A Review of the Fossil Record of Turtles of the Clade *Baenidae*

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ABSTRACT

The fossil record of the turtle clade *Baenidae* ranges from the Early Cretaceous (Aptian–Albian) to the Eocene. The group is present throughout North America during the Early Cretaceous, but is restricted to the western portions of the continents in the Late Cretaceous and Paleogene. No credible remains of the clade have been reported outside of North America to date. Baenids were warm-adapted freshwater aquatic turtles that supported high levels of diversity at times through niche partitioning, particularly by adapting to a broad range of dietary preferences ranging from omnivorous to molluscivorous. Current phylogenies place *Baenidae* near the split of crown-group Testudines. Within *Baenidae* three more inclusive, named clades are recognized: *Baenodda*, *Palatobaeninae* and *Eubaeninae*. A taxonomic review of the group concludes that of 49 named taxa, 30 are nomina valida, 12 are nomina invalida and 7 are nomina dubia.

KEYWORDS

Phylogeny, biogeography, paleoecology, *Baenidae*, *Baenodda*, *Eubaeninae*, *Palatobaeninae*

Introduction

The name *Baenidae* was originally coined by Cope in 1873 to highlight the distinct nature of several newly described turtles that had been found in Eocene deposits in Wyoming (Cope 1873b). The name was consistently used in subsequent years to unite all turtles that were thought to be more closely related to *Baena arenosa* Leidy, 1870 from the Eocene of North America than to *Pleurosternon bullockii* (Owen, 1842) from the Late Jurassic of Europe (e.g., Cope 1884; Hay 1908; Williams 1950; Gaffney 1972), and the group never included any living turtle. Lyson and Joyce (2011) codified this usage through a phylogenetic definition, and we follow this definition herein. Although the exact etymology of the name is uncertain, it appears that *Baena* is derived from a Native American language, such as Arapahoe, where the word for turtle is "*be'enoo*" (Salzmann 1983). To emphasize that the name was to be pronounced with three syllables (e.g., *Ba-en-na*), the name was consistently written with a dieresis (i.e., *Baëna*) by early authors (e.g., Leidy 1871a, 1871b; Cope 1872, 1873a, 1873b; Hay 1908). However, we herein omit this glyph, as the International Code of Zoological Nomenclature (ICZN 1999) does not allow for the usage of diacritical marks.

In his thorough review of the fossil turtles of North America, Hay (1908) grouped a diverse assemblage of taxa from the Campanian to Eocene of North America into *Baenidae*, which closely resembles the list of taxa presented herein. The only exception is *Naomichelys speciosa* Hay, 1908, which was only known by a single, large entoplastron and has since been shown to be a representative of the clade *Solemydidae* (Hirayama et al. 2000; Joyce et al. 2014). Williams (1950) recognized a similar set of turtles from the Late Cretaceous to Eocene of North America, his Baenoidea, but also included *Meiolaniidae* on the basis of the presence of a biconvex cervical vertebra IV, but this characteristic is now interpreted as a homoplasy and meiolaniids are no longer thought to be closely related to baenids (e.g., Gaffney 1996; Joyce 2007; Anquetin 2012; Sterli et al. 2013). The influential classification of Gaffney (1972) was centered on the same set of

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Late Cretaceous to Eocene turtles, similar to previous authors, but *Baenidae* was expanded to include *Trinitichelys hiatti* Gaffney, 1972 from the Early Cretaceous (Aptian–Albian) of Texas and the idiosyncratic *Compsemys victa* Leidy, 1856 from the Late Cretaceous to Paleocene of the American West (Lyson and Joyce 2011). All recent global (e.g., Joyce 2007; Anquetin 2012; Sterli et al. 2013) and local phylogenetic analyses (e.g., Lyson and Joyce 2009a, 2009b, 2010, 2011; Lyson et al. 2011; Larson et al. 2013) have reproduced the overall grouping of Gaffney (1972), with the exception of *Compsemys victa*, which is retrieved outside of *Baenidae* (Lyson and Joyce 2011).

The first baenid species were described in the early 1870s from the newly discovered rich Eocene fossil beds near Fort Bridger in southwestern Wyoming, in particular *Baena arenosa*, "*Baena*" *affinis* Leidy, 1871a, *Chisternon undatum* (Leidy, 1871b) and *Chisternon hebraica* Cope, 1872/1873a. In contrast to other groups of turtles from North America, such as *Trionychidae* (Vitek and Joyce 2015), these baenids were universally based on relatively complete specimens, particularly shells. More strikingly, and again in stark contrast to Trionychidae (Vitek and Joyce 2015), no new species were named for the rest of the 19th century, perhaps because baenids were not diagnosed by nuances in shell sculpturing, as was commonly done for trionychids. At the beginning of the 20th century, Lambe (1902, 1906a) and Hay (1901, 1904a, 1904b) named six new species of baenid turtles from Late Cretaceous deposits in Alberta, Montana and Wyoming. It is notable that most of those taxa are also based on relatively complete shells or skulls. Hay (1908) significantly increased the known diversity of baenids by naming 11 more species, based on relatively complete shells, from the Early Cretaceous to Eocene of North America. A parataxonomic problem becomes apparent at this time, however, as most species are based on shells (e.g., "*Baena*" *hayi* Gilmore, 1916a), but others on skulls (e.g., "*Baena*" *latifrons* (Hay, 1908)) only, and because few specimens were available that preserved both anatomical regions. In a series of papers, Gilmore (1916a, 1916b, 1916c, 1920, 1935) added 11 additional taxa to the list of named baenids, based solely on relatively complete shell material ranging from the Late Cretaceous to the Eocene. Isolated, additional species were otherwise named during this time period by Hay (1909), Parks (1933) and Russell (1934). Until this point, baenids had regularly been named, but, with exception of "*Baena*" *affinis*, never synonymized (Leidy 1873).

In a series of papers, Gaffney thoroughly described the morphology of baenids and thoughtfully revised the taxonomy of the group. This revision resulted in the reorganization of the previously named 36 taxa into 14 valid species and the naming of four new species (Gaffney and Hiatt 1971; Gaffney 1972, 1982a, 1982b). The lack of significant new material, however, did now allow for any shell- and skull-based taxa to be synonymized.

The discovery of new material has spawned much research on baenid turtles over the course of the last two decades. This includes the discovery of a new species from the Early Cretaceous of Maryland (Lipka et al. 2006); the description of a new baenid from the Santonian of Canada (Larson et al. 2013); the redescription of Campanian taxa from Canada (Brinkman and Nicholls 1991, 1993; Brinkman 2003a); the description of abundant material from the Maastrichtian of North Dakota, including the description of three new species (Lyson and Joyce 2009a, 2009b, 2010); the description of a turtle fauna from the Campanian of Utah, including one new species (e.g., Hutchison et al. 2013; Lively, in press); and the description of three new Paleogene taxa, one from the Paleocene of California (Hutchison 2004), one from the Paleocene of New Mexico (Lyson et al., in press) and the last from the Eocene of Wyoming (Archibald and Hutchison 1979). The stratigraphic range of various baenid taxa was furthermore investigated based on shell fragments (e.g., Lillegraven and Eberle 1999; Holroyd et al. 2001, 2014; Holroyd and Hutchison 2002; Lyson et al. 2011). Although the parataxonomy of the group largely remains unresolved, phylogenetic and stratigraphic methods now allow identifying potentially synonymous shell and skull taxa, which in return permits a more realistic assessment of diversification and extinction rates for the group (Lyson and Joyce 2010; Lyson et al. 2011).

For institutional abbreviations see Appendix 1. Named baenid genera are listed in Appendix 2.

Skeletal Morphology

Cranium

The skulls and mandibles of baenids preserve readily compared with those in many other groups of turtles, and much literature is therefore available regarding their morphology. The following, alphabetically organized list summarizes the available literature: *Arundelemys dardeni* Lipka et al., 2006 (Lipka et al. 2006); *Baena arenosa* (Hay 1908; Gaffney 1972, including skull of "*Baena sima*"; note that the skulls figured by Gaffney [1972] are chimeras); "*Baena*" *affinis* (Hay 1908, including skull of "*Baena riparia*"); *Boremys pulchra* (Lambe, 1906a) (Brinkman and Nicholls 1991); *Cedrobaena brinkman* Lyson and Joyce, 2009b (Case 1939; Lyson and Joyce 2009b); *Ce. putorius* (Gaffney, 1972) (Gaffney 1972; Lyson and Joyce 2009b); *Chisternon undatum* (Gaffney 1972, 1982b); *Eubaena cephalica* (Hay, 1904b) (Hay 1904b, 1908; Gaffney 1972, 1982a, 1982b); *Gamerabaena sonsalla* Lyson and Joyce, 2010 (Lyson and Joyce 2010); *Goleremys mckennai* Hutchison, 2004 (Hutchison 2004); *Hayemys latifrons* (Hay 1908; Gaffney 1972); *Neurankylus eximius* Lambe, 1902 (Brinkman and Nicholls 1993); *Neurankylus lithographicus* Larson et al., 2013 (Larson et al. 2013); *Neurankylus torrejonensis* Lyson et al., in press (Lyson et al., in press); *Palatobaena bairdi* Gaffney, 1972 (Gaffney 1972, 1982a, 1982b [late Paleocene material only]); *Palatobaena cohen* Lyson and Joyce, 2009a (Lyson and Joyce 2009a; Gaffney 1982a, 1982b [Maastrichtian and early Paleocene material]); *Palatobaena gaffneyi* Archibald and Hutchison, 1979 (Archibald and Hutchison 1979); *Plesiobaena antiqua* (Lambe, 1902) (Gaffney 1982b; Brinkman 2003a); *Stygiochelys estesi* Gaffney and Hiatt, 1971 (Gaffney and Hiatt 1971; Gaffney 1972, 1982b); and *Trinitichelys hiatti* Gaffney, 1972 (Gaffney 1972, 1982a).

The skulls of basal and omnivorous baenids are relatively elongate (Figure 1A), but increasingly molluscivorous taxa have wider skulls with broad triturating surfaces (Figure 1B, C). Baenids generally have poorly developed lower temporal emarginations, but deep upper temporal emarginations. However, temporal emarginations appear to reduce convergently in multiple lineages following the Cretaceous/Tertiary (K/T) extinction event, perhaps as a result of directed selective pressures from newly emerging small, predatory mammals (Lyson and Joyce 2009a). The surface of the skull has a crenulated texture in basal representatives (e.g., *Trinitichelys hiatti*), but is smooth in most derived taxa. Scute sulci are commonly present on the skull roof.

In basal baenids, the nasals are relatively large, but they are reduced in size in derived baenids and often fuse to the frontals (Figure 1). The prefrontals are relatively large in representatives of *Neurankylus*, but they do not contact one another along the midline in those taxa. The prefrontals of all other baenids are small and often contribute little to nothing to the dorsal skull roofing. The reduction of the prefrontals is compensated through expanded frontals. The parietals are large, paired elements and typically do not contact the squamosals posterolaterally. The postorbitals are elongate bones that typically contribute to the upper temporal emargination. The jugals are relatively small bones and their contribution to the orbit has taxonomic significance, although it is important to note that this character can change with ontogeny (Lyson and Joyce 2009a). The quadratojugals are relatively large elements that anteriorly frame the cavum tympani. The squamosals form the posterodorsal portion of the cavum tympani and define a voluminous antrum postoticum.

The triturating surfaces are mostly formed by the premaxillae and maxillae, but the palatines, pterygoids and jugal can contribute minutely as well, but never the vomer (see Figure 1). Low labial ridges usually frame the triturating surfaces. The presence and extent of lingual ridges is taxonomically significant. The foramen palatinum posterius is relatively small. A broad lingual groove universally separates the right and left triturating surfaces. No baenid is therefore known to develop a true secondary palate.

The pterygoids are large elements that fully floor the cranio-quadrate space and posteriorly contact the basioccipital (see Figure 1). The size and shape of the external pterygoid process is greatly variable and has taxonomic significance. The internal carotid artery enters the skull halfway along the contact between the pterygoid and basisphenoid, but splits immediately within the skull into the palatine and cerebral branches (Gaffney 1975). It is therefore a question of semantics whether a true foramen posterius canalis

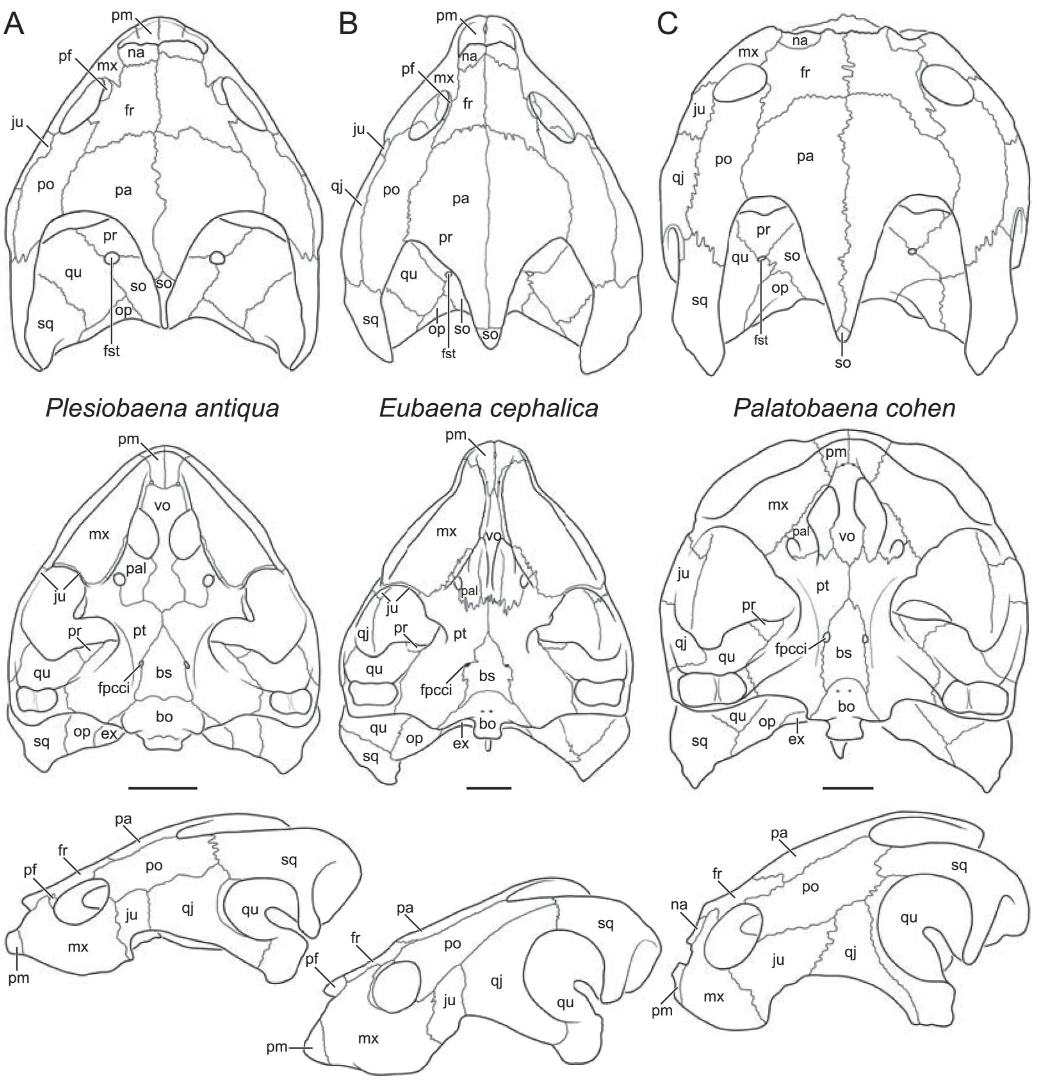

Figure 1. Cranial morphology of *Baenidae* as exemplified by three species. **A,** *Plesiobaena antiqua* (redrawn from Brinkman 2003a). **B,** *Eubaena cephalica* (redrawn from Gaffney 1972). **C,** *Palatobaena cohen* (redrawn from Lyson and Joyce 2009a). *Abbreviations*: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fpcci, foramen posterius canalis carotici interni; fr, frontal; fst, foramen stapedio-temporale; ju, jugal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Scale bars approximate 1 cm.

carotici interni is present or, rather, tightly spaced foramina posterius canalis carotici palatinum and cerebralis (sensu Rabi et al. 2013). The quadrates form a large cavum tympani and low mandibular condyles. The incisura columella auris is broad and universally remains open posteriorly.

Together with the prootic, the quadrate forms a broad processus trochlearis oticum that protrudes only modestly into the temporal fossa (see Figure 1). The foramen stapedio-temporale is set on top of the otic chamber, and the possible contributions of the opisthotic and/or supraoccipital to that foramen has taxonomic significance. The supraoccipital often contributes to the most posterior aspects of the dorsal skull roofing but only forms a short crista supraoccipitalis.

Shell

Shells of baenids preserve readily, but only rarely in association with a skull. The following, alphabetically organized list summarizes the available literature: *Baena arenosa* (*Baena clara*, *Baena emiliae* and *Baena sima* of Hay, 1908; the specimen figured in Gaffney 1972 is "*Baena*" *affinis*); "*Baena*" *affinis* (Leidy 1871a; *Baena riparia* of Hay 1908; *Baena inflata* of Gilmore, 1916c; *Baena arenosa* of Gaffney, 1972); "*Baena*" *escavada* Hay, 1908 (Hay 1908); *Boremys grandis* Gilmore, 1935 (Gilmore 1935; Sullivan et al. 2013); *Boremys pulchra* (Gaffney 1972, material from Judith River Group/Formation only; Brinkman and Nicholls 1991); *Cedrobaena brinkman* (Case 1939; Lyson and Joyce 2009b); *Chisternon undatum* (Hay 1908; Gaffney 1972); *Denazinemys nodosa* (Gilmore, 1916b) (Gilmore 1916b; Wiman 1933; Sullivan et al. 2013); *Eubaena hatcheri* (Hay, 1901) (Hay 1901, 1908); *Neurankylus baueri* Gilmore, 1916b (Gilmore 1916b; Wiman 1933; Sullivan et al. 2013); *Neurankylus eximius* (Lambe 1902; Larson et al. 2013); *Neurankylus lithographicus* (Larson et al. 2013); *Neurankylus torrejonensis* (Lyson et al., in press); *Palatobaena cohen* (Lyson and Joyce 2009a); *Plesiobaena antiqua* (Brinkman 2003a); *Protobaena wyomingensis* (Gilmore, 1920) (Gilmore 1920); *Scabremys ornata* (Gilmore, 1935) (Gilmore 1935; Sullivan et al. 2013); "*Baena*" *hayi* (Gilmore 1916a); *Thescelus insiliens* Hay, 1908 (Hay 1908; figure in Gaffney 1972 is a chimera); *Thescelus rapiens* Hay, 1908 (Hay 1908); and *Trinitichelys hiatti* (Gaffney 1972).

The shell of baenids resembles that of many other aquatic turtles by being moderately domed, teardrop shaped in lateral view and by the presence of a relatively large plastron that covers much of the shell from below (Figure 2). The surface of the shell of basal baenids (e.g., *Trinitichelys hiatti*, *Protobaena wyomingensis*) and an eclectic mix of more derived taxa (e.g., *Thescelus insiliens*) is covered with fine crenulations that resemble those of pleurosternids. The shells of the remaining baenids are either decorated by welt-like pustules (e.g., *Denazinemys nodosa*), midline crenulations (e.g., "*Baena*" *affinis*) or lack distinctive sculpturing (e.g., *Plesiobaena antiqua*).

The carapace consists of the usual set of bones seen in most turtles. With few exceptions (e.g., *Plesiobaena antiqua*; Figure 2B), fontanelles are absent in skeletally mature specimens. The neural series is complete and never interrupted by medial contacts of the costals. A preneural is apparent in several eubaenines (e.g., *Chisternon undatum*). The nuchal is typically a wide, rectangular element, but sometimes shows a deep nuchal notch (e.g., *Thescelus insiliens*). Basal baenids have a regular count of 11 peripherals (e.g., *Neurankylus* spp.; Figure 2A), but the number appears to increase among derived baenids (e.g., *Pl. antiqua*; see Figure 2B), although fusion and/or damage makes it difficult to rigorously assess this number for most taxa. Basal baenids also have one or two suprapygals in addition to the pygal, but this number is typically reduced to one among baenodds (Figure 2C).

A single cervical, five vertebrals, four pairs of pleurals and a complete ring of 12 pairs of marginal scutes cover the carapace of basal baenids (e.g., *Neurankylus* spp.; see Figure 2A). In baenodds, vertebral V fully separates the marginal ring along the midline and thereby contributes to the posterior margin of the shell (see Figure 2B, C). This contact is typically associated with the formation of a broad pygal notch and is often framed by small, supernumerary marginals. In eubaenines, the cervical breaks up into multiple scutes and a prepleural is consistently present (see Figure 2C). Supramarginals are furthermore present in *Boremys* spp., whereas a nuchal scute is apparent in some eubaenines (e.g., *Eubaena hatcheri*; see Figure 2C).

The plastron of baenids is well developed and consists of an entoplastron and paired epi-, hyo-, meso-, hypo- and xiphiplastra. Dorsal epiplastral processes (sensu Lyson et al. 2013) are absent. The mesoplastra are well developed and, with few exceptions (e.g., *Chisternon undatum*), contact one another broadly along the midline. Plastral fontanelles are universally absent and the bridges are broad. The anterior plastral buttress is well developed and broadly contacts the costals and thoracic rib I, whereas the posterior plastral buttress contacts costals V and/or VI. Basal baenids have a pair of equally sized gulars and extragulars (see Figure 2A). The extragulars typically contact one another along the midline posterior to the gulars in baenodds (see Figure 2B). All baenids have four pairs of inframarginals, with the exception of "*Baena*" *affinis*, which only has three that form an interrupted row, thereby allowing a contact of the pectoral scute with the marginal ring.

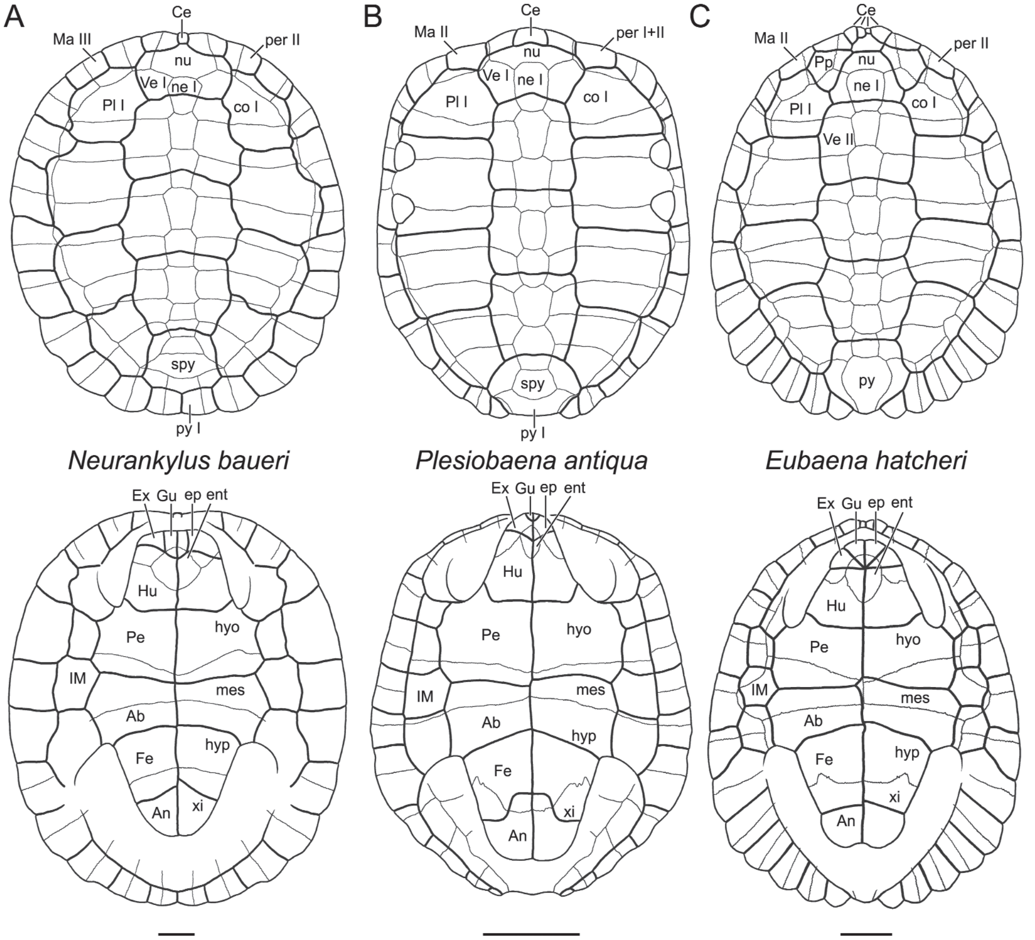

Figure 2. Shell morphology of *Baenidae* as exemplified by three species. **A,** *Neurankylus baueri* (USNM 8344). **B,** *Plesiobaena antiqua* (redrawn from Brinkman 2003a). **C,** *Eubaena hatcheri* (redrawn from Hay 1908). *Abbreviations*: Ab, abdominal scute; An, anal scute; Ce, cervical scute; co, costal; ent, entoplastron; ep, epiplastron; Ex, extragular scute; Fe, femoral scute; Gu, gular scute; Hu, humeral scute; hyo, hyoplastron; hyp, hypoplastron; IM, inframarginal scute; Ma, marginal scute; mes, mesoplastron; ne, neural; nu, nuchal; Pe, pectoral scute; per, peripheral; Pl, pleural scute; Pp, prepleural scute; py, pygal; spy, suprapygal; Ve, vertebral scute; xi, xiphiplastron. Scale bars approximate 5 cm.

The anal-femoral sulcus of baenids is either straight (see Figure 2A, C) or forms a broad omega-shaped sulcus that crosses the xiphiplastra-hypoplastral suture (see Figure 2B).

Postcranium

The nonshell postcranium of baenids is rarely preserved and rarely described. Information is available for the following taxa: “*Baena*” *affinis* (*Ba. arenosa*, *Ba. sima*, *Ba. riparia* of Hay 1908); *Boremys pulchra* (Brinkman and Nicholls 1993); *Cedrobaena brinkman* (Case 1939; Lyson and Joyce 2009b); *Chisternon undatum* (*Ch. hebraica* of Hay 1908); *Plesiobaena antiqua* (Brinkman 2003a); *Thescelus insiliens* (Russell 1934).

The neck of baenid turtles consists of anteroposteriorly short, but dorsoventrally tall vertebrae that have a distinct ventral keel. Reduced cervical ribs are only known from *Boremys pulchra*, where they articulate with the centra along parapophyses and transverse processes set at the middle of the centrum. The three-dimensional shape of the vertebrae of *Chisternon undatum* is intermediate between those of pleurodires and cryptodires, and likely allowed the animal to ventrolaterally tuck its head below the carapace (Werneburg, Hinz et al. 2015; Werneburg, Wilson et al. 2015). The tail is notably long whenever preserved (e.g., *Thescelus insiliens*).

A partial hand and complete foot have been reported for *Cedrobaena brinkman* (Case 1939; Lyson and Joyce 2009b). These are consistent in general morphology with those of other freshwater aquatic turtles, but lack specializations as seen in marine turtles or soft-shelled turtles. The ansula (sensu Joyce et al. 2013) is well developed and digit V lacks a claw.

The scapulacoracoid of baenids is a triradiate element consisting of three processes that lack interconnecting bony webbings. The dorsal margin of the ilium is notable for being oriented obliquely, not horizontal, as in most other turtles. The posterolateral process of the ischium is long and thin. The pelvis of mature individuals is fused and is adorned by a well-ossified epipubis.

Phylogenetic Relationships

In parallel with naming the taxon *Baenidae*, Cope (1873b) provided one of the first phylogenetic hypotheses of turtles in the form of a dendrogram, in which he placed *Baenidae* in a "polytomy" with *Pleurodira* Cope, 1865 and a polyphyletic assemblage of cryptodires with well-developed shells. However, Cope (1873b) did not discuss any particular characters that would allow him to establish this arrangement. In a revised dendrogram, Cope (1884) placed baenids as the direct descendants of *Trionychidae* Gray, 1825, but ancestral to *Pleurodira*, again with no character support. Dollo (1886) similarly placed baenids as sister to pleurosternids within the taxon Clidosterna, which is now recognized as a highly polyphyletic group of aquatic and terrestrial taxa. None of these early arrangements had much impact on subsequent studies.

In his influential classification of turtles, Lydekker (1889) proposed a grouping of turtles named Amphichelydia, which included various primitive turtles, including *Baenidae*, that were thought to be ancestral to both pleurodires and cryptodires. This classification was followed, among others, by Baur (1891), Hay (1905, 1908) and Williston (1925), and was only modified slightly by Williams (1950) through the elevation of various taxa to higher ranks and the addition of *Meiolaniidae*.

Using cladistic arguments, Gaffney (1975) outlined that Amphichelydia was a paraphyletic taxon and suggested instead that *Baenidae* and *Pleurosternidae* (his Glyptopsidae) form a monophyletic group, *Paracryptodira*, situated at the base of the cryptodiran stem lineage. The monophyly of *Paracryptodira* is currently under debate, as some analyses retrieve them as monophyletic (e.g., Joyce 2007; Anquetin 2012; Gaffney et al. 2007; Rabi et al. 2013), but others as paraphyletic (e.g., Sterli et al. 2013). All analyses agree that baenids diverged very close to the base of crown *Testudines*, but there is disagreement if they are situated at the base of *Pan-Cryptodira* (e.g., Joyce 2007), just outside of crown *Testudines* (e.g., Sterli et al. 2013) or in an unresolved polytomy (e.g., Anquetin 2012).

Early authors did not invest much effort into resolving the internal relationships within *Baenidae*, but instead simply highlighted some taxa as unique by placing them in separate genera, thereby rendering "*Baena*" a classic wastebasket taxon (e.g., Hay 1908; Gilmore 1935). Gaffney (1972) produced the first phylogenetic hypothesis of the group, though sampling was restricted to taxa preserving skulls. In addition to identifying the basal taxa *Trinitichelys hiatti* and *Hayemys latifrons*, Gaffney (1972) recognized the derived clade *Baenodda* (his Baenodd) consisting of a Late Cretaceous to Paleocene clade of turtles (i.e., *Plesiobaena*/*Eubaena*/*Stygiochelys*), as sister to an Eocene clade (i.e., *Baena*/*Chisternon*). Brinkman and Nicholls (1991) suggested that *Boremys pulchra* is situated within the former clade as well, whereas Brinkman and Nicholls (1993) suggest that *Neurankylus eximius* is placed outside of *Baenodda*. Part of this sample was integrating into various global analyses of turtles (e.g., Joyce 2007; Anquetin 2012; Sterli et al. 2013), but these did not provide new insights of the interrelationships of baenids.

In a series of papers, Lyson and Joyce developed a number of interrelated character/taxon matrices that densely sample baenid turtles (Lyson and Joyce 2009a, 2009b, 2010, 2011; Lyson et al. 2011, in press). These analyses universally retrieve the basal baenids identified by Gaffney (1972) and Brinkman and Nicholls (1993), but the available character evidence retrieves a different arrangement within *Baenodda* (Figure 3). To facilitate communication, we herein define three

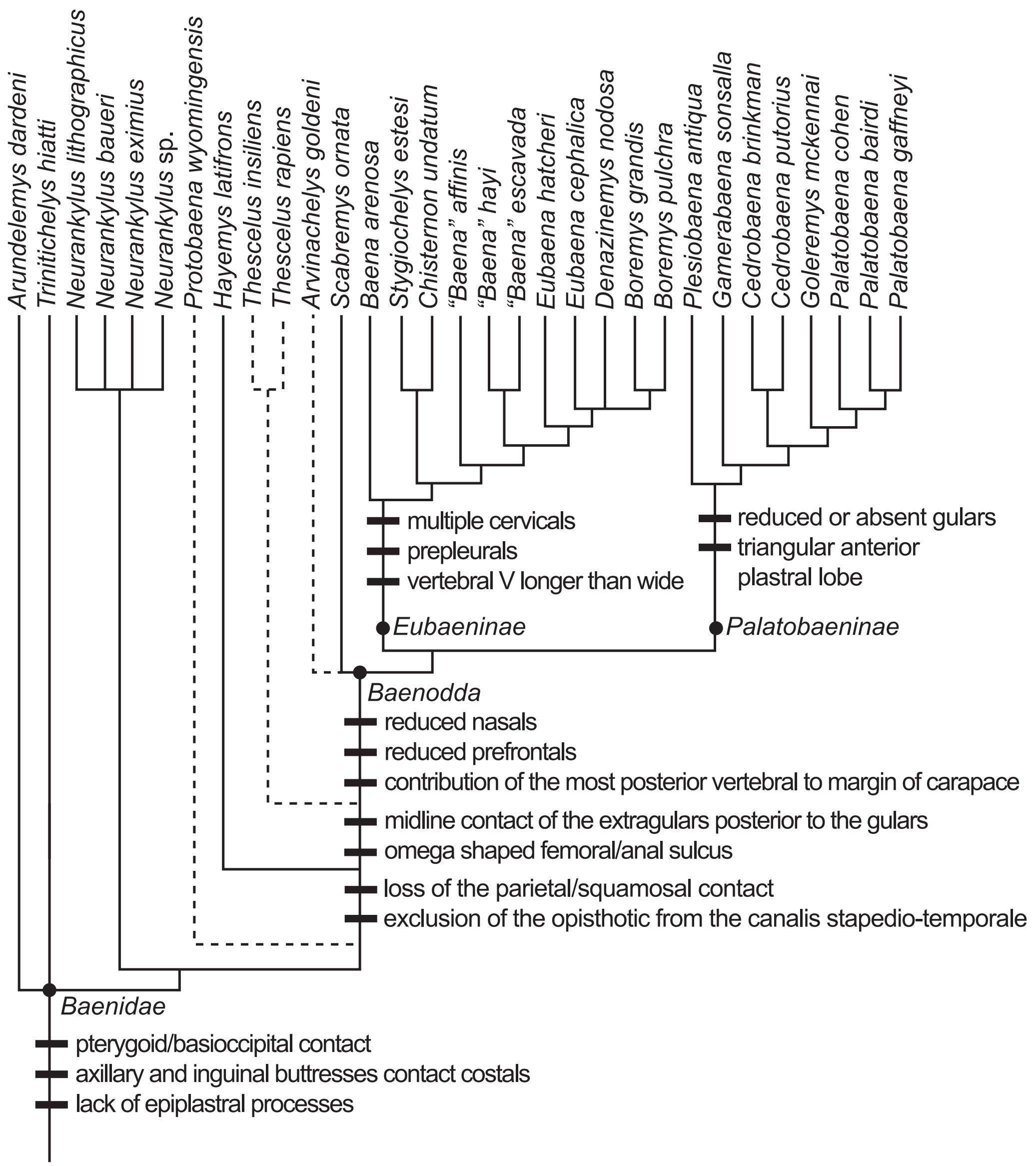

Figure 3. A phylogenetic hypothesis of valid baenid taxa, with diagnostic characters for the most important clades (Lyson et al., in press). Dashed lines highlight taxa that were not included in the analysis and were secondarily inserted using diagnostic characteristics.

internested baenid clades. Following Gaffney and Meylan (1988), *Baenodda* is referred to the clade that originates from the first ancestor of *Baena arenosa* to have evolved a marginal ring that is separated at the midline and allows contribution of the most posterior vertebral to the margin of the carapace. The name *Eubaeninae* Gaffney, 1972 is referred to the most inclusive clade that includes *Eubaena cephalica*, but not *Palatobaena bairdi*. The name *Palatobaeninae* Gaffney, 1972 is referred to the most inclusive clade that includes *Pa. bairdi*, but not *Eu. cephalica*. It is important to note that *Eubaeninae* and *Palatobaeninae* combined may, but do not have to be synonymous with *Baenodda*. The cladogram used herein follows that of Lyson et al. (in press; see Figures 3, 4).

Paleoecology

Baenid turtles are universally found in freshwater aquatic sediments and have tacitly been assumed to inhabit rivers and lakes, likely because of the hydrodynamic shape of the shell. Although the limbs were only partially known, Hay (1908:44) already noted that they were adapted to swimming, but "lacked specializations," presumably those seen in marine turtles. Although baenids are common in the fossil record, only the holotypes of *Cedrobaena brinkman* and *Baena longicauda* (herein referred to *Thescelus insiliens*) preserve partial hands and feet (Russell 1934; Case 1939). Although the manus of turtles is more diagnostic for their habitat preferences (Joyce and Gauthier 2004), the pes is greatly elongated and therefore consistent with aquatic habitats. Hutchison (1984) noted that "*Baena arenosa*" (two species in this review) is dominant in fluvial sediments and may therefore have been a riverine turtle, whereas the coeval *Chisternon undatum* is more common in lacustrine sediments and therefore may have been a pond turtle. In our experience, such sedimentological differences are also apparent for other baenid turtles and should be systematically applied to the group to further understand niche partitioning, as has been done for trionychids (Joyce and Lyson 2011) and dinosaurs (Lyson and Longrich 2011). Sullivan et al. (1988) reported a specimen of *Neurankylus* from the early Paleocene of New Mexico that, uniquely among fossil turtles worldwide, preserves a color pattern over much of the carapace. The pattern consists of small, dark spots set against a light background and Sullivan et al. (1988) interpreted this as being consistent with freshwater aquatic habitat preferences.

Low lingual and labial ridges typically adorn the triturating surfaces in the jaws of baenids, but strong serrations or "teeth" are universally missing. This contrasts with the morphology seen in herbivorous testudinoids (Joyce and Bell 2004) and is therefore more consistent with generalized feeding. The triturating surfaces of numerous baenid turtles are greatly expanded, in concert with a reduction of the lingual and labial ridges. This morphology is developed to the extreme in representatives of *Palatobaena*, and Archibald and Hutchison (1979) suggested that this was indicative of a molluscivorous diet. Although no other taxon has such broad palates, a full spectrum of intermediates is apparent and Lyson et al. (2011) therefore suggested that the high diversity of baenids seen in the Late Cretaceous was, in part, supported by niche partitioning, with taxa ranging from regular omnivores to hyperspecialized molluscivores. In contrast to some extant molluscivorous taxa, in particular *Graptemys* spp. (Ernst and Barbour 1989), there is no apparent niche partitioning between the sexes, as would become apparent from strong sexual dimorphism.

Baenids are common in the fossil record, not only because they live in environments where sediments are being deposited (i.e., lakes and rivers), but also because their shells often fuse into a single unit when reaching skeletal maturity, thereby greatly increasingly their likelihood of being preserved (Hutchison 1984). However, Hutchison (1984) observed among large populations of Eocene baenids, that the shells fuse only in skeletally mature individuals of some taxa (his *Baena arenosa*), while remaining open until maturity in others (*Chisternon undatum*). The difference can be used to aid in the identification of baenids (Hutchison 1984), but also explains why some baenids are more commonly preserved than others. The record of the otherwise Late Cretaceous (Campanian) *Boremys* lineages, for example, was only recently extended by about 11 million years through the rare finding of poorly ossified shells in early Paleocene (Puercan North American Land Mammal Age [NALMA]) sediments (Lyson et al. 2011).

Baenids are notably absent from Arctic regions throughout their fossil record, in contrast to other turtles (West and Dawson 1977; Brinkman and Tarduno 2005). Indeed, whereas baenids are common occurrences in early Campanian rocks exposed in Alberta, they are notably rare in that region following the late Campanian, which coincides with a global cooling trend at that time (Brinkman 2003b, 2013; Brinkman and Eberth 2006). The distribution of baenids may therefore have been restricted by their need for higher temperatures. Among others, this may be one reason why the group never dispersed to other northern continents along various Arctic routes that were available throughout the Cretaceous and Paleogene (D. Brinkman, pers. comm.).

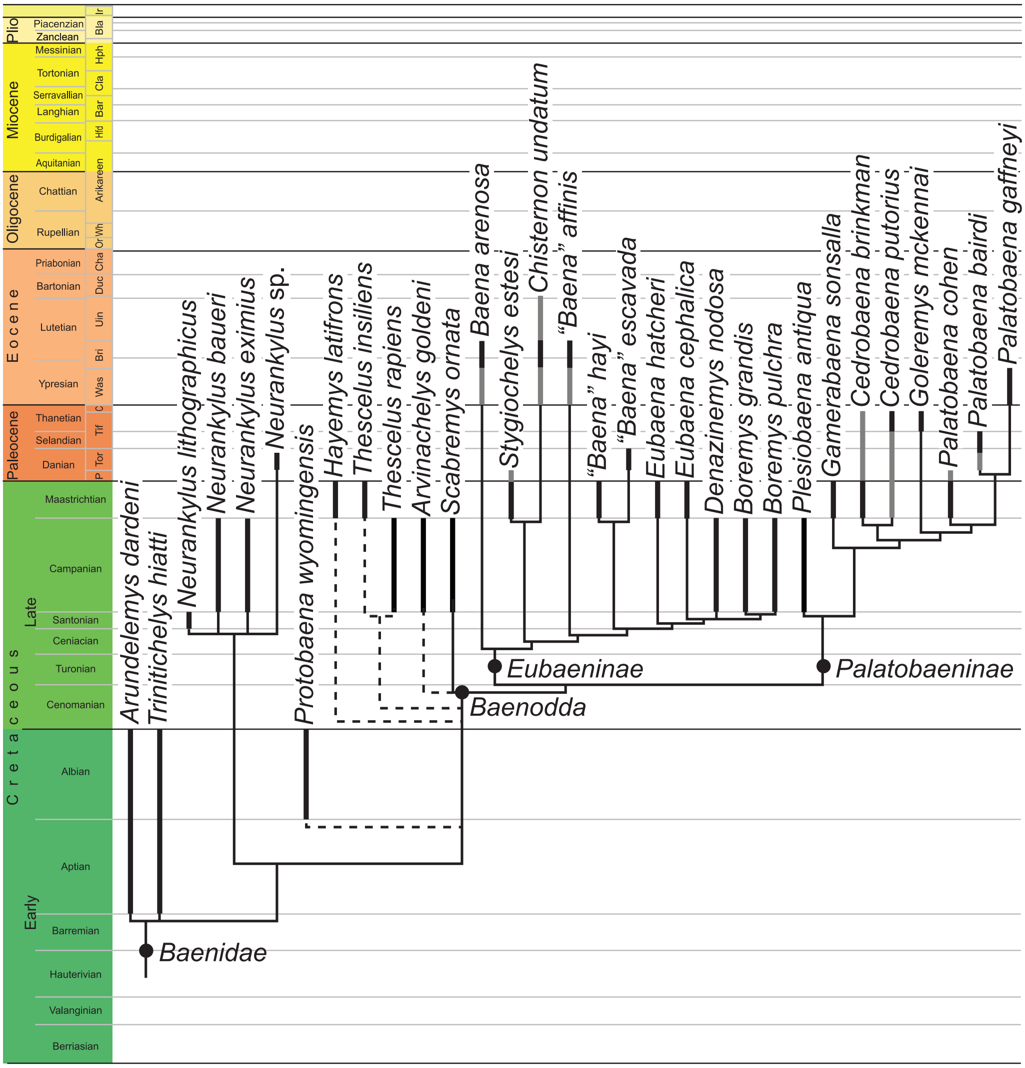

FIGURE 4. The stratigraphic and biogeographic distribution of valid baenid taxa. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material.

Paleobiogeography

The oldest baenids are known from Early Cretaceous (Aptian–Albian) deposits throughout North America, including *Arundelemys dardeni* from Maryland (Lipka et al. 2006), *Protobaena wyomingensis* (Gilmore, 1920) from Wyoming, *Trinitichelys hiatti* from Texas and fragmentary remains from Montana (Figure 5; see also Appendix 3). These early baenids universally have a shell sculpturing reminiscent of Late Jurassic pleurosternids, and it is therefore highly likely that they are the descendants of that group of turtles.

A significant hiatus exists in the fossil record of baenids, which ranges from the Cenomanian to Turonian. During this time range, a broad seaway fully dissected North America into western and eastern landmasses, Laramidia and Appalachia, respectively. Although terrestrial to near-coastal deposits are known from the Late Cretaceous and Paleogene of Appalachia that preserve a rich turtle fauna (e.g., Hay 1908; Weems 1988, 2014; Hutchison and Weems 1998), not a single, even fragmen-

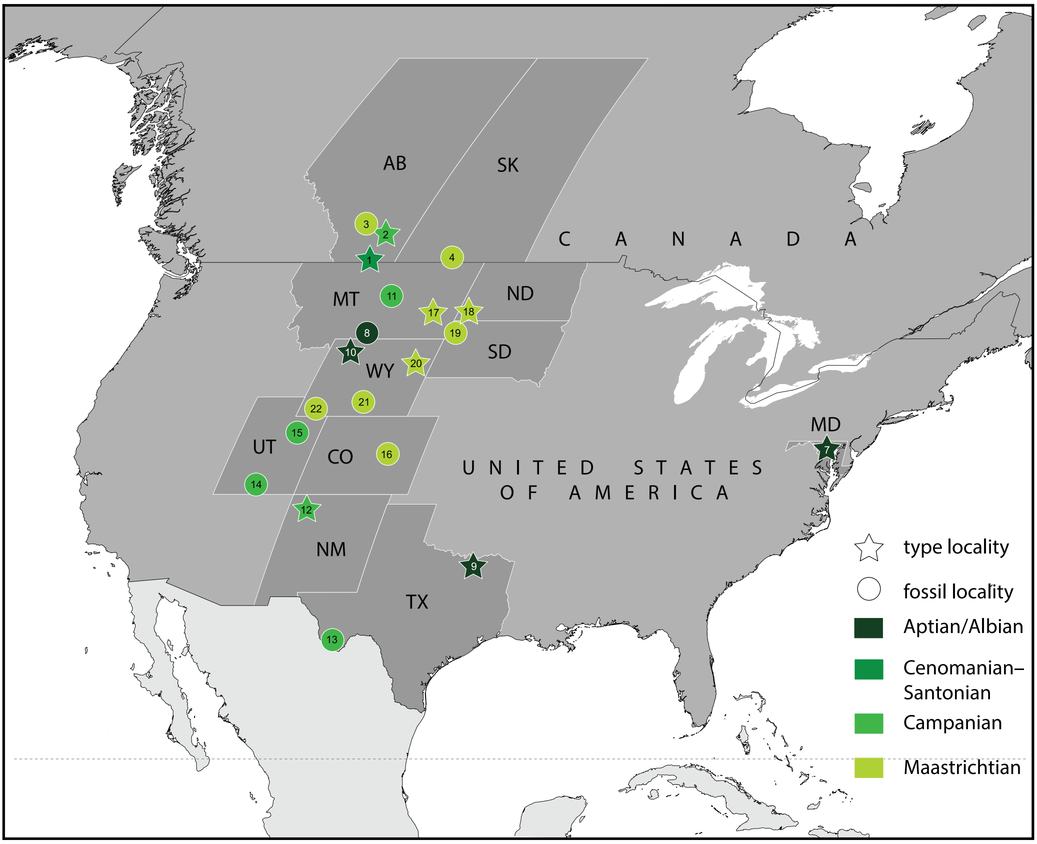

Figure 5. The geographic distribution of figured baenids from the Cretaceous. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: AB, Alberta; CO, Colorado; MD, Maryland; MT, Montana; ND, North Dakota; NM, New Mexico; SD, South Dakota; SK, Saskatchewan; TX, Texas; UT, Utah; WY, Wyoming.

tary baenid has been reported to date. It therefore appears all but certain that baenids went extinct on Appalachia and exclusively continued their evolution on Laramidia.

The Late Cretaceous baenid record starts in the Santonian of Canada with the appearance of *Neurankylus lithographicus* (Larson et al. 2013; see Figure 5). The Campanian rock record is significantly greater throughout Laramidia, and baenids are abundant in the northern deposits of Alberta and Montana and the southern deposits of New Mexico, Texas and Utah. We recognize three northern taxa (i.e., *Boremys pulchra*, *Neurankylus eximius* and *Plesiobaena antiqua*) as opposed to six southern taxa (i.e., *Arvinachelys goldeni*, *Boremys grandis*, *Denazinemys nodosa*, *Neurankylus baueri*, *Scabremys ornata* and *Thescelus rapiens*), and this great difference may well represent a latitudinal diversity gradient, as previously noted by Brinkman (2003b) and Hutchison et al. (2013). Campanian taxa are not affected by parataxonomy. Although unfigured remains of *Neurankylus* have been reported (Brinkman and Rodriguez de la Rosa 2006), it is notable that the rich turtle faunas of Coahuila, Mexico, appear to mostly lack baenids (Rodriguez-de la Rosa and Cevallos-Ferriz 1998; Brinkman and Rodriguez de la Rosa 2006).

The Maastrichtian record of baenids is rich, but unfortunately restricted entirely to the northern basins of Alberta, Colorado, Montana, Wyoming, North Dakota, South Dakota and Saskatchewan. We recognize nine valid baenid taxa and one lineage from this region, but note that that number is likely inflated by parataxonomy, as four taxa are known from skulls only (*Gamerabaena sonsalla*, *Eubaena cephalica*, *Hayemys latifrons* and *Stygiochelys estesi*), four from

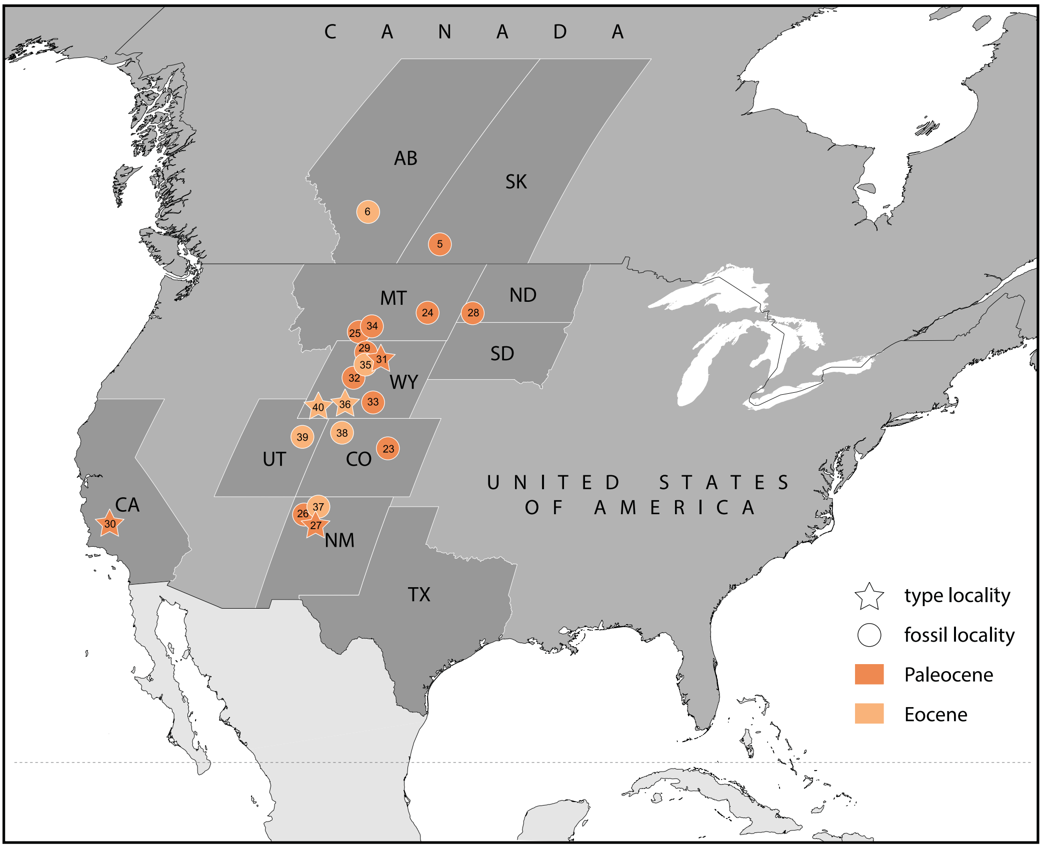

FIGURE 6. The geographic distribution of figured baenids from the Paleogene. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: AB, Alberta; CA, California; CO, Colorado; MT, Montana; ND, North Dakota; NM, New Mexico; SD, South Dakota; SK, Saskatchewan; TX, Texas; UT, Utah; WY, Wyoming.

shells only (*Boremys* sp., *Eubaena hatcheri*, "*Baena*" *hayi* and *Thescelus insiliens*), but only two from skull and shells (*Palatobaena cohen* and *Cedrobaena brinkman*). We are herein able to propose several possible synonymies among the skull and shell taxa (i.e., *Eu. cephalica* with *Eu. hatcheri*; *St. estesi* with "*Ba.*" *hayi*; and *H. latifrons* with *Th. insiliens*; see Systematic Paleontology below), but all of these must remain conjectural hypotheses until the appropriate associations are found.

Although the Paleocene record of baenid turtles is far less extensive than that of the Late Cretaceous, rich earliest Paleocene fossil sites in the northern basins of North Dakota, Montana and Wyoming (Holroyd and Hutchison 2002; Holroyd et al. 2014; Lyson and Joyce 2009a, 2009b; Lyson et al. 2011; Figure 6) document that the vast majority of baenid lineages survived the K/T extinction event (Lyson and Joyce 2009b, 2010; Lyson et al. 2011). The diversity of baenids is less well understood for the northern basins in the late Paleocene. However, excellent sites in Wyoming document the persistent presence of *Cedrobaena brinkman* and *Ce. putorius* combined with the possibly anagenetic appearance of *Palatobaena bairdi* (Gaffney 1972; Lyson and Joyce 2009a, 2009b).

After a long hiatus that spans the Maastrichtian, the fossil record of baenids reemerges in the early Paleocene of the southern basins of New Mexico. Although much material is available, only three taxa have been reported to date: "*Baena*" *escavada*, *Neurankylus torrejonensis* and *Palatobaena* sp. (Hay 1908; Lucas 1982; Sullivan and Lucas 1986; Sullivan et al. 1988; Lyson et al., in press). The finding of *Goleremys mckennai* in the late Paleocene of California is particularly significant, as this is the only record of a baenid west of the North American Cordillera (Hutchison 2004).

Although fragmentary remains have been reported from the Eocene of New Mexico (Lichtig and Lucas 2015) and Saskatchewan (Hutchison and Storer 1998), the vast majority of Eocene baenid material is described from Utah and Wyoming (Hay 1908; Gilmore 1916c). We recognize a total of four baenid taxa in the Eocene: *Baena arenosa*, *Chisternon undatum*, *Palatobaena gaffneyi* and "*Baena*" *affinis*. The last *Pa. gaffneyi* is reported from the early Eocene (Wasatchian NALMA; Holroyd et al. 2001) and the last *Chisternon undatum* from the early late Eocene (early Uintan NALMA; Hutchison 1992). Turtles ascribed to *Baena arenosa*, our *Baena arenosa* and "*Baena*" *affinis*, are reported from as late as the early late Eocene (late Uintan NALMA). No later records are known throughout North America, and the group therefore appears to be extinct by the latest Eocene (Hutchison 1992, 1996).

Riabinin (1938) reported the possible presence of baenids from Late Cretaceous sediments exposed in Kazakhstan, but he did not substantiate this claim with any specimens. All current reviews on the turtle faunas of Asia agree that baenids never occurred on this continent (e.g., Sukhanov 2000). Karl and Tichy (2002) more recently interpreted a partial skull from the Late Cretaceous of Chile as a new species of baenid, *Australobaena chilensis*. Parham et al. (2014) highlighted the surprising nature of this identification, but were reluctant to provide an authoritative reassessment of this taxon, as the holotype is fragmentary and demands a better description. We here note that all baenids, even fully molluscivorous forms such as *Palatobaena* spp., lack true secondary palates and never exhibit a vomerine contribution to the triturating surfaces, in contrast to various radiations of marine turtles, including *A. chilensis* (Parham et al. 2014). We therefore conclude with confidence that *Australobaena chilensis* is not a baenid. The fossil record of the group is therefore fully restricted to North America.

Systematic Paleontology

Valid Taxa

See Appendix 4 for the hierarchical taxonomy of *Baenidae* as described in this work.

Baenidae Cope, 1873b

Phylogenetic definition. Following Lyson and Joyce (2011), we here refer the name *Baenidae* to the most inclusive clade that includes *Baena arenosa* Leidy, 1870 but not *Pleurosternon bullockii* (Owen, 1842) or any extant species of turtle.

Diagnosis. Representatives of Baenidae are currently diagnosed relative to other turtles by the presence of the following derived characters: pterygoid-basioccipital contact, axillary and inguinal buttresses that reach the costals and lack of epiplastral processes. Baenids symplesiomorphically possess a processus trochlearis oticum, a foramen posterius canalis carotici interni that is located halfway along the pterygoid-basisphenoid contact and mesoplastra.

Arundelemys dardeni Lipka et al., 2006

Taxonomic history. *Arundelemys dardeni* Lipka et al., 2006 (new species).

Type material. USNM 497740 (holotype), a nearly complete cranium mostly lacking the posterior dermal roofing bones (Lipka et al. 2006, figs. 2, 3).

Type locality. Hotton locality, near Muirkirk, Prince George's County, Maryland, USA (see Figure 5); Potomac Formation, late Albian to early Aptian, Early Cretaceous (Lipka et al. 2006).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Arundelemys dardeni* is diagnosed as a baenid by the presence of a pterygoid-basioccipital contact, a processus trochlearis oticum and a foramen posterius canalis carotici interni that is located halfway along the pterygoid-basisphenoid contact. *Arundelemys dardeni* is differentiated from all other baenids by its elongate skull, deep upper temporal emargination, crenulated skull roof, moderately developed dorsal prefrontal exposure, large nasals and the exclusion of the jugal from the orbit margin.

Comments. *Arundelemys dardeni* is based on a well-preserved partial cranium that was found in isolation in an Early Cretaceous clay pit near Muirkirk, Maryland (Lipka et al. 2006). Clay pits in the vicinity of Muirkirk have yielded fragmentary shell remains of at least three turtle taxa over the course of the last century, including the coarsely ornamented solemydid *Naomichelys speciosa*, the finely ornamented "*Glyptops caelatus*" (see Invalid Taxa below) and an unnamed turtle with a smoothly textured shell (Kranz 1998). At this point, it is only evident that *A. dardeni* cannot be considered a solemydid, as the skull categorically differs from that of *Naomichelys speciosa* (Joyce et al. 2014). Although it appears likely that the shell taxon "*G. caelatus*" will eventually be shown to belong to the skull taxon *A. dardeni*, we agree with Lipka et al. (2006) that it is currently not possible to synonymize these taxa, as this material was not found in direct association. Phylogenies universally retrieve *A. dardeni* as a basal baenid (e.g., Lipka et al. 2006; Lyson et al. 2011; Larson et al. 2013).

Hayemys latifrons (Hay, 1908)

Taxonomic history. *Eubaena latifrons* Hay, 1908 (new species); *Hayemys latifrons* Gaffney, 1972 (new combination).

Type material. AMNH 6139 (holotype), a crushed, partial cranium (Hay 1908, figs. 69, 70; Gaffney 1972, figs. 6, 7, 48).

Type locality. Seven Mile Creek, Niobrara or Weston County, Wyoming, USA (Hay 1908; see Figure 5); Lance Formation (Gaffney 1972), Maastrichtian, Late Cretaceous.

Referred material and range. No specimens have been referred to date.

Diagnosis. *Hayemys latifrons* is diagnosed as part of Baenidae by a pterygoid-basioccipital contact, a processus trochlearis oticum and a foramen posterius canalis carotici interni that is located halfway along the pterygoid-basisphenoid. *Hayemys latifrons* is currently differentiated from other baenids by having large nasals, a relatively large contribution of the prefrontal to the skull roof, a jugal contribution to the orbit margin, deep upper temporal emargination and frontals that are larger than the parietals.

Comments. *Hayemys latifrons* is a skull taxon based on a partially crushed cranium from the Maastrichtian Lance Formation of Wyoming (Hay 1908). No other skulls of similar morphology have been found to date, and *H. latifrons* is therefore one of the most poorly understood baenid turtles. Gaffney (1972) tentatively placed *H. latifrons* outside of *Baenodda*, and most subsequent analyses have agreed with this placement (e.g., Lyson and Joyce 2009a, 2009b; Lyson et al., in press). The phylogenetic analysis of Lyson and Joyce (2010) furthermore placed *H. latifrons* in a polytomy with the shell taxon *Thescelus insiliens*, which also originates from the Late Cretaceous (Maastrichtian) of Wyoming, and they consequently proposed a tentative synonymy for these two taxa. A skull–shell association is once again needed to support this assessment. However, given that we lack external data that would allow us to corroborate or disprove this association, we do not emphasize this possible synonym in our figures.

Neurankylus Lambe, 1902

Type species. *Neurankylus eximius* Lambe, 1902.

Diagnosis. *Neurankylus* is diagnosed as a baenid by the complete list of characters listed for that clade above. *Neurankylus* is currently differentiated from all other baenids by their large size (carapacial length more than 50 cm), a smooth rounded shell that lacks both nuchal and pygal notches, a complete ring of marginals, wide vertebrals, a undivided cervical that is taller than wide, lack of contact between the extragulars, broad exposure of the prefrontals on the dorsal skull roof, large nasals, little to no upper temporal emargination, small and triangular basisphenoid and a deep and distinctly hooked dentary.

Neurankylus baueri Gilmore, 1916b

Taxonomic history. *Neurankylus baueri* Gilmore, 1916b (new species); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* = *Neurankylus baueri* Gaffney, 1972 (junior synonym); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* = *Neurankylus baueri* = *Neurankylus wyomingensis* Brinkman and Nicholls, 1993 (junior synonym); *Neurankylus baueri* Larson et al., 2013 and Sullivan et al., 2013 (nomen validum).

Type material. USNM 8344 (holotype), a complete shell (Gilmore 1916b, figs. 32, 33, pls. 64, 65; Gaffney 1972, fig. 38; Larson et al. 2013, fig. 21.1c; Sullivan et al. 2013, fig. 20.6a, b).

Type locality. Ah-shi-sle-pah Wash/Meyers Creek, middle branch, San Juan County, New Mexico, USA (see Figure 5); Hunter Wash Member, Kirtland Formation, Campanian, Late Cretaceous (Sullivan et al. 2013).

Referred material and range. Late Cretaceous (Campanian), Kirtland and Fruitland Formations of New Mexico (referred material of Sullivan et al. 2013) and Kaiparowits Formation of Utah (material referred to *Neurankylus* type A and B by Hutchison et al. 2013).

Diagnosis. *Neurankylus baueri* is currently diagnosed as a baenid by axillary and inguinal buttresses that reach the costals, a lack of epiplastral processes and the presence of well-developed mesoplastra, and as a representative of *Neurankylus* by its large size, a smooth shell that lacks both anterior and posterior notches, a complete ring of marginals, wide vertebrals, a small undivided cervical that is taller than wide and lack of contact between the extragulars. *Neurankylus baueri* is currently differentiated from other *Neurankylus* by a narrow vertebral V, a scalloped posterior edge of the shell, rectangular posterior neural bones and the development of a weak, disrupted median keel on the carapace.

Comments. *Neurankylus baueri* is based on a well-preserved and near-complete shell from the Late Cretaceous (Campanian) of New Mexico (Gilmore 1916b). In his review of *Baenidae*, Gaffney (1972) synonymized *N. baueri* with *N. eximius* from similarly dated sediments in southern Alberta, therefore creating a taxon that eventually was thought to have a large spatial and temporal distribution through the referral of material ranging from the Santonian to Paleocene (see *N. eximius*). However, new finds have shown that the northern and southern Campanian specimens differ systematically (Sullivan et al. 2013), and we therefore agree that they represent two separate lineages.

Hutchison et al. (2013) described a number of specimens from the Late Cretaceous (Campanian) of Utah and referred them to two informal taxa, *Neurankylus* A and B. The primary differences diagnosing *Neurankylus* A are the relative length and width of the anterior plastral lobe, but in our experience, this character is highly variable within baenids. *Neurankylus* B is similarly diagnosed by its large size and broader marginals, characters which eventually may turn out to systematically diagnose a taxon, but that are here interpreted to be interspecific variation as well. We therefore refer all Campanian material from Utah to *N. baueri* and await the discovery of additional material that will help test our taxonomic assertions.

Neurankylus eximius Lambe, 1902
(= *Baena fluviatilis* Parks, 1933
= *Charitemys captans* Hay, 1908)

Taxonomic history. *Neurankylus eximius* Lambe, 1902 (new species); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys* *captans* = *Neurankylus baueri* Gaffney, 1972 (senior synonym); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* = *Neurankylus baueri* = *Neurankylus wyomingensis* Brinkman and Nicholls, 1993 (senior synonym); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* Larson et al., 2013 (senior synonym).

Type material. CMN 1504 (holotype), fragmentary posterior half of carapace (Lambe 1902, fig. 7; Hay 1908, fig. 90; Larson et al. 2013, fig. 21.2).

Type locality. Red Deer River, Alberta, Canada (Lambe 1902; see Figure 5); Judith River Group, probably Dinosaur Park Formation, Campanian, Late Cretaceous (Larson et al. 2013).

Referred material and range. Late Cretaceous (Campanian) of Alberta, Canada, and Montana, USA (referred material of Brinkman and Nicholls 1993 and Larson et al. 2013, including type material of *Baena fluviatilis* and *Charitemys captans*).

Diagnosis. *Neurankylus eximius* is currently diagnosed as a baenid by the full list of characters listed above for that clade, and as a representative of *Neurankylus* by its large size, smooth shell that lacks both anterior and posterior notches, complete ring of marginals, wide vertebrals, small, undivided cervical that is taller than wide, lack of contact between the extragulars, large exposure of the prefrontal on the dorsal skull roof and small and triangular basisphenoid. *Neurankylus eximius* is currently differentiated from other *Neurankylus* by a wide vertebral V, no scalloping on the posterior edge of the shell, hexagonal posterior neural bones, the development of a weak, disrupted median keel on the carapace and moderate upper temporal emargination in the skull.

Comments. *Neurankylus eximius* is based on the posterior half of a shell collected from Campanian deposit in southern Alberta, Canada (Lambe 1902). Gaffney (1972) concluded in his taxonomic review of baenid turtles that *N. eximius* is the only valid species of *Neurankylus* and that this species therefore has a broad Campanian distribution ranging from Alberta, Montana and New Mexico and a single find from the Maastrichtian of Montana. A number of additional specimens were provisionally assigned to this taxon in subsequent years, thereby explicitly or implicitly expanding its distribution significantly to the Santonian of Canada (Brinkman 2003b), the Campanian of Texas (Tomlinson 1997), the Maastrichtian of Colorado (Hutchison and Holroyd 2003), North Dakota and Montana (Holroyd and Hutchison 2002) and the early Paleocene (Puercan and Torrejonian NALMA) of New Mexico (Lucas 1982; Sullivan et al. 1988).

We herein follow the new taxonomic arrangement of Larson et al., 2013, who recognize a Santonian taxon from Alberta (*N. lithographicus*), a Campanian taxon from Alberta and Montana (*N. eximius*) and a Campanian taxon from New Mexico (*N. baueri*). Of the remaining specimens formerly referred to *N. eximius*, we here assign the newly described material from Utah to *N. baueri*, but refer all others to *Neurankylus* sp. until they have been further evaluated.

We are aware of significant material of *Neurankylus* from Wyoming and Montana that is housed, among others, at UCMP and YPM, but unfortunately these specimens are undescribed to date. Given that this material is temporarily and spatially "intermediate" relative to *N. eximius* and *N. baueri*, it may have an important impact on the taxonomy of the group, and we therefore urge study of this material.

Neurankylus lithographicus Larson et al., 2013

Taxonomic history. *Neurankylus lithographicus* Lambe, 1902 (new species).

Type material. TMP 2007.035.0045 (holotype), poorly preserved anterior half of a shell (Larson et al. 2013, figs. 21.1a, 4, 5); TMP 1991.113.0001 (paratype), fragmentary carapace, plastron, caudal vertebrae, limb elements and possible squamosal (not figured); TMP 1991.113.0009 (paratype), plastral fragment (Larson et al. 2013, fig. 21.5).

Type locality. 1.5 km east of Writing-On-Stone Provincial Park, Alberta, Canada (see Figure 5); Deadhorse Coulee Member, Milk River Formation, 26.5 m above Virgelle Member, Santonian, Late Cretaceous (Larson et al. 2013). The paratypes were found in the vicinity of the holotype in outcrops of equivalent age (Larson et al. 2013).

Referred material and range. Late Cretaceous (Santonian) of the vicinity of Writing-On-Stone Provincial Park, Alberta, Canada (hypodigm of Larson et al. 2013).

Diagnosis. *Neurankylus lithographicus* is currently diagnosed as a baenid by presence of a processus trochlearis oticum, axillary and inguinal buttresses that reach the costals, lack of epiplastral processes and the development of mesoplastra, and as a representative of *Neurankylus* by its large size, smooth shell that lacks both anterior and posterior notches, complete ring of marginals, wide vertebrals and a small, undivided cervical that is taller than wide. *Neurankylus lithographicus* is currently differentiated from all *Neurankylus* by a wide vertebral V, extragulars that are smaller than the gulars and that contact one another along the midline and the lack of a posterior scalloped shell margin.

Comments. *Neurankylus lithographicus* is based on a number of partial specimens recovered from Late Cretaceous (Santonian) sediments within the immediate vicinity of Writing-On-Stone Provincial Park, Alberta. The available material does not preserve many important anatomical features, but we agree that enough character evidence is available to diagnose a valid taxon. Additional finds will hopefully allow diagnosing this taxon more thoroughly in the future.

Neurankylus torrejonensis Lyson et al., in press

Taxonomic history. *Neurankylus torrejonensis* Lyson et al., in press (new species).

Type material. NMMNHS P-9049, a fragmentary skeleton, including skull, lower jaws, shell and associated postcranial elements (Lyson et al., in press, figs. 2–5).

Type locality. SW1/4SE1/4SE1/4 Section 32, T 21 N, R 4 W, east flank of Torreon (a.k.a. Torrejon) Wash, Sandoval County, New Mexico, USA; Nacimiento Formation, 25 m below the unconformable contact of the overlying San Jose Formation, Torrejonian NALMA, Danian, early Paleocene (Lyson et al., in press).

Referred material and range. No specimens are referred. The specific affinities of slightly older (Puercan NALMA) material from nearby localities (e.g., Sullivan et al. 1988) remains uncertain.

Diagnosis. *Neurankylus torrejonensis* is currently diagnosed as a baenid by presence of a processus trochlearis oticum, axillary and inguinal buttresses that reach the costals, lack of epiplastral processes and the development of mesoplastra, and as a representative of *Neurankylus* by its large size, smooth shell that lacks both anterior and posterior notches, complete ring of marginals, wide vertebrals, small, undivided cervical that is taller than wide, lack of contact between the extragulars, broad exposure of the prefrontals on the dorsal skull roof, large nasals, no upper temporal emargination, small and triangular basisphenoid and a deep and distinctly hooked dentary. *Neurankylus torrejonensis* is currently differentiated from other *Neurankylus* by a wide vertebral V, extragulars that are smaller than the gulars, the lack of a posterior scalloped edge of the shell, broad exposure of the parietals dorsal to the supraoccipital and a large prefrontal exposure on the dorsal skull roof.

Comments. The holotype of *Neurankylus torrejonensis* was initially reported by Lucas (1982) and was used to inform the cranial scoring of *N. eximius* (sensu Gaffney 1972) in several cladistic analyses (e.g., Brinkman and Nicholls 1993; Lyson and Joyce 2009a, 2009b, 2010, 2011), but the specimen remained undescribed until recently. Although all four named species of *Neurankylus* only differ from one another in minor details (Lyson et al., in press), we agree that four taxa can be recognized that range from the Santonian of Canada to the Paleocene of New Mexico.

Thescelus Hay, 1908

Type species. *Thescelus insiliens* Hay, 1908.

Diagnosis. *Thescelus* is diagnosed as a baenid by the presence of axillary and inguinal buttresses that reach the costals, lacking epiplastral processes, and mesoplastra, and partially resembles baenodds by an omega-shaped femoral-anal sulcus and midline contact of the extragulars posterior to the gulars. *Thescelus* is currently differentiated from other baenids by the presence of marginals that prevent the vertebral V from forming part of the shell margin, a wide and unbroken cervical, a deep nuchal notch and extremely large extragulars.

Thescelus insiliens Hay, 1908
(= *Baena longicauda* Russell, 1934)

Taxonomic history. *Thescelus insiliens* Hay, 1908 (new species); *Thescelus insiliens* = *Baena longicauda* = *Thescelus rapiens* = *Thescelus hemispherica* Gaffney, 1972 (senior synonym); *Thescelus insiliens* Sullivan et al., 2013 (nomen validum).

Type material. AMNH 1108 (holotype), a near-complete shell (Hay 1908, pls. 24, 25; Gaffney 1972, fig. 42).

Type locality. Seven Mile Creek, about 5 miles (8 km) north of the Cheyenne River, Ogallala County, Wyoming, USA (Hay 1908; see Figure 5); Lance Formation (Gaffney 1972), Maastrichtian, Late Cretaceous.

Referred material and range. Late Cretaceous (Maastrichtian) of Montana, USA (referred material of Hutchison and Archibald 1986 and Holroyd et al. 2014) and Saskatchewan, Canada (Russell 1934; Gaffney 1972; type material of *Baena longicauda*).

Diagnosis. *Thescelus insiliens* is diagnosed as a baenid and a representative of *Thescelus* by the complete list of shell characters listed for these clades above. *Thescelus insiliens* is currently differentiated from other *Thescelus* by the presence of a shell with crenulated texture, absence of prepleurals and presence of small gulars.

Comments. *Thescelus insiliens* is based on a single, well-preserved shell from the Lance Formation of Wyoming (Hay 1908). Gaffney (1972) united *Baena longicauda* and all three then-known species of *Thescelus* into a single taxon, but the recent review of Sullivan et al. (2013) reinstated the three *Thescelus* species. Given the small number of specimens that are available, we find it difficult to arrive at a rigorous taxonomic conclusion. However, given that many other baenid taxa have northern and southern representatives, and that there are systematic differences in humeral morphology and shell pattern among the Campanian southern material and the Maastrichtian northern material, we recognize the northern *Th. insiliens* and the southern *Th. rapiens*. The holotype of *B. longicauda* displays enough characters to allow referring it to *Thescelus*, and we refer it to *Th. insiliens* on the bais of temporal and stratigraphic considerations. The holotype of *Thescelus hemispherica*, by contrast, does not clearly display characters of any particular baenid taxon, and we therefore declare it a nomen dubium (see below).

Thescelus insiliens appears to be an exceedingly rare taxon, given that it is only known from the holotype from Wyoming, the holotype of *B. longicauda* and a single referred specimen from the Hell Creek Formation of Montana (Hutchison and Archibald 1986; Holroyd et al. 2014). *Thescelus insiliens* is retrieved in an unresolved polytomy with *Hayemys latifrons* in some phylogenies (e.g., Lyson and Joyce 2010), a rare skull taxon known from a single specimen, and it is therefore possible that these taxa are synonymous, but skull–shell associations are needed to rigorously test this hypothesis.

Thescelus rapiens Hay, 1908

Taxonomic history. *Thescelus rapiens* Hay, 1908 (new species); *Thescelus insiliens* = *Baena longicauda* = *Thescelus rapiens* = *Thescelus hemispherica* Gaffney, 1972 (junior synonym); *Thescelus rapiens* Sullivan et al., 2013 (nomen validum).

Type material. AMNH 6066 (holotype), a partial shell, missing much of the margins (Hay 1908, figs. 91, 92; Sullivan et al. 2013, fig. 20.8a, b).

Type locality. Ojo Alamo, San Juan County, New Mexico, USA; De-na-zin Member, Kirtland Formation (see Figure 5); Campanian, Late Cretaceous (Sullivan et al. 2013).

Referred material and range. Late Cretaceous (Campanian), New Mexico, USA (hypodigm of Wiman 1933).

Diagnosis. *Thescelus rapiens* is diagnosed as a baenid and a representative of *Thescelus* by the complete list of shell characters listed for these clades above. *Thescelus rapiens* is currently differentiated from other *Thescelus* by absence of a crenulated shell texture, absence of prepleurals and large gulars.

Comments. *Thescelus rapiens* is based on a partial shell from the Late Cretaceous (Campanian) of New Mexico. Although Gaffney (1972) synonymized this taxon with *Thescelus insiliens*, we agree with Sullivan et al. (2013) that it is valid (see above), but consider *Thescelus hemispherica* to be a nomen dubium. Given that no new specimens of *Thescelus* have been reported in the last several decades, our hypodigm overlaps with that of Wiman (1933). The phylogenetic position of *Thescelus* spp. still remains unresolved (see *Th. insiliens* above).

Trinitichelys hiatti Gaffney, 1972

Taxonomic history. *Trinitichelys hiatti* Gaffney, 1972 (new species).

Type material. MCZ 4070 (holotype), a partial skeleton, lacking mandibles, caudal vertebrae, distal limbs and posterior part of shell (Gaffney 1972, figs. 2–5, 47; Gaffney 1982a, fig. 3).

Type locality. One mile from Hardee, Montague County, Texas, USA (Gaffney 1972; see Figure 5); Antlers Formation (Trinity Sands of Gaffney 1972), Aptian–Albian, Early Cretaceous (Joyce et al. 2014).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Trinitichelys hiatti* is diagnosed as a baenid by the full list of characters listed above for that clade. *Trinitichelys hiatti* is differentiated from all other baenids by the presence of a narrow, undivided cervical, an elongate skull, small prefrontal that does not form part of the dorsal skull roof and a crenulated texture on both the skull and shell.

Comments. *Trinitichelys hiatti* is only known from a partial skeleton (Gaffney 1972) from the Early Cretaceous (Aptian–Albian) of Texas and is therefore temporally similar in age to *Protobaena wyomingensis* from Wyoming and the dubious taxon *Glyptops pervicax* from Montana. Phylogenetic analyses typically retrieve this taxon as a relatively basal baenid outside of the clade formed by *Neurankylus* and *Baenodda* (Gaffney 1972; Lipka et al. 2006; Lyson et al. 2011) but a more derived position relative to *Neurankylus*, but outside of *Baenodda* has also been retrieved (Larson et al. 2013). The available material of *Tr. hiatti* and *Pr. wyomingensis* does not overlap greatly and it is therefore difficult to evaluate a potential synonymy. Small differences are apparent in the shape of the posterior vertebrals, but we do not give this much weight, as both taxa are known from only a single specimen and with little overlapping skeletal material. We nevertheless retain both taxa as valid based on spatial considerations.

Protobaena wyomingensis (Gilmore, 1920), gen. nov., comb. nov.

Taxonomic history. *Neurankylus wyomingensis* Gilmore, 1920 (new species); [*Neurankylus wyomingensis*] Gaffney, 1972 (nomen dubium); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* = *Neurankylus baueri* = *Neurankylus wyomingensis* Brinkman and Nicholls, 1993 (junior synonym); *Neurankylus wyomingensis* Larson et al., 2013 (nomen validum).

Type material. USNM 7581 (holotype), posterior half of shell (Gilmore 1920, pls. 29, 30).

Type locality. Shoshone River, near Cody, Big Horn County, Wyoming, USA (Gilmore 1920; see Figure 5); Thermopolis Shale (formerly Colorado Shale; Gilmore 1920), Albian, Early Cretaceous (Rice 1976).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Protobaena wyomingensis* is diagnosed as a baenid by the presence of inguinal buttresses that reach the costals, and mesoplastra. *Protobaena wyomingensis* is differentiated from all other baenids by a large crenulated shell, a pygal notch and by the conflation of the posterior skin-scute sulcus with the posterior margin of the shell.

Comments. *Protobaena wyomingensis* is based on the posterior portions of a damaged shell that was recovered from Early Cretaceous sediments in Wyoming (Gilmore 1920). This turtle is therefore broadly equivalent in age to the type material of "*Glyptops pervicax*" from nearby Montana and of *Trinitichelys hiatti* from Texas. The taxon was originally diagnosed by the crenulated sculpturing on the shell, which distinguished it from other members of *Neurankylus*, the genus to which it was originally assigned (Gilmore 1920). The spatially close type material of "*Glyptops pervicax*" does not allow a detailed comparison with this taxon and is confirmed to be a nomen dubium herein (see Invalid Taxa below). Gaffney (1972) noted that *Pr. wyomingensis* and *T. hiatti* are broadly equivalent in their surface sculpturing, but he nevertheless thought *Pr. wyomingensis* to lack diagnostic traits and declared it a nomen dubium as well. Brinkman and Nicholls (1993), by contrast, synonymized *Pr. wyomingensis* with the Campanian *Neurankylus eximius*, but did not provide any justification for that decision.

Gilmore (1920) originally stated that the holotype of *Protobaena wyomingensis* is from the Colorado Shale exposed along the Shoshone River near the city of Cody. Larson et al. (2013) reasoned that this stratigraphic unit corresponds to the Late Cretaceous (Coniacian) Cody Shale, but the Colorado Shale in the Bighorn Basin was actually renamed Thermopolis Shale (Lupton 1916) and the current geological map of Wyoming confirms that the Thermopolis Shale crops out along the Shoshone River at Cody. The holotype of *Pr. wyomingensis* is therefore of Lower Cretaceous (Albian) age (Rice 1976). Larson et al. (2013:390) resurrected *Pr. wyomingensis* given that it "appears to possess a unique combination of features." They furthermore retained *Pr. wyomingensis* within the genus *Neurankylus*, perhaps due to temporal considerations, but noted that it is notably different from all other *Neurankylus* species, particularly in regard to its surface texture, and may therefore hold a different phylogenetic position.

The figures of Gilmore (1920) clearly reveal that the skin-scute sulcus of the marginals converges with the posterior margin of the shell in the pygal region for a short distance, but only on the visceral side of the carapace, and we were able to confirm this observation based on personal observations of this specimen. This feature is symplesiomorphically lacking in the vast majority of turtles, including basal baenids such as *Neurankylus* spp., and is intermediate to the defining characteristic of the clade *Baenodda*. We therefore tentatively hypothesize that *Protobaena wyomingensis* is the sister to *Baenodda* (see Figure 3) and refer it to the new genus *Protobaena*. The possible synonymy of *Pr. wyomingensis* with *Trinitichelys hiatti*, as briefly discussed by Gaffney (1972), stands in conflict to most phylogenetic hypotheses, because these two have two different positions within the tree (e.g., Gaffney 1972; Lipka et al. 2006; Lyson et al. 2011), but would be consistent with some of the topologies obtained by Larson et al. (2013), which place both taxa in a derived position relative to *Neurankylus*. A formal restudy of the type specimen is nevertheless warranted, as it remains possible that the posterior margin of the type specimen is damaged and that the morphology, as discussed above, is a preservational artifact (J. Lively, pers. comm.).

Baenodda Brinkman, 2003a

Phylogenetic definition. The name *Baenodda* is referred to the clade that originates from the first ancestor of *Baena arenosa* Leidy, 1870 to have evolved a marginal ring that is separated at the midline and thereby allows contribution of the most posterior vertebral to the margin of the carapace.

Diagnosis. *Baenodda* is diagnosed as part of *Baenidae* by the full list of characters listed above for that clade. *Baenodda* is primarily differentiated from all other baenids by the autapomorphy by which it is defined (i.e., a contribution of the most posterior vertebral to the margin of the carapace). Baenodds are otherwise currently diagnosed by reduced nasals and prefrontals, loss of the parietal-squamosal contact (also present in *Hayemys latifrons*), exclusion of the opisthotic from the canalis stapedio-temporale (also present in *Hayemys latifrons*), a midline contact of the extragulars posterior to the gulars and an omega-shaped femoral-anal sulcus.

Comments. Gaffney (1972) presented a Linnaean classification of Baenidae, for which he created new ranks, as his classification demanded more ranks than officially provided by the ICZN (1999). These new ranks include two “infrafamilies” with the unmelodious names Hayemdood and Baenodd. Holroyd and Hutchison (2002) suggested Baeninae as a replacement for Baenodd, whereas Brinkman (2003a) suggested the modification Baenodda. Given that most subsequent authors utilized the latter name (e.g., Lucas and Sullivan 2006; Lyson and Joyce 2009a, 2009b; Larson et al. 2013; Sullivan et al. 2013), we herein formalize the name Baenodda by tying it to one of the characters used by Gaffney and Meylan (1988) to define this taxon. Following the recommendations of Joyce et al. (2004), we assign authorship to Brinkman (2003a) as he created the name as currently spelled.

Arvinachelys goldeni Lively, in press

Taxonomic history. *Arvinachelys goldeni* Lively, in press (new species).

Type material. UMNH 21151 (holotype), a partial skeleton consisting of a cranium, mandible, shell, partial right limbs and partial cervical and caudal series (Lively, in press, figs. 1, 2, 4, 5a, 6a, 7, 8).

Type locality. UMNH VP Locality 951, Grand Staircase-Escalante National Monument, Kane County, Utah, USA; 170 m above formational contact, Kaiparowits Formation, Campanian, Late Cretaceous (Lively, in press).

Referred material and range. Late Cretaceous (Campanian), Kaiparowits Formation of Utah (referred material of Lively, in press).

Diagnosis. *Arvinachelys goldeni* is diagnosed as a baenid and a baenodd by the full list of characters listed for those clades above. *Arvinachelys goldeni* is currently differentiated from other baenodds by the presence of large nasals, divided external nares and the absence of a well-developed lingual ridge.

Comments. *Arvinachelys goldeni* is currently in the process of being named on the basis of several specimens, including complete shells and skulls, from the Late Cretaceous (Campanian) of Utah. The shell displays numerous characters typical of palatobaenine turtles, especially the reduction of the gulars and the plesiomorphic absence of supernumerary scutes and bone, but the skull is highly apomorphic, in particular through the subdivision of the external nares. This taxon was not yet integrated into the new global phylogenetic analysis of Lyson et al. (in press), but Lively (in press) hypothesized it to be a basal baenodd and sister to *Hayemys latifrons*. Given that our topology differs considerably from that of Lively (in press), we manually inserted *Ar. goldeni* in an unresolved polytomy at the base of *Baenodda*, as it clearly exhibits the defining characteristic of that taxon, and await further analysis.

Scabremys ornata (Gilmore, 1935)

Taxonomic history. *Baena ornata* Gilmore, 1935 (new species); *Denazinemys ornata* Lucas and Sullivan, 2006 (new combination); *Scabremys ornata* Sullivan et al., 2013 (new combination).

Type material. USNM 13229 (holotype), a nearly complete shell (Gilmore 1935, figs. 7, 8, pl. 14; Lucas and Sullivan 2006, fig. 3; Sullivan et al. 2013, fig. 20.3).

Type locality. Three miles (4.5 km) northeast of Hunter’s Store, SW1/4 T 24 N, R 13 W, San Juan County, New Mexico, USA (Gilmore 1935; see Figure 5); Hunter Wash Member, lower Kirtland Formation, Campanian, Late Cretaceous (Sullivan et al. 2013).

Referred material and range. Late Cretaceous (Campanian), Kirtland Formation of New Mexico (referred material of Gilmore 1935).

Diagnosis. *Scabremys ornata* is diagnosed as a baenid by the presence of axillary and inguinal buttresses that reach the costals, lacking epiplastral processes, and mesoplastra, and as a baenodd by a vertebral contribution to the posterior margin of the carapace and midline contact of the extragulars posterior to the gulars. The highly reduced gulars are diagnostic of *Palatobaeninae* (see below), but phylogenetic analyses currently place this taxon outside of that clade. *Scabremys ornata* is currently differentiated from other baenids by the presence of a pustular textured shell, a wide and unbroken cervical, loss/reduction of extragulars and the absence of a preneural bone and prepleurals.

Comments. *Scabremys ornata* is a based on a near-complete shell from the Late Cretaceous (Campanian) of New Mexico. The species greatly resembles the coeval eubaenine *Denazinemys nodosa* from the same basin by having a carapace that is decorated by elongate, welt-like knobs, but varies systematically by exhibiting various palatobaenine characteristics, such as the absence of prepleurals, presence of a single cervical and reduction of the extragulars. We therefore agree with Sullivan et al. (2013) that this is a valid taxon, while noting that current phylogenies cannot fully resolve the placement of this taxon relative to Eubaeninae or Palatobaeninae (Lyson et al., in press). Tomlinson (1997) assigned a number of incomplete specimens from the Late Cretaceous (Campanian) of Texas to *Scabremys ornata*, but we agree with Sullivan et al. (2013) that this material is too incomplete to support this taxonomic decision.

Eubaeninae Gaffney, 1972

Phylogenetic definition. We here define *Eubaeninae* as referring to the most inclusive clade that includes *Eubaena cephalica* (Hay, 1904b), but not *Palatobaena bairdi* Gaffney, 1972.

Diagnosis. *Eubaeninae* is diagnosed as being situated within *Baenidae* and *Baenodda* by the full list of characters listed for those clades above. *Eubaeninae* is differentiated from other baenodds by the presence of several cervicals, by vertebrals III that are longer than wide and the presence of prepleurals.

Comments. Following the rules of the ICZN (1999), authorship for this taxon should be granted to Williams (1950), as he was the first to name a family group taxon typified by *Eubaena cephalica* (i.e., Eubaenidae). However, we herein follow the recommendations of Joyce et al. (2004) and assign authorship to Gaffney (1972), as he was the first to author the name with this exact spelling.

Baena arenosa Leidy, 1870 (= *Baena clara* Hay, 1908 = *Baena emiliae* Hay, 1908 = *Baena sima* Hay, 1908)

Taxonomic history. *Baena arenosa* Leidy, 1870 (new species); *Baena arenosa* = *Baena affinis* Hay, 1908 (senior synonym); *Baena arenosa* = *Baena affinis* = *Baena sima* = *Baena clara* = *Baena riparia* = *Baena emiliae* = *Baena inflata* Gaffney, 1972 (senior synonym).

Type material. USNM 103 (holotype), a partial shell (Leidy 1873, pl. 13.1, 2).

Type locality. Junction of the Big Sandy and Green Rivers (Leidy 1873), Sweetwater County, Wyoming, USA (see Figure 6); lowest part of the Bridger Formation (Hay 1908), Black Fork Member, Bridger Formation, Bridgerian NALMA, Early Eocene, Ypresian–Lutetian (Murphey and Evanoff 2007).

Referred material and range. Eocene (Uintan NALMA, Lutetian) of Utah (Hay 1908, type material of *Baena emiliae*); Eocene (Bridgerian NALMA, Ypresian–Lutetian) of Wyoming (Leidy 1870; Hay 1908, type material of *Baena clara* and *Baena sima*).

Diagnosis. *Baena arenosa* is diagnosed as a baenodd by contribution of vertebral V to the margin of the carapace, midline contact of the extragulars posterior to the gulars, an omega-shaped femoral-anal sulcus, and as a eubaenine by the presence of several cervicals, vertebral III longer than wide and prepleurals. *Baena arenosa* is differentiated from other eubaenines by the absence of a prepleurals, undivided cervical, presence of vertebrals II–IV that are longer than wide, the lack of a sigmoidal humeral-extragular sulcus, thick dorsal skull roof, well-developed skull roof with little to no upper temporal emargination and distinctly hooked dentary.

Comments. Leidy (1870, 1871a, 1871b), Cope (1872, 1873a), Hay (1908) and Gilmore (1916c) named a total of 11 baenids from Bridgerian and Uintan deposits in Utah and Wyoming. Gaffney (1972) had been rather conservative with his taxonomic assessments among Cretaceous and Paleocene baenids and maintained the validity of numerous taxa that are based on rather complete specimens but had uncertain phylogenetic relationships (e.g., *Baena marshi*, *Baena callosa*, *Denazinemys nodosa*, *Eubaena hatcheri*, "*Baena*" *hayi*). However, although Eocene baenids display a similar amount of morphological disparity as their predecessors, he interpreted most disparity as intraspecific variability and recognized only two taxa, *Chisternon undatum* and *Baena arenosa*.

Although we agree that much intraspecific variation is apparent among Eocene baenids, our work with Cretaceous specimens (e.g., Lyson and Joyce 2009a, 2009b, 2010; Lyson et al. 2011; unpublished data) has demonstrated that shell characters are less variable among baenids than assumed by Gaffney (1972). Indeed, it appears that Gaffney's (1972) disregard of shell characters was the result of his taxonomic assessment.

Among the 11 named Eocene baenids, three (*gigantea*, *hebraica* and *undatum*) stand out by being large and by possessing preneural bones and nuchal and prepleurals, and we agree with Gaffney (1972) that these should be synonymized into *Chisternon undatum*. However, among the eight taxa grouped by Gaffney (1972) into *Baena arenosa*, we recognize at least two consistent morphotypes.

Three taxa (*affinis*, *inflata* and *riparia*) are distinguished by the presence of prepleurals (though with a lack of a preneural bone and nuchal scute), crenulated vertebrals and the unique presence of three inframarginals combined with a contact of the pectoral with a marginal, and we therefore group these into "*Baena*" *affinis*. Among the referred specimens, the holotype of *riparia* is the most notable, as it consists of a beautifully preserved shell and a skull.

Three other taxa (*clara*, *emiliae* and *sima*) are united by the plesiomorphic absence of all supernumerary bones, and we group these into *Baena arenosa*. This characteristic is unique among Eocene baenids and always occurs symmetrically on both sides of the shell. We are therefore confident that this character is not an anomaly. It is important to note that the type of *B. arenosa* lacks all diagnostic areas and that we would prefer to declare this taxon a nomen dubium. However, this would have dire taxonomic consequences, as this is the type of *Baena* and *Baenidae*. For the sake of nomenclatural stability, we therefore refer *clara*, *emiliae* and *sima* to *arenosa* even though characters are absent that would support this decision. The validity of "*Baena*" *affinis* relative to *Baena arenosa* is independently supported by numerous skull characters that were highlighted by Gaffney (1972) between the type material of *Ba. sima* (now *Ba. arenosa*) and *Ba. riparia* (now "*Baena*" *affinis*), but that were interpreted as intraspecific variation.

We emphasize that our taxonomic assessment of the Eocene baenids can only be considered preliminary, because we were not able to view most material firsthand. We therefore encourage a thorough review of this group of turtles, which should include improved preparation of all type material and careful illustration of all relevant specimens. Given that it is only possible to identify material using relatively complete shells, we refer only sufficiently figured material to *Baena arenosa* and "*Baena*" *affinis*.

"*Baena*" *affinis* Leidy, 1871a
(= *Baena riparia* Hay, 1908
= *Baena inflata* Gilmore, 1916c)

Taxonomic history. *Baena affinis* Leidy, 1871a (new species); *Baena arenosa* = *Baena affinis* Leidy, 1873 (junior synonym); *Baena arenosa* = *Baena affinis* = *Baena sima* = *Baena clara* = *Baena riparia* = *Baena emiliae* = *Baena inflata* Gaffney, 1972 (junior synonym).

Type material. ANSP 10055 (holotype), a shell (Leidy 1873, pl. 13.3).

Type locality. Church Buttes on Black's Fork of Green River, 3 miles (4.5 km) north of Fort Bridger, Uinta County, Wyoming, USA (Leidy 1873; see Figure 6); level B (Hay 1908), Black Fork Member, Bridger Formation, Bridgerian NALMA, Early Eocene, Ypresian–Lutetian (Murphey and Evanoff 2007).

Referred material and range. Eocene (Bridgerian NALMA, Ypresian–Lutetian) of Wyoming (Leidy 1871a; Hay 1908; including type material of *Baena riparia* and *Baena inflata*) and Eocene (Uintan NALMA, Lutetian) of Wyoming (Gilmore 1916c, type material of *Baena inflata*).

Diagnosis. "*Baena affinis*" is diagnosed as a baenodd by contribution of vertebral V to the posterior margin of the shell, midline contact of the extragulars posterior to the gulars and an omega-shaped femoral-anal sulcus, and as a eubaenine by the presence of multiple cervicals, vertebral III that is longer than wide and prepleurals. "*Baena*" *affinis* is differentiated from other eubaenines by vertebrals II–IV that are longer than wide, the lack of a sigmoidal humeral-extragular sulcus, the presence of only three inframarginals, mesoplastra that do not contact one another in some specimens and a thick dorsal skull roof.

Comments. "*Baena*" *affinis* is based on a partial shell from Bridgerian deposit in Wyoming. Leidy (1871a) originally diagnosed this taxon, among others, by the reduced count of inframarginals, which permits a lateral contact of the pectorals with the marginal ring, but after the discovery of new material from Wyoming, he reinterpreted this character as intraspecific variation and synonymized "*Baena*" *affinis* with *Baena arenosa* (Leidy 1873). We here reinstate "*Baena*" *affinis* as a valid taxon, because several Eocene specimens, including the types of "*Ba.*" *riparia* and "*Ba.*" *inflata*, document the consistent presence of the reduced inframarginal count noted by Leidy (1871a) in full synchrony with the presence of prepleurals (see *Ba. arenosa* for more extensive discussion). It is somewhat ironic that, of all taxa, we reestablish *affinis*, given that this was the only baenid taxon to be synonymized with another prior to the modern taxonomic review of Gaffney (1972) and has been thought to be invalid for nearly 150 yr.

"*Baena*" *escavada* Hay, 1908

Taxonomic history. *Baena escavada* Hay, 1908 (new species).

Type material. AMNH 2013, a relatively complete, slightly crushed shell (Hay 1908, figs. 42, 43, pl. 11).

Type locality. "At the head of Escavada Creek" (Hay 1908), "Rio Arriba County, New Mexico" (label at AMNH), USA (see Figure 6); Nacimiento Formation, Torrejonian NALMA (Sullivan and Lucas 1986), Selandian, early Paleocene.

Referred material and range. No specimens have been referred to date.

Diagnosis. "*Baena*" *escavada* is diagnosed as a baenodd by the contribution of the most posterior vertebral to the carapacial margin, midline contact of the extragulars posterior to the gulars and an omega-shaped femoral-anal sulcus, and as a eubaenine by the presence of a vertebral III that is longer than wide. The presence of multiple cervicals and prepleurals is uncertain for this taxon. "*Baena*" *escavada* is differentiated from other eubaenines by the presence of an undivided cervical, vertebrals II–IV that are longer than wide, the lack of a sigmoidal humeral-extragular sulcus and a rectangular anterior plastral lobe.

Comments. "*Baena*" *escavada* is based on a relatively complete shell (Hay 1908) and is the only named Paleogene baenid from the American Southwest. This taxon is not mentioned by Gaffney (1972) and therefore appears to have slipped through the cracks of his otherwise exhaustive review. We here note that the narrow, highly elongate vertebrals of "*Baena*" *escavada* greatly resembles those of the Eocene taxa *Baena arenosa* and *Chisternon undatum*, but there is too little character evidence to rigorously clarify the interrelationships of these three species, although the loss of prepleurals at least on one side of the shell is indicative of a position closer to *Ba. arenosa*. Given that rich baenid material is available from the Paleocene of New Mexico, we are confident that future analyses will resolve this issue. Until this point, we highlight the taxonomic uncertainty by placing the genus assignment in quotation marks.

"*Baena*" *hayi* (Gilmore, 1916a), comb. nov.

Taxonomic history. *Baena hayi* Gilmore, 1916a (new species).

Type material. USNM 6728 (holotype), a nearly complete shell missing parts of the posterior margins (Gilmore 1916a, pls. 32, 33).

Type locality. Lance Creek, Niobrara County, Wyoming, USA (Gilmore 1916a; see Figure 5); Lance Formation (Gilmore 1916a), Maastrichtian, Late Cretaceous.

Referred material and range. No specimens have been referred to date (see Comments below, however, regarding possible synonymy with *Stygiochelys estesi*).

Diagnosis. "*Baena*" *hayi* is diagnosed as a baenodd by the contribution of vertebral V to the posterior margin of the carapace, midline contact of the extragulars posterior to the gulars and an omega-shaped femoral-anal sulcus, and as a eubaenine by the presence of several cervicals and the presence of prepleurals (W.G. Joyce and T.R. Lyson, pers. obs. of type material). "*Baena*" *hayi* is differentiated from other eubaenines by the presence of only small prepleurals, presence of square vertebrals, lack of a sigmoidal humeral-extragular sulcus and a triangular anterior plastral lobe.

Comments. "*Baena*" *hayi* is a shell taxon from the Late Cretaceous (Maastrichtian) Powder River Basin of Wyoming. Even though the outer surface of the shell of this taxon is decorated by a dense pattern of ridges, much as in pleurosternids and basal baenids, fragmentary material has not yet been attributed to this taxon (e.g., Holroyd and Hutchison 2002; Holroyd et al. 2014).

The phylogenetic analysis of Lyson and Joyce (2010) placed "*Baena*" *hayi* at the base of *Palatobaeninae* and Lyson and Joyce (2010) therefore concluded that the shell taxon "*Ba.*" *hayi* may be synonymous with the coeval skull taxon *Gamerabaena sonsalla*. However, the updated phylogenetic hypothesis of Lyson et al. (in press) places this taxon within *Eubaeninae*. The sculpturing pattern of "*Ba.*" *hayi* greatly resembles that of published, but unfigured specimens of *Stygiochelys estesi* (UCMP 113316–17, Gaffney 1982b) and both "*Ba.*" *hayi* and *St. estesi* originate from the northern basins of Wyoming and Montana. We therefore cautiously suggest a possible synonymy of "*Ba.*" *hayi* with *St. estesi*, but refrain from referring *hayi* to *Stygiochelys* for the moment, as this synonymy remains somewhat conjectural.

Boremys Lambe, 1906b

Type species. *Baena pulchra* Lambe, 1906a.

Diagnosis. *Boremys* is diagnosed as a baenodd and a eubaenine by the full list of characters listed for those clades above. *Boremys* is differentiated from other eubaenines by the presence of supramarginals, a nuchal scute, weakly scalloped anterior margins of the shell, and a rectangular anterior plastral lobe and deep upper temporal emargination.

Boremys grandis Gilmore, 1935

Taxonomic history. *Boremys albertensis* Gilmore, 1920 (new species); *Boremys pulchra* = *Boremys albertensis* = *Boremys grandis* Gaffney, 1972 (junior synonym); *Boremys grandis* Brinkman and Nicholls, 1991 (nomen validum).

Type material. USNM 12979 (holotype), a near-complete shell missing a portion of its margins (Gilmore 1935, figs. 9, 10, pl. 15; Sullivan et al. 2013, fig. 20.5a, b).

Type locality. SW1/4 T 24 N, R 13 W, 3 miles (4.5 km) northeast of Hunter's Store, San Juan County, New Mexico, USA (Gilmore 1935; see Figure 5); De-na-zin Member, upper Kirtland Formation, Campanian, Late Cretaceous (Sullivan et al. 2013).

Referred material and range. Late Cretaceous (Campanian), Kirtland and Fruitland Formations of New Mexico (referred material of Sullivan et al. 2013) and Kaiparowits Formation of Utah (Hutchison et al. 2013).

Diagnosis. *Boremys grandis* is diagnosed as a eubaenine by the presence of multiple cervicals, vertebral III that is longer than wide and the presence of prepleurals, and as a representative of *Boremys* by all characters listed for that clade above. *Boremys grandis* is differentiated from other *Boremys* by its large size (carapace length greater than 50 cm) and presence of two irregular rows of supramarginals.

Comments. *Boremys grandis* is based on a large, nearly complete shell from Campanian deposits in the San Juan Basin of New Mexico. In the type description, Gilmore (1935) referred a shell to this taxon that had previously been assigned to *Denazinemys nodosa* by Wiman (1933). However, without further analysis, we cannot distinguish if this is a highly abnormal *D. nodosa* or *Bo. grandis* as the shell is covered by numerous highly irregular scutes.

In his review of the North American *Baenidae*, Gaffney (1972) united all then-known *Boremys* specimens into a single taxon, *Boremys pulchra*, with a distribution ranging from New Mexico to Alberta. However, the later review by Brinkman and Nicholls (1991) revealed that the northern material varies systematically from the southern and that two separate species are therefore present, *Bo. pulchra* and *Bo. grandis*. Sullivan et al. (2013) reported additional material of *Bo. grandis* from the Campanian of New Mexico, whereas Hutchison et al. (2013) referred additional material from the Campanian of Utah. We agree with Tomlinson (1997) that the partial shell she reported from the Campanian of Texas is too fragmentary to allow confident assignment to any particular taxon, or even *Boremys*.

Boremys pulchra (Lambe, 1906a)
(= *Boremys albertensis* Gilmore, 1920)

Taxonomic history. *Baena pulchra* Lambe, 1906a (new species); *Boremys pulchra* Lambe, 1906b (new combination); *Boremys pulchra* = *Boremys albertensis* = *Boremys grandis* Gaffney, 1972 (senior synonym); *Boremys pulchra* = *Boremys albertensis* Brinkman and Nicholls, 1991 (senior synonym).

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

Type locality. Near the mouth of Berry Creek, Red Deer River, Dinosaur Provincial Park, Alberta, Canada (see Figure 5); Judith River Group, Campanian, Late Cretaceous (Lambe 1906a; Brinkman and Nicholls 1991).

Referred material and range. Late Cretaceous (Campanian), Judith River Group, Alberta (referred material of Lambe 1914; Gilmore 1920; Parks 1933; Brinkman and Nicholls 1991, including type material of *Boremys albertensis*) and Montana (Fiorillo 1989).

Diagnosis. *Boremys pulchra* is diagnosed as a eubaenine by the presence of multiple cervicals, vertebral III that is longer than wide and the presence of prepleurals, and as a representative of *Boremys* by all characters listed for that clade above. *Boremys pulchra* is differentiated other *Boremys* by its small size (carapace length less than 30 cm) and presence of a single row of supramarginals.

Comments. *Boremys pulchra* and *Boremys albertensis* are both based on shell material from the Judith River deposits of Alberta and have been synonymized over the course of the last decades (Gaffney 1972, Brinkman and Nicholls 1991). Gaffney (1972) furthermore added *Bo. grandis* from the Campanian of New Mexico to this taxon, but Brinkman and Nicholls (1991) have since shown that the northern material differs consistently from the southern material and we agree with this assessment. Brinkman and Nicholls (1991) furthermore provided a comprehensive summary of the morphology of this taxon.

Fragmentary material of *Boremys* has been reported from Campanian deposits in Montana (e.g., Dodson 1984; Blob and Fiorillo 1996) and Saskatchewan (Storer 1993), but we cannot support these identifications because all material remains undescribed. However, we agree that the plastron figured by Fiorillo (1989) is diagnostic of *Boremys*, and we refer it to *Boremys pulchra* on the basis of geographic considerations.

Lyson et al. (2011) figured and described fragmentary remains of *Boremys* sp. from the Maastrichtian and relatively complete shells from the early Paleocene (Puercan NALMA), all from North Dakota, but these remains lack key areas and it is therefore not possible to assign them to any particular species with confidence. The nuchals figured by Lyson et al. (2011), however, reveal that the partial nuchal referred to Eubaenina indet. by Hutchison and Holroyd (2003) from the Denver Basin is attributable to *Boremys* sp. The Santonian material from Alberta referred to *Boremys* sp. by Brinkman (2003b) remains unfigured, and we therefore cannot assess the taxonomic affinities of this material.

Chisternon undatum (Leidy, 1871b)
(= *Baena hebraica* Cope, 1872
= *Baena gigantea* Gilmore, 1916c)

Taxonomic history. *Baena undata* Leidy, 1871b (new species); *Chisternon undatum* Leidy, 1872 (new combination); *Chisternon undatum* = *Baena gigantea* = *Baena hebraica* Gaffney, 1972 (senior synonym).

Type material. ANSP 10040 (holotype), a partial shell (Leidy 1873, pl. 14).

Type locality. "[A] few miles from Fort Bridger," (Leidy 1873:169) Uinta County, Wyoming, USA (see Figure 6); Bridger Formation (Gaffney 1972), Bridgerian NALMA, Early Eocene, Ypresian–Lutetian.

Referred material and range. Early Eocene (Wasatchian NALMA, Ypresian) of Wyoming (Holroyd et al. 2001); middle Eocene (Bridgerian NALMA, Ypresian–Lutetian) of Wyoming (Leidy 1871b; Cope 1872; Gaffney 1972; including type material of *Baena hebraica*); middle Eocene (Uintan NALMA, Lutetian) of Utah (Gilmore 1916c; Gaffney 1972; including type material of *Baena gigantea*).

Diagnosis. *Chisternon undatum* is diagnosed as a baenodd and a eubaenine by the full list of characters listed above for those clades. *Chisternon undatum* is differentiated from other eubaenines by its large size (carapace length greater than 50 cm), unsutured mature shell, nuchal scute, longer than wide vertebrals II–IV, lack of a sigmoidal humeral-extragular sulcus, triangular anterior plastral lobe, moderate development of the upper temporal emargination and posteriorly notched orbit.

Comments. Among the 11 named baenid taxa from the Eocene, three are easily distinguished by their large size and the presence of a preneural bone and nuchal scute. These three taxa were historically considered to be valid (Hay 1908; Gilmore 1916c), but we agree with Gaffney (1972) that all material should be combined into a single taxon, *Chisternon undatum*, as they differ only in minor nuances. However, additional finds in Wasatchian, Bridgerian and Uintan deposits may eventually support the recognition of several chronospecies, similar to those that we recognize for *Palatobaena* (see above), in which case the Wasatchian *Ch. gigantea* would be reinstated. Given that *Ch. undatum* is easily distinguished from coeval baenids, we readily accept all referred material, even if it is not figured (e.g., Gaffney 1972; Holroyd et al. 2001).

Denazinemys nodosa (Gilmore, 1916b)

Taxonomic history. *Baena nodosa* Gilmore, 1916b (new species); *Denazinemys nodosa* Lucas and Sullivan, 2006 (new combination).

Type material. USNM 8345 (holotype), a nearly complete shell (Gilmore 1916b, figs. 34, 35, pl. 76; Sullivan et al. 2013, fig. 20.2a, b).

Type locality. Locality 60, Willow Wash, 2 miles (3 km) northwest of Ojo Alamo store, San Juan County, New Mexico, USA (see Figure 5); De-na-zin Member, Kirtland Formation, Campanian, Late Cretaceous (Sullivan et al. 2013).

Referred material and range. Late Cretaceous (Campanian), Kirtland and Fruitland Formations of New Mexico (referred material of Gilmore 1916b, 1919; Wiman 1933; Sullivan et al. 2013), Kaiparowits Formation of Utah (Hutchison et al. 2013) and Aguja Formation of Texas, USA (Tomlinson 1997).

Diagnosis. *Denazinemys nodosa* is diagnosed as a baenodd by the contribution of vertebral V to the posterior margin of the carapace, midline contact of the extragulars posterior to the gulars and an omega-shaped femoral-anal sulcus, and as a eubaenine by the presence of multiple cervicals, vertebral III that is longer than wide and the prepleurals. *Denazinemys nodosa* is differentiated from other eubaenines by its welt-like sculpturing.

Comments. Campanian deposits in New Mexico and Utah have yielded a total of three taxa that are diagnosed by the presence of a welt-like sculpturing, *Boremys grandis*, *Denazinemys nodosa* and *Scabremys ornata* (Hutchison et al. 2013; Sullivan et al. 2013), and it is therefore difficult to distinguish these taxa on the basis of fragmentary shell material. However, all three taxa are easily distinguished if more complete specimens are available. In particular, *Boremys grandis* is very large and displays numerous supernumerary scutes, *Denazinemys nodosa* is greatly splayed posteriorly and exhibits prepleurals, while *Scabremys ornata* is round in outline, lacks prepleurals and has reduced gulars. The validity of *Denazinemys nodosa* is uncontroversial.

Eubaena Hay, 1908

Type species. *Baena cephalica* Hay, 1904b.

Diagnosis. *Eubaena* is diagnosed as a baenodd and a eubaenine by the full list of characters provided above for those clades. *Eubaena* is differentiated from other eubaenines by open sutures in the skull and shell of adults, presence of a nuchal scute, extragulars that only weakly contact one another along the midline, lack of an omega-shaped femoral-anal sulcus, presence of an incipient secondary palate, exclusion of the jugal from the margin of the orbit, small orbit, broadly expanded posterior triturating surfaces, swollen maxillae and an elongate snout.

Eubaena cephalica (Hay, 1904b)

Taxonomic history. *Baena cephalica* Hay, 1904b (new species); *Eubaena cephalica* Hay, 1908 (new combination).

Type material. YPM VP 001785[(holotype, now lost), a cranium (Hay 1904b, pl. 12; Hay 1908, pls. 19.4, 21.1, 2; Gaffney and Hiatt 1971, fig. 5; Gaffney 1972, figs. 18, 19, 57).

Type locality. Converse or Niobrara County, Wyoming, USA (Hay 1908; Gaffney 1972; see Figure 5); Lance Formation, Maastrichtian, Late Cretaceous (Gaffney 1972).

Referred material and range. No specimens have been referred to date (see Comments below, however, regarding possible synonymy with *Eubaena hatcheri*).

Diagnosis. *Eubaena cephalica* is diagnosed as a baenodd, a eubaenine and a representative of *Eubaena* by the full list of cranial characters provided for those clades. *Eubaena cephalica* cannot be rigorously diagnosed from *Eubaena hatcheri* as the former is only known from skull material and the other from shell material. Future finds may show these taxa to be synonymous (see Comments below).

Comments. *Eubaena cephalica* is based on a beautifully preserved skull from the Late Cretaceous (Maastrichtian) sediments exposed in the Powder River Basin of Wyoming (Hay 1904b), but the type specimen appears to have been stolen from an office while under study (E.S. Gaffney, pers. comm., 2001). Given that the type specimen was figured and/or illustrated in great detail by Hay (1904b, 1908), Gaffney and Hiatt (1971) and Gaffney (1972), there is no need for the designation of a neotype as the application of the taxon name is unambiguous.

It appears highly likely that the skull taxon *E. cephalica* is synonymous with the shell taxon *E. hatcheri*, but we refrain from formally synonymizing the two until a shell–skull association has been found (see *E. hatcheri* below). We nevertheless highlight this probable synonymy in our phylogeny (see Figure 3) and stratigraphic summary (Figure 4).

Eubaena hatcheri (Hay, 1901), comb. nov.

Taxonomic history. *Baena hatcheri* Hay, 1901 (new species).

Type material. CM 115 (holotype), a near-complete shell with some damage to the posterior margins (Hay 1901, pl. 15; Hay 1908, figs. 40, 41, pls. 9, 10; Gaffney 1972, fig. 43).

Type locality. "A sandstone bluff on the south side of Lance Creek, opposite the mouth of Dogie Creek," Niobrara County, Wyoming, USA (see Figure 5); Lance Formation; Maastrichtian, Late Cretaceous (Hay 1908; with corrections from Gaffney 1972).

Referred material and range. No specimens have been referred to date (see Comments below, however, regarding possible synonymy with *Eubaena cephalica*).

Diagnosis. *Eubaena hatcheri* is diagnosed as a baenodd, a eubaenine and a representative of *Eubaena* by the full list of shell characters provided for those clades. *Eubaena hatcheri* cannot be rigorously diagnosed from *Eubaena cephalica* as the former is only known from shell material and the other from skull material. Future may show these taxa to be synonymous (see Comments below).

Comments. *Eubaena hatcheri* is based on a well-preserved shell that was collected in Late Cretaceous (Maastrichtian) deposits in Wyoming. The shell lacks a notable sculpturing pattern, and fragmentary material has therefore never been referred to this taxon (e.g., Holroyd and Hutchison 2002; Holroyd et al. 2014). The only specimen that has been formally referred to *E. hatcheri*, a partial shell from the Campanian of Alberta (Lambe 1902), now serves as the holotype of *Boremys pulchra* (Lambe 1906a).

The phylogenetic analysis of Lyson and Joyce (2010) retrieved a number of taxon pairs that consist of a shell and skull taxa from the same stratigraphic interval and geographic area. The shell taxon *Eubaena hatcheri* and the skull taxon *E. cephalica*, both from the Powder River Basin of Wyoming, also form such a taxon pair and Lyson and Joyce (2010) therefore tentatively suggested that they may be synonymous, while refraining from formally proposing a synonymy, because actual skull–shell associations were lacking. New, undescribed fossil material from North Dakota appears to further support this synonymy, but formal analysis of these specimens is outstanding. We therefore decided to transfer "*Baena*" *hatcheri* to *Eubaena* and to graphically highlight the possible synonymy of *E. cephalica* and *E. hatcheri* in our phylogeny (see Figure 3) and stratigraphic summary (see Figure 4).

Stygiochelys estesi Gaffney and Hiatt, 1971

Taxonomic history. *Stygiochelys estesi* Gaffney and Hiatt, 1971 (new species).

Type material. AMNH 2601 (holotype), a near-complete cranium (Gaffney and Hiatt 1971, figs. 1, 2, 4, 6a; Gaffney 1982a, fig. 4).

Type locality. SW1/4NW1/4, Section 1, T 15 N, R 55 E, near Glendive, Dawson County, Montana, USA; Hell Creek Formation (Gaffney and Hiatt 1971), Maastrichtian, Late Cretaceous.

Referred material and range. Early Paleocene (Puercan NALMA, Danian) of Montana (specimens referred by Gaffney 1982b).

Diagnosis. *Stygiochelys estesi* is diagnosed as a baenodd and a eubaenine by the complete list of cranial characters listed for those clades above. *Stygiochelys estesi* is differentiated from other eubaenines by open sutures in the adult skull, a point contact between the pterygoids, small contribution of the jugal to the orbit margin, large and notched orbit, posterior triturating surfaces broadly expanded and swollen maxillae.

Comments. *Stygiochelys estesi* is a skull-based taxon from the Maastrichtian Hell Creek Formation of Montana (Gaffney and Hiatt 1971). Although no additional specimens have been assigned to this taxon to date from the Late Cretaceous, at least two skull–shell associations are known from the locality Baenid Badlands, just above the K/T (Gaffney 1972), and this taxon is therefore known to have survived the extinction event at this boundary. A possible synonym with "*Baena*" *hayi* is plausible, but not certain (see Comments for that taxon below).

Palatobaeninae Gaffney, 1972

Phylogenetic definition. We here define *Palatobaeninae* as referring to the most inclusive clade that includes *Palatobaena bairdi* Gaffney, 1972, but not *Eubaena cephalica* (Hay, 1904b).

Diagnosis. *Palatobaeninae* is diagnosed as being situated within *Baenidae* and *Baenodda* by the full list of characters listed for those clades above. *Palatobaeninae* is differentiated from other baenodds by the symplesiomorphic absence of prepleurals and subdivided cervicals and presence of a triangular anterior plastral lobe and reduced to absent gulars.

Cedrobaena Lyson and Joyce, 2009b

Type species. *Plesiobaena putorius* Gaffney, 1972.

Diagnosis. *Cedrobaena* is diagnosed as a baenodd and a palatobaenine by the full list of characters listed for those clades above. *Cedrobaena* is differentiated from other palatobaenines by the absence of an incipient secondary palate, parietal overhang overlying supraoccipital well developed, short preorbital skull length and jugal exposed in the orbit margin.

Cedrobaena brinkman
(Lyson and Joyce, 2009b), comb. nov.

Taxonomic history. *Peckemys brinkman* Lyson and Joyce, 2009b (new species).

Type material. UMMP 20490 (holotype), an almost complete skeleton (Case 1939, figs. 1–18; Lyson and Joyce 2009b, figs. 4, 6–11).

Type locality. "Near Fort Peck" (Case 1939), Valley County, Montana, USA (see Figure 5); Hell Creek Formation, Maastrichtian, Late Cretaceous (Lyson and Joyce 2009b).

Referred material and range. Late Cretaceous (Maastrichtian) of Colorado, Montana, North Dakota and Wyoming, and Late Paleocene (Tiffanian NALMA, Selandian–Thanetian) of Wyoming (hypodigm of Lyson and Joyce 2009b).

Diagnosis. *Cedrobaena brinkman* is diagnosed as a baenodd, a palatobaenine and a representative of *Cedrobaena* by the full list of characters listed for those clades above. *Cedrobaena brinkman* is differentiated from *Cedrobaena putorius* by its small size, parallel labial and lingual ridges and weaker development of the parietals dorsal to the supraoccipital.

Comments. The type specimen of *Cedrobaena brinkman* is a near-complete skeleton from the Hell Creek Formation of Montana that was described in detail by Case (1939), but, strangely, not assigned to any taxon. See *Ce. putorius* for historical background that led to the naming of this taxon. Although we loathe naming monotypic genera, because they are redundant with the species epithet, our 2009 analysis (Lyson and Joyce 2009b) forced us to place this taxon in its own genus, *Peckemys*. However, given that more recent analyses place this taxon as sister to *Ce. putorius*, we abandon use of the otherwise redundant name *Peckemys*.

Cedrobaena putorius (Gaffney, 1972)

Taxonomic history. *Plesiobaena putorius* Gaffney, 1972 (new species); *Cedrobaena putorius* Lyson and Joyce, 2009b (new combination).

Type material. YPM VPPU 014984 (formerly PU 14984), a partial cranium (Gaffney 1972, fig. 14; Lyson and Joyce 2009b, fig. 1a).

Type locality. Cedar Point Quarry, SW1/4 Section 23, T 55 N, R 95 W, Bighorn County, Wyoming, USA (see Figure 6); Fort Union Formation, early Tiffanian NALMA (Gaffney 1972), Selandian–Thanetian, Paleocene.

Referred material and range. Late Cretaceous (Maastrichtian) of North and South Dakota and Paleocene (Torrejonian + Tiffanian NALMA, Danian–Thanetian) of Wyoming (hypodigm of Lyson and Joyce 2009a).

Diagnosis. *Cedrobaena putorius* is diagnosed as a baenodd, a palatobaenine and a representative of *Cedrobaena* by the full list of cranial characters listed for those clades above. *Cedrobaena putorius* is differentiated from *Cedrobaena brinkman* by its larger size, better developed parietal overhang with parallel sides and stronger posterior expansion of the triturating surfaces of the maxilla.

Comments. *Cedrobaena putorius* is based on a partial cranium from the Tiffanian (late Paleocene) Cedar Point Quarries of Wyoming (Gaffney 1972). In his expansive review of baenid turtles, Gaffney (1972) united a number of fossil finds ranging from the Campanian to Paleocene in the taxon *Plesiobaena* and recognized two species: the Campanian to Maastrichtian *Plesiobaena antiqua* and the late Paleocene *Plesiobaena putorius*. A review of the Campanian material led Brinkman (2003a) to conclude that it is distinct from the Maastrichtian material, but he fell short of naming a new species. The differences highlighted by Brinkman (2003a) were supported by the description of new Maastrichtian material by Lyson and Joyce (2009b) leading to the naming of a new taxon, "*Plesiobaena*" *brinkman*, which includes Maastrichtian to late Paleocene material and which is diagnosable to contemporary material referable to "*Plesiobaena*" *putorius*.

The phylogenetic analysis of Lyson and Joyce (2009b) revealed that all named *Plesiobaena* species form a paraphyletic grade relative to *Palatobaena* spp. Although the rules of nomenclature do not demand that monophyletic groups are named (ICZN 1999), it is common practice to avoid paraphyletic genera and Lyson and Joyce (2009b) therefore placed all *Plesiobaena* species in separate genera: *Plesiobaena antiqua*, *Cedrobaena brinkman* and *Ce. putorius*. Given that we disapprove of the unnecessary proliferation of monotypic genera, we strongly encourage the reduction of the number of genera within *Palatobaeninae*, if future researchers retrieve previously unrecognized monophyletic groups.

Gamerabaena sonsalla Lyson and Joyce, 2010

Taxonomic history. *Gamerabaena sonsalla* Lyson and Joyce, 2010 (new species).

Type material. ND 06-14.1 (holotype), a partial cranium (Lyson and Joyce 2010, figs. 1, 3b).

Type locality. Near Marmarth, Bucklin Township, Slope County, North Dakota, USA (see Figure 5); approximately 66 m below the Fort Union formational contact, Hell Creek Formation, Maastrichtian, Late Cretaceous.

Referred material and range. No material has been referred to date.

Diagnosis. *Gamerabaena sonsalla* is diagnosed as a baennod and palatobaenine by the skull characters listed above for these clades. *Gamerabaena sonsalla* is currently differentiated from other palatobaenines by the moderate expansion of the prefrontal on the dorsal skull roof that excludes the frontal from entering the orbit margin, laterally indented maxillae, exclusion of the jugal from the orbit margin and notched frontals that extend posteriorly well beyond the orbit margin.

Comments. *Gamerabaena sonsalla* is only known from the type skull, which originates from Late Cretaceous (Maastrichtian) Hell Creek Deposits of North Dakota (Lyson and Joyce 2010). Though rare, this taxon is well diagnosed relative to other baenids and its validity is therefore uncontroversial. The phylogenetic analysis of Lyson and Joyce (2010) placed *Ga. sonsalla* in a similar phylogenetic position as the shell taxon "*Baena*" *hayi* from coeval deposits, and they therefore suggest that these two taxa may be synonymous. We here argue that "*Ba.*" *hayi* is a eubaenine and therefore an unlikely candidate for synonymy (see "*Ba.*" *hayi* below).

Goleremys mckennai Hutchison, 2004

Taxonomic history. *Goleremys mckennai* Hutchison, 2004 (new species).

Type material. UCMP 179519 (holotype), a well-preserved cranium (Hutchison 2004, fig. 1).

Type locality. UCMP Locality V99042, Kern County, California, USA (see Figure 6); Goler Formation, early Tiffanian NALMA, Selandian, Paleocene.

Referred material and range. No material referred to date.

Diagnosis. *Goleremys mckennai* is diagnosed as a baenodd and a palatobaenine by the full list of cranial characters listed for those clades above. *Goleremys mckennai* is differentiated from other palatobaenines by large nasals, deep cheek emargination, a broad contribution of the jugal to the orbit margin and small, triangular parietals.

Comments. *Goleremys mckennai* was named on the basis of a well-preserved skull from early Paleocene Goler Formation exposed in California (Hutchison 2004). The specimen is particularly notable, as it is the only baenid remain found on the western side of the Western Cordillera. The validity of this taxon is uncontroversial.

Palatobaena Gaffney, 1972

Type species. *Palatobaena bairdi* Gaffney, 1972.

Diagnosis. *Palatobaena* is diagnosed as a baenodd and a palatobaenine by the full list of characters listed for those clades above. *Palatobaena* is differentiated from other palatobaenines by its round skull, extremely expanded posterior triturating surfaces, dorsally oriented orbits and narial sulcus.

Palatobaena bairdi Gaffney, 1972

Taxonomic history. *Palatobaena bairdi* Gaffney, 1972 (new species).

Type material. YPM VPPU 016839 (holotype, formerly PU 16839), right half of a slightly crushed cranium (Gaffney 1972, figs. 22–24, 51; Archibald and Hutchison 1979, fig. 6e).

Type locality. Cedar Point Quarry, SW1/4 Section 23, T 55 N, R 95 W, Bighorn County, Wyoming, USA (see Figure 6); Fort Union Formation, early Tiffanian NALMA (Gaffney 1972), Selandian, Paleocene.

Referred material and range. Paleocene (Torrejonian + Tiffanian NALMA) of Wyoming and Montana (Gaffney 1972; Archibald and Hutchison 1979; Lyson and Joyce 2009a).

Diagnosis. *Palatobaena bairdi* is diagnosed as a baenodd, a palatobaenine and a representative of *Palatobaena* by the full list of cranial characters listed for those clades above. *Palatobaena bairdi* is differentiated from other *Palatobaena* spp. by its deep upper temporal emargination, posteriorly pointed parietals, broad contribution of the jugal to the orbit margin and well-developed contact between the pterygoids.

Comments. *Palatobaena bairdi* is typified on a partial skull from the late Paleocene (Tiffanian NALMA, Selandian–Thanetian), but a number of fragmentary specimens from the Late Cretaceous (Maastrichtian) were attributed to this taxon in the type description. Holroyd and Hutchison (2002) noted that the Maastrichtian material shows differences from the late Paleocene material, but they did not name a new species, likely because appropriate type material was missing. Lyson and Joyce (2009a) were able to describe a series of well-preserved skulls and shells from the Late Cretaceous (Maastrichtian) of North Dakota that supported the taxonomic assessment of Holroyd and Hutchison (2002). In addition to the new material from North Dakota, Lyson and Joyce (2009a) referred all material from the Maastrichtian and early Paleocene (Puercan) to the new taxon, *Pa. cohen*, that had previously been referred to *Pa. bairdi* (Gaffney 1972, 1982b; Archibald and Hutchison 1979; Hutchison and Archibald 1986; Holroyd and Hutchison 2002; Hutchison and Holroyd 2003) on the basis of apomorphies or stratigraphic considerations. *Palatobaena cohen* appears to possess the ancestral morphology for *Pa. bairdi* and may therefore be its direct ancestor (Lyson and Joyce 2009a).

Palatobaena cohen Lyson and Joyce, 2009a

Taxonomic history. *Palatobaena cohen* Lyson and Joyce, 2009a (new species).

Type material. YPM VP 057498 (holotype), a complete skull, including mandible, and shell (Lyson and Joyce 2009a, figs. 3, 5, 6.1).

Type locality. Near Marmarth, Bucklin Township, Slope County, North Dakota, USA (see Figure 5); approximately 65 m below the Fort Union formational contact; Hell Creek Formation, Maastrichtian, Late Cretaceous (Lyson and Joyce 2009a).

Referred material and range. Late Cretaceous (Maastrichtian), Montana and North Dakota and early Paleocene (Puercan NALMA, Danian) of Montana and Colorado (hypodigm of Lyson and Joyce 2009a).

Diagnosis. *Palatobaena cohen* is diagnosed as a baenodd, a palatobaenine and a representative of *Palatobaena* by the full list of characters listed for those clades above. *Palatobaena cohen* is differentiated from other *Palatobaena* by its deep upper temporal emargination, pointed parietals, posterior extension of the frontals beyond the orbit margin, large orbits, broad contribution of the jugal to the orbit margin and well-developed contact between the pterygoids.

Comments. *Palatobaena cohen* is based on a beautifully preserved skull that was found in close association with a shell from the Late Cretaceous (Maastrichtian) Hell Creek Formation of North Dakota. See *Palatobaena bairdi* for historical background.

Palatobaena gaffneyi
Archibald and Hutchison, 1979

Taxonomic history. *Palatobaena gaffneyi* Archibald and Hutchison, 1979.

Type material. UCMP 114529 (holotype), nearly complete, slightly crushed skull (Archibald and Hutchison 1979, figs. 5, 6a–c, f, 7c, d).

Type locality. UCMP Locality V71238, Sweetwater County, Wyoming, USA (see Figure 6); Wasatch Formation, Wasatchian NALMA (Archibald and Hutchison 1979), Ypresian, Eocene.

Referred material and range. Early Eocene (Wasatchian NALMA, Ypresian) of Wyoming (Holroyd et al. 2001), *Baenidae* indet. ("Baena" of Holroyd et al. 2001).

Diagnosis. *Palatobaena gaffneyi* is diagnosed as a baenodd, a palatobaenine and a representative of *Palatobaena* by the full list of cranial characters listed for those clades above. *Palatobaena gaffneyi* is differentiated from other *Palatobaena* by its moderately deep temporal emargination, rounded parietals that cover the supraoccipital, broad contribution of the supraoccipital to the dorsal skull roof, small contribution of the jugal to the orbital margin and point contact between the pterygoids.

Comments. *Palatobaena gaffneyi* is based on a rather complete, though heavily fragmented skull from Wasatchian deposits in Wyoming (Archibald and Hutchison 1979). The taxon is well diagnosed relative to other species of *Palatobaena*, and its taxonomic status is therefore uncontroversial. Given that all three *Palatobaena* species have nonoverlapping temporal ranges and that older taxa are symplesiomorphic relative to younger ones, however, it is possible that *Pa. gaffneyi* is the final link in a series of chronospecies (Lyson and Joyce 2009a).

Plesiobaena antiqua (Lambe, 1902)
(= *Baena callosa* Hay, 1904a)

Taxonomic history. *Baena antiqua* Lambe, 1902 (new species); *Plesiobaena antiqua* Gaffney, 1972 (new combination).

Type material. CMN 1648 (holotype), an anterior plastral lobe and partial anterior carapace (Lambe 1902, fig. 10; Hay 1908, fig. 38).

Type locality. Below mouth of Berry Creek, Red Deer River, Dinosaur Provincial Park, Alberta, Canada (see Figure 5); Judith River Group, Campanian, Late Cretaceous (Lambe 1902; Brinkman 2003a).

Referred material and range. Late Cretaceous (Campanian), Judith River Group of Alberta (sequentially referred material of Gilmore 1920; Parks 1933; Russell 1934; and Brinkman 2003a) and Montana (Hay 1904a, type material of *Baena callosa*).

Diagnosis. *Plesiobaena antiqua* is diagnosed as a baenodd and a palatobaenine by the full list of characters listed for those clades above. *Plesiobaena antiqua* is differentiated from other palatobaenines by pointed parietals that cover the supraoccipital, exclusion of the jugal from the orbit margin, weak cheek emargination, point contact between the pterygoids, weakly expanded posteriorly triturating surfaces and fontanelles between costals and peripherals in all but the most skeletally mature specimens.

Comments. *Plesiobaena antiqua* is the most common turtle in the Campanian Judith River deposits of Canada, and its anatomy is therefore well understood (Brinkman 2003a). We here show (see Invalid Taxa below) that the type material of *Baena callosa* from the Campanian of northern Montana falls within the documented range of variation for *Pl. antiqua*, and we therefore synonymize these two taxa. Gaffney (1972) assigned material from the Maastrichtian of Montana and Wyoming to *Pl. antiqua* as well, but subsequent work (e.g., Brinkman 2003a; Lyson and Joyce 2009b) demonstrated that this material represents a new taxon, now termed *Cedrobaena brinkman*. Hutchison et al. (2013) recently described two relatively complete shells from the Campanian of Utah as *Plesiobaena* sp., but this has since been named as a new species, *Arvinachelys goldeni* (see above). The morphology of *Pl. antiqua* was most recently revised by Brinkman (2003a).

Invalid and Problematic Taxa

Baena callosa Hay, 1904a (junior synonym of *Plesiobaena antiqua* (Lambe, 1902))

Taxonomic history. *Baena callosa* Hay, 1904a (new species).

Type material. CM 330 (holotype), an incomplete shell (Hay 1904a, figs. 1, 2, pl. 9; Hay 1908, figs. 35, 36, pl. 8.1).

Type locality. Willow Creek Area, 10 miles (16 km) north of Musselshell, Musselshell County (not Gallatin County sensu Hay 1908), Montana, USA (Stanton and Hatcher 1905; see Figure 5); Judith River Formation (Stanton and Hatcher 1905), Late Cretaceous (Campanian).

Comments. *Baena callosa* has been largely been ignored by researchers since its naming. Following the realization that *Baena* sensu stricto is restricted to the Eocene, Gaffney (1972) listed this taxon among those that should be removed from *Baena*, but he did not explore possible synonymies with other taxa. We note that *Baena callosa* resembles the coeval taxon *Plesiobaena antiqua* by being relatively small, lacking prepleurals and by having a narrow anterior plastral lobe and an omega-shaped anal-femoral sulcus, and the arrangement of the gulars is within the documented variation for *Pl. antiqua*. We therefore refer *Baena callosa* to *Pl. antiqua*.

Baena clara Hay, 1908 (junior synonym of *Baena arenosa* Leidy, 1870)

Taxonomic history. *Baena clara* Hay, 1908 (new species); *Baena arenosa* = *Baena affinis* = *Baena sima* = *Baena clara* = *Baena riparia* = *Baena emiliae* = *Baena inflata* Gaffney, 1972 (junior synonym).

Type material. AMNH 1675 (holotype, listed as AMNH 6075 in plate captions of Hay 1908), a nearly complete shell (Hay 1908, figs. 57, 58, pl. 16).

Type locality. "Exact level and locality not known" (Hay 1908:74); Wyoming, USA (see Figure 6); Bridger Formation (Hay 1908), Bridgerian NALMA, Early Eocene, Ypresian–Lutetian.

Comments. For extensive discussion see *Baena arenosa*.

Baena emiliae Hay, 1908 (junior synonym of *Baena arenosa* Leidy, 1870)

Taxonomic history. *Baena emiliae* Hay, 1908 (new species); *Baena arenosa* = *Baena affinis* = *Baena sima* = *Baena clara* = *Baena riparia* = *Baena emiliae* = *Baena inflata* Gaffney 1972 (junior synonym).

Type material. AMNH 1925 (holotype), nearly complete shell (Hay 1908, figs. 67, 68, pl. 20).

Type locality. White River, Uinta County, Utah, USA (Gaffney 1972; see Figure 6); Level B, Uinta Formation, Uintan NALMA, Lutetian, middle Eocene.

Comments. For extensive discussion see *Baena arenosa*.

Baena fluviatilis Parks, 1933 (junior synonym of *Neurankylus eximius* Lambe, 1902)

Taxonomic history. *Baena fluviatilis* Parks, 1933 (new species); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* = *Neurankylus baueri* Gaffney, 1972 (junior synonym); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* = *Neurankylus baueri* = *Neurankylus wyomingensis* Brinkman and Nicholls, 1993 (junior synonym); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* Larson et al., 2013 (junior synonym).

Type material. ROM 854 (holotype, formerly listed as ROM 5724), partial shell lacking most peripheral elements (Parks 1933, figs. 1, 2, pl. 7).

Type locality. Sand Creek, Red Deer River, Alberta, Canada (Parks 1933; see Figure 5); "probably Dinosaur Park Formation" (Larson et al. 2013:392), Judith River Group, Campanian, Late Cretaceous (Brinkman 2003b).

Comments. The type specimens of *Baena fluviatilis* and *Neurankylus eximius* originate from the Judith River Group of southern Alberta (Lambe 1902; Parks 1933). All taxonomic reviews of the last decades have concluded that these taxa are synonymous (Gaffney 1972; Brinkman and Nicholls 1993; Larson et al. 2013), and we agree with this straightforward assessment.

Baena gigantea Gilmore, 1916c (junior synonym of *Chisternon undatum* (Leidy, 1871b))

Taxonomic history. *Baena gigantea* Gilmore, 1916c (new species); *Chisternon undatum* = *Baena gigantea* = *Baena hebraica* Gaffney, 1972 (junior synonym).

Type material. CM 3441 (holotype), nearly complete shell primarily lacking posterior margins (Gilmore 1916c, figs. 5–7, pl. 20).

Type locality. Wagonhound Bend, White River, Uinta County, Utah (Gilmore 1916c); Lower Uinta B, Uinta Formation (Gilmore 1916c), Uintan NALMA, Lutetian, middle Eocene (Prothero 1996).

Comments. *Baena gigantea* is based on a large shell discovered in Uintan deposits in Utah (Gilmore 1916c). We agree with Gaffney (1972) that this taxon is synonymous with the Bridgerian taxon *Chisternon undatum* (see above). This synonymy is uncontroversial.

Baena hebraica Cope, 1872/1873a (junior synonym of *Chisternon undatum* (Leidy, 1871b))

Taxonomic history. *Baena hebraica* Cope, 1872/1873a (new species); *Chisternon hebraica* Hay, 1908 (new combination); *Chisternon undatum* = *Baena gigantea* = *Baena hebraica* Gaffney, 1972 (junior synonym).

Type material. USNM 2275 (holotype), anterior half of shell (Cope 1884, pl. 19.1, 2).

Type locality. Black's Fork of Green River, SW Wyoming, USA (Cope 1884, see Comments below; see Figure 6); Bridger Formation (Hay 1908), Bridgerian NALMA, Ypresian–Lutetian, Eocene.

Comments. *Baena hebraica* is based on a partial shell from Bridgerian deposits in Wyoming. Cope (1872, 1873a) reports the type to be from Cottonwood Creek, but in 1884 he reports the locality as Black's Fork. Similar inconsistencies are apparent for numerous trionychid taxa from Cottonwood Creek or Black's Fork (Vitek and Joyce 2015). Many small rivers were historically referred to as Cottonwood Creek, and it is therefore unclear which river Cope (1872, 1873a) referred to. A river called Cottonwood Creek exists north of the Bridger Basin, but current geological maps do not reveal any Eocene deposits in its vicinity. We therefore presume that the type locality is indeed at Black's Fork, which is situated near Fort Bridger.

Gaffney (1972) synonymized *Baena hebraica* with the coeval taxon *Chisternon undatum*, and we agree with this assessment. We also agree that all specimens referred by Hay (1908) to *Ba. hebraica* should instead be referred to *Ch. undatum*.

Baena inflata Gilmore, 1916c (junior synonym of "*Baena*" *affinis* Leidy, 1871a)

Taxonomic history. *Baena inflata* Gilmore, 1916c (new species); *Baena arenosa* = *Baena affinis* = *Baena sima* = *Baena clara* = *Baena riparia* = *Baena emiliae* = *Baena inflata* Gaffney, 1972 (junior synonym).

Type material. CM 3406 (holotype), a nearly complete shell missing the posterior margins (Gilmore 1916c, figs. 2, 3, pl. 19).

Type locality. McCook Canyon, White River, Uinta County, Utah (Gilmore 1916c); near top of Horizon A, Uinta Formation (Gilmore 1916c), Uintan NALMA, Lutetian, middle Eocene (Prothero 1996).

Comments. For extensive discussions see *Baena arenosa* and "*Baena*" *affinis*.

Baena longicauda Russell, 1934 (junior synonym of *Thescelus insiliens* Hay, 1908)

Taxonomic history. *Baena longicauda* Russell, 1934 (new species); *Thescelus insiliens* = *Baena longicauda* = *Thescelus rapiens* = *Thescelus hemispherica* Gaffney, 1972 (junior synonym).

Type material. CMN 8678 (holotype), a partial skeleton consisting of the posterior portions of the carapace and plastron, seven caudal vertebrae, left manus, and articulated pelvic girdle, hind limbs and tail (Russell 1934, pls. 1–3).

Type locality. SE1/4 Section 23, T 1, R 5, W 3rd Meridian, Morgan Creek, east branch of Rocky Creek, Saskatchewan, Canada (see Figure 5); Frenchman Formation (formerly lower Ravenscrag Formation), Maastrichtian, Late Cretaceous (Russell 1934).

Comments. *Baena longicauda* is based on a partial skeleton from the Late Cretaceous (Maastrichtian) of southern Saskatchewan (Russell 1934). We synonymize this taxon with the coeval *Thescelus insiliens* on the basis of the presence of a complete ring of marginal elements, an omega-shaped anal-femoral sulcus, the presence of fine crenulations on the surface of the shell and the presence of a deep nuchal notch.

Baena marshi Hay, 1904b nomen dubium

Taxonomic history. *Baena marshi* Hay, 1904b (new species).

Type material. YPM VP 000299 (holotype), a near-complete plastron with articulated peripheral elements (Hay 1904b, fig. 1, pl. 11; Hay 1908, fig. 39, pl. 8.2).

Type locality. Between Buck and Lance Creek, Converse County, Wyoming, USA (Hay 1904b; see Figure 5); Lance Formation, Maastrichtian, Late Cretaceous (Gaffney 1972).

Comments. *Baena marshi* is primarily based on a plastron from the Late Cretaceous (Maastrichtian) of Wyoming. The plastron exhibits well-developed gular and extragulars and a straight anal-femoral sulcus, and can therefore be placed with confidence within *Eubaeninae*, but characters are lacking that would allow distinguishing it from various described or undescribed *Eubaena* and *Stygiochelys* species. We therefore find *Baena marshi* to lack diagnostic characters and declare it a nomen dubium.

Baena platyplastra Gilmore, 1916c nomen dubium

Taxonomic history. *Baena platyplastra* Gilmore, 1916c (new species).

Type material. CM 3227 (holotype), a partial plastron (Gilmore 1916c, fig. 8, pl. 18.2).

Type locality. "Northeast of Well No. 2," Uinta County, Utah (Gilmore 1916c:120); Uinta B, Uinta Formation (Gilmore 1916c), Uintan NALMA, Lutetian, middle Eocene (Prothero 1996).

Comments. *Baena platyplastra* is based on a partial specimen from Uintan deposits in Utah, which was differentiated from other baenids by its large size and thin plastral bones (Gilmore 1916c). The anterior plastral lobe and the carapace are missing completely, and it is therefore not possible to observe many important characters. Gaffney (1972) rejected this taxon as a nomen dubium, but referred it nevertheless to *Baena arenosa*, a minor internal inconsistency. We agree with the former assessment and declare this taxon a nomen dubium.

Baena riparia Hay, 1908 (junior synonym of "*Baena*" *affinis* Leidy, 1871a)

Taxonomic history. *Baena riparia* Hay, 1908; *Baena arenosa* = *Baena affinis* = *Baena sima* = *Baena clara* = *Baena riparia* = *Baena emiliae* = *Baena inflata* Gaffney, 1972 (junior synonym).

Type material. AMNH 5977 (holotype), a near-complete, slightly damaged skeleton (Hay 1908, figs. 59–66, pls. 17, 18, 19.1–3; Gaffney 1972, fig. 31).

Type locality. Grizzly Buttes, Uinta County, Wyoming, USA (Hay 1908; see Figure 6); level B (Hay 1908), Black Fork Member, Bridger Formation, Bridgerian NALMA, Early Eocene, Ypresian–Lutetian (Murphey and Evanoff 2007).

Comments. For extensive discussions see *Baena arenosa* and "*Baena*" *affinis*.

Baena sima Hay, 1908 (junior synonym of *Baena arenosa* Leidy, 1870)

Taxonomic history. *Baena sima* Hay, 1908; *Baena arenosa* = *Baena affinis* = *Baena sima* = *Baena clara* = *Baena riparia* = *Baena emiliae* = *Baena inflata* Gaffney, 1972 (junior synonym).

Type material. AMNH 5971 (holotype), partial skeleton, including skull and shell (Hay 1908, figs. 52, 53, pls. 13.2, 3, 14.4–6); AMNH 5965 (paratype), a shell (Hay 1908, pl. 15); AMNH 5907 (paratype), shell and fragments of skull, pelvis and limb bones (Hay 1908, figs. 54–56).

Type locality. Little Dry Creek, south of Fort Bridger, Uinta County, Wyoming, USA (Hay 1908; see Figure 6); level B (Hay 1908), Black Fork Member, Bridger Formation, Bridgerian NALMA, Early Eocene, Ypresian–Lutetian (Murphey and Evanoff 2007). The paratypes both originate from the same level of the nearby Grizzly Buttes locality.

Comments. For extensive discussion see *Baena arenosa*.

Boremys albertensis Gilmore, 1920 (junior synonym of *Boremys pulchra* (Lambe, 1906a))

Taxonomic history. *Boremys albertensis* Gilmore, 1920 (new species); *Boremys pulchra* = *Boremys albertensis* = *Boremys grandis* Gaffney, 1972 (junior synonym); *Boremys pulchra* = *Boremys albertensis* Brinkman and Nicholls, 1991 (junior synonym).

Type material. USNM 8803 (holotype), a near-complete shell missing its left lateral and posterior margins (Gilmore 1920, figs. 3, 4, pls. 33, 34).

Type locality. South Branch of Sand Creek, Red Deer River, Alberta, Canada (Gilmore 1920; see Figure 5); 200 feet below the top of the Belly River Formation, Oldman Formation (Gaffney 1972), Judith River Group, Campanian, Late Cretaceous (Brinkman 2003b).

Comments. *Boremys albertensis* is based on a relatively complete shell that was diagnosed relative to *Bo. pulchra* by its larger size and numerous variations to the number and size of the carapacial scutes (Gilmore 1920). A taxonomic review of *Boremys* material from North American revealed that much variation is present to the number of carapacial scutes, but that the northern material varies consistently from the southern material (Brinkman and Nicholls 1991). We therefore agree that *Bo. albertensis* is the junior synonym of *Bo. pulchra*.

Charitemys captans Hay, 1908 (junior synonym of *Neurankylus eximius* Lambe, 1902)

Taxonomic history. *Charitemys captans* Hay, 1908 (new species); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys cap-*

tans = *Neurankylus baueri* Gaffney, 1972 (junior synonym); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* = *Neurankylus baueri* = *Neurankylus wyomingensis* Brinkman and Nicholls, 1993 (junior synonym); *Neurankylus eximius* = *Baena fluviatilis* = *Charitemys captans* Larson et al., 2013 (junior synonym).

Type material. AMNH 6098 (holotype), two quadrates and fragmentary carapace and plastron remains (Hay 1908, figs. 93–95).

Type locality. Montana, USA (Hay 1908; see Figure 5); Judith River Formation, Campanian, Late Cretaceous (Gaffney 1972).

Comments. The holotype of *Charitemys captans* was recovered from the Judith River deposits of Montana, just south of the type locality of *Neurankylus eximius* in neighboring Alberta. Gaffney (1972), Brinkman and Nicholls (1993) and Larson et al. (2013) suggested that these taxa are synonymous, and we agree with this assessment. It is interest to note that the type specimen of *Charitemys captans* remains the only described representative of *Neurankylus eximius* from Montana to date, although numerous specimens exist at UCMP (D. Brinkman, pers. comm.).

Chisternon interpositum Hay, 1909
nomen dubium

Taxonomic history. *Chisternon interpositum* Hay, 1909 (new species); [*Chisternon interpositum*] Gaffney, 1972 (nomen dubium).

Type material. USNM 6058 (holotype), anterior portions of shell (Hay 1909, figs. 1, 2).

Type locality. T 5 S, R 19 E, Carbon County, Montana (Hay 1909); early Paleocene (see Comments below).

Comments. *Chisternon interpositum* is based on a partial shell that preserves that the central, anterior portion of the carapace and much of the anterior plastral lobe (Hay 1909). According to the geological map of Montana, the Lebo and Tongue River Members of the Fort Union Formation crop out within the 36 square mile (about 93 km^2) "type locality" and this specimen is therefore likely "middle" Paleocene in age (i.e., Torrejonian–Tiffanian).

The holotype preserves preneurals, prepleurals and well-developed gulars, and can therefore be diagnosed with confidence as a eubaenine. However, important anatomical areas are missing and it is therefore not possible to diagnose this fossil relative to other eubaenines. We therefore agree with Gaffney (1972) that this taxon is a nomen dubium.

Glyptops caelatus Hay, 1908
nomen dubium

Taxonomic history. *Glyptops caelatus* Hay, 1908 (new species); [*Glyptops caelatus*] Gaffney, 1972 (nomen dubium).

Type material. USNM 5880 (holotype, originally catalogued as USNM 1930; Hay 1908), articulated right costal I and right peripherals I and II (Hay 1908, figs. 28–31, pl. 7.1, 2).

Type locality. Muirkirk, Prince George's County, Maryland, USA (see Figure 5); Potomac Formation, late Albian to early Aptian, Early Cretaceous (Hay 1908; Lipka et al. 2006).

Comments. *Glyptops caelatus* is based on a shell fragment consisting of the right costal I and right peripherals I and II that was recovered from an Early Cretaceous clay pit near Muirkirk, Maryland (Hay 1908), in the immediate temporal and spatial vicinity of the type material of *Arundelemys dardeni* (Lipka et al. 2006). Although it is likely that these two taxa are synonymous, it is currently not possible to refer one to the other, because material of both taxa has not yet been found in direct association and because the available material of *G. caelatus* is too fragmentary to allow resolving its phylogenetic placement. The exterior surfaces of the available shell material of *G. caelatus* are decorated by a finely sculptured pattern that generally resembles that of many pleurosternids and baenids (including the skull of *A. dardeni*), and its paracryptodiran affinities therefore appear certain. However, we agree with Gaffney (1979) that the type material lacks diagnostic characters and that this taxon should therefore be regarded as a nomen dubium.

Glyptops pervicax Hay, 1908
nomen dubium

Taxonomic history. *Glyptops pervicax* Hay, 1908 (new species); [*Glyptops pervicax*] Gaffney, 1979 (nomen dubium).

Type material. AMNH 1018 (holotype), a poorly preserved partial shell (Hay 1908, fig. 32).

Type locality. Push Creek, 13 miles (21 km) east of Pryor, Bighorn County, Montana, USA (see Figure 5); Sykes Mountain Formation, Albian, Early Cretaceous (Moberly 1960).

Comments. *Glyptops pervicax* is based on a poorly preserved partial shell from the Early Cretaceous Sykes Mountain Formation of Montana, which is broadly equivalent in age to type localities of *Protobaena wyomingensis* about 150 km to the northeast and *Trinitichelys hiatti* about 2,000 km to the southeast. Given the extremely poor preservation of the type specimens, Hay (1908) was only able to provide the sketch of the plastron, which lacks meaningful diagnostic characters. We therefore conclude that possible synonymies cannot be evaluated for this taxon and agree with Gaffney (1979) that it is best interpreted as a nomen dubium.

Polythorax missuriensis Cope, 1876
nomen dubium

Taxonomic history. *Polythorax missuriensis* Cope, 1876 (new species); [*Polythorax missuriensis*] Gaffney, 1972 (nomen dubium).

Type material. A partial shell, the whereabouts of which are unknown (Hay 1908; Gaffney 1972).

Type locality. Montana; "Fort Union Beds" (Cope 1876); associated dinosaur fossils indicate a Late Cretaceous age, but a lack of additional locality information precludes associating this find with the Campanian Judith River Beds or the Maastrichtian Hell Creek Formation (Gaffney 1972).

Comments. *Polythorax missuriensis* is based on a partial shell that was never figured and now appears to be lost (Hay 1908; Gaffney 1972). We agree with Gaffney (1972) that it is even uncertain if this taxon represents a baenid (contra Hay 1908) and that this taxon must be considered a nomen dubium.

Thescelus hemispherica Gilmore, 1935
nomen dubium

Taxonomic history. *Thescelus hemispherica* Gilmore, 1935 (new species); *Thescelus insiliens* = *Baena longicauda* = *Thescelus rapiens* = *Thescelus hemispherica* Gaffney, 1972 (senior synonym); *Thescelus hemispherica* Sullivan et al., 2013 (nomen validum).

Type material. USNM 12818 (holotype), partial shell missing much of the carapacial margins and the posterior plastral lobe (Gilmore 1935, figs. 11, 12, pl. 16; Sullivan et al. 2013, fig. 20.7a, b).

Type locality. Three miles (4.5 km) northeast of Hunter's Store, Bisti Post Office, SW1/4 T 24 N, R 13 W, San Juan County, New Mexico; Hunter Wash Member, Kirtland Formation; Campanian, Late Cretaceous (Sullivan et al. 2013).

Comments. *Thescelus hemispherica* is based on a partial shell from Campanian deposits in New Mexico (Gilmore 1935). The taxon was synonymized with *Th. insiliens* by Gaffney (1972), but Sullivan et al. (2013) recently reinstated its validity. The holotype of *Th. hemispherica* is notable in that the carapace is covered by thick welts similar to those seen in *Boremys grandis*, *Denazinemys nodosa* and *Scabremys ornata* from coeval deposits, but the shell, as preserved, does not display enough details to rigorously distinguish it from these taxa. We suggest that this specimen be cleaned and prepared to allow more rigorously assessing Gilmore's (1935) interpretation, especially in regard to the distribution of the scutes. Until this has been accomplished, we consider this taxon to be a nomen dubium.

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Appendix 1
Institutional Abbreviations

AMNH	American Museum of Natural History, New York, New York, USA
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
CMN	Canadian Museum of Nature, Ottawa, Canada
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
ND	North Dakota Heritage Center, Bismarck, North Dakota, USA
NMMNHS	New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA
ROM	Royal Ontario Museum, Toronto, Canada
TMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Canada
UCMP	University of California Museum of Paleontology, Berkeley, California, USA
UMMP	University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA
UMNH	Natural History Museum of Utah, Salt Lake City, Utah, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
YPM VP	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA
YPM VPPU	Division of Vertebrate Paleontology (Princeton University Collection), Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

Appendix 2
Named Baenid Genera

Arundelemys Lipka et al., 2006 (type species: *Arundelemys dardeni* Lipka et al., 2006)
Arvinachelys Lively, in press (type species: *Arvinachelys goldeni* Lively, in press)
Baena Leidy, 1870 (type species: *Baena arenosa* Leidy, 1870)
Boremys Lambe, 1906b (type species: *Baena pulchra* Lambe, 1906a)
Cedrobaena Lyson and Joyce, 2009b (type species: *Plesiobaena putorius* Gaffney, 1972)
Charitemys Hay, 1908 (type species: *Charitemys captans* Hay, 1908)
Chisternon Leidy, 1872 (type species: *Baena undata* Leidy, 1871b)

Denazinemys Lucas and Sullivan, 2006 (type species: *Baena nodosa* Gilmore, 1916b)

Eubaena Hay, 1908 (type species: *Baena cephalica* Hay, 1904b)

Gamerabaena Lyson and Joyce, 2010 (type species: *Gamerabaena sonsalla* Lyson and Joyce, 2010)

Goleremys Hutchison, 2004 (type species: *Goleremys mckennai* Hutchison, 2004)

Hayemys Gaffney, 1972 (type species: *Eubaena latifrons* Hay, 1908)

Neurankylus Lambe, 1902 (type species: *Neurankylus eximius* Lambe, 1902)

Palatobaena Gaffney, 1972 (type species: *Palatobaena bairdi* Gaffney, 1972)

Peckemys Lyson and Joyce, 2009b (type species: *Peckemys brinkman* Lyson and Joyce, 2009b)

Plesiobaena Gaffney, 1972 (type species: *Baena antiqua* Lambe, 1902)

Protobaena gen. nov. (type species: *Neurankylus wyomingensis* Gilmore, 1920)

Polythorax Cope, 1876 (type species: *Polythorax missuriensis* Cope, 1876)

Scabremys Sullivan et al., 2013 (type species: *Baena ornata* Gilmore, 1935)

Stygiochelys Gaffney and Hiatt, 1971 (type species: *Stygiochelys estesi* Gaffney and Hiatt, 1971)

Thescelus Hay, 1908 (type species: *Thescelus insiliens* Hay, 1908)

Trinitichelys Gaffney, 1972 (type species: *Trinitichelys hiatti* Gaffney, 1972)

Appendix 3
Biogeographic Summary of Baenid Turtles

Numbers in brackets reference Figures 4 and 5.
Abbreviation: TL, Type locality.

Canada

[1] Late Cretaceous, Santonian; Alberta; *Neurankylus lithographicus* (TL) (Larson et al. 2013)

[2] Late Cretaceous, Campanian; Alberta; *Boremys pulchra* (TL) (Lambe 1906a, 1914; Gilmore 1920; Parks 1933; Brinkman and Nicholls 1991, including type material of *Boremys albertensis*), *Neurankylus eximius* (TL) (Lambe 1902; Parks 1993; Brinkman and Nicholls 1993; Larson et al. 2013), *Plesiobaena antiqua* (TL) (Lambe 1902; Gilmore 1920; Parks 1933; Russell 1934; Brinkman 2003a, 2003b)

[3] Late Cretaceous, Maastrichtian; *Baenidae* indet. (Brinkman and Eberth 2006)

[4] Late Cretaceous, Maastrichtian; Saskatchewan; *Eubaeninae* indet. (= *Baena hatcheri* of Russell 1934), *Palatobaeninae* indet. (= *Baena antiqua* of Russell 1934), *Thescelus insiliens* (= *Baena longicauda* of Russell 1934)

[5] Paleocene; Alberta; *Baenidae* indet. (Brinkman 2013)

[6] Eocene, Uintan NALMA, Lutetian; Saskatchewan; *Baenidae* indet. (= *Baena* indet. of Hutchison and Storer 1998)

United States of America

[7] Early Cretaceous, Aptian/Albian; Maryland; *Arundelemys dardeni* (TL), *Paracryptodira* indet. (Lipka et al. 2006)

[8] Early Cretaceous, Aptian/Albian; Montana, Clark's Fork Basin; *Paracryptodira* indet. (= "*Glyptops pervicax*" of Hay 1908)

[9] Early Cretaceous, Aptian/Albian; Texas; *Trinitichelys hiatti* (TL) (Gaffney 1972)

[10] Early Cretaceous, Albian; Wyoming, Bighorn Basin; *Protobaena wyomingensis* (TL) (Gilmore 1920)

[11] Late Cretaceous, Campanian; Montana; *Boremys pulchra* (= *Boremys* sp. of Fiorillo 1989), *Neurankylus eximius* (Gaffney 1972; = *Charitemys captans* of Hay 1908), *Plesiobaena antiqua* (= *Baena callosa* of Hay 1904a)

[12] Late Cretaceous, Campanian; New Mexico, San Juan Basin; *Boremys grandis* (TL) (Gilmore 1935; Sullivan et al. 2013), *Denazinemys nodosa* (TL) (Gilmore 1916b, 1919; Wiman 1933; Sullivan et al. 2013), *Neurankylus baueri* (TL) (Gilmore 1916b, 1919, 1935; Wiman 1933; Sullivan et al. 2013), *Scabremys ornata* (TL) (Gilmore 1935), *Thescelus rapiens* (TL) (Hay 1908; Wiman 1933)

[13] Late Cretaceous, Campanian; Texas; *Denazinemys nodosa*, *Neurankylus* sp. (Tomlinson 1997)

[14] Late Cretaceous, Campanian; Utah, Kaiparowits Plateau; *Arvinachelys goldeni* (Lively, in press = *Plesiobaena* sp. of Hutchison et al. 2013), *Boremys grandis* (Hutchison et al. 2013), *Neurankylus baueri* (= *Neurankylus* A + B of Hutchison et al. 2013), *Denazinemys nodosa* (Hutchison et al. 2013)

[15] Late Cretaceous, Campanian; Utah, Uinta Basin; *Baenidae* indet. (= *Thescelus insiliens* of Gaffney 1972)

[16] Late Cretaceous, Maastrichtian; Colorado, Denver Basin; *Boremys* sp. (= "Eubaenina indet." of Hutchison and Holroyd 2003); *Neurankylus* sp. (Hutchison and Holroyd 2003); *Cedrobaena brinkman* (Lyson and Joyce 2009b; = *Plesiobaena* cf. *antiqua* of Hutchison and Holroyd 2003)

[17] Late Cretaceous, Maastrichtian; Montana, Powder River/Williston Basin; *Neurankylus* sp. (Holroyd and Hutchison 2002), *Palatobaena cohen* (Lyson and Joyce 2009a; = *Pa. bairdi* of Gaffney 1972, 1982b; Archibald and Hutchison 1979; Hutchison and Archibald 1986; Holroyd and Hutchison 2002), *Cedrobaena brinkman* (TL) (Lyson and Joyce 2009b; Case 1939; = *Plesiobaena antiqua* of Gaffney 1972), *Stygiochelys estesi* (TL) (Gaffney and Hiatt 1971; Gaffney 1982b), *Thescelus insiliens* (Hutchison and Archibald 1986; Holroyd et al. 2014)

[18] Late Cretaceous, Maastrichtian; North Dakota, Williston Basin; *Boremys* sp. (Lyson et al. 2011), *Cedrobaena putorius* (Lyson and Joyce 2009b), *Gamerabaena sonsalla* (TL) (Lyson and Joyce 2010), *Neuranky-*

lus sp. (Holroyd and Hutchison 2002), *Palatobaena cohen* (TL) (Lyson and Joyce 2009a; = *Pa. bairdi* of Holroyd and Hutchison 2002), *Cedrobaena brinkman* (Lyson and Joyce 2009b)

[19] Late Cretaceous, Maastrichtian; South Dakota, Williston Basin; *Cedrobaena putorius* (Lyson and Joyce 2009b)

[20] Late Cretaceous, Maastrichtian; Wyoming, Powder River Basin; *Eubaeninae* indet. (= *Baena marshi* of Hay 1904b), *Eubaena cephalica* (TL) (Hay 1904b), *Eubaena hatcheri* (TL) (Hay 1901), *Hayemys latifrons* (TL) (Hay 1908), *Cedrobaena brinkman* (Lyson and Joyce 2009b; = *Eubaena cephalica* of Estes 1964), "*Baena*" *hayi* (TL) (Gilmore 1916a), *Thescelus insiliens* (TL) (Hay 1908)

[21] Late Cretaceous, Maastrichtian; Wyoming, Hanna Basin; *Baenidae* indet. (Lillegraven and Eberle 1999)

[22] Late Cretaceous, Maastrichtian; Wyoming, Green River Basin; *Baenidae* indet. (Breithaupt 1982)

[23] Early Paleocene, Puercan NALMA, Danian; Colorado, Denver Basin; *Palatobaena cohen* (Lyson and Joyce 2009a; = *Pa. bairdi* of Archibald and Hutchison 1979; Hutchison and Holroyd 2003)

[24] Early Paleocene, Puercan NALMA, Danian; Montana, Williston Basin; *Palatobaena cohen* (Lyson and Joyce 2009a; = *Pa. bairdi* of Archibald and Hutchison 1979), *Stygiochelys estesi* (Gaffney 1982b)

[25] Early Paleocene, Torrejonian NALMA, Danian; Montana, Powder River Basin; *Palatobaena bairdi* (Gaffney 1972; Archibald and Hutchison 1979)

[26] Early Paleocene, Puercan NALMA, Danian; New Mexico, San Juan Basin; *Neurankylus* sp. (Sullivan et al. 1988), *Palatobaena* sp. (Sullivan and Lucas 1986)

[27] Early Paleocene, Torrejonian NALMA, Danian; New Mexico, San Juan Basin; "*Baena*" *escavada* (TL) (Hay 1908), *Neurankylus* sp. (Lucas 1982)

[28] Early Paleocene, Puercan NALMA, Danian; North Dakota, Williston Basin; *Boremys* sp. (Lyson et al. 2011)

[29] Early Paleocene, Torrejonian NALMA, Danian; Wyoming, Bighorn Basin; *Cedrobaena putorius* (Gaffney 1972; Lyson and Joyce 2009b), *Palatobaena bairdi* (Gaffney 1972)

[30] Late Paleocene, Tiffanian NALMA, Selandian/Thanetian; California; *Goleremys mckennai* (TL) (Hutchison 2004)

[31] Late Paleocene, Tiffanian NALMA, Selandian/Thanetian; Wyoming, Bighorn Basin; *Cedrobaena putorius* (TL) (Gaffney 1972; Lyson and Joyce 2009b), *Palatobaena bairdi* (TL) (Gaffney 1972)

[32] Late Paleocene, Tiffanian NALMA, Selandian/Thanetian; Wyoming, Wind River Basin; *Cedrobaena putorius* (Lyson and Joyce 2009b)

[33] Late Paleocene, Tiffanian NALMA, Selandian/Thanetian; Wyoming, Hanna Basin; *Cedrobaena brinkman* (Lyson and Joyce 2009b)

[34] Paleocene; Montana, Clark's Fork Basin; *Eubaeninae* indet. (= *Chisternon interpositum* of Hay 1909)

[35] Early Eocene, Wasatchian NALMA, Ypresian; Wyoming, Big Horn Basin; *Chisternon undatum*, *Palatobaena gaffneyi* (Holroyd et al. 2001), *Baenidae* indet. ("*Baena*" of Holroyd et al. 2001)

[36] Early Eocene, Wasatchian NALMA, Ypresian; Wyoming, Green River Basin; *Palatobaena gaffneyi* (TL) (Archibald and Hutchison 1979)

[37] Early Eocene, Wasatchian NALMA, Ypresian; New Mexico, San Juan Basin; *Baenidae* indet. (= *Baena arenosa* of Lichtig and Lucas 2015)

[38] Middle Eocene, Uintan NALMA, Lutetian; Colorado; *Baenidae* indet. (= *Baena arenosa* of Stucky et al. 1996)

[39] Middle Eocene, Uintan NALMA, Lutetian; Utah, Uinta Basin; *Baena arenosa* (= *Baena emiliae* of Hay 1908), *Chisternon undatum* (Gaffney 1972; = *Baena gigantea* of Gilmore 1916c), "*Baena*" *affinis* (= *Baena inflata* of Gilmore 1916c)

[40] Middle Eocene, Bridgerian NALMA, Ypresian/Lutetian; Wyoming, Green River Basin; *Baena arenosa* (TL) (Leidy 1870; Hay 1908; including type material of *Baena clara* and *Baena sima*), *Chisternon undatum* (TL) (Leidy 1871b; Cope 1872; Gaffney 1972; including type material of *Baena hebraica*), "*Baena*" *affinis* (TL) (Leidy 1871a; Hay 1908; including type material of *Baena riparia*)

Appendix 4
Hierarchical Taxonomy of *Baenidae*

- *Baenidae* Cope, 1873b
  - *Arundelemys dardeni* Lipka et al., 2006
  - *Hayemys latifrons* (Hay, 1908)
  - *Neurankylus* Lambe, 1902
    - *Neurankylus baueri* Gilmore, 1916b
    - *Neurankylus eximius* Lambe, 1902
    - *Neurankylus lithographicus* Larson et al., 2013
    - *Neurankylus torrejonensis* Lyson et al., in press
- *Trinitichelys hiatti* Gaffney, 1972
- *Protobaena wyomingensis* (Gilmore, 1920)
- *Baenodda* Brinkman, 2003a
  - *Scabremys ornata* (Gilmore, 1935)
  - *Thescelus* Hay, 1908
    - *Thescelus insiliens* Hay, 1908
    - *Thescelus rapiens* Hay, 1908
  - *Eubaeninae* Gaffney, 1972
    - *Baena arenosa* Leidy, 1870
    - "*Baena*" *affinis* Leidy, 1871a
    - "*Baena*" *escavada* Hay, 1908
    - "*Baena*" *hayi* (Gilmore, 1916a)
  - *Boremys* Lambe, 1906b
    - *Boremys grandis* Gilmore, 1935
    - *Boremys pulchra* (Lambe, 1906a)
  - *Chisternon undatum* (Leidy, 1871b)
  - *Denazinemys nodosa* (Gilmore, 1916b)
  - *Eubaena* Hay, 1908

Eubaena cephalica (Hay, 1904b)
Eubaena hatcheri (Hay, 1901)
Stygiochelys estesi Gaffney and Hiatt, 1971
Palatobaeninae Gaffney, 1972
Cedrobaena Lyson and Joyce, 2009b
Cedrobaena brinkman (Lyson and Joyce, 2009b)
Cedrobaena putorius (Gaffney, 1972)
Gamerabaena sonsalla Lyson and Joyce, 2010
Goleremys mckennai Hutchison, 2004
Palatobaena Gaffney, 1972
Palatobaena bairdi Gaffney, 1972
Palatobaena cohen Lyson and Joyce, 2009a
Palatobaena gaffneyi Archibald and Hutchison, 1979
Plesiobaena antiqua (Lambe, 1902)

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Editor's note: This article is intended to be included with others in a forthcoming book being coordinated by Walter G. Joyce to elucidate the fossil record of turtles. The individual articles that will form the components of this book are being published separately in the next several volumes of the *Bulletin of the Peabody Museum of Natural History*.