

A REVISION OF *PLESIOBAENA* (TESTUDINES: BAENIDAE) AND AN ASSESSMENT OF BAENID ECOLOGY ACROSS THE K/T BOUNDARY

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ABSTRACT—Over the course of the last two decades, the baenid taxon *Plesiobaena* has typically been thought to consist of two named species, *Plesiobaena antiqua* (Campanian) and *Plesiobaena putorius* (Paleocene), along with an unnamed species from the Maastrichtian, but the interrelationship of these three taxa was never explored in an explicit phylogenetic context. Herein we present or re-describe a number of relevant specimens and provide a cladistic analysis of Baenidae using species only as terminal taxa. The phylogenetic analysis clearly reveals that *Plesiobaena* in the traditional sense is a paraphyletic assemblage relative to the clade formed by *Gamerabaena sonsalla* and *Palatobaena* spp., thus demanding some nomenclatural adjustments. In particular, *Plesiobaena putorius* is moved to a new genus, *Cedrobaena*, and the unnamed taxon from the Maastrichtian is formally named *Peckemys brinkman*. Many of the new *Cedrobaena putorius* and *Peckemys brinkman* specimens described herein were found at the Turtle Graveyard locality in Slope County, North Dakota, along with four other turtle taxa, increasing the turtle diversity of this locality to at least six taxa. Although this indicates that Turtle Graveyard is the world's most diverse fossil turtle thanatocoenosis, a comparable diversity is found in modern river systems in the southeastern United States today. Our phylogenetic analysis indicates that seven out of nine latest Cretaceous baenid turtle lineages survived into the Paleocene, four of which are interpreted as being durophagous.

INTRODUCTION

BAENIDAE IS a clade of paracryptodiran turtles endemic to North America (Gaffney, 1972; Hutchison, 1984; Hutchison and Archibald, 1986; Holroyd and Hutchison, 2002; Hutchison and Holroyd, 2003; Joyce, 2007). These largely riverine, bottom-dwelling turtles have an excellent fossil record and thus have received considerable attention (Gaffney, 1972, 1982a, 1982b; Archibald and Hutchison, 1979; Hutchison and Archibald, 1986; Brinkman and Nicholls, 1991, 1993; Brinkman, 2003; Hutchison, 2006; Lyson and Joyce, 2009; Lyson and Joyce, in press). The group appears to be the most speciose Late Cretaceous (Campanian to Maastrichtian) North American clade of turtles where 14 to 17 baenid species are currently recognized (Lyson and Joyce, in press).

Gaffney (1972) provided the first thorough systematic analysis of Baenidae, including the description of several new species and genera. Among others, Gaffney (1972) erected the genus *Plesiobaena* and recognized two species, the type species *Plesiobaena antiqua* (Lambe, 1902) and *Plesiobaena putorius* Gaffney, 1972. The holotype of *Pl. antiqua* is a partial shell (NMC 1648) from the Oldman Formation (Campanian) of Alberta, while the holotype of *Pl. putorius* is a slightly crushed skull from the Fort Union Formation (Tiffanian) of Wyoming. Gaffney broadly referred a number of Cretaceous (Campanian and Maastrichtian) specimens to *Pl. antiqua* and attributed only Paleocene (Torrejonian and Tiffanian) material to *Pl. putorius*. Additional *Plesiobaena* material available to Archibald (1977) led him to speculate that the Campanian and Maastrichtian *Pl. antiqua* specimens represent two discrete species. Brinkman (2003) described several new skeletons from the Campanian and noted several systematic differences between Campanian and Maastrichtian material referred to *Plesiobaena antiqua* specimens, thus confirming Archibald's speculation that the Mesozoic material repre-

sents two distinct species. However, while Brinkman provided an excellent diagnosis and description for a restricted interpretation of *Pl. antiqua* to the Campanian, he did not formally name the Maastrichtian taxon.

Plesiobaena was regarded as the most basal representative of the subclade Baenodda in Gaffney's (1972) early cladistic analysis, and most analyses have confirmed this phylogenetic placement (Archibald, 1977; Gaffney and Meylan, 1988; Brinkman and Nicholls, 1991; Hutchison, 2005; Joyce, 2007). However, more recent analyses focused on baenid phylogeny indicate that Baenodda consists of two primary clades, with *Plesiobaena* as the most basal member of one of the groups (Lyson and Joyce, 2009; Lyson and Joyce, in press). However, given that all previous analyses assumed a monophyletic *Plesiobaena* and only scored the better known taxon *Pl. antiqua*, and given that the original diagnosis of Gaffney (1972) for *Plesiobaena* consists of characters that are now understood to be plesiomorphic for Baenodda (Lyson and Joyce, 2009), it is highly plausible that this taxon actually represents a basal Baenodda grade.

The purpose of this study is to analyze the three *Plesiobaena* taxa (two named, as well as the unnamed Maastrichtian taxon) in a parsimony cladistic framework. Given that we ultimately conclude that these three taxa form a paraphyletic grade, we herein assign *Pl. putorius* to *Cedrobaena* nov. gen. and formally name the unnamed taxon *Peckemys brinkman* gen. et sp. nov. We furthermore discuss the number of baenid turtle lineages that survived from the Cretaceous into the Paleocene and the dietary preference of those that crossed the boundary. The taxonomic nomenclature used herein follows that of Joyce et al. (2004) as applied to the phylogeny of Joyce (2007).

Institutional Abbreviations.—FMNH, Field Museum of Natural History, Chicago, Illinois; MRF, Marmarth Research Foundation, Marmarth, North Dakota; NMC, Canadian Museum of Nature, Ottawa, Ontario; UCMP, University of



FIGURE 1—*Cedrobaena putorius*, gen. nov., material from the Cedar Point Quarry, Early Tiffanian, Paleocene. A. Partially crushed holotype skull (YPM PU14984) in dorsal, ventral, and right lateral views (left to right). B. Referred *Cedrobaena putorius* skull (YPM PU 16837) from a juvenile individual in right lateral view. C. Referred *Cedrobaena putorius* skull (YPM PU 20600) in dorsal, ventral, and right lateral views (left to right). Arrows indicate autapomorphies for *Ce. putorius*: posterior extension of frontals ends within orbit; well developed parietal overhang overlying supraoccipital with parallel sides; and posteroventral closure of the incisura columellae.

California Museum of Paleontology, Berkeley, California; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; UW, University of Wyoming, Laramie; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Linnaeus, 1758
PARACRYPTODIRA Gaffney, 1975
BAENIDAE Cope, 1882
PLESIOBAENA Gaffney, 1972

Type species.—*Plesiobaena antiqua* (Lambe, 1902).

Included species.—*Plesiobaena antiqua*.

PLESIOBAENA ANTIQUA (Lambe, 1902)

Type specimen.—NMC 1648, the anterior lobe of the plastron and the anterior central portion of the carapace.

Type locality.—"...below the mouth of Berry Creek, Red Deer River..." (Lambe, 1902), Alberta, Canada.

Type horizon.—"Belly River series..." (Lambe, 1902), Dinosaur Park Formation, Campanian, Late Cretaceous (Brinkman, 2003).

Distribution.—Campanian of Alberta.

Referred material.—See hypodigm of Brinkman (2003).

CEDROBAENA gen. nov.
Figures 1–3

Synonymy.—*Plesiobaena putorius* Gaffney, 1972.

Etymology.—*Cedro*, Latin for cedar, in reference to Cedar Point Quarry where the type specimen was found. *Baena*, speculated to mean turtle in a native American language.

Type species.—*Cedrobaena putorius* nov. comb. (Gaffney, 1972).

Included species.—*Cedrobaena putorius* nov. comb.

Diagnosis.—Same as for the type species, *Cedrobaena putorius* nov. comb.

CEDROBAENA PUTORIUS nov. comb. (Gaffney, 1972)
Figures 1–3

Type specimen.—YPM PU 14984, an almost complete partially crushed skull (Fig. 1).

Type locality.—Cedar Point Quarry, Bighorn Basin, Wyoming.

Type horizon.—Fort Union Formation, Early Tiffanian, Paleocene.

Referred material based on autapomorphies.—YPM PU 16837, the right 1/3 of a skull, above Rock Bench level,

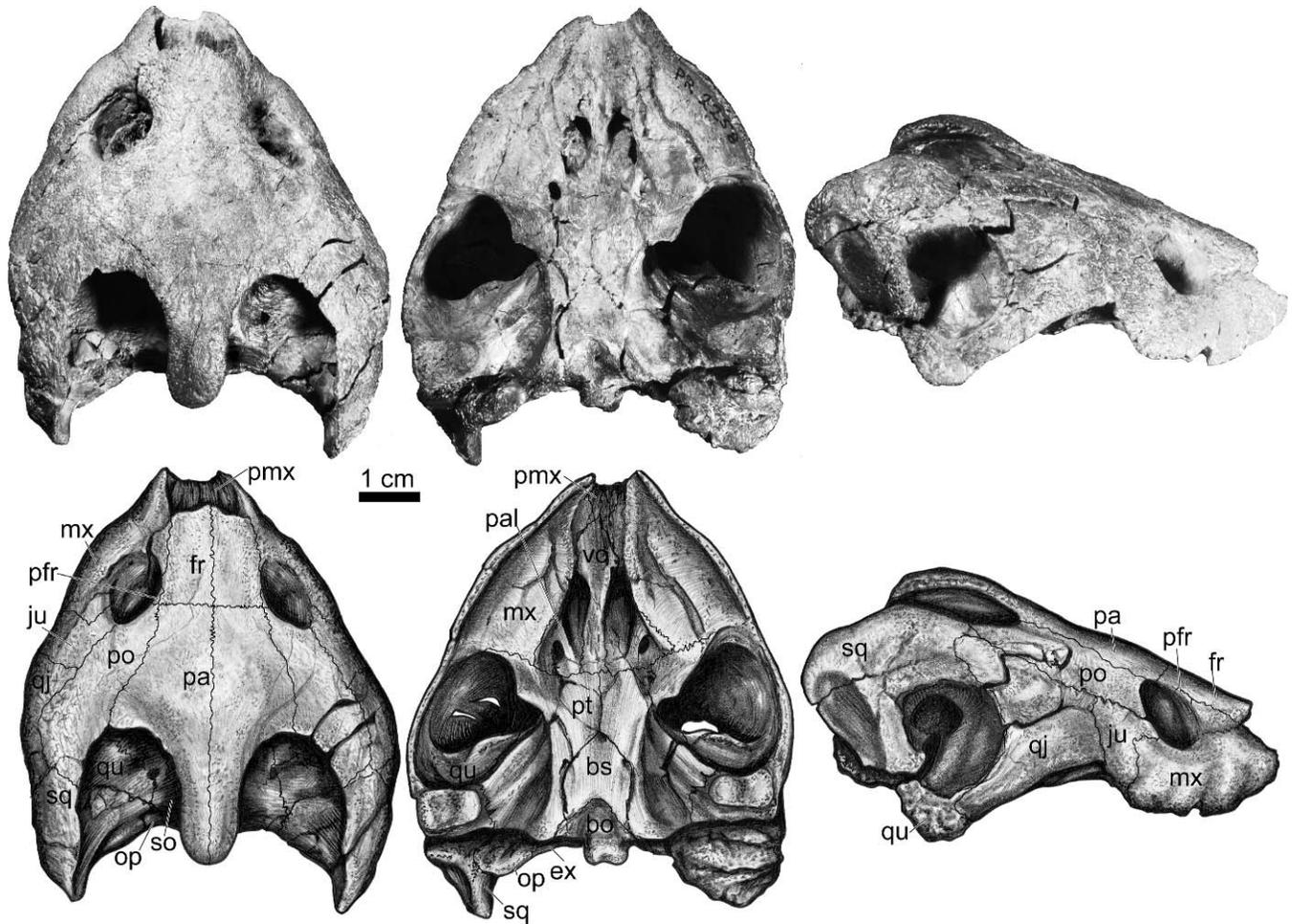


FIGURE 2—*Cedorbaena putorius* skull (FMNH PR 2258) from the Hell Creek Formation (latest Maastrichtian) of South Dakota. Illustrations (bottom) and photographs (top) in dorsal (left), ventral (middle), and right lateral (right) views. Abbreviations: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pfr, prefrontal; pmx, premaxilla; po, postorbital; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

probably Torrejonian, Wyoming (Fig. 1); YPM PU 18011, posterior portion of parietals, Rock Bench Quarry beds, Torrejonian; YPM PU 14986, posterior portion of parietals, Cedar Point Quarry, Tiffanian, Wyoming; YPM PU 20600, a mostly complete, uncrushed skull, Cedar Point Quarry, Tiffanian, Wyoming (Fig. 1); FMNH PR 2258, a complete skull, Hell Creek Formation, South Dakota (Fig. 2); MRF 239, a complete skull, Hell Creek Formation, North Dakota (Fig. 3); UW 3348, skull, lower jaws, and partial shell, Fort Union Formation, Tiffanian, Wyoming.

Distribution.—Hell Creek Formation (latest Maastrichtian) of South Dakota and North Dakota and Fort Union Formation (Torrejonian and Tiffanian) of Wyoming.

Diagnosis.—Diagnosed as being within Baenidae by location of the foramen posterius canalis carotici interni between the pterygoid and halfway along the basisphenoid; triturating surface posteriorly expanded with lingual ridge reduced posteriorly; and well-developed pterygoid and basioccipital contact. Part of the *Plesiobaena*/*Palatobaena* clade based on greater development of parietal overlying crista supraoccipitalis compared to *Eubaena cephalica* (Gaffney, 1972), *Stygiochelys estesi* Gaffney and Hiatt, 1971, and *Palatobaena cohen* Lyson and Joyce, 2009; deep temporal emargination; no incipient secondary palate; short preorbital skull length compared to *Boremys* spp. and *E. cephalica*; jugal exposed in orbital margin.

Autapomorphies include: parallel sided parietal overhang overlying supraoccipital; incisura columellae auris loosely enclosed posteroventrally by a dorsal process of the quadrate that contacts the squamosal; frontal and parietal suture located at middle of orbit; relatively thick stapes with the diameter more than double that of other baenids from which a stapes is known; lingual ridge curves laterally.

Similarities with *Pl. antiqua* include: cheek emargination shallow, reaching only to ventral border of orbit.

Similarities with *Pe. brinkman* include: nasals either lost or fuse early with frontals; jugal enters orbital margin; broad medial contact between pterygoids.

Differences compared to *Pl. antiqua* and *Pe. brinkman*: sulci for scales on dorsal skull roof present; supraoccipital not exposed on dorsal skull roof; dorsally oriented orbits; orbits inset into maxilla.

Similarities with *Palatobaena* spp.: large mandibular condyles; posterior portion of triturating surface greatly expanded; poorly developed pterygoideus externus; dorsally oriented orbits; orbits inset in maxilla.

Comments regarding postcranial material.—Baenid taxa known from the Campanian are easily diagnosed by their shells, but this does not hold true for taxa from the Maastrichtian and Paleocene. Three baenid shell morphs are currently known to occur in the Maastrichtian and Paleocene

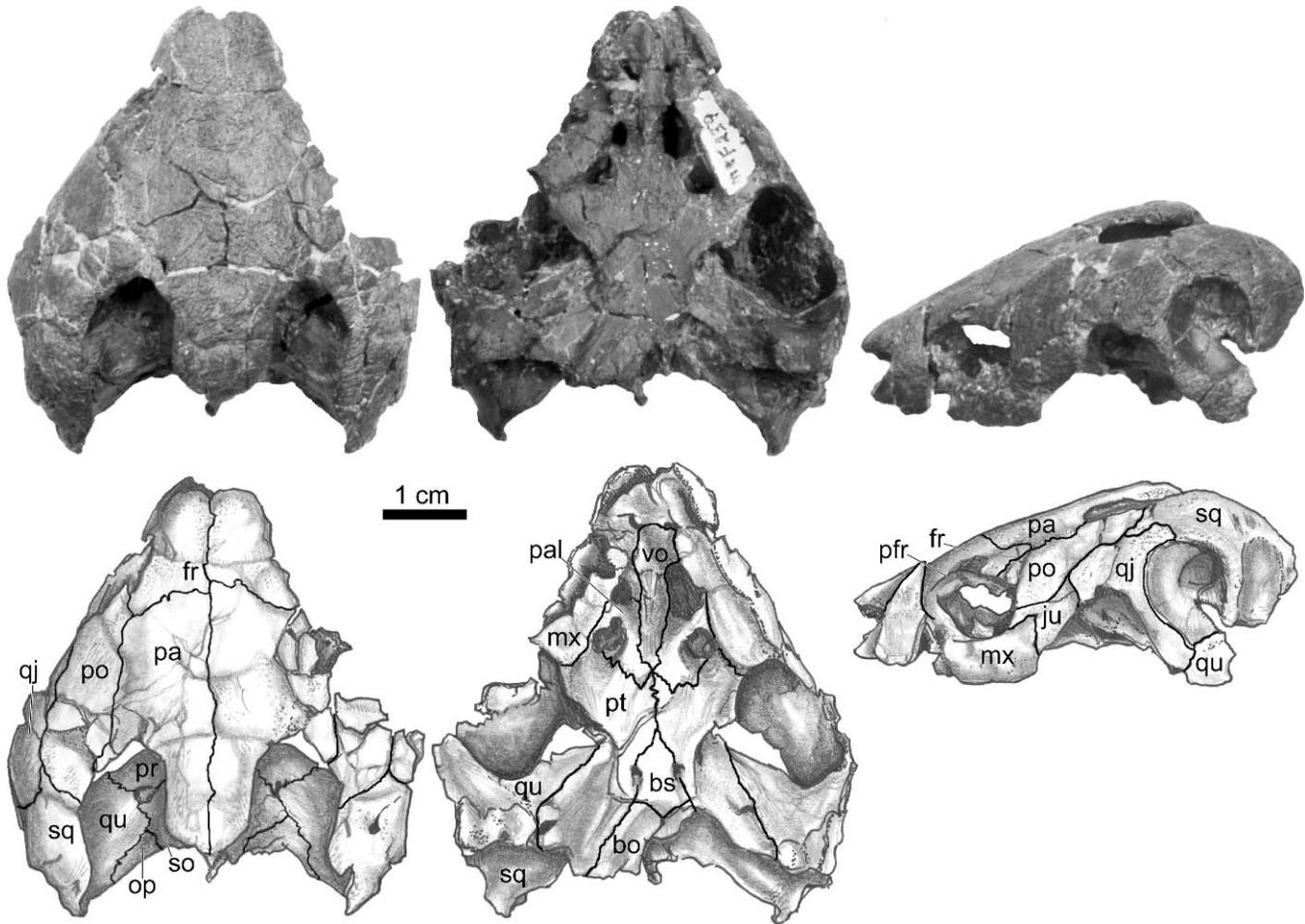


FIGURE 3—*Cedorbaena putorius* skull (MRF 239) from Turtle Graveyard locality in the Hell Creek Formation (latest Maastrichtian) of southwestern North Dakota. Illustrations (bottom) and photographs (top) in dorsal (left), ventral (middle), and left lateral (right) views. Abbreviations: bo, basioccipital; bs, basisphenoid; fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pfr, prefrontal; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

that reflect the three primary evolutionary lineages present at that time: the *Neurankylus* lineage, the *Plesiobaena*+*Palatobaena* lineage, and the *Eubaena*+*Stygiochelys* lineage. Shells of the *Neurankylus* lineage are large, have a finely crinkled sculpture pattern, and a complete ring of marginals, the basal condition for crown Testudines (Joyce, 2007). All known shells of the *Plesiobaena*+*Palatobaena* lineage (i.e., *Pl. antiqua*, *Pe. brinkman*, and *Pa. cohen*) share the following characters: lack of supramarginal scutes, lack of a nuchal scute (scute located between the cervical scute and first vertebral scute), weak scalloping, anal scute located entirely on the xiphiplastron (only sometimes the case in *Pl. antiqua*, Brinkman, 2003), and reduced or absent gular scutes. Finally, known shells of the *Eubaena*+*Stygiochelys* lineage (i.e., *E. cephalica*, *S. estesi*) all share the following characters: anterior supramarginal scales present, broken cervical scute, nuchal scute present, strongly scalloped posterior edge of shell, anal scute laps onto the hypoplastron, and well developed gular scutes. Although representatives of these three lineages can be readily distinguished from one another, identifying taxa within a particular lineage is more challenging.

Of the six hypothesized Maastrichtian and Paleocene representatives of the *Plesiobaena*+*Palatobaena* lineage, only *Pe. brinkman* gen. et. sp. nov. and *Pa. cohen* are known from shells. The shells of these two taxa are nearly identical except

for the strong nuchal projection present in *Pa. cohen*. As a consequence, until additional material is found, the remaining four taxa must be hypothesized to have similar shells as well, and the identification of solitary shells beyond the lineage level is problematic and should generally be avoided.

PECKEMYS gen. nov.

Figures 4–11

Etymology.—*Peck*, in reference to Fort Peck, Montana where the type specimen was found. *Emys*, Greek for turtle.

Type species.—*Peckemys brinkman* gen. et sp. nov.

Included species.—*Peckemys brinkman* gen. et sp. nov.

Diagnosis.—Same as for the type species, *Peckemys brinkman* gen. et sp. nov.

PECKEMYS BRINKMAN sp. nov.

Figures 4–11

Etymology.—*Brinkman*, in honor of Dr. Donald Brinkman, who has written numerous papers on baenid morphology and systematics and who recognized that Maastrichtian representatives of *Plesiobaena* belong to a species distinct from *Plesiobaena antiqua*. The species epithet is here formed and used explicitly as a noun in apposition, as is permitted by Article 31.1 of the ICZN.

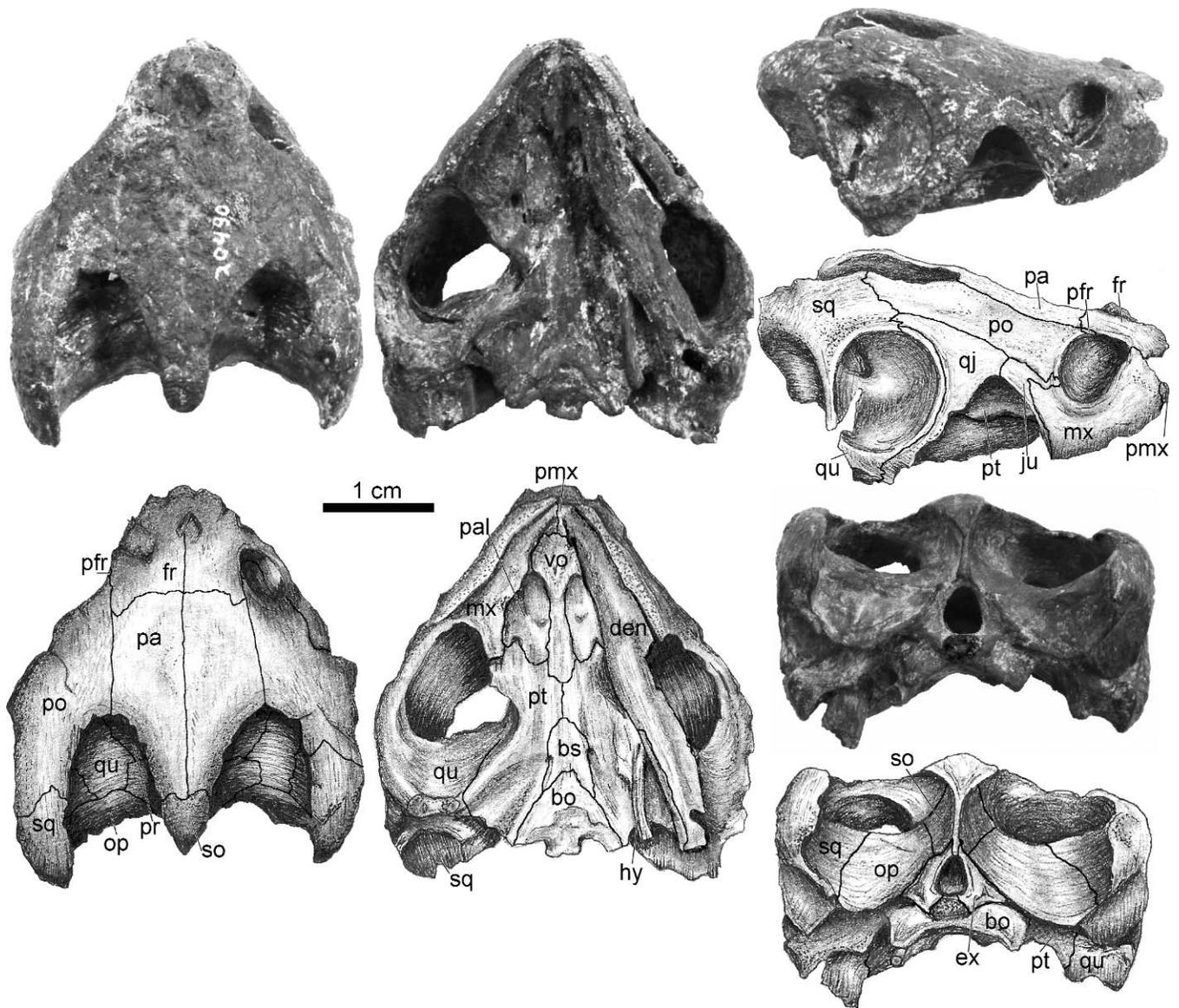


FIGURE 4—*Peckemys brinkman* (gen. et sp. nov.) skull (UMMP 20490, holotype) from the Hell Creek Formation of northeastern Montana, near Fort Peck. Photograph (top) and illustration (bottom) in dorsal (left), ventral (middle), right lateral (top right), and posterior (bottom right) views. Abbreviations: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pfr, prefrontal; pmx, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

Type specimen.—UMMP 20490 (Case, 1939, pp. 1–19, figs. 1–18), an almost complete skeleton (Figs. 4, 6–11).

Type locality and horizon.—“...near Fort Peck, Montana...” (Case, 1939); “...Lance Beds...” (Case, 1939); Hell Creek Formation (latest Maastrichtian).

Referred specimens based on autapomorphies.—MRF 231, a complete uncrushed skull, Turtle Graveyard Locality, Hell Creek Formation, North Dakota (Fig. 5); UCMP 49795, a complete uncrushed skull with lower jaws, Locality: UCMP V-5620, Lull 2 quarry, Lance Formation (Maastrichtian), Wyoming (figs. 8 and 9 in Gaffney (1972); UCMP 113318, a skull with lower jaws and fragmentary shell, Baenid Badlands, Hell Creek Formation, Montana; UCM 49318, a fused posterior part of skull, UCM locality: 78193, Laramie Formation (Maastrichtian), Colorado; UW 28085, a complete, partially crushed skull, Locality V90069, Hannah Formation, Tiffanian, Wyoming. Additional shell material may be present but cannot be referred with any confidence (see comments under *Ce. putorius* above).

Distribution.—Hell Creek Formation (latest Maastrichtian) of North Dakota and Montana, Lance Formation (latest Maastrichtian) of Wyoming, Hannah Formation (Tiffanian) of Wyoming, and Laramie Formation (latest Maastrichtian) of Colorado.

Diagnosis.—Diagnosed as being part of Baenidae by the location of the foramen posterius canalis carotici interni between the pterygoid and halfway along basisphenoid; triturating surface moderately expanded with lingual ridge reduced posteriorly; and well developed pterygoid and basioccipital contact. Member of *Plesiobaena/Palatobaena* grade based on greater development of parietal overlying crista supraoccipitalis compared to *E. cephalica*, *S. estesi*, and *Pa. cohen*; deep temporal emargination; no incipient secondary palate; short preorbital skull length compared to *Boremys* spp. and *E. cephalica*; jugal exposed in orbital margin.

Autapomorphies include: bar between orbit and cheek emargination less than half the diameter of the orbit; small squamosal and quadratojugal contact.

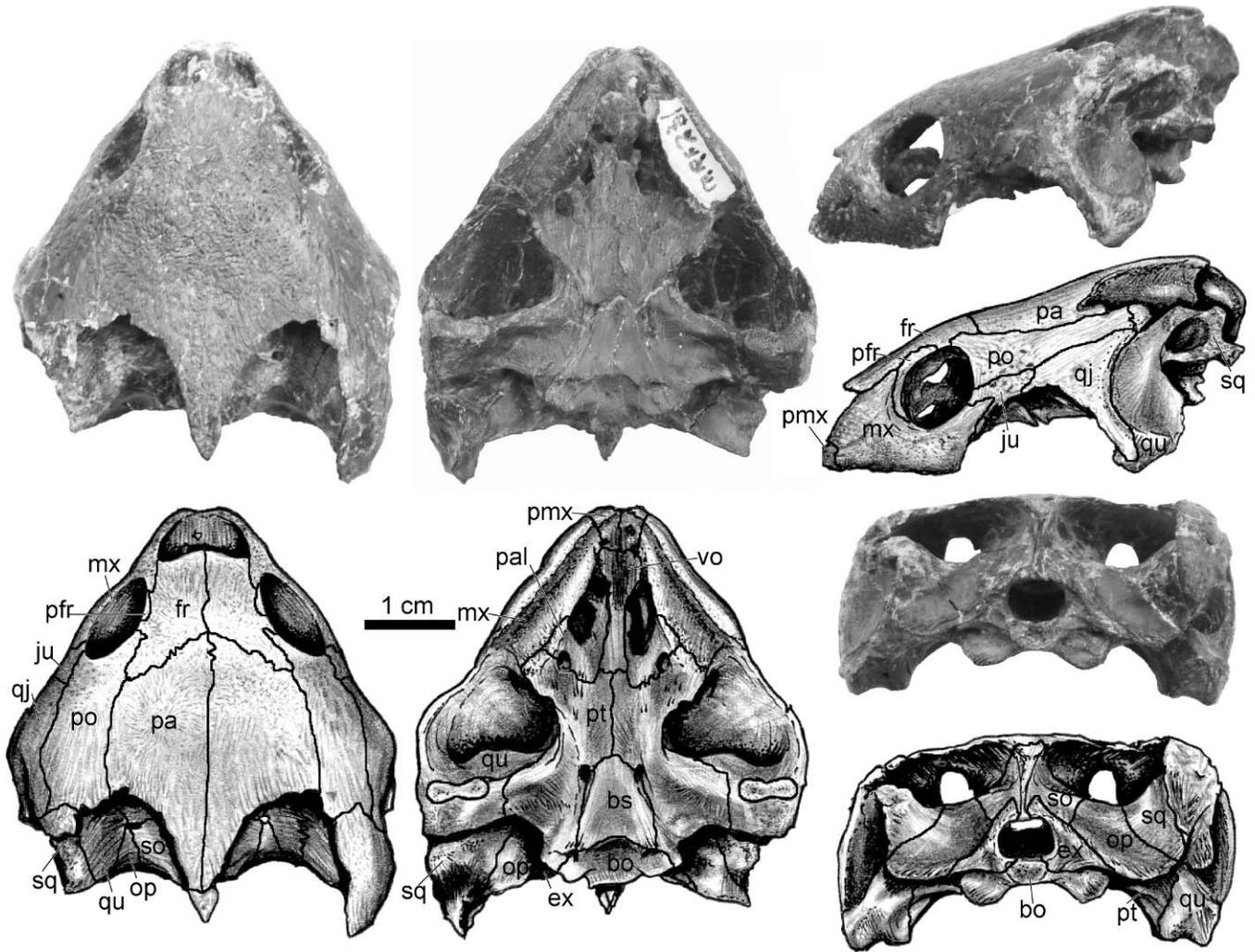


FIGURE 5—*Peckemys brinkman* skull (MRF 231) from Turtle Graveyard locality in the Hell Creek Formation (latest Maastrichtian) of southwestern North Dakota. Photograph (top) and illustration (bottom) in dorsal (left), ventral (middle), left lateral (top right), and posterior (bottom right) views. Abbreviations: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pfr, prefrontal; pmx, premaxilla; po, postorbital; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

Similarities with *Pl. antiqua* include: small mandibular condyles; vertically oriented orbits; orbit not inset into maxilla; posterior triturating surface only weakly expanded; frontals extend posteriorly to posterior margin of orbit; cheek emargination deep, extends dorsally to level midline with orbital margin; dorsal prefrontal exposure on skull roof; lacks process on quadrate which superficially closes lateral portion of Eustachian tube; four pleural scutes; vertebral scutes wider than long; first vertebral wide anteriorly, narrows posteriorly; anal/hypoplastron sulcus entirely on xiphiplastron; reduced/absent gulars.

Similarities with *Ce. putorius* include: well developed medial contact between pterygoids; well developed parietal overhang overlying supraoccipital; small portion of jugal enters orbital margin; temporal emargination does not extend anteriorly to anterior portion of prootic.

DESCRIPTION OF *CEDROBAENA PUTORIUS*

Skull.—Overall, the skull of *Ce. putorius* is large, much larger than either *Pl. antiqua* or *Pe. brinkman*. The skull is as large as that of various *Palatobaena* spp., *Chisternon undatum* (Leidy, 1871), and *S. estesi*. The skull is wedge shaped. As in *Pl. antiqua* and *Pe. brinkman*, the skull length (occipital

condyle to premaxillae) is approximately equal to the maximum skull width at the quadrates. The upper temporal emargination is deep as in *Pl. antiqua* and *Pe. brinkman* and reaches to the anterior portion of the prootic. The cheek emargination is relatively shallow, only reaching to the ventral portion of the orbital margin. The distance between the orbits is wide. The orbit is large, larger than the depth of the underlying maxilla, but not as large as the cavum tympani. The orbits are inset into the maxilla and are oriented dorsally as in *Gamerabaena sonsalla* Lyson and Joyce, in press and *Palatobaena* spp. The triturating surface is greatly expanded posteriorly, as great as that found in *S. estesi*, but not as broad as the triturating surface of *Palatobaena* spp. (Figs. 1–3).

Nasals.—The presence of nasals cannot be determined in any of the specimens examined despite the fact that two of the specimens (FMNH PR2258 and MRF 239) have open sutures (Figs. 2 and 3). Whether the nasals fused with the frontals early in development or are lost cannot be determined at the moment.

Prefrontals.—The dorsal plate of the prefrontal is visible in the Maastrichtian specimens but cannot be determined in the Paleocene specimens. In those specimens where it is visible, the dorsal plate of the prefrontal is greatly reduced, as in most

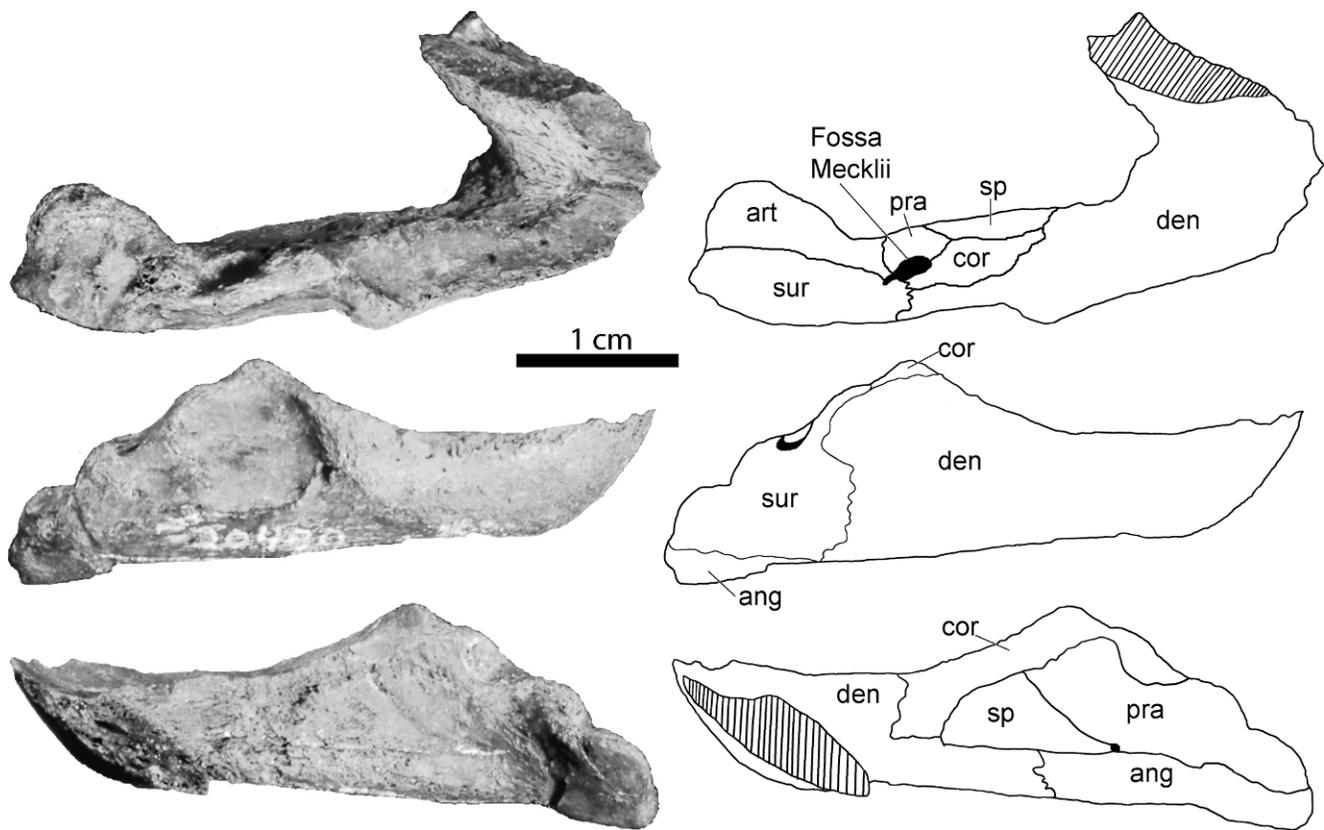


FIGURE 6—*Peckemys brinkman* lower jaw (UMMP 20490, holotype) photographs (left) and line drawings (right) in dorsal (top), right lateral (middle), and medial (bottom) views. Abbreviations: ang, angular; art, articular; cor, coronoid; den, dentary; pra, prearticular; sp, splenial; sur, surangular.

other derived baenids. The amount of exposure is similar to that seen in *Palatobaena* spp., *E. cephalica*, *Pl. antiqua*, and *Pe. brinkman*. The prefrontal forms the anterior portion of the orbit margin, which prevents the frontal from widely entering the orbital margin. The descending process of the prefrontal extends anterolaterally and forms the posterolateral wall of the fossa nasalis and the anterior wall of the fossa orbitalis. The descending process contacts the maxilla laterally, the vomer ventromedially, and the palatine ventrolaterally.

Frontals.—The frontals are small rectangular elements that are slightly longer than their maximum combined width. The frontals are posteriorly truncated, extending only to the middle of the orbit, whereas the frontals extend even with or beyond the posterior portion of the orbital margin in *Pe. brinkman* and *Pl. antiqua*. This appears to be an autapomorphy for *Ce. putorius*. As in *Pe. brinkman* and *Pl. antiqua*, a small portion of the frontal enters the orbital margin in lateral view. The contribution of the frontal to the orbital margin is constricted anteriorly by the prefrontal and posteriorly by an anterior projection of the postorbital. The frontal contacts the maxilla anterolaterally as in most other baenids. Since the presence of nasals cannot be determined, it is unknown whether the frontals enter the apertura narium externa. The frontals form a straight contact with the parietals.

Parietals.—As is generally the case in baenids, with the exception of *Hayemys latifrons* Gaffney, 1972, *Baena arenosa* Leidy, 1870, and *Ch. undatum*, the parietals are longer than their maximum combined width. The parietal overhang that roofs a portion of the upper temporal fossa is well developed. Unlike other taxa with a well-developed parietal overhang, the sides of the overhang are parallel in *Ce. putorius*. There is no squamosal and parietal contact as the upper temporal

emargination is deep. Sulci for scales are visible on the skull roof on every specimen except FMNH PR 2258. Unlike other baenids except *B. arenosa* and *Ch. undatum*, the parietals do not thin out posteriorly but are rather thick until the very end.

Jugal.—The jugal forms a large portion of the cheek region. It contacts the maxilla anteriorly, the postorbital dorsally, and the quadratojugal posteriorly. As in *Pe. brinkman*, but unlike *Pl. antiqua*, the jugal enters the orbital margin and its contribution to the orbital margin is greater than that found in *Pe. brinkman*. As in *Pe. brinkman*, its contribution to the orbital margin is constricted by a posterodorsal projection of the maxilla. Unlike either *Pe. brinkman* or *Pl. antiqua*, the ventral process of the jugal does not extend ventrally to contribute to the labial ridge. As in all baenids except *Palatobaena* spp., the jugal is slender in ventral view and lacks any significant muscle scars within the temporal cavity.

Quadratojugal.—The quadratojugal is a large, C-shaped bone with the dorsal extension reaching over the top of the cavum tympani to a level equal with the ventral extension of the quadratojugal. It forms the majority of the cheek emargination. As in *Pl. antiqua*, the cheek emargination is relatively shallow, reaching dorsally to the ventral margin of the orbit.

Squamosal.—The squamosal is a cone-shaped bone that sits posterodorsally to the quadrate at the very posterolateral portion of the skull. The squamosal forms the posterolateral rim of the upper temporal emargination. As in all baenids except *Pe. brinkman*, the squamosal has a broad contact with the quadratojugal anteriorly.

Postorbital.—The postorbital is a broad bar on the dorsolateral portion of the skull extending from the orbital margin to the temporal emargination. A process of the

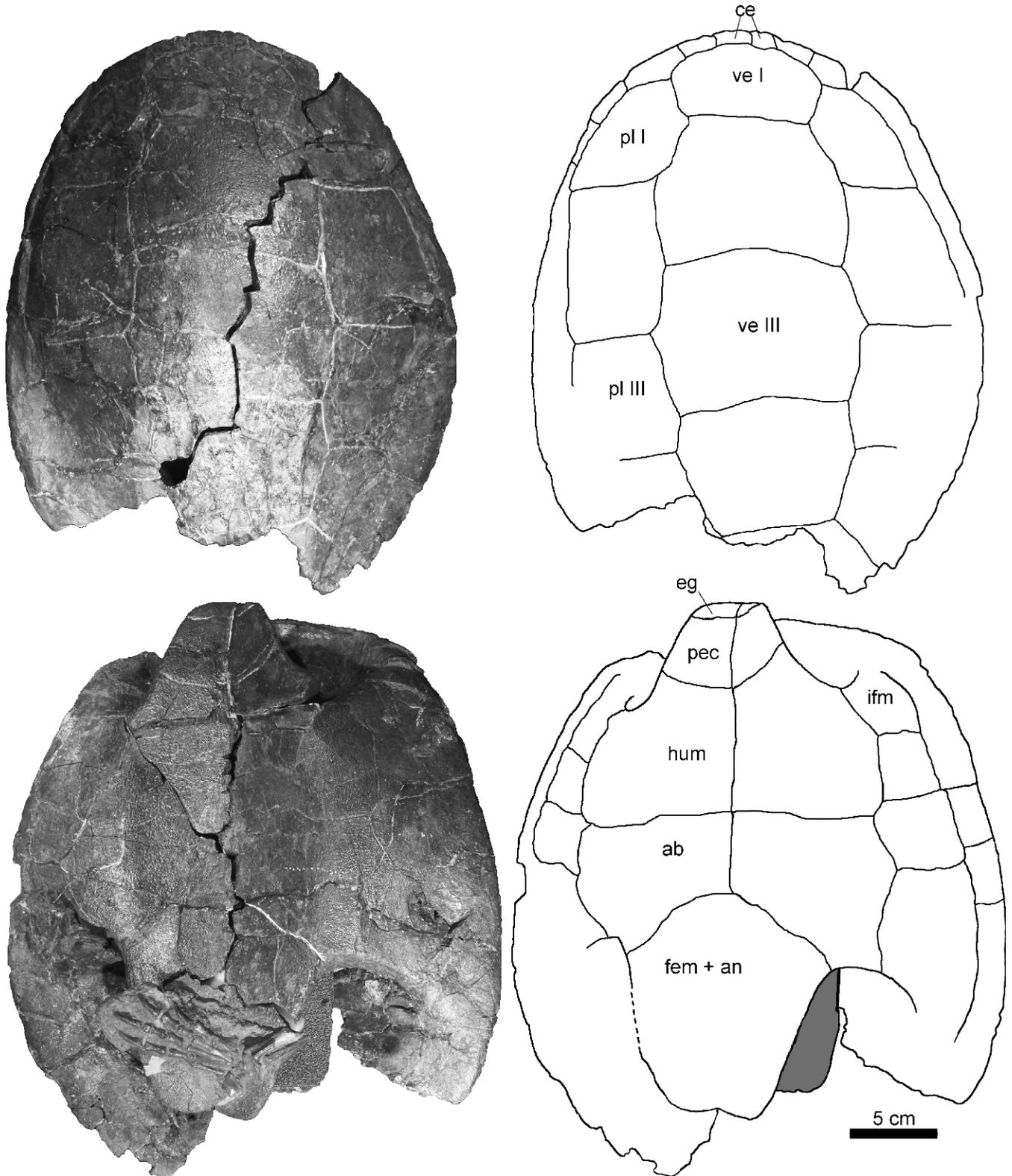


FIGURE 7—*Peckemys brinkman* shell (UMMP 20490, holotype) photographs (left) and line drawing (right) in dorsal (top) and ventral (bottom) views showing the scute morphology. Abbreviations: ab, abdominal; an, anal; ce, cervical; eg, extragular; fem, femoral; hum, humeral; ifm, inframarginal; pec, pectoral; pl, pleural; ve, vertebral. Shaded area in line drawing represents foam padding.

postorbital extends over the top of the orbit, further restricting the frontals' contribution to the orbital margin. Similar to *Pe. brinkman*, the postorbital does not contact the maxilla. The postorbital contacts the prefrontal anteriorly, the jugal

anteroventrally, the quadratojugal posteroventrally, the squamosal posteriorly, and the parietal medially.

Premaxilla.—The premaxilla is roughly triangular in ventral view and forms the ventral portion of the apertura narium

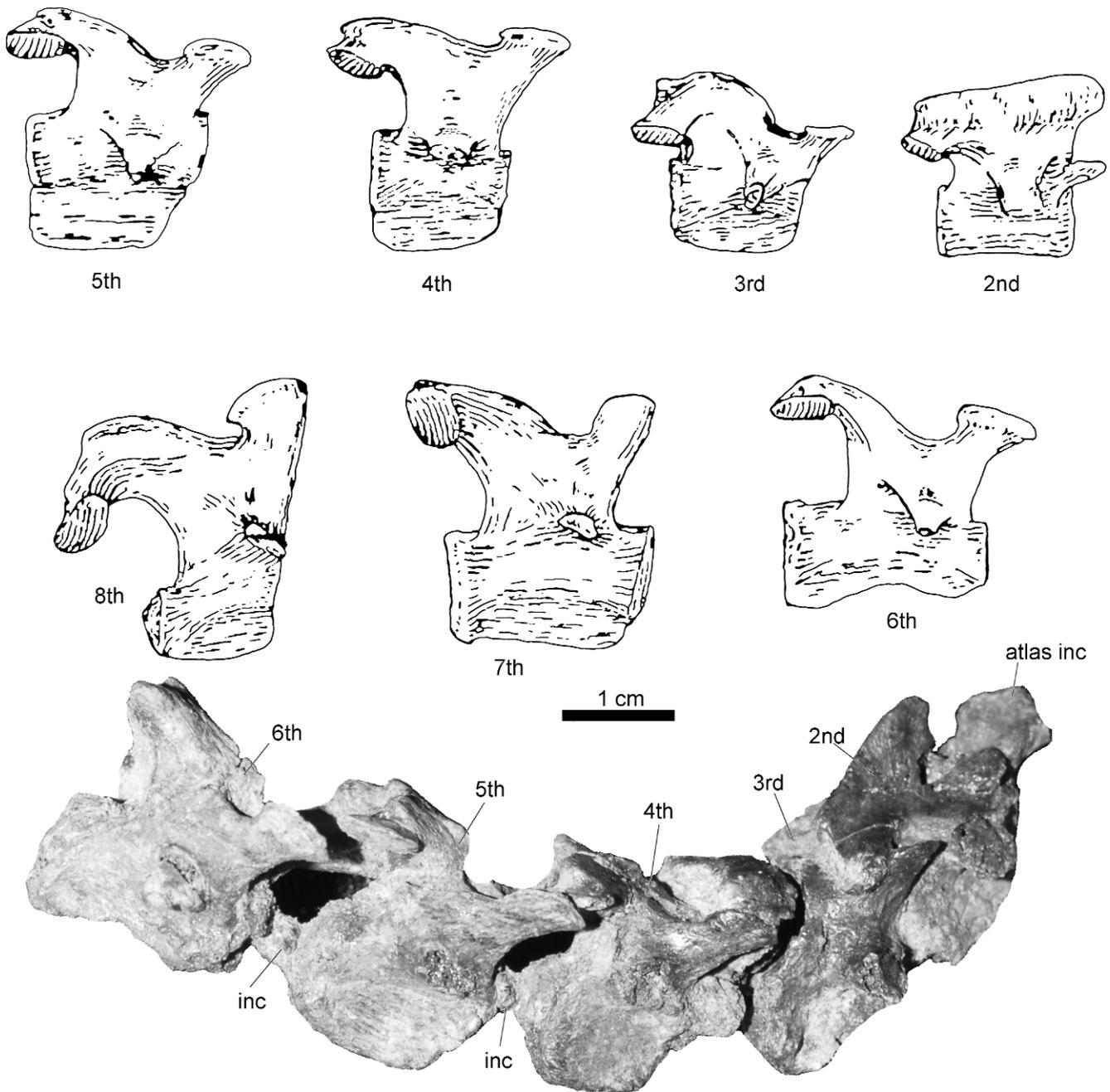


FIGURE 8—*Peckemys brinkman* cervical vertebrae (UMMP 20490, holotype) line drawing of the 2nd–8th cervical vertebrae (top) in right lateral view modified from Case (1939) and photograph of 2nd–6th cervical vertebrae (bottom) in right lateral view.

externa. The premaxilla contacts the other premaxilla medially, the maxilla posterolaterally, and the vomer posteriorly. As in *Pl. antiqua* and *Pe. brinkman*, the foramen praepalatinum is located between the premaxillae, maxilla, and vomer contact. Similar to *Pl. antiqua*, but unlike *Pe. brinkman*, the premaxillae protrude well beyond the anterior portion of the skull roof creating a nasal opening that is oriented dorsally.

Maxilla.—The maxilla forms a broad bar underneath the orbit. The anterodorsal process of the maxilla forms the lateral portion of the apertura narium externa and extends dorsally to contact the frontal. As in *Ga. sonsalla* and *Palatobaena* spp., the orbit is inset into the maxilla and is oriented dorsally. Ventrally, the maxilla forms most of the triturating surface. As in *S. estesi*, *B. arenosa*, *Ch. undatum*, *Ga. sonsalla*, and

Palatobaena spp., the labial ridge is swollen posteriorly and is thickened. As in most other baenids, a lingual ridge is present, and it is restricted to the anterior portion of the triturating surface. Unlike other baenid taxa, the anterior portion of the lingual ridge curves laterally as you move anteriorly, constricting the anterior portion of the triturating surface. The anterior constriction results in a more pronounced posterior expansion of the triturating surface. The posterior expansion of the triturating surface is wide, as wide as *S. estesi* and *Ga. sonsalla*, but not quite as wide as *Palatobaena* spp. The laterally directed lingual ridges also result in a wide tongue groove. The maxilla contacts the vomer and premaxilla anteromedially, the palatine medially, the pterygoid posteromedially, and the jugal posteriorly.

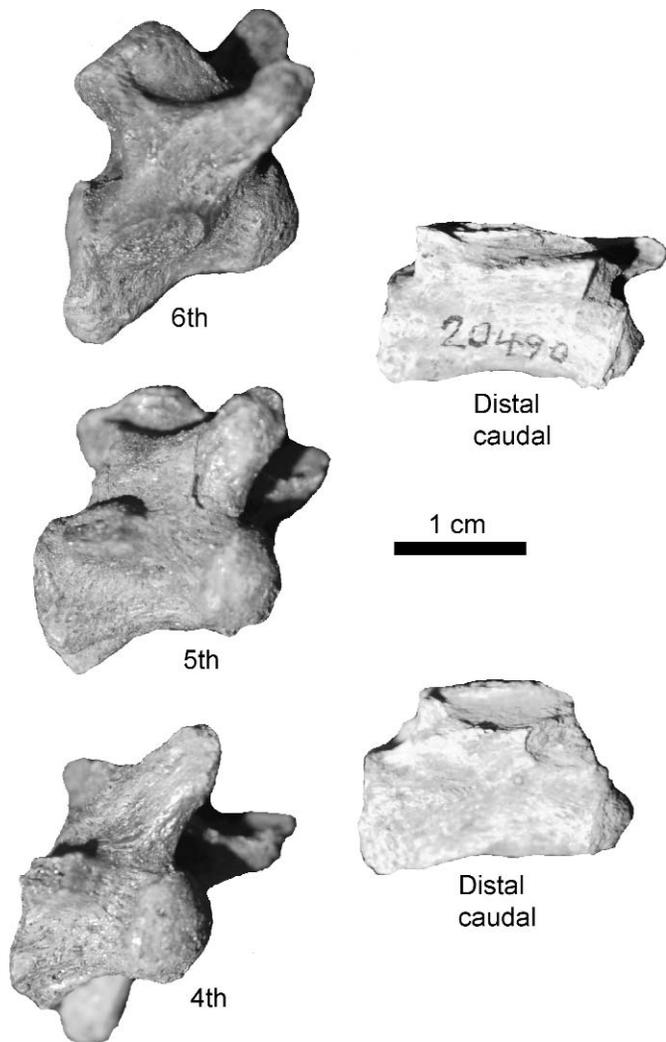


FIGURE 9—*Peckemys brinkman* caudal vertebrae (UMMP 20490, holotype) photograph in right lateral view.

Vomer.—As in all crown group turtles, the vomer is a single element. The vomer has an anterior expansion that contacts the premaxillae and maxillae. The posterior contact with the pterygoids is straight. The vomer contacts the palatine laterally and the descending process of the prefrontal anterodorsally.

Palatine.—The palatine is subrectangular in shape and roofs the internal choanae. All of the specimens except FMNH PR 2258 have the foramen palatinum posterius located between the palatine and pterygoid suture. In FMNH PR 2258, the foramen palatinum posterius is located entirely within the palatine, as in *S. estesi* and *Ch. undatum* (Fig. 2). The foramen palatinum posterius in MRF 239 is very large, larger than in any other baenid (Fig. 3). Similar to *Palatobaena* spp., *Pl. antiqua*, and *Pe. brinkman*, a small lateral process of the palatine forms a small portion of the lingual ridge of the triturating surface.

Quadrate.—The quadrate is a stout bone that forms the posterolateral portion of the skull. Anterolaterally the quadrate contacts the prootic and forms with it the processus trochlearis oticum. The quadrate forms the roughly circular cavum tympani. The cavum tympani opens laterally and is larger than the orbit. Similar to other baenids and pleurodires, the incisura columellae auris is elongate, enclosing the stapes

and, presumably, the Eustachian tube. The incisura columellae auris is a relatively narrow slit. A partial stapes is preserved in the holotype (YPM PU 14934) and it is a relatively robust structure; its diameter is more than double the diameter of the stapes found in *Eubaena* sp., *Pe. brinkman*, and *Palatobaena cohen*. In lateral view, a posterodorsal process extends dorsally from below the cavum tympani and contacts the squamosal, broadly enclosing the incisura columellae auris and presumably the Eustachian tube as well. A similar condition is found in *Compsemys victa* Leidy, 1856 (Hutchison and Holroyd, 2003), *Meiolania platyceps*, and various pleurodires (Gaffney, 1982; Joyce, 2007). Above the incisura, the antrum postoticum extends posterodorsally into the squamosal. Similar to *Palatobaena* spp., the condylus mandibularis is large. As in cryptodires, the quadrate has a broad sutural contact with the posterior portion of the pterygoid.

Pterygoid.—As in cryptodires, the pterygoids are widely exposed on the posterior margin of the skull. The pterygoids form a broad contact with one another as in *Pe. brinkman*, but unlike *Pl. antiqua*. The pterygoids contact the palatines and vomer anteriorly, the basisphenoid and basioccipital ventromedially, the quadrate ventrolaterally, and the prootic and parietal dorsally. There is no sign of an epipterygoid ossification in any of the four specimens examined. However, given the size of the specimens examined, the epipterygoid most likely had already fused with the parietal, as has been shown to be the case for larger individuals of *Pl. antiqua* (Brinkman, 2003).

Supraoccipital.—Unlike either *Pl. antiqua* or *Pe. brinkman*, the supraoccipital is not exposed on the skull roof. Instead the parietals completely cover the supraoccipital. The supraoccipital contacts the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteriorly. As in other paracryptodires, the supraoccipital forms the dorsal portion of the foramen magnum.

Exoccipital.—The exoccipitals form the lateral walls of the foramen magnum. They form the dorsolateral portion of the condylus occipitalis and are prevented from contacting one another by the basioccipital ventrally and the supraoccipital dorsally. They contact the opisthotic dorsolaterally, the supraoccipital dorsally, and the basioccipital ventrally. The exoccipitals form a small portion of the tuberculum basioccipitale.

Basioccipital.—The basioccipital is triangular to subrectangular in shape and is situated posterior to the basisphenoid. The basioccipital forms the majority of the condylus occipitalis. Wing-like processes extend posteroventrally from the basioccipital and contact the exoccipitals dorsally. These processes, along with the pterygoids, form the tuberculum basioccipitale. As in all baenids except *Pa. cohen* and *Pe. brinkman*, the tubercula basioccipitale are blocky elements that do not have significant posteriorly projecting processes.

Prootic.—The prootic forms the anterior portion of the bony inner ear. It contacts the parietal anterodorsally, the supraoccipital posterodorsally, the quadrate laterally, the pterygoid ventrally, and the basisphenoid medially.

Opisthotic.—The opisthotic forms the posterior portion of the bony inner ear. As in all baenids except *Ch. undatum* and *S. estesi*, the opisthotic does not enter the foramen stapediotemporale.

Basisphenoid.—As in other derived baenids, the basisphenoid is a large pentagonal-shaped element. As in baenids and pleurosternids, the foramen posterior canalis carotici interni are located midway along the length of the basisphenoid and pterygoid suture. Posteriorly, the basisphenoid contacts the

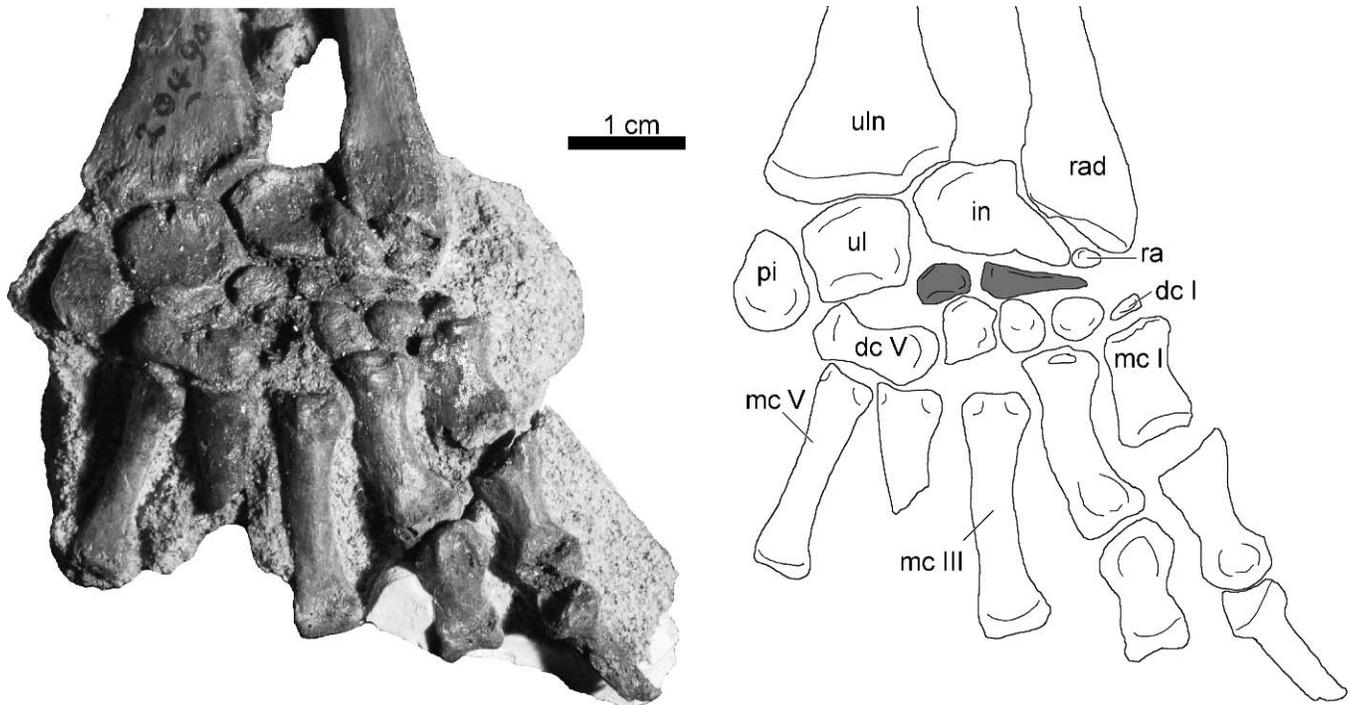


FIGURE 10—*Peckemys brinkman* left manus (UMMP 20490, holotype) photograph (left) and line drawing (right) in ventral view. Abbreviations: dc I, distal carpal I; ca V, distal carpal V; in, intermedium; mc I, metacarpal I; mc III, metacarpal III; mc V, metacarpal V; pi, pisiform; ra, radiale; rad, radius; ul, ulnare; uln, ulna. Lateral centrale (left) and medial centrale (right) are shaded gray.

basioccipital and the contact between these two bones is anteriorly convex.

Mandible.—A single specimen (UW 3348) has a skull and lower jaw association. Gaffney (1982) examined this specimen and wrote that it is virtually indistinguishable from the lower jaw of *Pl. antiqua* except for a medial expansion of the triturating surface found in *Ce. putorius*. He further indicated that it has a narrow triturating surface, large splenial, and a low coronoid process, as in *Pl. antiqua* and *Pe. brinkman*.

DESCRIPTION OF *PECKEMYS BRINKMAN*

Skull.—Overall, the skulls examined are relatively small. In the holotype (UMMP 20490, Fig. 4) and UCMP 49759 specimens, many of the sutures are fused and these specimens are presumably from adult individuals. MRF 231 is smaller than these two specimens and has open sutures and thus likely represents a juvenile individual (Fig. 5). The skull is triangular in shape. The holotype is 48.8 mm wide (quadrate to quadrate) and 50.6 mm long (premaxillae to occipital condyle). Only *Goleremys mckennai* Hutchison, 2005 and *Pl. antiqua* are of similarly small size. The upper temporal emargination is deep, reaching to the anterior part of the prootic. The cheek emargination is also deep, extending dorsally to the middle of the orbit. The distance between the orbits is wide as in *Palatobaena* spp., *Ga. sonsalla*, *Pl. antiqua*, and *Ce. putorius*. The orbit is large, larger than the depth of the underlying maxilla, but not as large as the cavum tympanum. As in *Pl. antiqua*, but unlike *Ce. putorius*, the orbits are situated vertically. Unlike most other baenids, the premaxillae do not extend beyond the overlying skull roof. The triturating surface is slightly expanded posteriorly, but not as expanded as in *Palatobaena* spp., *Eubaena cephalica*, *S. estesi*, *Ch. undatum*, *B. arenosa*, *Pl. antiqua*, and *Ce. putorius*. The weakly posteriorly expanded triturating surface more closely resembles that of *Pl. antiqua* than *Ce. putorius*.

Laterally, the bar between the orbit and cheek emargination is thin, less than half the diameter of the orbit. This is an autapomorphy for *Pe. brinkman*.

Nasals.—The presence of nasals cannot be determined in either the holotype (UMMP 20490) or the referred specimens examined (UCMP 49759, UW 28085, and MRF 231). Whether the nasals fused with the frontals or are truly lost as is hypothesized for *B. arenosa* (Gaffney, 1982) cannot be determined objectively. However, all of the sutures are clearly visible in the smaller specimen, MRF 231, indicating that the nasals either fused with the frontals early in development or that they are simply lost. Notably, nasals are present in *Pl. antiqua* (Brinkman, 2003).

Prefrontals.—As in other derived baenids, the dorsal plate of the prefrontal is greatly reduced. The amount of exposure is similar to that seen in *Palatobaena* spp., *E. cephalica*, *Pl. antiqua*, and *Ce. putorius*. The exposure is greater than that seen in *S. estesi*, *Boremys pulchra* (Lambe, 1906), *B. arenosa*, *Ch. undatum*, and *Go. mckennai* but not as great as *Ga. sonsalla*, *H. latifrons*, and *Neurankylus eximius* Lambe, 1902. The prefrontal forms the anterior portion of the orbital margin, blocking the frontal from widely entering the orbital margin. The prefrontal contacts the maxilla laterally, the vomer ventromedially, and the palatine ventrolaterally.

Frontals.—The length of the frontal is slightly longer than their combined width. As in *Pl. antiqua*, but unlike *Ce. putorius*, the frontals extend slightly beyond the posterior most portion of the orbit, similar to the condition found in other baenids except *H. latifrons*, *N. eximius*, *Trinitichelys hiatti* Gaffney, 1982, and *Ga. sonsalla*. As in *Pl. antiqua* and *Ce. putorius*, a very small portion of the frontal enters the orbital margin in lateral view; its contribution is constricted anteriorly by the prefrontal and posterolaterally by the postorbital. As in other baenids except *N. eximius* and *T. hiatti*, the frontal contacts the maxilla anterolaterally. The presence of nasals

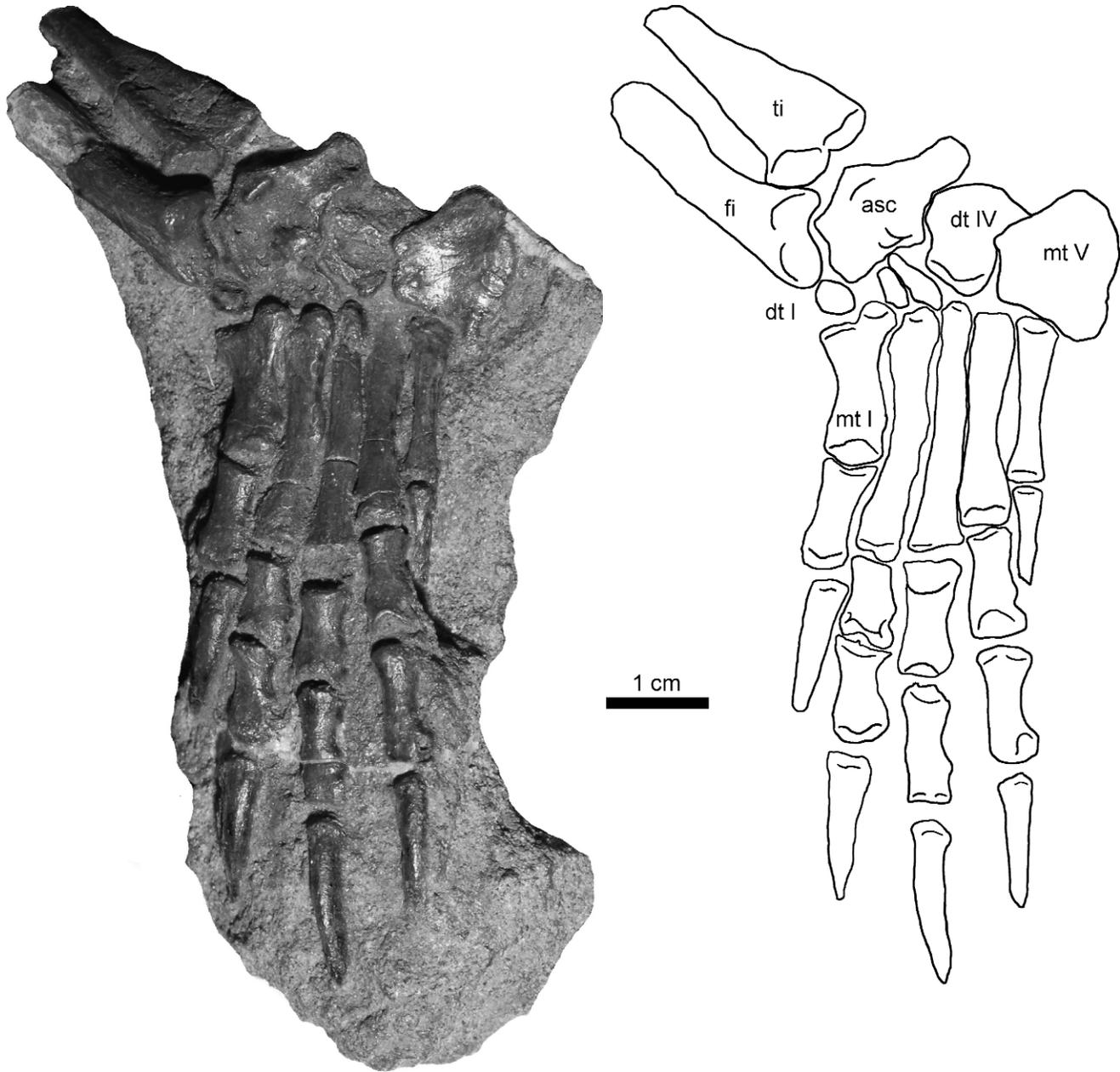


FIGURE 11—*Peckemys brinkman* left pes (UMMP 20490, holotype) photograph (left) and line drawing (right) in dorsal view. Abbreviations: asc, astragalocalcaneum; dt I, distal tarsal I, dt IV, distal tarsal IV; fi, fibula; mt I, metatarsal I; mt V, metatarsal V; ti, tibia.

cannot be determined, and it is unknown whether the frontals enter the external narial opening. The frontals have a relatively straight contact with the postorbitals laterally.

Parietals.—The parietals are longer than their maximum combined width. They form a straight contact with the frontals anteriorly as is found in *Pl. antiqua*, *Ce. putorius*, *B. arenosa*, and *S. estesi*. As in other baenids, the parietals form the majority of the margin of the upper temporal emargination. The portion of the parietals overlying the supraoccipital is well developed, but unlike *Ce. putorius*, the sides of the parietal are not parallel to one another. Unlike *T. hiatti*, *Ch. undatum*, and *B. arenosa* there is no squamosal and parietal contact as the temporal emargination is deep, reaching to the anterior of the post oticum. The parietals form the majority of the skull roof. Unlike *Ce. putorius*, but similar to *Pl. antiqua*, no sulci for scales are visible on the skull roof in any of the

specimens examined. Furthermore, the parietals thin out posteriorly as in *Pl. antiqua*.

Jugal.—The jugal is small, smaller than in any other baenid. A small portion of the jugal enters the orbital margin in lateral view. Its contribution to the orbital margin is constricted by a posterodorsal projection of the maxilla. The jugal's contribution to the orbit is intermediate between *Pl. antiqua* where the jugal is restricted from entering the orbital margin and *Ce. putorius* where the jugal has a relatively large contribution to the orbital margin. As in *Palatobaena* spp. and *Pl. antiqua*, a ventral process of the jugal forms the posteriormost portion of the labial ridge. The jugal forms the region between the orbit and the cheek emargination. This region is very slender; its width is approximately half the diameter of the orbit. This appears to be an autapomorphy of *Pe. brinkman*. As in all baenids

except *Palatobaena* spp., the jugal is slender in ventral view and lacks any significant muscle scars along the inside.

Quadratojugal.—The quadratojugal is a flat, C-shaped bone with the dorsal extension reaching around the cavum tympanum to a level equal with the ventral extension of the quadratojugal. The quadratojugal contacts the jugal anteriorly, the postorbital dorsally, and the quadrate and a small portion of the squamosal posteriorly. The quadratojugal forms the posterior portion of the cheek emargination. The cheek emargination is quite deep, reaching dorsally to the middle of the orbit. In lateral view, the external pterygoid process is visible through the cheek emargination.

Squamosal.—The squamosal is similar to other baenids'. It is a cone-shaped bone that sits posterodorsally to the quadrate. The squamosal forms the lateral portion of the temporal emargination. Anteriorly the squamosal contacts the postorbital and a small portion of the quadratojugal. As in other baenids, the antrum postoticum is well developed.

Postorbital.—As in other baenids, the postorbital forms a broad bar on the dorsolateral portion of the skull. The postorbital forms the majority of the posterodorsal portion of the orbital margin. A small process of the postorbital extends dorsally over the orbit, further constricting the frontal contribution to the orbital margin. Posteriorly, the postorbital forms a large portion of the lateral part of the upper temporal emargination. Unlike *Pl. antiqua*, but similar to *Ce. putorius*, the postorbital does not contact the maxilla. The postorbital contacts the jugal anteroventrally and the quadratojugal posteroventrally. Posteriorly, the postorbital contacts the squamosal.

Premaxilla.—The premaxilla is similar to other baenids'. It is roughly triangular in ventral view and forms the ventral margin of the apertura narium externa. The premaxilla contacts the other premaxilla medially, the maxilla posterolaterally, and the vomer posteriorly. A small portion of the lingual ridge extends onto the posterolateral most portion of the premaxilla. The foramen praepalatium is situated between the premaxillae, maxilla, and vomer, as in *T. hiatti*, *Pl. antiqua*, *Pe. brinkman*, and *Go. mckennai*. In contrast, the foramen praepalatium is located entirely within the premaxillae in *B. arenosa*, *Ch. undatum*, and *S. estesi*, between the premaxillae and vomer in *Palatobaena* spp., and between the premaxillae and maxillae in *E. cephalica*. Unlike in most baenids, the premaxilla ends even with the overlying dorsal skull roof and the nasal opening is thus oriented to the anterior.

Maxilla.—The maxilla forms a broad bar underneath the orbit. An ascending postorbital process reaches half way up the posterior orbital margin. The anterior ascending process frames the anterior of the orbit, contacts the prefrontal within the orbit, and contacts the frontal dorsally. This process also forms the lateral portion of the apertura narium externa. The orbit is situated vertically and is not inset into the maxilla as in *Ce. putorius*, *Ga. sonsalla*, and *Palatobaena* spp. (Lyson and Joyce, In Press). Ventrally, the maxilla forms the major portion of the triturating surface. The labial ridge is a thin vertical plate that is not swollen as in *Ce. putorius*, *Palatobaena* spp., *S. estesi*, *B. arenosa*, and *Ch. undatum*. The lingual ridge is restricted to the anterior portion of the maxilla as in other baenid taxa that have a lingual ridge. A wide tongue groove (i.e., choanal channel) is present between the lingual ridges as in *S. estesi*, *B. arenosa*, *Ch. undatum*, *Palatobaena* spp., *Pl. antiqua*, and *Ce. putorius*. Similar to *T. hiatti*, the triturating surface is not greatly expanded posteriorly, but only slightly expanded. This is unlike the greatly

posteriorly expanded triturating surface found in all other baenid taxa in which the triturating surface is preserved. The maxilla contacts the vomer and premaxilla anteromedially, the palatine medially, the pterygoid posteromedially, and the jugal posteriorly.

Vomer.—The vomer is a single anteriorly expanded element. The vomer contacts the premaxillae anteriorly, the prefrontals dorsolaterally, the palatines laterally, and the pterygoids posteriorly. In ventral view the vomer is concave. The anterior portion of the vomer is slightly higher than the posterior portion. The lateral edges of the vomer form the medial margins of the large internal choanae. In the holotype, the vomer extends beyond the posterior level of the palatines to form a rounded contact with the pterygoids, similar to that found in *B. arenosa* and *Ch. undatum*. However, in MRF 231 the vomer does not reach the posterior limit of the palatines, similar to *E. cephalica* and *B. pulchra*. There is no vomer and basisphenoid contact due to the well-developed medial contact of the pterygoids.

Palatine.—The palatine is similar to that of other baenids. It is a plate-like structure that roofs the internal choanae. As in all baenids except *Ch. undatum* and *S. estesi*, the foramen palatinum posterius is located in the palatine and pterygoid suture. A small lateral process of the palatine forms a small portion of the lingual ridge of the triturating surface as in *Palatobaena* spp., *Pl. antiqua*, and *Ce. putorius*.

Quadrate.—The quadrate is a stout C-shaped bone. Anterolaterally the quadrate forms a broad contact with the prootic. The anterior end of this contact forms the processus trochlearis oticum, with the suture running down the middle of this process. Ventrally the quadrate forms a vertical suture with the pterygoid. The quadrate forms the cavum tympani. The cavum tympani are circular cavities that open laterally and are larger than the orbit, similar to the condition found in all baenids except *S. estesi* and *Ch. undatum*. As in other baenids, the incisura columellae auris is a relatively narrow slit enclosing both the stapes and the Eustachian tube. The stapes is preserved in the holotype and is a slender rod, much thinner than the stapes found in *Ce. putorius*. Above the incisura, the antrum postoticum extends posterodorsally into the squamosal. Anteriorly the quadrate has a long C-shaped contact with the quadratojugal. Unlike the *Palatobaena* taxa and *Ce. putorius*, but similar to other baenids', the condylus mandibularis is quite small. As in other baenids, the quadrate encloses the anterior margin of the antrum postoticum.

Pterygoid.—Combined, the pterygoids are shaped like butterfly wings. As in cryptodires, the pterygoids are widely exposed on the posterior edge of the skull. The pterygoids contact one another medially, the vomer anteromedially, the palatine and maxilla anteriorly, a small portion of the jugal anterolaterally, the basisphenoid and basioccipital posteromedially, the prootic and parietal dorsally, and the quadrate posterolaterally. There is no sign of an epipterygoid ossification. However, given that all available specimens appear to be adult, it is likely that the epipterygoids fused to the pterygoids, as demonstrated for *Pl. antiqua* (Brinkman, 2003). As in *Ce. putorius*, but unlike *Pl. antiqua*, the contact between the pterygoids is well developed. The external pterygoid process is moderately developed. The entry foramen for the internal carotid artery is formed by the pterygoid and basisphenoid. The remaining systematically important carotid artery information cannot be discerned from the fully articulated skulls.

Supraoccipital.—As in all baenids except *N. eximius*, *T. hiatti*, *B. arenosa*, and *Ce. putorius*, the supraoccipital is exposed on the skull roof. The crista supraoccipitalis is short

and high, similar to most other baenids'. Anterodorsally the supraoccipital is overlain by the parietals, anterolaterally it contacts the prootic, posterolaterally it meets the opisthotic, and posteriorly it forms a small suture with the exoccipital.

Exoccipital.—The exoccipitals are situated lateral to the foramen magnum. Dorsolaterally the exoccipital contacts the opisthotic, dorsally the supraoccipital, and ventrally the basioccipital. As in other baenids, the exoccipitals do not contact one another, but are separated by the basioccipital and supraoccipital. The exoccipitals form the lateral portion of the condylus occipitalis. The exoccipitals form the dorsolateral portion of the tuberculum basioccipitale.

Basioccipital.—The basioccipital is a triangular to subrectangular bone situated posterior to the basisphenoid. It forms most of the condylus occipitalis. The condylus occipitalis has a central pit at its posterior end. Laterally, the basioccipital forms a long contact with the pterygoids. There are two wing-like processes on the basioccipital that extend posteroventrally and contact the exoccipitals dorsally. Posteriorly, these processes form together with the pterygoids the tubercula basioccipitales. Similar to *Pa. cohen*, the tubercula basioccipitales have posteriorly projecting processes.

Prootic.—The prootic is a small bone that forms the anterior portion of the inner ear. The prootic contacts the parietal anterodorsally, the supraoccipital posterodorsally, the quadrate laterally, the pterygoid ventrally, and the basisphenoid medially.

Opisthotic.—The opisthotic forms the posterior portion of the bony inner ear. Like all baenids except *Ch. undatum* and *S. estesi*, the opisthotic does not enter the foramen stapedio-temporale.

Basisphenoid.—As in other derived baenids, the basisphenoid is a large pentagonal shaped element. As in baenids and pleurosternids, the foramen posterior canalis carotici interni is located midway along the length of the basisphenoid and pterygoid suture. Posteriorly, the basisphenoid contacts the basioccipital and the contact between these two bones is anteriorly convex.

Hyoid.—Case (1939, p. 9) described two hyoid elements preserved in articulation in the holotype, but the right element has since been removed to gain access to the palate. These elements are interpreted to be the cornu branchiale I horns of the hyoid apparatus based on their position, size, and shape (Meylan, 1987). The posterior portion of the left cornu branchiale I has subsequently been separated from the skull but is still present as a loose element. The cornu branchiale I is an elongate structure, with the posterior portion more rod-like, while the anterior portion is more spatula-shaped. The element is situated in the palate and lies roughly parallel with the lower jaw. The hyoid extends from the middle of the lower jaw around the posterior portion of the skull. It is bent at roughly a 90° angle. Overall, the cornu branchiale I is very similar to that in other baenids where this bone is preserved (*Stygiochelys* sp. and *Eubaena* sp.) Similar to these taxa, the cornu branchiale II and corpus hyoidis are not present, because they were likely not ossified.

Mandible.—Overall, the lower jaw is very similar to the lower jaw of *Pl. antiqua* and *Ce. putorius* (Fig. 6). The angle between the rami is narrow. The angle is slightly narrower in *Pe. brinkman* than in *Pl. antiqua*, and both are significantly narrower than the angle between the rami in any other baenid.

Dentary.—The dentaries are connected medially by a broad symphysis. The triturating surface is very narrow as in *Pl. antiqua* and *Ce. putorius*. In addition, the labial and lingual ridges are approximately parallel to one another as is found in

Pl. antiqua, *Ce. putorius*, *B. arenosa*, and *Ch. undatum*. The labial ridge extends anterodorsally to form a slight symphyseal hook, not nearly as well developed as that found in *Glyptops plicatulus* (Cope, 1877). A small tubercle is present on the posterolateral portion of the dentary, similar to the situation in *Palatobaena* spp., *Pl. antiqua*, *Ce. putorius*, and *S. estesi*.

Articular.—The articular is situated between the prearticular and the surangular. The morphology is similar to that of cryptodires. It forms the majority of the area articularis mandibularis. The articular extends posteriorly to form a weak retroarticular process.

Splenial.—As in *Palatobaena* spp., *Ce. putorius*, and *Pl. antiqua*, a large splenial is present. It is a flat bone that forms the medial margin of the foramen intermandibularis medius and the anteromedial wall of the Fossa Meckelii.

Coronoid.—As in *Pl. antiqua*, the processus coronoideus is weakly developed. An anteromedial process of the coronoid extends anteriorly along the medial surface of the ramus to form a small medial portion of the triturating surface.

Angular.—The angular covers the posteroventral portion of the lower jaw. An anteromedial portion contacts the splenial. The foramen intermandibularis caudalis is located between the angular and prearticular as in *Pl. antiqua*, *Ce. putorius*, and *Palatobaena* spp.

Prearticular.—The prearticular covers the posteromedial portion of the lower jaw, anterior to the articular, dorsal to the angular, and lateral to the Fossa Meckelii. The prearticular has a broad anterior contact with the splenial, as is the case with other baenids where a splenial is present.

Surangular.—The surangular forms a relatively large portion of the lateral surface of the lower jaw. As in *Palatobaena* spp., the surangular and dentary contact is relatively straight.

Shell.—The shell and postcranial elements of the holotype were previously illustrated by Case (1939, Figs. 1–3), and a photograph of the shell was provided by Gaffney (1972, Fig. 13). The carapace is broken roughly along the midline into two pieces, and it is missing its posterior margin. The shell is oblong in shape, and the posterior portion that is preserved indicates that it is weakly scalloped posteriorly (Fig. 7). The shell is completely fused, obliterating all of the sutures; thus only the scute morphology will be discussed. Five vertebral scutes are present. These scutes are wider than they are long. As in *N. eximius*, *T. hiatti*, and *Pl. antiqua*, the first vertebral is wide anteriorly and narrows posteriorly. The remaining baenid taxa have a first vertebral that is narrow anteriorly and wide posteriorly. The second vertebral is hexagonal in shape as in *N. eximius* and *T. hiatti*, but this shape is notably absent in *Pl. antiqua*, which has a rectangular-shaped second vertebral. The third through fifth vertebrae are rectangular in shape. The posterior portion of the shell is damaged in the holotype and the relationship of the fifth vertebral to the shell margin cannot be determined. The sulcus between the fourth and fifth vertebral is straight.

Contrary to the description by Case (1939), we interpret the cervical scute as being subdivided into two elements. His original interpretation of a small cervical flanked by marginals would mean the left portion of the first vertebral scute contacts three marginal scutes while the right portion only contacts two marginal scutes. So instead of this asymmetrical arrangement we interpret the cervical scute as asymmetrically subdivided. The cervical scute in the population of *Eubaena* sp. from the Turtle Graveyard site ranges from undivided to subdivided into several pieces (pers. obs. TRL). Combined, the subdivided cervical scute is large, as large as that found in *Pl.*

antiqua and *Pa. cohen*. Only four pleural scales are present and all types of supramarginal scutes found in other baenids are missing. Sulci for marginal scutes are mostly obliterated. However, the first five left marginals are visible. The first vertebral scute contacts the first two marginal scutes. The second through fifth marginal scutes contact the first pleural scute.

Extragular scutes are present, but gulars scutes are notably absent. Extragular scutes are also absent in *Pa. cohen* and are greatly reduced in *Pl. antiqua*. The pectoral scutes are similar to those in other baenid turtles. They are located on the posterior portion of the anterior plastral lobe. The anterior plastral lobe is subtriangular in shape, as in *Pl. antiqua* and *Pa. cohen*. The humeral scutes are similar to those of other baenids. The lateral portion of the humeral contacts three inframarginal scutes laterally. The abdominal scutes are also similar to the abdominal scutes of other baenids. Case (1939, Fig. 2) illustrated the abdominal and femoral sulcus as lying entirely on the xiphiplastron; however this portion of the shell is covered up by the articulated left pes and the placement of this sulcus cannot be determined. The posterior plastral lobe is long and rectangular-shaped, as in other baenids. Both plastral lobes end prior to the margin of the carapace. The anterior lobe appears to extend beyond the carapacial margin, but this is an artifact of deformation.

Postcranial elements.—Postcranial elements are only known for the holotype specimen.

Cervical vertebrae.—Cervical vertebrae have been described for the following baenids: *N. eximius* (Wiman, 1930), *Ch. undatum* (Hay, 1908), *B. pulchra* (Brinkman and Nicholls, 1991), and *Pl. antiqua* (Brinkman, 2003). The complete cervical series is preserved in the holotype UMMP 20490 (Fig. 8) and were figured in Case (1939, Fig. 8). As in all turtles, there are eight cervical vertebrae. As in the other baenids, they decrease in length from the second to the fifth, then increase in length between the sixth and seven, and finally decrease in length in the eighth.

The atlas consists of four elements: paired neural arches anterodorsally, an intercentrum anteroventrally, and a centrum posteriorly. The centrum is preserved in articulation with the second to fourth cervical vertebrae while the remaining elements are loose. The centrum is similar in shape to that of all other turtles. As in other turtles, the neural arch can be divided into two parts: a dorsal portion that covers the neural cord with a posteriorly directed postzygapophyseal flange that articulates with the axis and a ventral portion that has articular surfaces for the occipital condyle anteriorly, atlas centrum posteroventrally, and the atlas intercentrum posteroventrally. Unlike in *B. pulchra*, there do not appear to be any atlantal cervical ribs, as this region is completely articulated and very well preserved yet ribs are absent, as are articulation sites for the ribs (Brinkman and Nicholls, 1991). However, we cannot rule out that these ribs simply washed away prior to fossilization. In all other aspects the atlas of *Pe. brinkman* is similar to the atlas found in other turtles (Gaffney, 1990).

The remaining cervicals are short with well-developed transverse processes that are situated at the middle of the centrum, as in all non-cryptodires. The axis has a neural spine similar to those of *B. pulchra*, *N. eximius*, *Pl. antiqua* and *Ch. undatum*. The neural spine is low and elongate with the anterior portion situated slightly higher than the posterior portion. In both *Pe. brinkman* and *B. pulchra*, the anterior portion of this neural spine extends anteriorly almost to the posterior tip of the crista supraoccipitalis. The prezygapophyses of the axis are clearly developed in *Pe. brinkman* but

appear to have been lost in the available specimens of *Ch. undatum* and *N. eximius* (Case, 1939). A weakly formed keel is present on the ventral midline of its centrum. Similar to *Pl. antiqua*, *N. eximius*, and *Ch. undatum*, the 8th cervical vertebra has a neural spine, although it is less well developed than in the former two taxa. The remaining cervical vertebrae of *Pe. brinkman* lack neural spines. A neural spine is also present on the third cervical vertebrae in *B. pulchra* and *Ch. undatum* (Brinkman and Nicholls, 1991; Hay, 1908). A strong ventral midline keel is present on the 3rd–8th cervical vertebrae similar to the keel in other baenids; the keel is much better developed than that in *Pl. antiqua* (Brinkman, 2003). The zygapophyses extend dorsally, further than in *N. eximius*. Cervical vertebrae 6–8 are gracile and are not as complex as the robust and complex cervical vertebrae 6–8 in *N. eximius*.

Case (1939) describes the cervical vertebrae as opisthocoealous; however, examination of the specimen does not corroborate this observation. Instead, the 1st through 7th cervical vertebrae are slightly amphicoelous, as in *B. pulchra*, whereas the eighth cervical vertebra appears to be procoelous. The cervical formula is thus 1()2()3()4()5()6()7()8. The cervical formulae for other baenids is: *N. eximius*, ?1? (2()3()4()5()6()7()8); *Pl. antiqua*, 1()2()3()4()5()6()7()8); *B. pulchra*, 1()2()3()4()5()6()7()8?; and *Ch. undatum*, 1()2()3()4()5()6()7()8. Small round intercentrum bodies are preserved in the neck of *Pe. brinkman* between cervicals 3–6, which likely represent ossified notochordal discs, which we call intercentral bodies. A similar condition was hypothesized for *B. pulchra* between cervicals 5 and 6 based on the morphology of the 5th cervical vertebra (Brinkman and Nicholls, 1991). These round intercentral bodies form functional condyles between two vertebrae and are not known to occur in any other group of turtle (Williams, 1950). Tubercles are present above the postzygapophyses in cervical vertebrae 4, 5, 6, and 8 in *Pe. brinkman*.

Caudal vertebrae.—Case (1939, Figs. 9–10) describes nine caudal vertebrae, but only eight are presently with the skeleton; the ninth was presumably lost at some point since Case's (1939) description. The first six caudal vertebrae are preserved in articulation with the specimen, and two mid-caudal vertebrae that presumably eroded away from the skeleton and were found loose are also present (Fig. 9). All eight vertebrae are opisthocoealous (Case, 1939). This differs from *B. pulchra* where the first two caudals are amphicoelous, central ends of the 3rd caudal are unknown, the 4th through 12th are opisthocoealous, and the 13th–19th are procoelous (Brinkman and Nicholls, 1991). Like *B. pulchra*, *Pl. antiqua* has amphicoelous proximal caudal vertebrae, but the shape of the more distal vertebrae in *Pl. antiqua* is not described (Brinkman, 2003). Like both *B. pulchra* and *Pl. antiqua*, the proximal caudal vertebrae are short and have well-developed transverse processes and low neural spines (Brinkman and Nicholls, 1991; Brinkman, 2003). The distal caudal vertebrae are more elongate than the proximal vertebrae. The lengthening of the vertebrae posteriorly is also found in *Pl. antiqua*, *B. pulchra*, and *N. eximius* and was interpreted as a derived condition for baenids by Brinkman and Nicholls (1991). Poorly-developed haemal arches are present on the anterior-most vertebrae of *Pe. brinkman*, as in *B. pulchra* and *Pl. antiqua*. Better-developed haemal arches are present starting at the 5th caudal vertebra.

Scapula and coracoid.—The scapula and coracoid were figured by Case (1939, Figs. 11–12) and generally resemble those of other aquatic turtles in being a triradiate structure that is not fused at the glenoid despite the general skeletal

maturity of the holotype individual. The scapular process and the acromial process are both rod-like structures that together form an angle of approximately 100 degrees. The coracoid, in contrast, is about the length of the acromial process but is expanded distally into a narrow fan. As in all derived turtles, there are no ridges that run along the shaft of either the scapula or coracoid and contribute to the rim of the glenoid.

Pelvis.—Unfortunately the pelvis was encased in a sulfur concretion which has since largely disintegrated, largely destroying the pelvis. Thus this description is based mainly on Case's (1939, Figs. 13–14) illustrations. As in cryptodires, the ilium possesses a well-defined shaft at its base near the acetabulum and, in lateral view, expands rather systematically into a vertically oriented fan, thus resembling the ilium of most cryptodires. The pelvis is otherwise known for *Pl. antiqua* (Brinkman, 2003), *B. arenosa* and *Ch. undatum* (Hay, 1908) and in these taxa, the dorsal fan is only developed towards the posterior, thus resulting in a vertical anterior margin of the ilium. As in all baenids and unlike cryptodires, the lateral (metischial) process of the ischium is a well-developed vertical blade with an upwards-rounded poster-ventral margin. The lateral pubic (pectineal) process is mostly developed towards the ventrum and does not protrude significantly towards the anterior. Anteriorly, the main bodies of the pubes touch to form a short symphysis, but there is no posteromedial contact with the ischia. The thyroid fenestrae are consequently large and medially confluent. The acetabulum appears to be fused, confirming the assertion that this is a skeletally mature individual. That being said, *Pe. brinkman* appears to possess a pelvis that is significantly less ossified than that of *Ch. undatum*, where the pubes conjoin to form an enlarged and fully ossified epipubic process.

Humerus.—The left humerus was figured by Case (1939, Fig. 15) and is approximately 58 mm long and approximately one centimeter shorter than the length of the femur in the holotype individual. This contrasts with *Pl. antiqua*, where these two bones are subequal in length. As in other baenids, the two humeral trochanters are highly asymmetric in size and flare far apart to form a broad intertrochanteric fossa; the humeral head is distinct from the trochanters and relatively small; and a distinct entepicondylar canal is present.

Radius and ulna.—Similar to the condition found in all turtles, the radius is slightly longer than the ulna (Gaffney, 1990). The radius is approximately 42 mm long and the ulna is approximately 36 mm long. The radius and ulna are virtually undistinguishable from these elements found in other baenids.

Manus.—A portion of the left manus is preserved in the holotype of *Pe. brinkman* (Fig. 10). The 1st digit is the only complete digit and thus the phalangeal formula is 2:?:?:?:?. The 1st metacarpal is short and broad while the remaining metacarpals are more elongate. Five distal carpal bones are present and they increase in size moving from digit 1 to digit 5. The fifth distal carpal contacts both the 4th and 5th metacarpal. The medial centrale is larger than the lateral centrale. As in crown turtles (Gaffney, 1990), a pisiform is present on the lateral part of the hand next to the ulnare, but it is surprisingly large for a freshwater aquatic turtle. Large pisiforms are known from marine protostegids (e.g., Tong et al., 2006), and chelonioids and pisiforms of intermediate size are known from near-shore eurytternids (Meyer, 1860). The ulnare is a large rectangular element. The intermedium is large, and its anterior edge lies even with that of the radius. Finally, a small blocky bone is present just posterior to the radius and medial to the intermedium, which we regard as the

radiale. The general testudine condition is either a small or absent radiale (Gaffney, 1990).

Femur.—The left femur, figured in Case, (1939, Fig. 17) is slightly longer than the humerus. It is approximately 67 mm long. As in most other turtles, it is less robust than the humerus. It is virtually identical to the femora found in other baenids.

Tibia and fibula.—The tibia is approximately 47 mm long and the fibula is 43 mm long. As in other turtles, the tibia is more robust than the fibula and its distal end contacts the medial surface of the astragalus. The distal end of the fibula contacts the astragalocalcaneum. These elements are virtually indistinguishable from other turtles.

Pes.—The complete left foot is beautifully preserved in the holotype of *Pe. brinkman* (Fig. 11). There are five metatarsals, with the 5th one strongly hooked, as is generally the case in crown Testudines. The 1st metatarsal is short and broad, while the 2nd–4th metatarsals are more elongate, as in other baenids that have the pes preserved (*Eubaena* sp., *Pl. antiqua*, and *Stygiochelys* sp.). The 2nd and 3rd metatarsals are subequal in length while the 4th is slightly shorter. The phalangeal formula is 2:3:3:3:2, as in *Pl. antiqua*. As in cryptodires and pleurodires, the distal phalanx of the 5th toe does not bear a claw. As in other turtles, there are four distal tarsals. The first three distal tarsals are small, while the 4th distal tarsal is quite large. The 4th distal tarsal is situated between the 5th metatarsal and the astragalocalcaneum. The astragalocalcaneum is fused as in several other baenids (Hay, 1908; Russell, 1934). There is no sign of a centrale in *Pe. brinkman*, unlike *Eubaena* sp. (UCMP 107617), which shows the fused astragalocalcaneum and a partially separated suture between the astragalus and centrale (Archibald, 1979; Gaffney, 1990). In the basal paracryptodiran *Dinochelys whitei* Gaffney, 1979, the astragalus and calcaneum are partly fused with a sutured centrale (Gaffney, 1990). Centrales are also present in chelydrids and pleurodires (Gaffney, 1990). Unfortunately the feet of most fossil turtles are not preserved well enough to determine the presence or absence of this potentially important systematic character.

PHYLOGENETIC ANALYSIS

A maximum parsimony analysis was performed using the matrix of Lyson and Joyce (in press). Two character scorings for *Plesiobaena antiqua* were changed: Character 8, shape of the triturating surface, was changed from 0 to 1. The scoring of this character is not obvious from the figures in Brinkman (2003), but both he and Gaffney (1972) describe *Pl. antiqua*'s triturating surface as being more like *T. hiatti*'s, with a weak posterior expansion with the labial and lingual ridges roughly parallel. Character 13, frontal contribution to the external narial opening, was changed from 0 to 0&2. While the figure in Brinkman (2003) clearly shows the frontals excluded from the external narial opening, he describes other specimens in which the frontals extend between the nasals into the external narial opening. In addition, a single character was added to the analysis and is listed in Appendix 1. Four shell taxa included in the analysis of Lyson and Joyce (in press) (i.e., "*Baena*" *hayi* Gilmore, 1916, "*Baena*" *hatcheri* Hay, 1901, "*Baena*" *marshi* Hay, 1904, and *Thescelus insiliens* Hay, 1908) were removed from the analysis because they behave like wildcard taxa (Nixon and Wheeler, 1992). However, three other ingroup taxa were added to the analysis: *Goleremys mckennai*, *Cedrobaena putorius* gen et sp. nov, and *Peckemys brinkman* nov. comb, and this analysis thus includes all baenid taxa known from cranial material. A total of 72 osteological

characters and 19 taxa, including 17 ingroup taxa, were analyzed. Eight characters were considered to represent morphoclines and were ordered (7, 14, 16, 18, 28, 33, 36 and 70). The remaining characters were run unordered and all characters were left unweighted. Missing data was scored as “?”. The complete matrix can be found in Appendix 2. A maximum parsimony analysis was performed on the dataset using PAUP 4.0b10 (Swofford, 2003). *Glyptops plicatulus* and *Pleurosternon bullocki* Owen, 1842 were specified as the outgroup taxa, and a branch and bound search was used with minimum branch lengths set to collapse. Support for each node was measured by calculating the Bremer support (Bremer, 1994) for each clade, as well as bootstrap frequencies (Felsenstein, 1985), with 10,000 bootstrap replicates and 100 random sequence addition replicates. Bootstrap frequencies > 70% are considered strong support (Hillis and Bull, 1993).

The parsimony analysis resulted in a single most parsimonious tree (MPT) with a tree length of 138 steps, consistency index of 0.6029, retention index of 0.7523, and rescaled consistency index of 0.4579 (Fig. 12). The analysis hypothesizes that the assemblage of turtles traditionally referred to as *Plesiobaena* (*Pl. antiqua*, *Pl. putorius*, and the previously unnamed taxon) are a paraphyletic assemblage. The successive taxa outside of the clade formed by *Ga. sonsalla* and *Palatobaena* spp are *Ce. putorius*, *Pe. brinkman*, and *Pl. antiqua*. Overall, the topology is very similar to that obtained by Lyson and Joyce (2009, in press). Baenidae is strongly supported (100% frequency; Bremer support of 6). The subclade Baenodda is strongly supported as well (85% frequency; Bremer support of 3). As in previous analyses by Lyson and Joyce (2009, in press), there is strong support for *S. estesi* as sister taxon to the Eocene baenid clade, *B. arenosa* and *Ch. undatum* (90% frequency; Bremer support of 4).

DISCUSSION

The new *Ce. putorius* skulls described herein are more nearly complete and exhibit clearer sutures than does the previously described *Ce. putorius* cranial material and thus provide additional osteological data. The Cretaceous specimens FMNH PR 2258 and MRF 239 were attributed to *Ce. putorius* based on several characters shared with the Tiffanian holotype (YPM PU 14984), including the posteroventral closure of the incisura columellae auris, presence of a well-developed parietal overhang with parallel sides that partially covers the temporal fossa, greatly expanded posterior portions of the triturating surface, a jugal contribution to the orbital margin, dorsally oriented orbits, orbits inset into the maxilla, and well-developed anterolaterally-curved lingual ridges. Morphologically and phylogenetically *Ce. putorius* shares many features with *Palatobaena* spp. and *Ga. sonsalla*. Indeed, our phylogenetic analysis indicates that *Ce. putorius* is more closely related to *Ga. sonsalla* and *Palatobaena* spp. than it is to either *Pe. brinkman* or *Pl. antiqua*. *Cedrobaena putorius*, *Ga. sonsalla*, and *Palatobaena* spp. share dorsally oriented orbits, orbits inset into the maxilla, extreme posterior expansion of the triturating surface, excavated nasals, reduced external pterygoid processes, and large mandibular condyles.

Previous analyses assumed that *Plesiobaena* was monophyletic and only included the more nearly complete *Pl. antiqua* in their phylogenetic analyses (Archibald, 1977; Gaffney and Meylan, 1988; Brinkman and Nicholls, 1991; Joyce, 2007; Lyson and Joyce, 2009). However, this analysis indicates that the collection of turtles traditionally referred to *Plesiobaena* is actually paraphyletic (Fig. 12). This is not surprising given that Gaffney's (1972) diagnosis of *Plesiobaena* consists of

characters now known to be symplesiomorphies for the clade Baenodda. In order to maintain a monophyletic *Plesiobaena*, only the type species, *Pl. antiqua*, is herein retained in this genus and the traditionally referred species *Plesiobaena putorius* was moved to a new genus, *Cedrobaena putorius*. In addition, the unnamed Maastrichtian taxon of Archibald (1979) and Brinkman (2003) is named as a new genus and species, *Peckemys brinkman*.

The stratigraphic ranges for *Pe. brinkman* and *Ce. putorius* overlap. Indeed a referred specimen for each species was found in the Turtle Graveyard locality in Slope County, North Dakota (MRF 231, *Pe. brinkman*; MRF 239, *Ce. putorius*). Thus, these taxa occur contemporaneously and cannot represent an anagenetic sequence, as could be the case for various species referred to *Palatobaena* (Lyson and Joyce, 2009). In contrast, *Pl. antiqua* is restricted to the Campanian and its stratigraphic range does not appear to overlap with either *Pe. brinkman* or *Ce. putorius*, and thus the possibility remains for it being ancestral to either *Pe. brinkman* or *Ce. putorius*. However, *Pl. antiqua* has several apomorphies relative to the other *Plesiobaena* taxa, including the exclusion of the jugal from the orbital margin, the placement of the first marginal scute mostly on the nuchal bone, and the fusion of the first and second peripheral bones, demonstrating that this taxon appears to represent an independent early side lineage.

All representatives of the *Plesiobaena*/*Palatobaena* clade appear to be restricted to the northern latitudes (Brinkman, 2005). *Plesiobaena antiqua* is one of the most common turtles in the Campanian Belly River Group of Dinosaur Provincial Park but is less abundant in Montana and is notably absent from Campanian sediments in Utah, New Mexico, Texas, and Mexico (Brinkman, 2005). Similarly, *Pe. brinkman* is known from the Hell Creek Formation of North Dakota and Montana but is absent in sediments of comparable age further to the south. *Ce. putorius* is known from the Hell Creek Formation of North and South Dakota and the Fort Union Formation of Wyoming but has not been reported from any southern localities. Slightly more southerly shell material has been described from the Maastrichtian and Puercan of the Denver Basin (Hutchison and Holroyd, 2003), but our revision indicates that this material cannot be referred to any given taxon with confidence (see comments under *Ce. putorius* above). Finally, *Ga. sonsalla* and *Palatobaena* spp. are only known from northern localities (Montana, North Dakota, Wyoming).

Both Maastrichtian specimens of *Ce. putorius* were found in sandy overbank deposits. FMNH PR 2258 was found associated with the famous *Tyrannosaurus rex* specimen nicknamed “Sue” (FMNH PR 2081), and MRF 239 was found at the Turtle Graveyard locality (Lyson and Joyce, 2009). Both localities are thought to represent slow-moving water or oxbow depositional environments, indicating that *Ce. putorius* preferred slower-moving water. This is similar to the stream channel paleoenvironmental interpretation for other baenids, with the potential exclusion of *N. eximius*, which is thought to have preferred floodplains rather than active channel margins (Hutchison and Archibald, 1986; but see Brinkman, 2005). Given the similarity of the triturating surfaces of *Ce. putorius* relative to *S. estesi* and *Palatobaena* spp., it was likely molluscivorous. The swollen maxillae with a stout labial ridge and a broad posterior expansion of the triturating surface are thought to be an adaptation for crushing mollusks or other hard-shelled crustaceans. This is further supported by the presence of large muscle scars on the

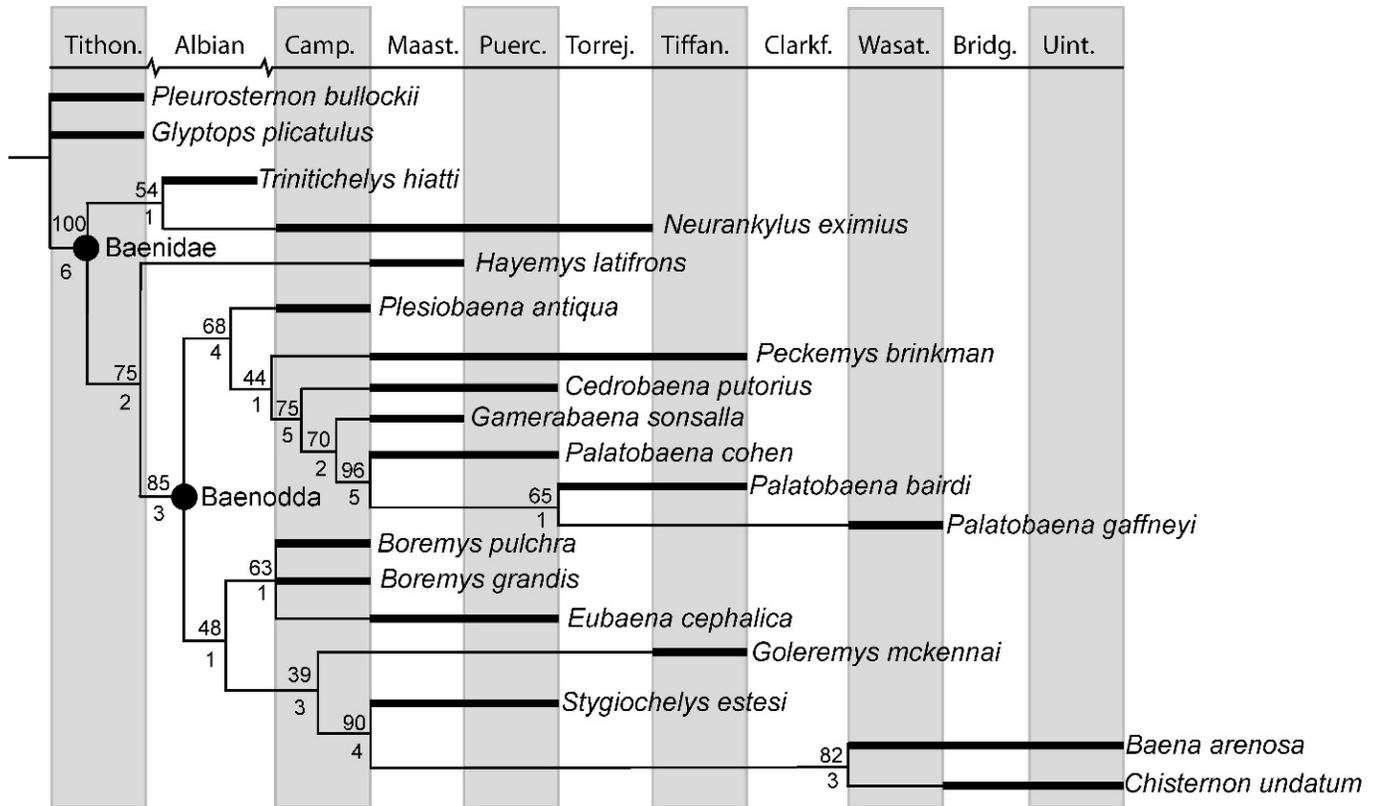


FIGURE 12—Baenidae cladogram mapped against the stratigraphic range from which each taxon has been reported (bold lines). Support for each node is measured using bootstrap frequency (top) and Bremer support for each clade (bottom).

crista supraoccipitalis that are not found in other baenids. The triturating surfaces of *Pl. antiqua* and *Pe. brinkman* are rather different compared to that of *Ce. putorius* by being more gracile and lacking the large posterior expansion. While *Pe. brinkman* is found in a similar depositional environment (i.e., slow-moving water or oxbow) as *Pe. brinkman*, its triturating surface indicates that it was likely a generalist rather than a molluscivore.

The description of two more taxa from the Turtle Graveyard locality in southwestern North Dakota increases this locality's turtle diversity to six: *Eubaena* sp., *Pa. cohen*, *Ce. putorius*, *Pe. brinkman*, *Axestemys* sp., and “*Aspideretes*” *lancensis* (likely a plastronid). While some microsite localities have comparable turtle diversity (e.g., Bug Creek Anthills, Hutchison and Archibald, 1986), these localities sample a much larger spatial area and temporal period compared to the thanatocoenosis found at Turtle Graveyard (Lyson and Joyce, 2009). The Turtle Graveyard is a true “snapshot in time” and provides a unique paleoecological glimpse into the early Hell Creek Formation. Interestingly, baenids dominate this locality in both number of individuals and number of taxa. The diversity of this locality is comparable to the local diversity of turtles in some southeastern North American river systems, which often contain four or five emydids, one or two chelydrids, one to two trionychids, and one to two kinosternids (Ernst and Barbour, 1989). Like most turtles, the turtles from Turtle Graveyard were likely mostly generalist feeders. However, given the diversity in triturating surfaces of these turtles, there was undoubtedly some resource partitioning among these taxa, as is again found in modern localities with comparable turtle diversity. The more gracile triturating surfaces found in *Eubaena* sp. and *Pe.*

brinkman indicate that these taxa were mostly generalists; the more robust and broadly expanding triturating surfaces and short faces of *Ce. putorius* and *Pa. cohen* indicate that these taxa were well adapted for crushing mollusks and were largely molluscivores; the secondary palate found in “*Aspideretes*” *lancensis* indicates it was likely durophagous; finally, the squarish and short snout, complete absence of a secondary palate, large size, and extremely long supraoccipital crest of *Axestemys* sp. indicates that it had a powerful bite that was largely used for cutting flesh.

The new species described herein, *Pe. brinkman*, increases the diversity of Maastrichtian baenids to 11. This number is likely inflated due to parataxonomic problems associated with named skull and shell species, and a more realistic estimation is eight baenid taxa (Lyson and Joyce, in press). Overall, this is comparable to the baenid diversity found during the whole of both the Campanian and Paleocene. However, the diversity within each given formation is significantly different. The Maastrichtian Hell Creek Formation is very diverse, with an estimated eight baenid taxa, while the Campanian Dinosaur Park Formation has an estimated three baenid taxa (Brinkman, 2005), and the Kirkland Formation has an estimated five baenid taxa. Either way, this indicates that baenids continuously held on to their ecological role from the latest Cretaceous into the Paleocene and continued to dominate riverine habitats in sheer numbers and diversity.

The addition of new material extends the range of *Ce. putorius* from the Paleocene into the Cretaceous and provides positive evidence for this taxon having survived the K/P extinction event. *Palatobaena cohen*, *S. estesi*, *Pe. brinkman*, *E. cephalica* (based on the presence of a lower jaw, YPM 56948 from the Puercan), and *N. eximius* are five other baenid

species also known to have survived the K/P extinction as suggested by the same line of evidence (Hutchison and Holroyd, 2003; Lyson and Joyce, 2009). In contrast, *Go. mckennai* is known from only a single Paleocene specimen, but our phylogenetic analysis (Fig. 12) predicts that its stem lineage must have extended into the Cretaceous as well. Thus a minimum of seven baenid lineages, specifically *Pa. cohen*, *Ce. putorius*, *Pe. brinkman*, *E. cephalica*, *N. eximius*, *S. estesi*, and the lineage leading to *Go. mckennai*, are now hypothesized to have survived the K/P extinction event. In contrast, a total of two baenid species are known from the Maastrichtian but appear to be missing in the Paleocene. These are *Ga. sonsalla* and *H. latifrons*. Three of these four taxa are based on single skulls, and their stratigraphic ranges are thus only poorly understood. If shell taxa are included (e.g., *Thesculus insiliens* Hay, 1908 and *Baena hayi* Gilmore, 1916), the number of species missing in the Paleocene would increase to six. However, several lines of evidence indicate that *Ga. sonsalla* and *B. hayi* as well as *H. latifrons* and *T. insiliens* are synonymous, indicating that only four baenid species may have gone extinct during or at the end of the Maastrichtian: *Ga. sonsalla*/*B. hayi*, *H. latifrons*/*T. insiliens*, *E. cephalica*, and *Pe. brinkman* (Lyson and Joyce, in press). Thus, seven out of nine baenid lineages appear to survive the K/P extinction event. Using similar lines of reasoning, six out of eight baenid lineages found in the Campanian are also found in the Maastrichtian, including *N. eximius* and the lineages leading to *H. latifrons*, *E. cephalica*, *Ce. putorius*, and *S. estesi*. This provides an estimation of the background extinction rate for baenids and it is only moderately lower than the extinction rate across the K/P boundary. The large percentage of baenids passing through the K/P boundary provides additional evidence for the continuity of the turtle group across the K/P boundary (Hutchison and Archibald, 1986; Brinkman, 2003).

Interestingly, four of the seven baenid lineages that survive the K/P extinction event are interpreted as durophagous. *Stygiochelys estesi*, *Pa. cohen*, *E. cephalica*, and *Ce. putorius* all have broad triturating surfaces and short faces, providing a broad surface and a strong bite for crushing shells. However, a significant number of freshwater mollusks from the Williston Basin of North America were thought to have gone extinct at the K/P boundary (Hartman, 1998). While many freshwater mollusk taxa may have gone extinct at the K/P boundary, it appears that the handful of remaining taxa flourished and provided a food source for these turtles. It is interesting that the taxa with a more specialist diet survived, while taxa that likely were more generalist (*Pe. brinkman* and *H. latifrons*) did not survive into the Paleocene.

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APPENDIX 1

Description of the single character added to the analysis of Lyson and Joyce (in press): 72. Lateral expansion of parietal: 0) maximum combined width of parietals is less than length; 1) maximum combined width of parietals is greater than length. This character was discussed in Gaffney (1982).

