 4 shows both lateral and dorsal views of the mandible. As with several other regions of the skull, owing to sutural 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 taller relative to the length of the mandible than in any other baenid. Most baenids appear to have a prominently developed coronoid process, with the exception of Eubaena cephalica (MRF 766), Denazinemys nodosa (BYU 19123), and Boremys pulchra (TMP 1988.02.10; TMP 2001.12.36), but the condition in Arvinachelys goldeni is particularly exaggerated compared with the modal baenid condition.

Anteriorly, the mandible possesses a prominent symphyseal hook. The two rami of the mandible come together at approximately an 88° angle, suggesting the angle measured for the upper jaw was not seriously affected by crushing. The mandible has a narrow triturating surface with parallel labial and lingual margins, unlike other taxa such as Palatobaena, which have robust, posteriorly expanded triturating surfaces. Although the labial ridge is prominent, Arvinachelys goldeni appears to lack a lingual ridge on the mandible, or it is weakly developed. 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. A similar tubercle also is seen in Palatobaena spp. (Lyson and Joyce, 2009a), Stygiochelys estesi (UCMP V73023/113316), and Baena arenosa (AMNH 5971). Posterior to the tubercle, a large fossa is present on the lateral surface of the mandible. The fossa, 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 was inferred previously for Palatobaena spp. (Archibald and Hutchison, 1979; Lyson and Joyce, 2009a). However, unlike Palatobaena, Arvinachelys did not have a posteriorly expanded, flat triturating surface.

**Carapace**

All three specimens of Arvinachelys preserve a relatively complete shell (Figs. 5, 6), but the carapace of UMHN VP 20451 is best preserved and provides the basis for most of the description here (Fig. 5C). Overall, the carapace is similar to that of Plesiobaena antiqua, with a few key differences; it is rounded anteriorly, lacks the nuchal projection of Plesiobaena antiqua (TMP 1992.36.681) and Palatobaena 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 Plesiobaena antiqua. This gives the carapace an almost torpido 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 Denazinemys nodosa. The posterior margin is strongly scalloped, as in Denazinemys nodosa (UMHN VP 20447) and Boremys spp. (TMP 1981.28.01; USNM 12979). This differs from the smooth to lightly scalloped posterior margin of Plesiobaena antiqua (TMP 1976.06.35) and the smooth margin of Palatobaena cohen (YPM 57498). As in other members of Bae- nodda, a pygal notch is present posteriorly, although it is shallow. A mid-dorsal ridge runs the length of the carapace, as in Plesiobaena antiqua (TMP 1976.06.35), Denazinemys nodosa (BYU 19123), and Boremys 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 costals that are not as pronounced as in Denazinemys nodosa, Boremys spp., or Scabremys ornata. For the most part, sutures between the carapace bones are closed in all specimens of Arvinachelys goldeni; 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. 5A). 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 divided. A similar condition is present in Thescelus spp., Scabremys ornata (USNM 13229), Plesiobaena antiqua (TMP 1976.06.35), and Palatobaena cohen (YPM 57498). This differs from the narrow, rectangular scute of basal baenids such as Trini- tichelys hiatti (MCZ 4070) and Neurankylus spp. and the divided cervical scutes of Baena arenosa (AMNH 5971), Chisteron undatum (AMNH 5961), Denazinemys nodosa (UCMP V95087/159703), Boremys spp., ‘Baena’ hayi (USNM 6728), and ‘Baena’ hatcheri, Hay, 1901 (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 serrations.

The vertebral scutes are wider than they are long, as in *Trinitichelys hiatti* (MCZ 4070), *Neurankylus* spp., *Thecesulus* spp., *Scabremys nodosa* (USNM 13229), *Plesiobaena antiqua* (TMP 1976.06.35), *Peckemys brinkman* (UMMP 20490; Lyson and Joyce, 2009b), and *Palatobaena 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 *Trinitichelys hiatti*, *Neurankylus* spp., and *Thecesulus* spp., the fifth vertebral is exposed on the posterior margin of the carapace. This character is used to distinguish members of the clade Baenodda. The size of the pleural scutes is restricted owing to the wide vertebrals. Pleural II has the largest exposure amongst this series of scutes. Prepleural scutes are absent, as in all baenids except *Denazinemys nodosa* (UCMP V95087/159703), *Boremys* spp., *Stygiochelys estesi* (UCMP V73023/113316), *Baena* spp., and *Chisteron undatum* (AMNH 5961).

**Plastron**

The anterior lobe of the plastron appears to exhibit some variation across specimens assigned to *Arvinachelys*. The anterior plastral lobe of the type specimen exhibits a condition similar to some specimens of *Denazinemys nodosa* (e.g., BYU 19125) in being subtriangular posteriorly, then becoming broader and more rounded anteriorly (Fig. 6A). In contrast, UMNH VP 20451 and 20183 possess a triangular anterior plastron with a blunt tip (Fig. 6B, C), nearly identical to the morphology observed in *Plesiobaena antiqua* (TMP 1985.58.45), *Peckemys brinkman* (UMMP 20490; Lyson and Joyce, 2009b), and *Palatobaena 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 the two referred specimens is the size of the humeral scutes, which are significantly smaller in UMNH VP 20451 and 20183 than in the type specimen (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 seem to 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 modal morphology of other baenids. The posterior plastral lobe is larger than the anterior, as in all other baenids except two undescribed species of *Neurankylus* from the Kaiparowits Formation (pers. observ.).

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 between these serrations.

The intergular scutes are absent, as in *Peckemys brinkman* (UMMP 20490; Lyson and Joyce, 2009b), *Palatobaena cohen* (YPM 57498), and some specimens of *Plesiobaena 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 has a broad contact with the pectoral scute in UMNH VP 20451, whereas that 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* Lamb, 1902 (TMP 2003.12.171), *Thecesulus hemispherica* Gilmore, 1935 (USNM 12818), *Boremys grandis* (USNM 12979), and *Stygiochelys estesi* (UCMP V73023/113316). This differs from *Neurankylus wyomingensis* (Gilmore, 1919) (USNM 7581), *Neurankylus baieri* (USNM 8344), *Trinitichelys hiatti* (MCZ 4070), and ‘Baena’ hayi (USNM 6728), which have narrower inframarginals than marginals. The inframarginals of *Plesiobaena antiqua* (TMP 2007.12.01), *Peckemys brinkman* (UMMP 20490; Lyson and Joyce, 2009b), *Denazinemys nodosa* (UMNH VP 20447), and *Baena arenosa* (AMNH 5970) differ in being wider than the ventral exposures of the marginals. The anal scute possesses an anterior projection with a truncated margin in all three specimens. The projection crosses the hypoplastron-xiphiplastron suture, as in all baenids except *Neurankylus* spp., *Trinitichelys hiatti* (MCZ 4070), and *Boremys* spp.

**Vertebrae**

As with other baenids (Brinkman and Nicholls, 1991; Lyson and Joyce, 2009b), the atlas is made up of four separate elements: two paramedian elements that constitute the neural arch, an anterior intercentrum, and a posterior centrum. Similar to *Peckemys brinkman*, but differing from *Boremys pulchra*, there do not appear to have been cervical ribs attached to the atlas (Brinkman and Nicholls, 1991; Lyson and Joyce, 2009b). However, it is possible that ribs became disarticulated prior to burial. The neural arches of the atlas are each made up of two plates. A flat dorsal plate is present and would have joined with the same structure of the other neural arch element dorsal to the spinal cord; a ventrally directed plate has 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 postzygophyseal 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 *Peckemys 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 axis of the holotype is preserved with both cervical ribs in situ. These are relatively flat elements with broad rib heads that rapidly taper posteroventrally down the shaft of the rib.

Three other incomplete cervical vertebrae of unknown position also are 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 *Peckemys brinkman* (Lyson and Joyce, 2009b), the fourth cervical of *Boremys pulchra* (Brinkman and Nicholls, 1991), and on a cervical of unknown position of *Neurankylus sp*. nov., from the Kaiparowits Formation (pers. observ.). These vertebrae suggest that at least a few of the centra in the cervical series were acrochous. The transverse process is short and robust and is displaced anteriorly from the center of the centrum. As in other baenids, the neural spines appear to be robust. The prezygophyses are prominent.

Four distal caudal vertebrae of unknown position are preserved. These are rod-like elements, lacking neural spines, hemal 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 caudals XVII and XIX figured by Brinkman and Nicholls (1991) for *Boremys pulchra*. 
Shoulder Girdle

The entire shoulder girdle is preserved in place in the holotype of *Arvinachelys*, gen. nov., although 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 scapular processes typically are approximately 90° apart, but less than that of *Chisternon undatum* (AMNH 5904), whose scapular and acromion processes are separated by approximately 125°. The coracoid is articulated with the scapula, exhibiting the typical turtle 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. 7). As in other baenids, a groove along the dorsomedian dorsal face of the distal portion of the humerus represents the entepicondylar groove. Only one side of the radius and ulna are exposed, and they appear 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 broad articulation with the medial facet of the ulna as in *Peckemys brinkman* (Lyson and Joyce, 2009b). A blocky bone just beyond the ulna is identified here as the ulnare and is shifted slightly lateral to its normal position. Two distal carpals are exposed; the medial element is rounded, similar to distal carpals II and III of *Chisternon undatum* (AMNH 5904), whose scapular and acromion processes are 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 posteroverentrally. This is similar to most other baenid specimens in which the ilium is preserved, with the exception of *Peckemys brinkman*, the ilial blade of which expands both anteriorly and posteriorly at the dorsal end. The ischium possesses a sharp, posteriorly projecting boot as in other baenids. The pubic apron is not exposed; but the ventral pubic tubercles are visible, and are rounded and robust.

Pelvis

Nearly the entire left pelvis of the holotype specimen is preserved in limited views. The left femur is in situ, still articulated with the acetabulum; 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 the digits can be made based on external molds of some of the phalanges preserved in the sandstone matrix of the specimen (Fig. 8). Metatarsals I–IV are present. The first metatarsal is a robust element that is the shortest of the first four metatarsals. However, compared with the same element figured by Lyson and Joyce (2009b) for *Peckemys brinkman*, the first metatarsal 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 *Peckemys 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 with phalanx I of any other digit, as is the case in *Peckemys brinkman*.

**FIGURE 7.** Photograph (left) and line drawing (right) of the right forelimb and manus of the holotype of *Arvinachelys goldeni* (UMNH VP 21151) in ventral view. Abbreviations: dc, distal carpals; hu, humerus; in, intermedium; mc, metacarpal; rad, radius; uln, ulna; ulnare. Scale bar equals 1 cm.

**PHYLOGENETIC ANALYSIS**

My phylogenetic analysis recovered 18 most parsimonious trees, with a length of 257 steps. Figure 9 shows the strict consensus of these most parsimonious trees. *Arvinachelys goldenii* was recovered as the sister taxon to *Hayemys latifrons* from the Maastrichtian Lance Formation of Wyoming. These taxa are united by the lack of a frontal contribution to the margin of the orbit (character 16[2]), the posterior palatine foramen forming only in the palate (character 27[1]), and the lateral expansion of the nasals (character 97[1]). *Arvinachelys goldenii* and *Hayemys latifrons* are placed within the clade Baenodda. *Scabremys ornata* and the clade of *Arvinachelys* + *Hayemys* form successively nested branches at the base of Baenodda; *Plesiobaena antiqua* is much more highly nested, as the sister group of a clade including ‘Baena’ hayi, *Goleremys*, *Stygiochelys*, *Baena*, *Chisternon*, *Eubaena*, *Denazinemys*, and *Boremys*. Other taxa
previously assigned to Plesiobaena (e.g., Cedrobaena and Peckemys) are spread paraphyletically between Arvinachelys and Plesiobaena antiqua, supporting their taxonomic separation from Plesiobaena. Baenodda is united by the presence of scalloping on the posterior margin of the carapace (character 36[1 and 2]), the contribution of the fifth vertebral to the posterior carapace margin (character 37[1]), the presence of a pygal notch (character 57[1]), and the anterior margin of the nuchal being even with the first peripheral (character 87[1]).

The consistency index is low for the phylogeny (0.502), indicating high homoplasy within the Baenidae dataset. Retention index is 0.710. Overall, bootstrap frequencies were low across the phylogeny, with most nodes below 50%; the highest bootstrap value within Baenidae was for the genus Thescelus (51%). Bremer support values were almost universally 1 or 2 within Baenidae, with the exceptions of Thescelus spp. + Baenodda (6), the branch leading to the Thescelus polytomy (6), the branch leading to Baenodda (6), Arvinachelys goldeni + Hayemys latifrons (4), Denażinemys nodosa + Eubaena cephalica + Boremys spp. (3). Denażinemys nodosa + Eubaena cephalica (3), and Boremys grandid + Boremys pulchr (3). The 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 taxon.

As noted above in the discussion of Arvinachelys goldeni’s cranial anatomy, the presence/absence of a contact between the frontal and maxilla was scored as unknown, owing to displacement of the dorsal ramus of the maxilla. To test the effects of this character change on baenid phylogeny, I reran the analysis, scoring character 17 as ‘0,’ and left all other character scorings the same. The resulting tree is identical to the strict consensus, except the clade of Hayemys latifrons + Arvinachelys goldeni, which is collapsed into a polytomy with a clade of more highly nested members of Baenodda. That analysis recovered 36 most parsimonious trees with a length of 258 steps.

Hayemys latifrons was suggested to be the junior synonym of Thescelus insiliens Hay, 1908, by Lyson and Joyce (2010) based on contemporaneity and a similar phylogenetic placement. To test the likelihood of this, I also performed a constraint analysis, placing Hayemys latifrons within Thescelus spp. This requires three additional steps, recovering 22 most parsimonious trees with a length of 260 steps. The topology that results from the analysis constraining Hayemys latifrons within Thescelus is identical to the strict consensus in my original analysis, with the exception of the placement of Hayemys and a collapse of the monophyletic Neurankylus clade into a basal polytomy outside of Thescelus + Baenodda.

Because material of Arvinachelys was previously assigned to Plesiobaena sp., I tested the number of steps required to constrain a tree topology with the clade of Arvinachelys + Plesiobaena antiqua. This requires 10 additional steps, recovering 2353 most parsimonious trees with a length of 267 steps. I also constrained a tree topology that included a monophyletic clade of Plesiobaena antiqua + Peckemys brinkman + Cedrobaena putorius + Gamera baena sonsalla + Palatoabaena spp., sensu Lyson and Joyce (2009a, 2009b, 2010) and Lyson et al. (2011). That required only two additional steps, recovering 108 most parsimonious trees with a length of 259 steps. The resulting topology is similar to that of Lyson and Joyce (2011) in which Plesiobaena antiqua and Peckemys brinkman form a polytomy with the clade Cedrobaena putorius + Gamera baena sonsalla + Palatoabaena spp.

DISCUSSION

Turtles formerly assigned to the genus Plesiobaena, including a previously unnamed Maastrichtian taxon (now Peckemys brinkman), Plesiobaena antiqua, and Plesiobaena putorius, were found previously to represent a paraphyletic group, placed on successively nested branches along the stem to Palatoabaena spp. (Lyson and Joyce, 2009b). Because of this, Lyson and Joyce (2009b) suggested that Maastrichtian taxa (i.e., Peckemys brinkman, Cedrobaena putorius, and Palatoabaena cohen) are not as easily diagnosed by shell morphology, but that Campanian shells of the ‘Plesiobaena grade’ still could be diagnosed as belonging to Plesiobaena antiqua (Lyson and Joyce, 2009b). The results of my phylogenetic analysis suggest otherwise. Until shells of ‘Plesiobaena sp.’ were identified by Hutchison et al. (2013) from the Kaiparowits Formation, Plesiobaena was known only from northern Laramidia. However, the discovery of the associated skull and shell described in my study demonstrates that isolated shells previously referred to Plesiobaena sp. belong to a taxon that is more closely related to Hayemys latifrons. The phylogenetic analyses by Lyson and Joyce (2009a, 2009b, 2010) indicated weak support for a monophyletic clade that included Plesiobaena antiqua, Peckemys brinkman, Cedrobaena putorius, Gamera baena sonsalla, and Plesiobaena spp. My analysis provides weak support for Plesiobaena antiqua being more closely related to the clade including Baena arenosa and Boremys pulchr. The topology recovered by Lyson and Joyce (2009a, 2009b, 2010), in which Plesiobaena antiqua is more closely related to Palatoabaena than Boremys, requires only two additional steps. This, coupled with the phylogenetic placement of Arvinachelys goldeni, indicates that the general shell morphology previously attributed to purported members of Plesiobaena 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 and suspect, although there are five characters that distinguish the shell of Arvinachelys goldeni from Plesiobaena antiqua (a hexagonal secund vertebral scute and a more prominently scalloped posterior margin in Arvinachelys; a more prominent nuchal projection, presence of carapacial fontanelles, and larger inframarginal width relative to marginal width in Plesiobaena).

The skull-based taxon Hayemys latifrons was suggested previously to be a junior synonym of the shell morphotype named Thescelus insiliens based on both stratigraphic and phylogenetic evidence (Lyson and Joyce, 2010). However, no directly associated specimen of skull and shell is known for either taxon. My hypothesis predicts instead that Hayemys latifrons may have
FIGURE 9. Strict consensus cladogram of 18 trees, with bootstrap frequencies (top/left) and Bremer support values (bottom/right). Nodes with bootstrap frequencies denoted with an asterisk (*) collapsed during the bootstrap analysis.
possessed a ‘Plesiobaena-grade’ shell, rather than a Thescelus-like shell. Key similarities that link Hayemys latifrons with Arvinachelys goldeni include a wedge-shaped skull with a laterally expanded rostrum, a posterior palatine foramen enclosed within the palate, the lack of frontal contribution to the orbital margin (visible in UMNH VP 21300), and premaxillae that do not extend beyond the anterior margin of the skull roof. The presence or absence of two distinct external nares in Hayemys latifrons cannot be assessed because of the crushed nature of the holotype specimen. There also are some key differences between the skulls of the two taxa, including relative interorbital width of the skull roof, morphology of the basioccipital tubercles, inset of the orbit into the maxilla, and the shape of the nasal-fronto-suture. Also, the occipital condyle of Hayemys latifrons is more prominent, with a weakly formed ‘neck’ anterior to the condyle, although that feature is not known to be a phyletogenetically informative character in other baenid taxa. Additionally, a clade formed by Thescelus spp. and Hayemys latifrons requires only three additional steps from the strict consensus of my phylogenetic analysis. It is possible, therefore, that the Arvinachelys-Hayemys skull morphology, like ‘Plesiobaena-type’ shells, may represent a morphological grade within Baenodda. Therefore, synonymy between Hayemys latifrons and Thescelus insilienteus cannot be ruled out (Lyson and Joyce, 2010; Larson et al., 2012), but it is not supported by available data and should not be assumed in phyleogenetic analyses.

Hayemys latifrons, from the Maastrichtian Lance Formation of Wyoming, historically possessed a temporally long ghost lineage, given its basal position outside Baenodda according to previous phylogenetic analyses (Lyson and Joyce, 2010). Arvinachelys goldeni partially fills that gap by extending the fossil record of the lineage into the late Campanian, 10 million years earlier than Hayemys. The new taxon also extends the geographic range of the lineage into southern Laramidia. Latitudinal differences in vertebrate assemblages during the Late Cretaceous were noted several decades ago (e.g., Lehman, 1987, 1997, 2001). Recent investigations into the dinosaur assemblage of the Kaiparowits Formation (e.g., Sampson et al., 2010) supported that 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 and five are diagnosable to recognized or new nid taxa are known from the Kaiparowits Formation of southern Utah. These data provide further support for the hypothesis of basin-scale endemism and differences overall between northern and southern Laramidian fossil assemblages from the Campanian.

CONCLUSIONS

Arvinachelys goldeni, gen. et sp. nov., represents a new, morphologically disparate taxon from the Campanian Kaiparowits Formation of southern Utah. Unlike any other baenid, it has two distinct external nares that are partially separated by a dorsal process of the premaxillae. The taxon is known from no other sedimentary basin across Laramidia; its restriction to southern Utah supports previous hypotheses of regional provinciality and basin-scale endemism across Laramidia during the Campanian. The hypothesized sister-taxon relationship of Arvinachelys goldeni and Hayemys latifrons from the Maastrichtian Lance Formation of Wyoming parallels previous observations of similarity between Campanian turtle assemblages from southern Laramidia and those from the Maastrichtian of northern Laramidia (e.g., Hutchison et al., 2013). Arvinachelys goldeni also increases the known diversity of Baenidae—already the most speciose clade of turtles during the Late Cretaceous.

The inclusion of Arvinachelys goldeni in my analysis supports a different phylogenetic hypothesis from those that were published in recent years (Lyson and Joyce, 2009a, 2009b, 2010; Lyson et al., 2011). However, all phylogenetic analyses, including my own, have low support for the placement of particular taxa, especially Plesiobaena antiqua and Peckemys brinkmanai. Phylogenetic uncertainty within Baenidae continues to be an issue, in spite of the taxonomically comprehensive nature of my analysis. The incompleteness of many baenid taxa likely promotes uncertainty of evolutionary relationships within this clade; over half of the ingroup taxa are represented by only crania or shells. Character choice is another possible source of phylogenetic uncertainty within Baenidae. As in other turtle clades (e.g., Joyce and Bell, 2004), the understanding of variation within Baenidae is limited. Ontogenetic variation in the contribution of the jugal to the orbital margin (character 18) was noted in the skull of Palatobaena coheni (Lyson and Joyce, 2009a). Variation also was observed in the ornamentation of shells assigned to Baena arenosa (pers. observ.). To properly test the utility of these and other characters in phylogenetic analyses, more baenid specimens need to be described in order to better understand intra-specific and interspecific variation within the clade.

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