

A NEW SPECIES OF *PALATOBAENA* (TESTUDINES: BAENIDAE) AND A MAXIMUM PARSIMONY AND BAYESIAN PHYLOGENETIC ANALYSIS OF BAENIDAE

TYLER R. LYSON^{1,2} AND WALTER G. JOYCE^{3,4}

¹Department of Geology and Geophysics, Yale University, 210 Whitney Avenue, New Haven, Connecticut 06511, <tyler.lyson@yale.edu>;

²Marmarth Research Foundation, Marmarth, North Dakota 58643; ³Institut für Geowissenschaften, University of Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany, <walter.joyce@uni-tuebingen.de>; and ⁴Division of Vertebrate Paleontology, Yale Peabody Museum of Natural History, New Haven, CT 06511.

ABSTRACT—New *Palatobaena* material from the Hell Creek Formation (Maastrichtian), including the first skull and shell association, from southwestern North Dakota represents a new species named herein *Palatobaena cohen*. The material consists of 4 skulls, 2 lower jaws, and 2 shells and represents a true biological population (spatially and temporally restricted), which provides unprecedented access to ontogenetic and other intraspecific variation found in this taxon. The skull's round shape and lack of a lingual ridge on the greatly expanded triturating surface indicate its *Palatobaena* affinities, but it differs from both previously existing *Palatobaena* taxa in a number of features. The addition of shell characters to the most inclusive baenid phylogenetic analyses (Maximum parsimony and Bayesian) to date indicate that *Pa. cohen* is sister taxon to the other *Palatobaena* taxa. Notably, both the maximum parsimony analysis and Bayesian analysis provide strong support for *Plesiobaena antiqua* as sister to the *Palatobaena* clade. In addition, both analyses provide strong support for *Stygiochelys estesi* as sister to the Eocene clade of *Baena arenosa* and *Chisternon undatum*, which significantly reduces this clades' ghost lineage. The baenid topology reveals a demonstrably homoplastic trend towards the reduction of the temporal emargination and unique thickening of the posterior portion of the parietals that corresponds with the K/T boundary and is hypothesized to have provided limited protection from increasingly effective mammalian predators.

INTRODUCTION

BAENIDAE IS a species-rich group of paracryptodiran turtles (Joyce, 2007) endemic to North America that arose in the early Cretaceous, diversified in the latest Cretaceous, and went extinct in the Eocene (Gaffney, 1972; Russell, 1975; Hutchison, 1982). The group includes the enigmatic pug-nosed *Palatobaena*, a morphologically disparate turtle. Two species of *Palatobaena* are currently recognized, which combined have a referred age from the Late Cretaceous (Maastrichtian) to early Eocene (Gaffney, 1972; Archibald and Hutchison, 1979). Gaffney (1972) erected its type species *Palatobaena bairdi* based on a fragmentary skull from the Fort Union Formation of the Bighorn Basin of Wyoming. Due to the fragmentary nature of the then available Upper Cretaceous and early Paleocene material, he referred all material to this taxon. With the addition of more cranial material, Archibald and Hutchison (1979) described a second species, *P. gaffneyi*, on the basis of a complete skull from the Eocene (Wasatchian North American Land Mammal Age). Although Archibald and Hutchison (1979) did not undertake a revision of *Pa. bairdi*, they did note differences between the Cretaceous and Paleocene material referred to this taxon. More recently, Holroyd and Hutchison (2002) argued that a newly discovered Paleocene skull (UCMP 131953) indicated that the Cretaceous *Palatobaena* material represented a new species distinct from *Pa. bairdi*, but did not undertake a formal description of that taxon.

Palatobaena's position within Baenidae has long been uncertain due to the fragmentary nature of the available cranial material and the lack of referred shells. Gaffney (1972) tentatively regarded *Pa. bairdi* as sister to the Eocene baenid clade *Chisternon undatum* (Leidy, 1871) and *Baena arenosa* Leidy, 1870. With additional cranial material, Archibald and Hutchison (1979) re-evaluated *Palatobaena's* position and argued that it was most closely related to *Eubaena cephalica* (Hay, 1904), *Plesiobaena antiqua* (Lambe, 1902), and *Stygiochelys estesi* Gaffney and Hiatt, 1971 based on these taxa's expanded triturating surfaces. A larger analysis by Gaffney and Meylan (1988), which incorporated all baenids then known from skulls, placed *Pl. antiqua* in a basal

position and *Pa. bairdi* as sister taxon to *S. estesi*, which together were the most derived baenid taxa.

A previously undescribed locality from the Hell Creek Formation of southwestern North Dakota has yielded numerous *Palatobaena* specimens, including the first referable shells. This study confirms that the Upper Cretaceous material represents a new species of *Palatobaena*, which is formally named herein. The material from this single locality represents the most nearly complete skeleton known for *Palatobaena* and thus provides new information about skull and shell structure for this taxon. Furthermore, multiple *Palatobaena* specimens were recovered from the locality, which provides unprecedented access to ontogenetic and individual variation. Here we revisit all previously referred *Palatobaena* material, diagnose and describe the new species, describe the individual and ontogenetic variation found in the skull, and revise the phylogeny of Baenidae.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York City, New York; CCM, Carter County Museum, Ekalaka, Montana; FMNH, Field Museum of Natural History, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MRF, Marmarth Research Foundation, Marmarth, North Dakota; UCM, University of Colorado Museum, Boulder, Colorado; UCMP, University of California Museum of Paleontology, Berkeley, California; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut.

GEOLOGICAL SETTING AND TAPHONOMY

The locality is located in Bucklin Township, Slope County, near Marmarth, North Dakota. More detailed information is available to qualified persons upon request from MRF or YPM. Sediments exposed at the locality are part of the Hell Creek Formation (latest Maastrichtian) (Fig. 1). The site is located in the lower third of the formation, approximately 65 m below the formational contact with the Fort Union Formation. The locality, named Turtle Graveyard, has yielded an unsurpassed number of slightly disarticulated baenid turtle specimens including more than 70 shells, 35 skulls, and other postcranial remains of three baenid taxa, as well as

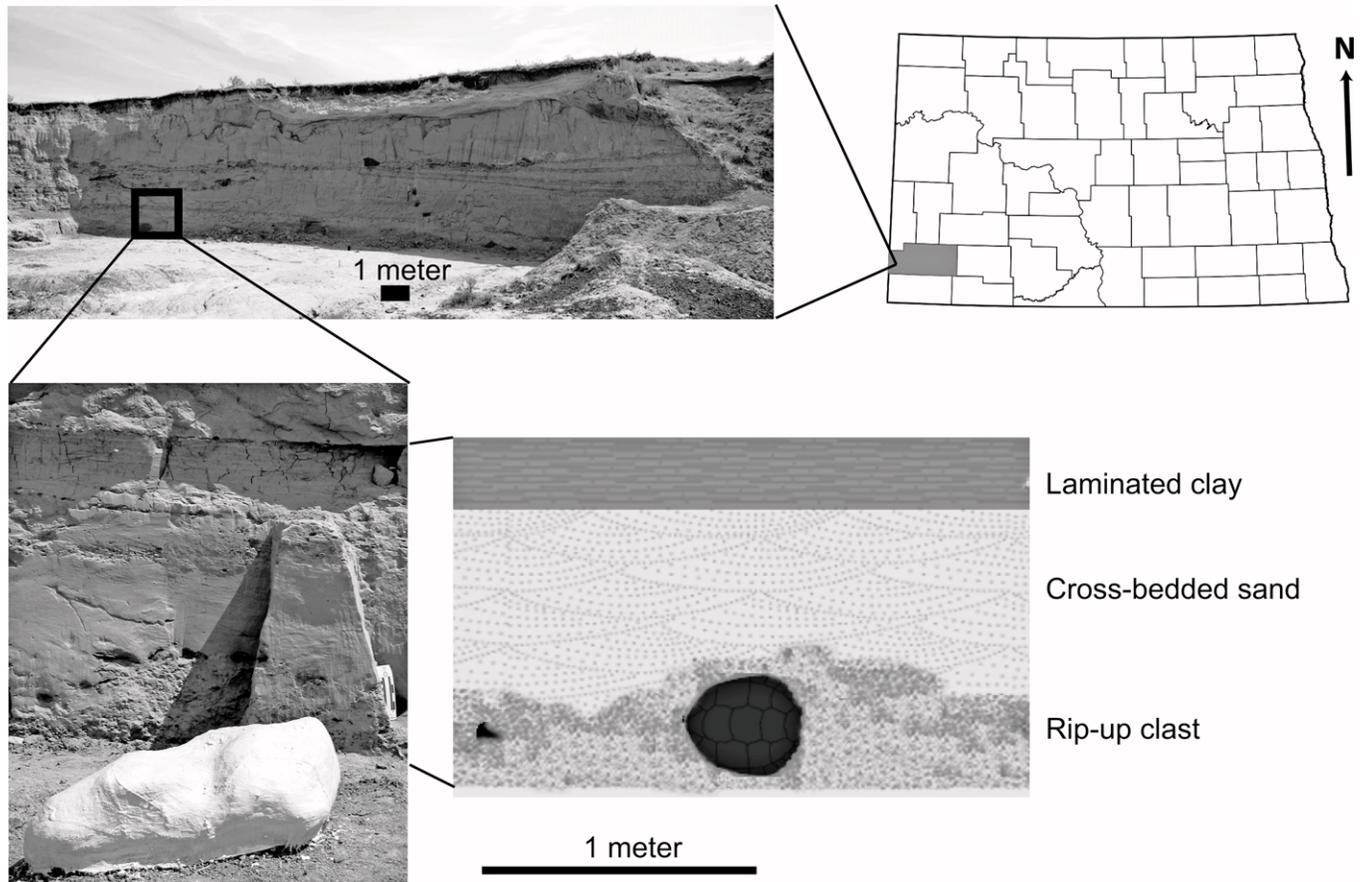


FIGURE 1—Turtle Graveyard locality located in Slope County southwestern North Dakota in the Hell Creek Formation (Maastrichtian). Turtles are buried in a structureless, unconsolidated sandstone unit with rip-up clast stringers, which is overlain by a cross bedded sand unit and laminated clay unit.

partial, disarticulated trionychid turtle skeletons, teeth, and cartilaginous jaw elements from the ray fish *Myledaphus*, a lone unidentified crocodile dentary, and a few isolated bones from an unidentified theropod (Fig. 2). *Palatobaena* specimens represent only a small fraction of the fossil material but nevertheless consist of four skulls, two lower jaws, and two shells.

The fossil-bearing layer varies laterally in thickness from 80–120 cm over a distance of 16 m (Fig. 1). It lies on top of an undulatory, tabular mudstone with scour marks bearing 245° southeast. Directly overlying the scoured bed is a structureless layer of rip-up clasts and sand that varies in thickness from 1–12 cm (Fig. 1). The clasts are typically 1 or 2 cm in diameter; however, clasts 3 to 4 cm in diameter are not uncommon. The fossil material, as well as numerous lignified logs, is found in or on top of this layer (Fig. 1). Hollow sandstone moulds up to 10 cm in diameter preserve many of these logs three dimensionally. Branches and turtle shells commonly extend into the overlying unconsolidated sandstone layer. The upper portion of this fining upward unit preserves heterolithic cross-beds dipping approximately 20° to the southeast. The bed is 60–70 cm thick in the southeastern part of the quarry and it pinches out into a laminated clay unit on the northwestern portion of the quarry. Discontinuous lag stringers with clay clasts ranging in size from a few mm to 3 cm in diameter are found throughout this portion of the sequence. This layer is overlain with a laminated clay unit, which varies laterally in thickness from 2–18 cm (Fig. 1). The textural and structural data indicate that the entire sequence was the result of deposition from fluvial currents of decreasing energy (Boggs, 2006).

The unit in which the fossils are preserved is overlain with a series of sandstone units, a large structureless conglomerate-like

unit with clay clasts up to 40 cm in diameter that cuts into the underlying sandstone unit and pinches out to the southeast, and a series of laminated clay units that lie in between sandstone units (Fig. 1). The alternating sequence of high velocity sandstone deposits and zero velocity laminated clay units, as well as the incising channels, indicate an ephemeral paleo-environment, such as a pond or shallow stream, which would periodically flood and dry out (Murphy et al., 2003).

An ephemeral pond interpretation is further supported by the presence of only omnivorous and molluscivorous turtles and small, molluscivorous ray fish (*Myledaphus*), and the absence of the normally ubiquitous actinopterygians (e.g., garfish), whose presence would indicate a larger, more stable body of water. A wide range in the degree of articulation, from mostly articulated skeletons to disarticulated shells, is evident, which indicates differences in the length of post-mortem decay. Most commonly, the fused baenid shells and skulls (Hutchison, 1984) are disarticulated from their appendicular skeleton, although articulated elements are not uncommon. Appendicular skeletons and skulls are often closely associated with their shells (determined via size comparisons), indicating that they were not transported a significant distance after their death. Significantly, many of the skulls have the stapes intact and some have the hyoid elements preserved, indicating that the skin was still attached to these specimens at time of deposition. Many of the specimens are preserved in close juxtaposition with the logs, which range in size from 6–38 cm in diameter. Overall, the sedimentology and the general layout of the specimens (Figs. 1, 2) indicate an after-death assemblage, or thanatocoenosis. In addition, the close association but differential preservation of the skeletons and number of large logs with very few leaves found at the site indicates a taphonomic history in

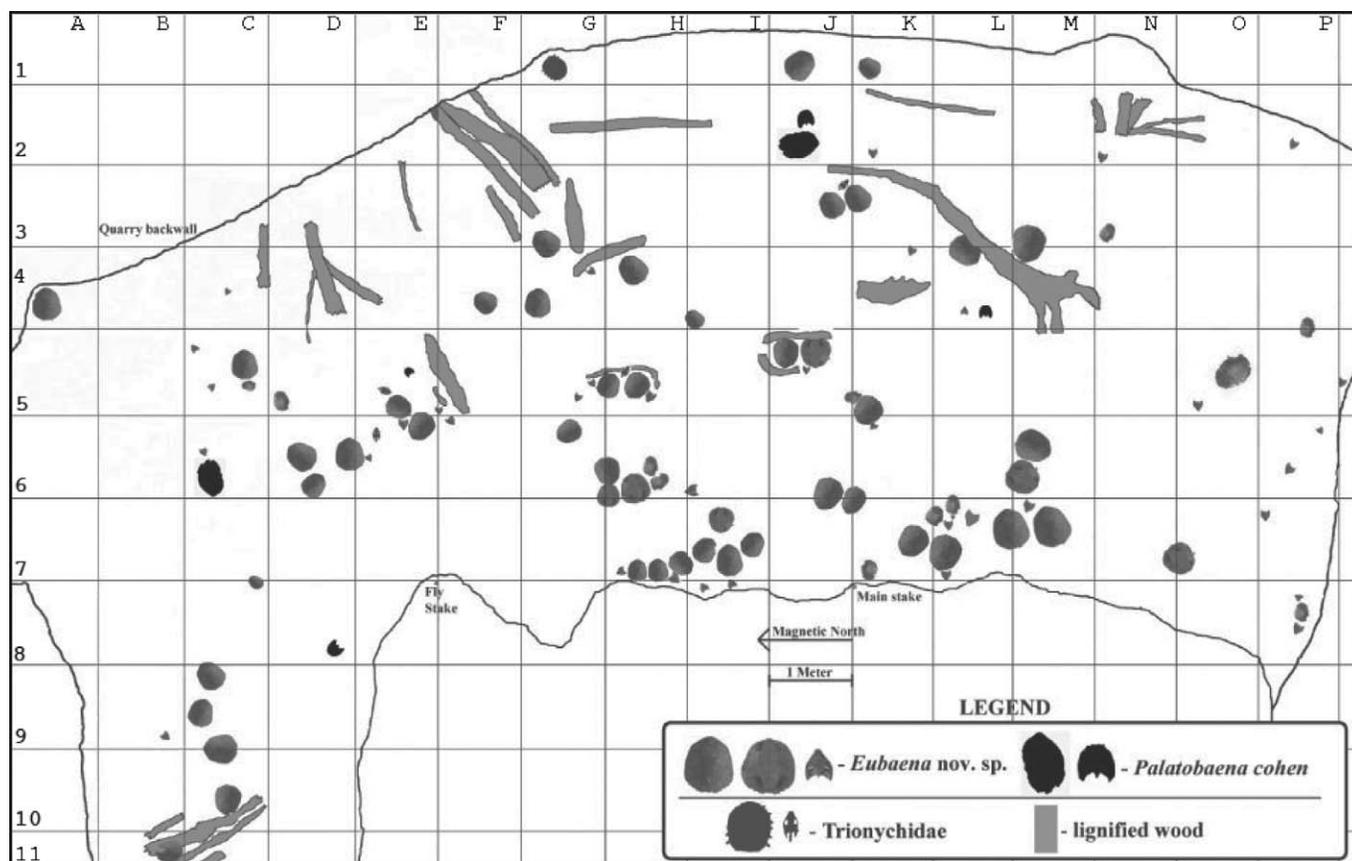


FIGURE 2—Digitized field map of Turtle Graveyard with coordinates of *Palatobaena cohen* material discussed in the text: J/2, YPM 57498 (type), skull, lower jaw and shell; L/4, MRF-257; C/6, MRF-123; D/8, MRF-259; E/5, MRF-263. The *P. cohen* material was found with abundant *Eubaena* material, as well as some trionychid individuals and several lignified logs.

which an oxbow or pond environment dried up during a drought, killing the trapped turtles, ray fish and surrounding trees at different time periods. The turtles were subsequently buried without being transported a significant distance in a debris-type flow deposit when a nearby river flooded. Most importantly, the thanatocoenosis appears to represent a true biological population (temporally and spatially restricted) of multiple species of turtle, one of which is the new species of *Palatobaena* presented herein.

ASSOCIATING SHELLS WITH SKULLS

Complete fossil turtle skeletons are exceedingly rare in the fossil record and most taxa are thus based on shells or skulls only. Although baenid systematics used to suffer from the resulting parataxonomy (see Gaffney, 1972), new finds have provided a few affirmative associations of skulls and shells (e.g., Brinkman and Nicholls, 1991; Brinkman and Nicholls, 1993). Both known species of *Palatobaena* are based on cranial material, and no shells have previously been found in close association with cranial material. As such, the possibility thus remains that *Palatobaena* is a junior synonym of a more historically recognized shell taxon, such as '*Baena*' *hatcheri* Hay, 1901 or *Thescelus insiliens* Hay, 1908.

Although we herein report confidently on the first skull/shell association for any species of *Palatobaena*, none of the referred specimens were found in actual articulation with one another. Instead, all referred cranial and shell material (four skulls, two mandibles, and two shells) was found in a single quarry (Fig. 2) intermixed with dozens of other skulls and shells (Fig. 2; also see Geological Setting above). Two primary considerations, however, allow us to associate this material. In particular, although more than 80 baenid shells were recovered from the quarry, the vast

majority can be classified as one shell morph whereas only two present a second shell morph. Similarly, of approximately 40 available skulls, the vast majority can be grouped in one skull morph (diagnostic of *Eubaena*) whereas only four comprise a second skull morph (diagnostic of *Palatobaena*). Interestingly, the more common shell and skull morph both comprise ontogenetic sequences, whereas the less common shell and skull morph are rather homogenous in size. More importantly, some of the common skull and shell morphs were found in articulation and thus unambiguously belong to the same taxon. What remains is the less common shell and skull morph. In addition, the holotype's skull, lower jaw, and shell were all found within a meter of one another (Fig. 2). Although it is possible that a large assemblage of turtles came to rest with little transport and that one less common species is known from skulls only and the other from shells only, we think it to be significantly more likely that the less common shell and skull morphs belong together. Additional finds will be able to test this assertion.

SYSTEMATIC PALEONTOLOGY

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

Type species.—*Palatobaena bairdi* Gaffney, 1972.

PALATOBAENA BAIRDI Gaffney, 1972

Type specimen.—YPM-PU 16839, a partially distorted right half of a skull.

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

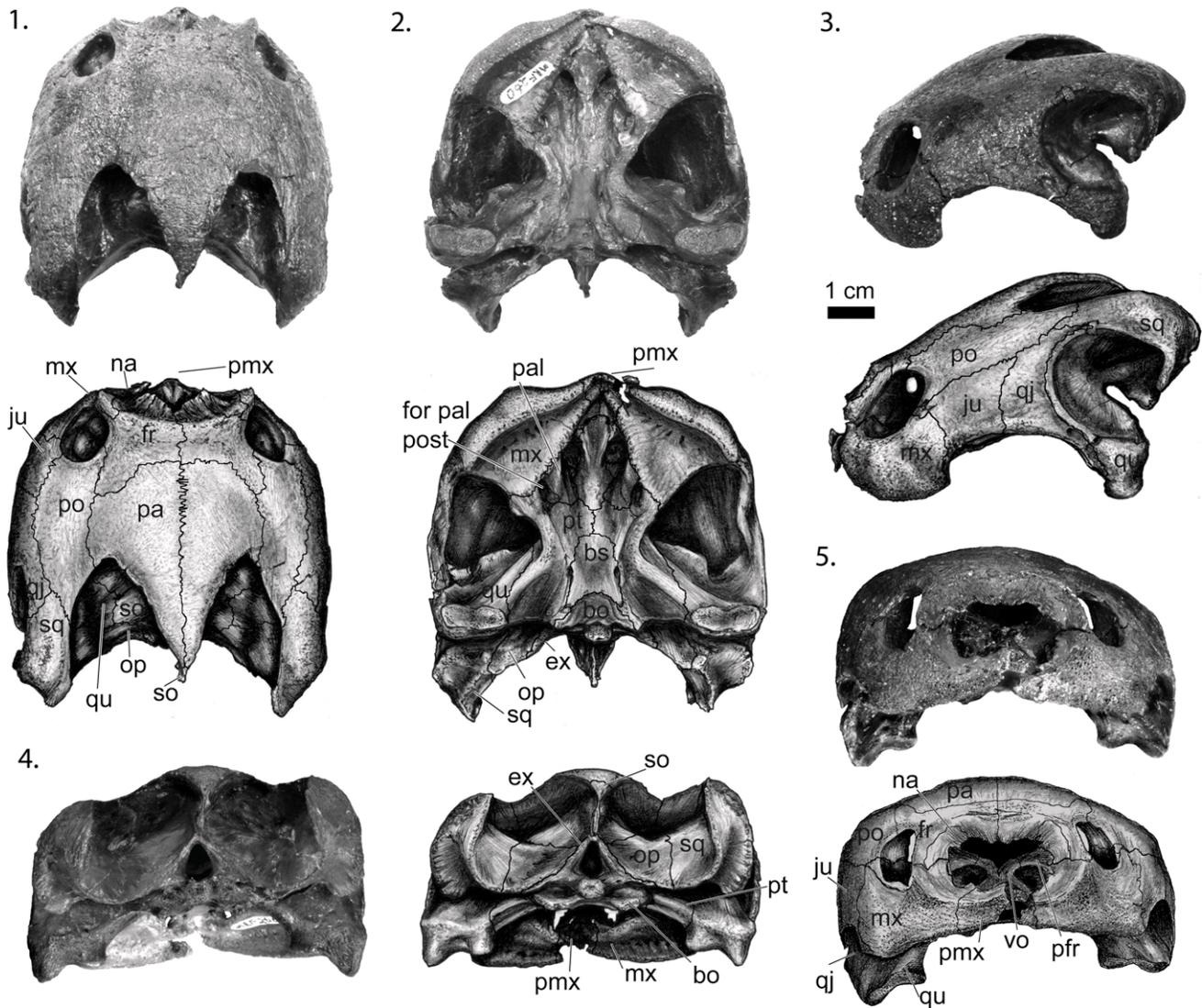


FIGURE 3.—*Palatobaena cohen* skull (YPM 57498, type) from Turtle Graveyard. 1, photograph (top) and illustration (bottom) in dorsal view; 2, photograph (top) and illustration (bottom) in ventral view; 3, photograph (top) and illustration (bottom) in lateral view; 4, photograph (left) and illustration (right) in posterior view; 5, photograph (top) and illustration (bottom) in anterior view. Abbreviations: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pmx, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadrate-jugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

Type horizon.—Fort Union Formation, early Tiffanian (late Paleocene).

Referred material based on synapomorphies.—CCM 77-11, complete skull; YPM-PU 17108, complete dentary.

Referred material based on equivalent stratigraphy.—YPM-PU 17153, right maxilla; YPM-PU 16947, right maxilla (list of material revised from that presented by Archibald and Hutchison, 1979).

PALATOBAENA GAFFNEYI Archibald and Hutchison, 1979

Type specimen.—UCMP 114529, nearly complete skull lacking the right orbital region.

Type locality.—UCMP V71238, Sweetwater County, Wyoming.

Type horizon.—Main body of Wasatch Formation, Wasatchian (early Eocene).

Referred material based on equivalent stratigraphy.—UCMP 173700, right and left dentary; UCMP 129724, juvenile right dentary.

PALATOBAENA COHEN, new species
(Figs. 3, 5, 6)

Type specimen.—YPM 57498, a complete uncrushed skull, mandible, and shell (see comments below).

Type locality and age.—Bucklin Township, Slope County, near Marmarth, North Dakota (More detailed information is available to qualified persons upon request from MRF or YPM); Hell Creek Formation (latest Maastrichtian), approximately 65 meters below the Fort Union formational contact.

Referred specimens based on synapomorphies.—MRF 257, complete skull and mandible; MRF 259, complete skull; MRF 263, complete skull; MRF 123, shell missing part of carapace; FMNH PR 829, anterior part of skull; UCM 37738, skull and jaw fragments; UCMP 114539, fragmentary skull and jaws; UCMP 131953, skull; UCMP 131952, fragmentary skull; AMNH 8277, complete lower jaws.

Other referred specimens based on equivalent stratigraphy.—UCMP 114680, right and left jaw halves; UCMP 114686, left maxilla; AMNH 2603, nearly complete lower jaws; MCZ

3515, right maxilla; UCMP 114644, left maxilla; UCMP 117154, dentary; UCMP 14656, right quadrate; UCMP 131701, incomplete skull; UCMP 131702, incomplete skull; UCMP 137358, left mandible; UCMP 172257, left maxilla; UCMP 129934, dentary; UCMP 159255, fragmentary skull; UCM 49229, left dentary; UCM 49230, right and left dentary. All of these specimens were previously referred to *Pa. bairdi* (Gaffney, 1972; Archibald and Hutchison, 1979; Gaffney, 1982; Hutchison and Archibald, 1986; Holroyd and Hutchison, 2002; Hutchison and Holroyd, 2003).

Etymology.—The species honors Steven Cohen, an avid supporter of fossil turtle research and the Marmarth Research Foundation.

Diagnosis.—Member of Baenidae based on location of the foramen posterius canalis carotici interni between the pterygoid and halfway along basisphenoid; posteriorly expanded triturating surfaces with lingual ridge reduced posteriorly; small or absent dorsal lappet of prefrontal; and well developed pterygoid and basioccipital contact. Member of *Palatobaena* based on oval skull shape, dorsally oriented orbits, rounded snout, processus pterygoideus externus nearly absent, lack of lingual ridge on triturating surface, lack of nasal midline contact, and obtuse angle formed between swollen maxillae. The following characters distinguish it from *Palatobaena bairdi* and *Palatobaena gaffneyi*: bone thin near the upper temporal emargination; slender crista supraoccipitalis that comes to a point posteriorly and has little to no exposure on the skull roof.

The following characters distinguishes *Pa. cohen* from *Pa. bairdi*: larger contribution of frontal to orbital margin; frontals extend posteriorly beyond posterior margin of orbit; upper temporal emargination extending anterior to the processus trochlearis oticum; smooth reflected rim on the dorsal margin of the cheek emargination; labial ridge deflected ventrally by about 20° maximum skull width greater than maximum skull length (Table 1); vomer about 60° from the plane of the basicranium.

The following characters distinguishes *Pa. cohen* from *Pa. gaffneyi*: orbit larger than maxillary shelf below orbit; well developed pterygoid contact; nasals excavated; processus inferior parietalis forming two distinct crista anteriorly; nasal sulcus extending across anterior margin of frontals; tubercula basioccipitale divergent and extending posteriorly nearly as far as occipital condyle articulation.

DESCRIPTION OF PALATOBAENA COHEN

Skull.—Holotype YPM 57498 (Fig. 3) includes a large, beautifully preserved skull with no distortion. The description of the skull is based on the holotype YPM 57498 and three other perfect skulls of varying sizes, MRF 257, MRF 259, MRF 263 (Table 1), all of which were collected from the same locality and thus document variation and growth within a single population (Fig. 4).

The skull is round with the width slightly greater than the length, as in *Palatobaena gaffneyi* (Table 1). The upper temporal emargination of the skull is deeper than that found in either *Palatobaena bairdi* or *Pa. gaffneyi*. It reaches anterior to the processus trochlearis oticum. In contrast to both *Pa. bairdi* and *Pa. gaffneyi*, the bone near this emargination is thin and the dorsal exposure of the crista supraoccipitalis is slight. Unlike *Pa. bairdi* and *Pa. gaffneyi*, which have a square or blunt posterior end/point to the crista supraoccipitalis, respectively, *Pa. cohen* has a slender crista supraoccipitalis that comes to a point beyond the level of the foramen magnum. As in other baenids, the cheek region is moderately emarginated, with the lower temporal emargination barely reaching dorsally to the level of the ventral margin of the orbit. The arc formed by the cheek emargination is asymmetrical; the maxillary portion is shorter and steeper than that of the quadratojugal and jugal. Similar to *Pa. gaffneyi*, the dorsal margin of the cheek emargination has a smooth, reflected rim. In dorsal view, the orbits are oriented dorsally and are partially inset in a

deep recess of the maxilla, as in the other *Palatobaena* taxa. Unlike *Pa. gaffneyi*, which has a small orbit, the orbit is large, its diameter being greater than the depth of the maxilla below the orbit. Like *Pa. gaffneyi* and *Pa. bairdi*, the inter-orbital width is wide, wider than in any other baenid. In dorsal view there is a broad curve to the anterior portion of the skull. Two of the four skulls have visible scale sulci on the skull roof (Fig. 4).

The parietals are longer than their maximum combined width. As in other baenids except *Hayemys latifrons* Gaffney, 1972, they are the major element of the dorsal skull roof. They have a broadly curved anterior edge that articulates with the frontal. Laterally, the parietal contacts the postorbital. Posteriorly the parietals come to a point over the crista supraoccipitalis with little to no overhang. Similar to all other baenids except the other *Palatobaena* taxa and *B. arenosa* and *C. undatum*, the parietal is very thin near the temporal emargination. The processus inferior parietalis contributes to the formation of the lateral wall of the braincase. The anterior tip of this process contacts the palatine. Between this contact and the foramen nervi trigemini, the process rests on the pterygoid. The parietal forms the anterior edge of the foramen nervi trigemini and sends a slender process along the prootic to form the posterior edge of that foramen as well.

The frontals are slightly rectangular with a posterolaterally protruding process. This lateral wing extends well posterior to the posterior-most portion of the orbital margin. The frontals are wider than long, and anteriorly they terminate before or at the posterior margin of the premaxillae. Each frontal contacts the nasal, maxilla, and prefrontal anteriorly. Unlike in other baenids, the frontals are the primary contributors to the external narial opening. Posteriorly, the frontals contact the parietals. A large portion of the frontal enters into the margin of the orbit between the prefrontal and postorbital.

In dorsal view, the nasals are small wedge-shaped elements that taper posterolaterally to form a small portion of the external narial opening. There is a distinct smooth sulcus surrounding the narial opening ventrally and laterally. The lateral rim of this sulcus is slightly flared, interrupting the otherwise rounded outline of the anterior portion of the skull. In anterior view, the sulcus forms a distinct point over the premaxillae. Both *Pa. cohen* and *Pa. bairdi* have a dorsal semi-circular ridge that runs around the external narial opening and over the frontals and is connected by an anterior-dorsal projection from each maxillae. In between this ridge and the external narial opening, the bone is very rugose, is lower than the rest of the skull roof, and is greatly reduced. This feature is absent in *Pa. gaffneyi*. In anterior view, the nasals are large strip-like elements that extend posteriorly well into the narial opening and medially contact the maxilla and prefrontal. The prefrontal is not exposed on the skull roof. As in other *Palatobaena* taxa, the maxilla is swollen compared to other baenids, i.e., the bone is greatly thickened along the labial margin. It is a broad suborbital bar that forms the lateral surface of the face. The maxilla forms the ventral margin and floor of the fossa orbitalis. It contacts the premaxillae, vomer, palatine and prefrontal medially, pterygoid and jugal posteriorly, and the nasal and frontal dorsally. A process on the posterior portion of the maxilla extends dorsally just posterior to the orbit in the two larger specimens, constricting the jugal's contribution to the orbit in these two specimens.

In ventral view, the triturating surface is a flat, wide, triangular crushing surface that lacks a lingual ridge both anteriorly and posteriorly. Posteriorly, the triturating surface is virtually flush with the palatine and pterygoid surfaces. The labial triturating surface is fat and blunt compared to other baenid taxa. The labial ridges meet to form an obtuse angle, approximately 110–120°, that is similar to the angle found in *Pa. gaffneyi*. The triturating surface narrows to a small sliver on the premaxillae, but nevertheless forms a complete upside down 'U'. The premaxillae are wedge-like elements that form the anterior edge of the foramen praepalatium. The premaxillae contact the maxillae and vomer

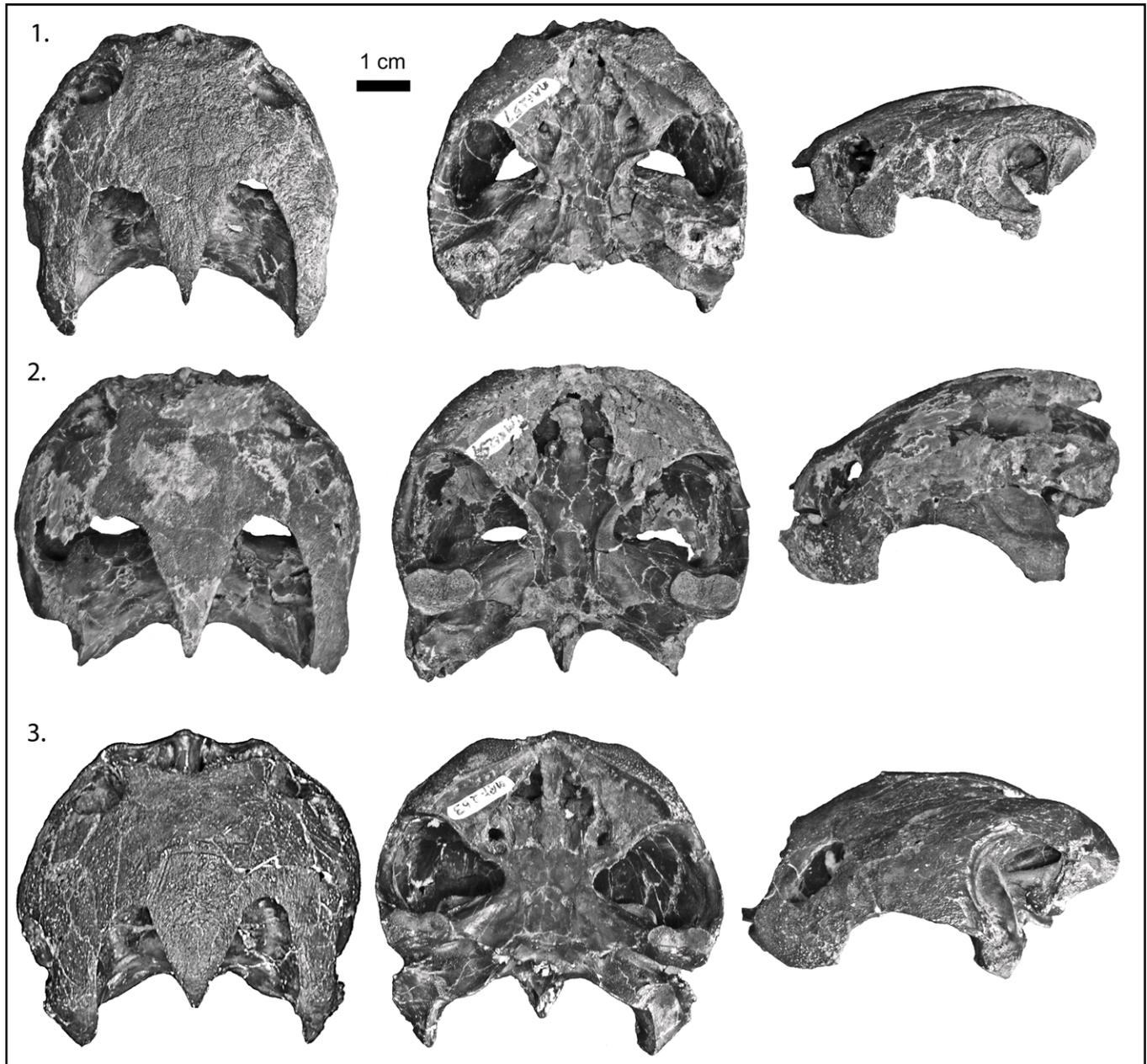


FIGURE 4—Photographs (left page) and illustrations (right page) of *Palatobaena cohen* skull material from Turtle Graveyard showing ontogenetic and other intraspecific variation; 1, MRF 257 in dorsal, ventral, and lateral view; 2, MRF 259 in dorsal, ventral, and lateral view; 3, MRF 263 in dorsal, ventral, and lateral view.

posteriorly. The vomer is large, as in the other *Palatobaena* taxa. The posterior portion of the vomer expands laterally and contacts the palatines laterally and the pterygoids posteriorly. As in the other *Palatobaena* taxa, the vomer's contact with the pterygoids is curved. The palatines and pterygoids form the foramen palatine posterius as in other baenids except *H. latifrons*, *Stygiochelys estesi*, and *Chisternon undatum*. The processus pterygoideus externus is greatly reduced, similar to the other *Palatobaena* taxa. The reduction appears to be linked with the high coronoid process of the lower jaw. This reduction of the processus pterygoideus externus probably allows the lower jaw to be fully closed without contacting bone. The muscle attachment site of the pterygoideus musculature runs as a crest along the entire length of the pterygoid and bifurcates into a lateral and medial crest just posterior to the foramen palatinum posterius. A pit is present between the

splitting crista and foramen palatinum posterius. The pit and lateral and medial crista around the foramen palatinum posterius is reduced in *Pa. bairdi* and absent in *Pa. gaffneyi*. Unlike in *Pa. gaffneyi*, a well-developed contact between the pterygoids is present. The basisphenoid is long and pentagonal in shape. The posterior foramen of the internal carotid artery is located halfway along the basisphenoid and pterygoid. The basisphenoid contacts the basioccipital posteriorly. The basioccipital forms a relatively long contact with the pterygoids posterolaterally. A pronounced basis tuberculi basalis is present dorsally to the basisphenoid and basioccipital. Posteriorly, the basioccipital tuberculum protrude to almost the level of the occipital condyle. These very thin, rectangular protuberances are flat mediolaterally and do not angle downward laterally.

In lateral view, the preorbital skull length is very short, giving

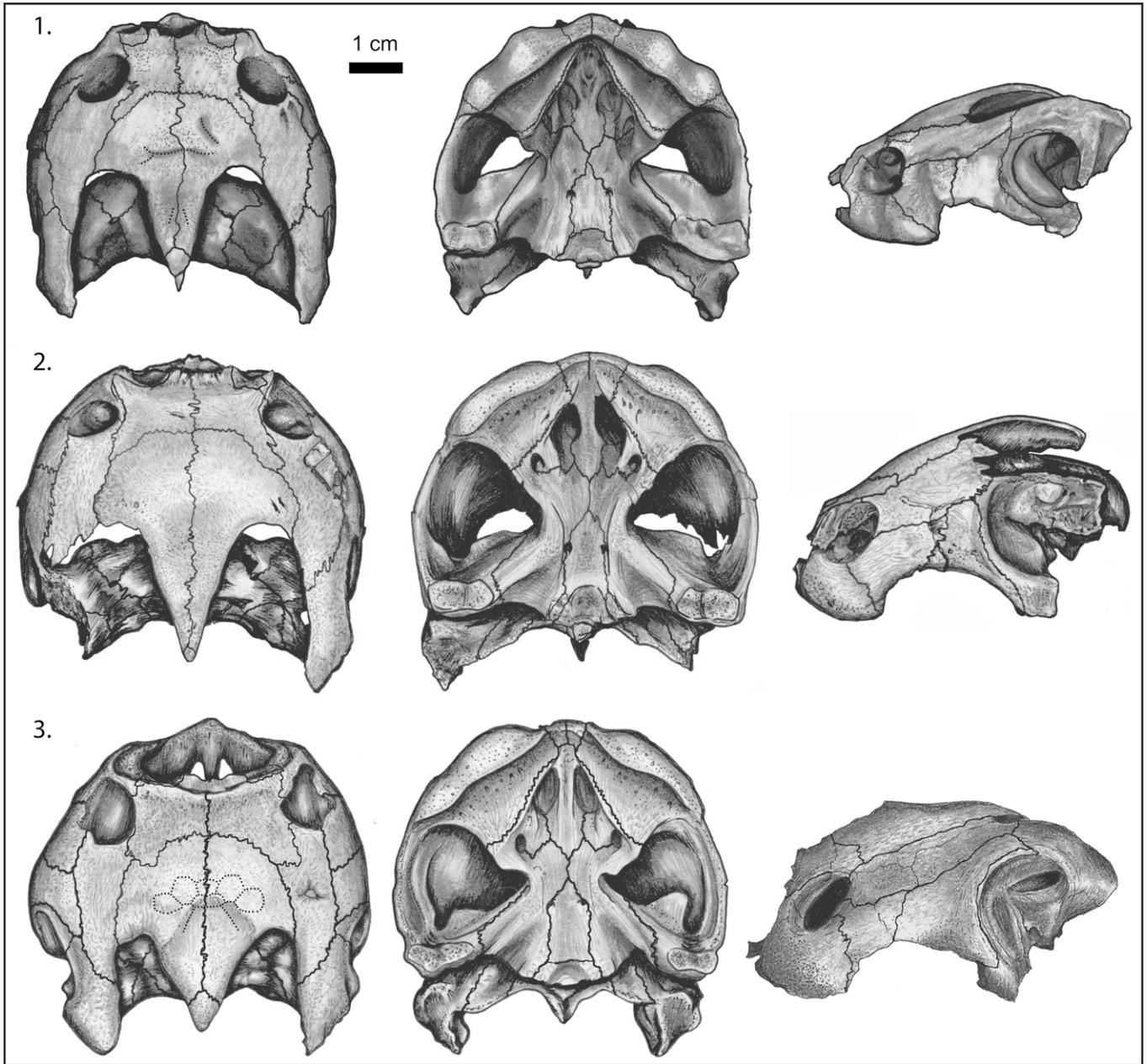


FIGURE 4—Continued.

the skull a very blunt appearance. The cheek region of the maxilla is as high as the vertical diameter of the orbit. The cavum tympani is kidney shaped, but the antrum postoticum is deep but not inflated. The jugal is a large bone that has a large exposure in the orbital margin in the smaller skulls, but has a limited exposure in the largest individual, thus perhaps hinting at an ontogenetic change. The jugal contacts the postorbital dorsally and the quadratojugal posteriorly. The postorbital is a broad bar that enters the orbital margin anteriorly and the temporal emargination posteriorly. The quadratojugal is C-shaped and lacks an anterior extension. The curved portion of the C-shape ends just anterior to the cavum tympanum. The quadratojugal overlies the quadrate ventrally and contacts a small portion of the squamosal dorsally. The anterior portion of the squamosal forms a wedge between the postorbital dorsally and the quadratojugal ventrally.

The ear region in *Pa. cohen* is overall quite similar to other

baenids. The incisura columella auris encloses a distinctly elongate space, which contains the Eustachian tube and stapes. Both stapes are preserved in the type and MRF 257 and have a long, slender, rod-like morphology. The supraoccipital and quadrate contact one another posterior to the stapedia foramen and thus exclude the opisthotic from entering that structure. The supraoccipital roofs the foramen magnum, which is oblong in shape. The occipital condyle below the foramen magnum is round and small.

Mandible.—The lower jaws of MRF 257 and YPM 57498 (type) were both found closely associated (<20 cm) with their skulls and, most importantly, articulate perfectly with them as well. These mandibles are consequently grouped with these crania with great confidence.

Overall, the dentary is very massive. The triturating surface formed by the dentary is flat, triangular, and anterolaterally tilted. As in *Pa. bairdi*, but unlike the case of all other baenids, the

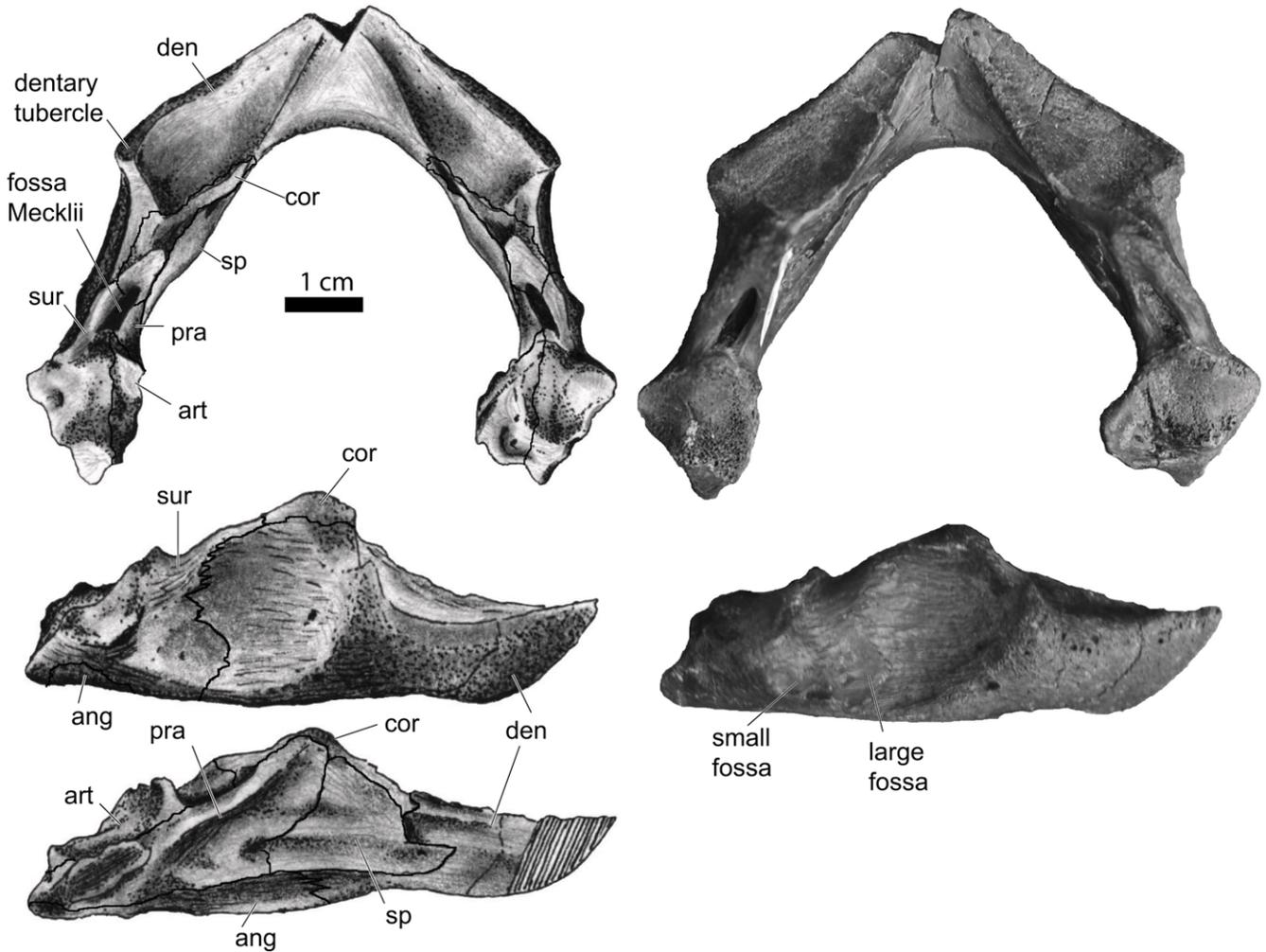


FIGURE 5—*Palatobaena cohen* lower jaw (YPM 57498, type) illustrations in dorsal, lateral, and medial view (left) and photographs in dorsal and lateral view (right). Abbreviations: ang, angular; art, articular; cor, coronoid; den, dentary; pra, prearticular; sp, splenial; sur, surangular.

labial ridge is thus higher than the lingual ridge. The labial ridges come together to form an approximately 45° angle, whereas the labial ridges form an approximately 115° angle. A distinct tubercle is present on the posterolateral surface of the dentary (Fig. 5). This tubercle is also present in *Pa. bairdi*, *Pa. gaffneyi*, *S. estesi*, and *B. arenosa*. The coronoid process is well developed, as in

other baenids. An anteromedial portion of the coronoid forms the posteromedial portion of the triturating surface. Medially, the coronoid contacts the splenial. The splenial is a large flat bone that forms the anterior edge of the intermandibular caudal foramen and the anteromedial wall of the fossa Meckelii. The splenial contacts the long, low-lying angular ventrally. These bones, along

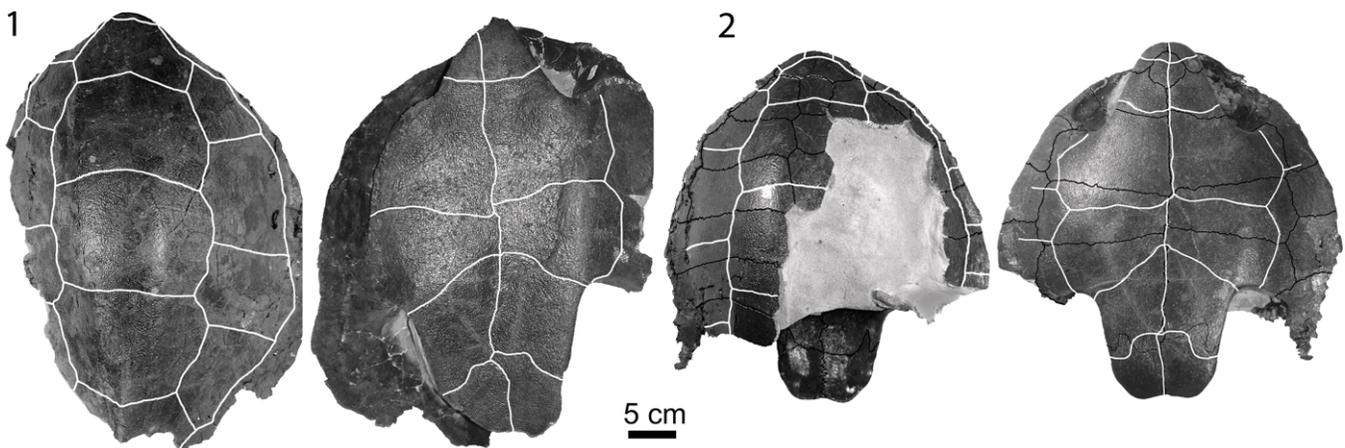


FIGURE 6—*Palatobaena cohen* shell. 1, YPM 57498 (type) shell in dorsal and ventral view; 2, MRF 123 shell in dorsal and ventral view.

TABLE 1—Measurements of the skull of *Palatobaena cohen*. The length of the skull roof is from the anterior, midline portion of the apertura narium externa to the posterior tip of the supraoccipital crest. The maximum width is measured just anterior to the quadrates.

Specimen	Length of skull roof	Occipital condyle to premaxillae width	Maximum width	Distance between orbits	Angle between maxillae
YPM 57498	61.75 mm	60 mm	76 mm	33 mm	120°
MRF 259	56 mm	54.25 mm	71.6 mm	29 mm	115°
MRF 263	49.5 mm	51.5 mm	73 mm	30 mm	120°
MRF 258	52 mm	51.25 mm	65 mm	25 mm	110°

with the prearticular, form the intermandibular caudal foramen. The posterior articular surface of the prearticular is well developed, more so than in *Pa. bairdi*. The prearticular, articular, coronoid, and surangular form the fossa Meckelii. A small fossa is present on the surangular, just posterior to the large adductor fossa ventral to the coronoid process. The surangular suture with the dentary is relatively straight, as in *Pa. bairdi*.

Shell.—The shell of YPM 57498 was found closely associated (<30 cm) with its skull and lower jaw. The posterior and left margin of the carapace of YPM 57498 was fractured prior to burial and is thus missing. The straight carapace length is 28.5 cm and shows no distortion. The shell is fully fused and all sutures are thus obscured. However, a second smaller shell, MRF 123, has open sutures allowing for both scute and sutural contacts to be reconstructed (Fig. 6).

The shell of *Pa. cohen* is generally similar to the shell of *Plesiobaena antiqua*. In dorsal view both shells are oblong (Brinkman, 2003). However, a distinct anterior nuchal projection is evident that is absent in all other baenids. Thus, the anterior half of the shell is triangular in shape. Similar to *Pl. antiqua*, but more distinctly so, the sides of *Pa. cohen*'s shell diverge so slightly that the width across the inguinal buttresses is greater than the width across the auxiliary buttresses. The posterior portion of the shell of the holotype is preserved past the point at which scallops are observed on other baenids and there is no sign of any scalloping otherwise, indicating that serrations were subdued or absent as in *Pl. antiqua* (Brinkman, 2003).

The pattern of scutes on the carapace (Fig. 6) resembles that of *Pl. antiqua* in that a single rectangular cervical scute is present anteriorly, the fifth vertebral scute opens on the posterior edge of the carapace, supramarginal scutes are absent, only four pleural scutes are present, and the vertebral scutes are wider than they are long (Brinkman, 2003). However, *Pa. cohen*'s cervical scute is almost twice as wide as *Pl. antiqua*'s cervical scute. Also, the vertebral scutes found on *Pa. cohen* are much wider than those found on *Pl. antiqua*. The five vertebral scutes cover a major portion of the carapace, a larger portion than in any other baenid. The four pleural scutes extend well onto the peripheral bones thus restricting the marginals to the peripherals.

The smaller shell, MRF 123, preserves the first six marginal scutes. Unlike those of other baenids, the first six marginal scutes are narrow and restricted to the peripheral series. Similar to *Pl. antiqua*, and unlike Maastrichtian forms of *Plesiobaena* sp., the first marginal scute is located entirely on the large, hexagonal shaped nuchal (Brinkman, 2003). The sulci between the remaining marginals are found in the middle portion of the peripheral series. Sutures can only be discerned for the anterior six peripherals. The suture between the first and second peripherals is overlain by the second marginal scute, as is the condition found in other primitive turtles (Brinkman, 2003).

The plastron (Fig. 6) is similar to *Pl. antiqua*'s plastron. The plastron has a subtriangular anterior lobe and a subrectangular posterior lobe that is longer than the anterior lobe. The plastral buttresses extend well onto the visceral surface of the costal

bones. The axillary buttress articulates with the first costal and the inguinal buttress articulates with the fifth costal.

The epiplastra contact each other anterior to the entoplastron. Ventrally, the entoplastron is sub-circular. The hypoplastra contact the posterior tip of the second peripheral element anteriorly and the tip of the fifth peripheral posteriorly. The mesoplastra contact each other along the midline and contact the fifth and sixth peripheral laterally. The hypoplastron contacts at least the fifth and sixth peripheral elements laterally, the mesoplastra anteriorly, one another medially, and the xiphoplastron posteriorly. The suture between the hypoplastron and the xiphoplastron is v-shaped pointing posteriorly.

The anterior region of the plastron may be unique for baenids in that there may be only one pair of gulars. This region is damaged in YPM 57498, but excellently preserved in MRF 123. Sulci are preserved excellently in this specimen, but only one pair of gulars, probably the extragulars, is apparent. The extragular/humeral sulcus passes through the anterior third of the entoplastron. The humeral/pectoral sulcus is relatively straight and is located in the posterior third of the anterior lobe. Laterally, the pectoral scute contacts the first three inframarginal scutes. The pectoral/abdominal sulcus runs fairly straight along the mesoplastron. The abdominal/femoral sulcus is located on the hypoplastron and runs from the base of the posterior lobe anteriorly to just posterior to the contact between the mesoplastra and hypoplastra. Laterally, the abdominal scute contacts the third and fourth inframarginals. Similar to *Pl. antiqua*, the femoral/anal sulcus is S-shaped. It curves anteriorly from the lateral edge of the xiphoplastron over the xiphoplastron-hypoplastron contact and then extends transversely across the midline. Four inframarginal scutes are present. All of them extend laterally onto the peripheral series.

PHYLOGENETIC ANALYSIS

To determine the phylogenetic affinities of *Pa. cohen*, as well as a number of other recently described baenid taxa, Bayesian and maximum parsimony phylogenetic analyses were performed. Sixteen species, consisting of fourteen ingroup and two outgroup taxa, were used in these analyses along with 54 osteological characters with 64 derived character states. A list of all materials and anatomical sources is given in Appendix 1, a list of characters is provided in Appendix 2, and the character matrix is presented in Appendix 3. Missing data was scored as "?." Of 10 multistate characters, five (7, 14, 18, 27, 35) represented morphoclines and were ordered. The remaining characters were run unordered and all characters were given equal weight. The parsimony analysis was performed using PAUP 4.0b10 (Swofford, 2001). The branch and bound search algorithm was used and minimum branch lengths were set to collapse. Support for each node was measured by calculating bootstrap (Felsenstein, 1985) values with 10,000 bootstrap replicates and 100 random sequence addition replicates. We regard bootstrap values of $\geq 70\%$ as strong support and bootstrap values of $\leq 70\%$ as weak support (Hillis and Bull, 1993), while noting that perfect sampling (i.e., a single synapomorphy for each node in a pectinate tree) will achieve bootstrap values no higher than 65%.

To explore its effects, a Bayesian analysis was performed using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). The M_k model for morphology (Lewis, 2001) was used with character type set to "standard" for discrete morphological characters and coding set to "variable" (Clarke and Middleton, 2008). This model is similar to the Jukes-Cantor model of nucleotide change except that it has a variable number of states (prset ratepr=variable) (Ronquist et al., 2005). Analyses were conducted with a random starting tree and run for 5×10^6 generations. Two simultaneous runs and four Markov Chains, one cold and three heated (utilizing default heating values), were sampled every 100 generations. Convergence between the two simultaneous runs was determined

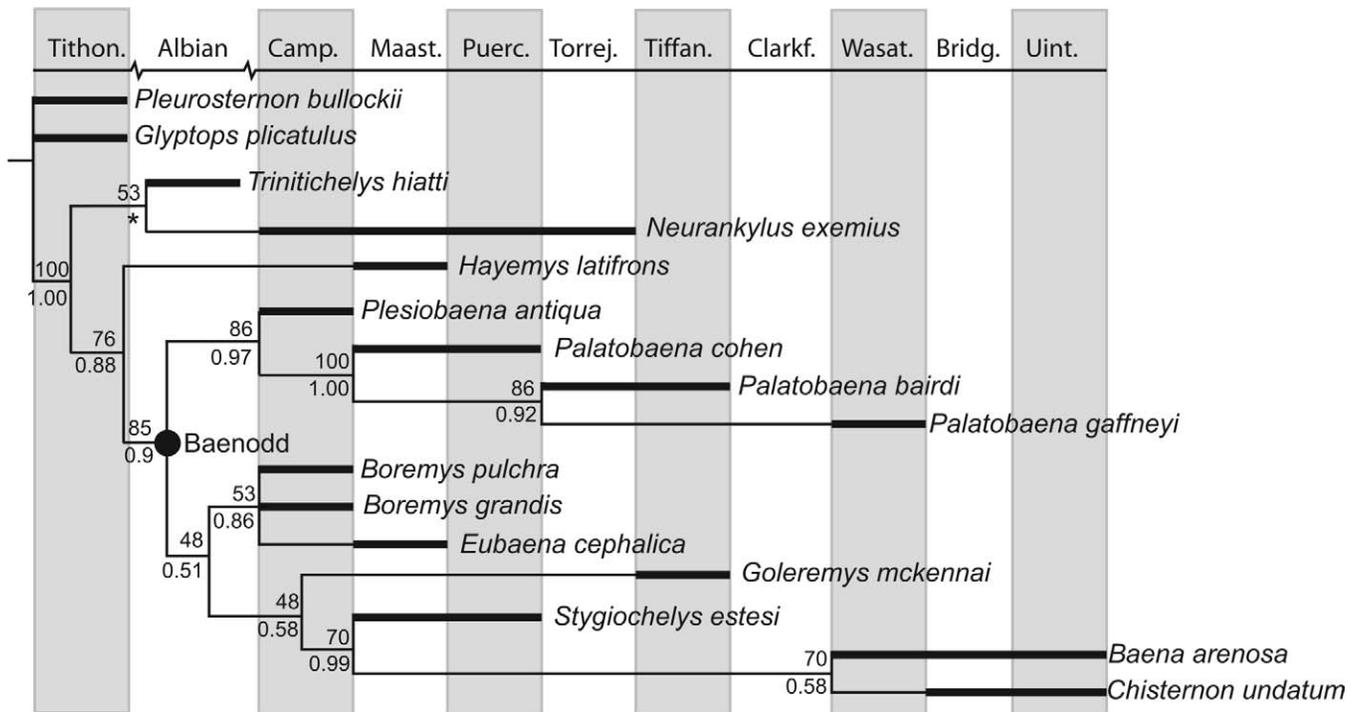


FIGURE 7—Baenidae cladogram mapped against the stratigraphic range from which each taxon has been reported (bold lines). Support for each node is measured using bootstrap frequency (top) and posterior probabilities (bottom). * indicates PP < 0.50.

by the stabilization of the standard deviation of the split frequencies below 0.01. The first 25% of samples (12,500 total) were eliminated in the burn-in. The topology and posterior probability (PP) for all clades in the final majority rule consensus tree are reported and compared to results obtained from maximum parsimony (Fig. 7). We consider PP values of >95% as strong support for a clade, although note that a perfectly sampled dataset would result in PPs no higher than 75%.

A single most parsimonious tree was obtained with a tree length of 98 steps, a consistency index (CI) of 0.6495, a retention index (RI) of 0.7639, and a rescaled consistency index (RC) of 0.4989 (Fig. 7). The tree is fully resolved except for a polytomy formed by *Boremys pulchra* (Lambe, 1906), *Boremys grandis* Gilmore, 1935, and *E. cephalica*. Baenidae is well supported (100% bootstrap) and is diagnosed by several unambiguous synapomorphies including the presence of a well developed labial ridge anteriorly only, midline contact between the pterygoids, small basisphenoid, reduced prefrontal exposure on skull roof and no dorsal epiplastral process. Similar to past phylogenetic analyses (Gaffney and Meylan, 1988; Brinkman and Nicholls, 1993; Joyce, 2007) *Trinitichelys hiatti* Gaffney, 1972, *Neurankylus eximius* Lambe, 1902 and *H. latifrons* are considered the basal most members of Baenidae. *T. hiatti* and *N. eximius* are weakly supported as a clade that is sister group to *H. latifrons* and baenodds. Similar to Brinkman and Nicholls (1993), *E. cephalica* is regarded as being closely related to *Boremys*. Contrary to previous phylogenetic analyses, there is strong support for *Pl. antiqua* as the sister group to *Palatobaena* (86% bootstrap). In addition, *S. estesi* is considered sister group to the *B. arenosa* and *C. undatum* clade (70% bootstrap) which together sit in a more derived topological position compared to previous hypotheses (Gaffney and Meylan, 1988; Joyce, 2007). The *Palatobaena* clade is strongly supported (100% bootstrap) with *Pa. cohen* situated basal to *Pa. bairdi* and *Pa. gaffneyi* (86% bootstrap). *Goleremys mckennai* Hutchison, 2005 is very weakly supported as sister to the *S. estesi* and *B. arenosa*/*C. undatum* clade.

The topology from the Bayesian analysis is nearly identical to

the most parsimonious tree with the only difference being that it does not regard *T. hiatti* and *N. eximius* as a clade. Instead, it places these two taxa in a basal polytomy with *H. latifrons* + Baenodds. As in the parsimony analysis Baenidae is strongly supported (PP = 1.00). There is moderately strong support for *H. latifrons* being more closely related to the baenodds than either *T. hiatti* or *N. eximius* (PP = 0.90). In addition, the Bayesian analysis strongly supports *Pl. antiqua* as sister group to *Palatobaena* (PP = 0.97). *Palatobaena* is strongly supported (PP = 1.00) with *Pa. cohen* as sister group to *Pa. bairdi* and *Pa. gaffneyi* (PP = 0.92). It provides strong support for *S. estesi* as sister to the *B. arenosa* and *C. undatum* clade (PP = 99). There is very weak support for *G. mckennai* as sister to the *S. estesi* and *B. arenosa*/*C. undatum* clade (PP = 0.58).

DISCUSSION

Since the *Pa. cohen* material was found in a single quarry that is both temporally and spatially restricted, all material is derived from a true biological population. True biological populations of fossil vertebrates are rare and, when found, provide access to the intraspecific variation of that taxon. The four skulls are slightly different in size and show minor differences, some of which is interpreted as ontogenetic (Figs. 3, 4). The most notable such change is a reduction of the contribution of the jugal to the orbit margin (Figs. 3, 4). This character is an important character that has been used traditionally to help diagnose many baenid taxa and the significant ontogenetic variation observed in *Pa. cohen* indicates that caution must be used when using this character. In addition, the degree of nasal excavation becomes more extreme in the larger individuals. In the smallest individual, the nasal region extends to the level of the anteriormost portion of the premaxillae, whereas in the larger individuals, the nasal region ends just anterior to the orbits.

A number of other differences among the four individuals do not correlate with size and are thus not attributed to ontogeny (Fig. 4). The amount of supraoccipital exposure on the dorsal skull roof varies, as does the midline contact of the pterygoid.

There is also some variation in the degree of temporal emargination and the angle between the maxillae ranged from 110 to 120°. Finally, the presence and development of scale sulci on the dorsal skull roof varies, with two of the skulls clearly having visible sulci. Despite these differences, the overall morphology is quite consistent within this population of *Pa. cohen*.

The stratigraphic ranges for the three species of *Palatobaena* appear not to overlap. As far as we can tell using diagnostic specimens, *Pa. cohen* extends from the Maastrichtian to the Puercan, *Pa. bairdi* from the Torrejonian to the Tiffanian, whereas *Pa. gaffneyi* is only known from the Wasatchian (Fig. 7). While the Puercan *Palatobaena* specimens are incomplete, three specimens (UCM 37738, UCM 131953, and UCM 131952) share characters with *Pa. cohen*, including a pointed supraoccipital (UCM 131952), frontals which extend posteriorly well beyond the margin of the orbit (UCM 37738 and UCM 131953), maximum width greater than maximum length (UCM 131953), and a relatively large contribution of the frontal to the orbit (UCM 131953). The remaining material is too fragmentary and was assigned to *Pa. cohen* or *Pa. bairdi* based on stratigraphic considerations. Given the three species' stratigraphic ranges do not overlap, their overall morphological similarity, and fragmentary nature of much of the material, it is possible that the three species represent an anagenetic sequence.

There are a number of general changes in the skull morphology between the Maastrichtian *Pa. cohen* to Wasatchian *Pa. gaffneyi*. There is a general preorbital shortening going from the Maastrichtian to Wasatchian *Palatobaena*. Furthermore, there is a reduction of the sulcus enclosing the apertura narium externus in *Pa. cohen* to *Pa. bairdi* to *Pa. gaffneyi*. As noted by Hutchison and Archibald (1979), there is a general downward rotation of the face going from the *Pa. cohen* to *Pa. bairdi* to a more extreme *Pa. gaffneyi*. Finally, there is an extension of the frontals and a reduction of the tubercula basioccipitalia from the Maastrichtian to Wasatchian *Palatobaena*. Most of these changes are correlated with the presence of a well-developed triturating surface and are likely minor modifications that aid with a molluscivorous diet. As in other vertebrates, a shortened preorbital length increases the force of the animal's bite, which in *Palatobaena*'s case would aid in crushing mollusk shells.

The Cretaceous lower jaws of *Pa. bairdi* thoroughly described by Gaffney (1982) are here considered to be *Pa. cohen* on the basis of the presence of a small fossa on the surangular just posterior to the large adductor fossa ventral to the processus coronoides and a medially expanded articular surface in both the lower jaw associated with the type of *Pa. cohen* (YPM 57498) and the Cretaceous material Gaffney (1982) referred to *Pa. bairdi*. The former character was used by Archibald and Hutchison (1979) to differentiate between a *Plesiobaena putorius* dentary, later identified as *Pa. bairdi* (Gaffney, 1982), and a Cretaceous *Pa. bairdi* dentary, here referred to as *Pa. cohen*, and the character is here used to differentiate between *Pa. bairdi* and *Pa. cohen*.

In contrast to the highly derived skulls of *Palatobaena*, the associated shells are strikingly primitive. The overall morphology is nearly identical to the basal-most baenodid *Pl. antiqua*. Unlike other baenodids, both taxa share the plesiomorphic condition of having 4 supramarginal scutes, an undivided cervical scute, vertebral scutes that are wider than long, scalloping greatly reduced posteriorly, and no preneural bone. While these two lineages share several plesiomorphic shell characters, they also share three shell synapomorphies: the presence of the first marginal scute mostly or entirely on the nuchal bone, presence of fontanelles in adult shells, and the reduction of the gulars. The shell of *Pa. cohen* also has a few autapomorphies including a strong anterior nuchal projection, vertebrals that are significantly wider than long, and the absence of extragulars. The addition of the shell characters for *Palatobaena* significantly changes its phylogenetic position within Baenidae. Previous cladistic and non-cladistic hypotheses

consistently placed *Palatobaena* relatively derived within the Baenidae tree (Gaffney and Meylan, 1988; Archibald, 1977; Archibald and Hutchison, 1979; Hutchison, 2006), usually as sister to *S. estesi*. However, the primitive shell, as well as a number of shell synapomorphies with *Pl. antiqua* pull *Palatobaena* to a more basal position within the tree as sister group to *Pl. antiqua* and the broad crushing surfaces of the jaws must now be considered as having evolved twice.

The new topology differs furthermore from previous cladistic hypotheses in placing the Cretaceous taxon *S. estesi* as sister to the Eocene *B. arenosa* and *C. undatum*. Previous cladistic hypotheses placed *B. arenosa* and *C. undatum* at a more basal position within the tree, thus predicting a long ghost lineage for this clade (Gaffney and Meylan, 1988; Joyce, 2007). Given that *S. estesi* is found in the Cretaceous and even survives into the Paleocene (Hutchison and Holroyd, 2003), the *B. arenosa* and *C. undatum* ghost lineage is significantly reduced. This clade shares a number of synapomorphies including the presence of a wide groove between the lingual ridges of the maxillae, a large posteriorly notched orbit, a jugal that enters the orbital margin, vertebral scutes that are significantly longer than wide, and presence of a nuchal scute.

The topology from the Bayesian phylogenetic analysis is virtually identical to that obtained in the maximum parsimony analysis. The only difference is that the Bayesian analysis does not regard *T. hiatti* and *N. exemius* as a clade, whereas the maximum parsimony analysis provides weak support for this clade. The overall similarity in topology obtained in the two analyses indicates the signal within the data is strong and it doesn't matter which evolutionary model is used (i.e., parsimony or M_k model). In general, the posterior probabilities (PP) from the Bayesian analysis were higher than the bootstrap frequencies from the maximum parsimony analysis. However, this is not the case for the *B. arenosa* and *C. undatum* node. Interestingly, while there is strong bootstrap support for this node (70%), the PP is very low (0.58). This is likely the result of several *B. arenosa* autapomorphies with respect to *S. estesi* and *C. undatum*, which in MrBayes increases its branch length and lowers its PP.

Some curious changes occur in post-Cretaceous baenids. In the *Palatobaena* lineage, *Plesiobaena* lineage, and the *S. estesi/B. arenosa/C. undatum* lineage, there is a demonstrably homoplastic trend towards the reduction of the temporal emargination combined with a demonstrably homoplastic and rather unique thickening of the posterior portion of the parietals. It is apparent that this notable parallelism must be driven by a similar selecting force. Among Paleogene to Eocene turtles, baenids stand out in that they are among the last representatives of the ancient North American lineage Paracryptodira (Joyce, 2007). Unlike various groups of invading turtles, paracryptodires stand out in their inability to retract their head and neck inside the shell for protection. This inability obviously did not pose a serious problem throughout the Cretaceous, as the fossil record demonstrates that this group flourished throughout this time period. However, with the spread of increasingly efficient mammalian predators following the K/T extinction, this inability may have been detrimental. Though speculative, we hypothesize that the growing ossification to the posterior rim of the skull may have been a response to mammalian predation, but that these modifications ultimately proved insufficient to help carry the lineage past the Eocene (Hutchison, 1982).

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APPENDIX 1—List of Specimens Used

Pleurostemon bullockii (hypodigm of Joyce, 2007), *Glyptops plicatulus* (hypodigm of Joyce, 2007), *Trinitichelys hiatti* (see Gaffney, 1972); *Neurankylus eximius* (see Gaffney, 1972 for Campanian shell, Brinkman and Nicholls, 1993 for Campanian skull); *Hayemys latifrons* (see Gaffney, 1972); *Plesiobaena antiqua* (not sensu Gaffney, 1972, because it combines what likely represents two different species, one from the Campanian and one from the Maastrichtian; hypodigm of Brinkman, 2003); *Boremys pulchra* (hypodigm of Brinkman and Nicholls, 1991); *Boremys grandis* (hypodigm of Brinkman and Nicholls, 1991); *Eubaena cephalica* (see Gaffney, 1972 for skull; lower jaw attributed by Gaffney, 1982 is not used because several described cranial taxa from the Maastrichtian lack jaws and because of observations on additional material to be published upon soon; postcranium attributed to *Eubaena cephalica* by Archibald, 1977, is not used because attribution is tenuous and because material is rather incomplete and thus uninformative); *Palatobaena cohen* (see hypodigm herein); *Palatobaena bairdi* (see hypodigm herein); *Palatobaena gaffneyi* (see hypodigm of Archibald and Hutchison, 1979); *Stygiuchelys estesi* (see Gaffney, 1972 for skull; material attributed by Archibald, 1977 used for postcranial characters); *Baena arenosa* (hypodigm of Gaffney, 1972); *Chisternon undatum* (hypodigm of Gaffney, 1972); *Goleremys mckennai* (see hypodigm of Hutchison, 2006).

APPENDIX 2—List of Characters Used

- Skull shape in dorsal view (Gaffney and Meylan, 1988, C3.1): 0 = oblong and rounded anteriorly; 1 = wedge shaped, skull tapers towards the anterior tip; 2 = short and rounded.
Comments: This character captures the two primary skull shapes apparent for the ingroup, as well as the one shape for the outgroup. Given that these three skull shapes do not form a logical morphocline, however, this character is left unordered in the analysis. As of now, all ingroup taxa clearly fall within one of the two categories used herein.
- Interorbital width: 0 = wide; 1 = narrow.
- Preorbital length (Brinkman and Nicholls, 1991, 11): 0 = short, snout shorter than orbit diameter; 1 = long, snout longer than orbit diameter.
Comments: The purpose of this character is to capture the relative lengthening of the preorbital portion of the skull (i.e., the lengthening of the snout) that is seen in some representatives of the ingroup. A long-snouted condition is most apparent for *Eubaena cephalica*. A long snout has also been reported for *Boremys pulchra*, but due to crushing seen in these specimens, this is somewhat questionable. We nevertheless retained that scoring for our analysis.

- 4) Orbit shape: 0 = circular to oval; 1 = generally circular, but with a distinct posterodorsal notch.
- 5) Orbit height relative to maxillary height (Brinkman and Nicholls, 1991, 19): 0 = orbit larger than maxillary height below orbit; 1 = orbit smaller than maxillary height below orbit.
- 6) Orientation of orbit: 0 = orbits mostly oriented laterally; 1 = orbits mostly oriented dorsally.
- 7) Development of the lingual ridge (in part Gaffney and Meylan, 1988, C2.3, C7.1): 0 = lingual ridge developed along the entire lingual margin of palate; 1 = lingual ridge only developed along the anterior half of the lingual margin of the palate; 2 = lingual ridge absent.
 Comment: The character states developed for this character form a morphocline and thus can be run ordered in an analysis.
- 8) Shape of triturating surface (in part Gaffney and Meylan, 1988, C2.3, C7.1; Brinkman and Nicholls, 1991, 1): 0 = lingual and labial margins more or less parallel; 1 = lingual and labial margins diverge posteriorly, triturating surface expanded posteriorly.
- 9) Intermaxillary arch/tongue groove (Gaffney and Meylan, 1988, C8.1): 0 = right and left triturating surface do not meet along midline; tongue groove, if present, narrow; 1 = right and left triturating surface contact another along the midline along a rounded bridge, the intermaxillary arch; tongue groove wide.
 Comment: The presence of an intermaxillary arch is a poorly described character that we interpret as a medial connection of the right and left triturating surfaces along the front of the skull resulting in a single, arch-shaped triturating surface. In our experience, the distribution of this character fully coincides with the presence of a wide tongue groove and both characters may thus be related. Until additional material is found that demonstrates that both are not factually correlated, we thus join both morphologies into a single character.
- 10) Palatine contribution to triturating surface: 0 = absent, the palatine sits below triturating surface, or contributes to it only very lightly; 1 = present, palatine contributes clearly to triturating surface.
- 11) Swollen maxillae: 0 = absent; labial ridge of maxillae gracile; 1 = present; labial margins of maxillae greatly thickened.
- 12) Nasal size (Gaffney and Meylan, 1988, C.1; in part Brinkman and Nicholls, 1991, 10): 0 = large, forms most of preorbital skull surface; 1 = reduced, form only small portion of preorbital skull surface.
- 13) Frontal contribution to external nares (in part Brinkman and Nicholls, 1991, 10): 0 = absent; 1 = present, frontals contribute to external nares by sending processes between nasals and maxillae; 2 = present, frontals contribute to external nares by sending processes along the midline between the nasals.
 Comments: Within the ingroup the frontals contribute to the external nares in two different ways that are not homologous with another. Given that the character states do not form a logical morphocline, this character is left unordered.
- 14) Prefrontal exposure on skull roof (Gaffney and Meylan, 1988, C2.1): 0 = prefrontals contribute significantly to the dorsal skull roof; 1 = prefrontal contribution to the skull roof greatly reduced to a small sliver; 2 = prefrontal contribution to skull roof completely absent.
 Comments: The character states of this character form a logical morphocline and thus can be run ordered in an analysis.
- 15) Contribution of frontal to the postorbital portion of the skull roof: 0 = frontals contribute to postorbital portion of skull similar to orbital portion of skull; 1 = frontal contribution to postorbital portion of skull greatly reduced relative to orbital portion.
- 16) Frontal contribution to orbits (Brinkman and Nicholls, 1991, 20): 0 = large; 1 = reduced to a small process; 2 = absent.
 Comments: The three character states used in this character form a logical morphocline and this character can thus be run ordered in an analysis.
- 17) Frontal contact with maxilla: 0 = absent, frontals and maxillae separated by prefrontals and/or nasals; 1 = present, frontals and maxillae contact between prefrontals and nasals.
- 18) Jugal contribution to orbit in adult individuals (Gaffney and Meylan, 1988, C6.4; Brinkman and Nicholls, 1991, 13): 0 = absent; 1 = reduced; 2 = large.
 Comments: In our experience, the contribution of the jugal to the orbit changes through ontogeny in that older individuals have a smaller contribution. Among others, this is apparent for *Palatobaena cohen* described herein. Nevertheless, a clear phylogenetic signal is apparent as well. We thus attempted to code individuals only that reasonable represent subadult to adult individuals. This character can be run ordered because the character states form a morphocline.
- 19) Jugal contribution to labial ridge: 0 = absent; 1 = present, jugal sends a narrow process ventrally that forms the most posterior portion of the labial ridge, just behind the maxilla.
- 20) Posterodorsal extension of quadratojugal above cavum tympani (Gaffney and Meylan, 1988, C6.5): 0 = present; 1 = absent.
- 21) Squamosal contact with parietal (Gaffney and Meylan, 1988, C6.3): 0 = present, upper temporal emargination shallow; 1 = absent, upper temporal emargination deep.
- 22) Posterior end of crista supraoccipitalis: 0 = crista supraoccipitalis ends in a point; 1 = crista supraoccipitalis expanded posteriorly and rounded.
 Comments: Almost all turtles in this analysis show some amount of upper temporal emargination and thus can be scored with ease in regards to this character. However, some individuals of *Baena arenosa* do not exhibit any upper temporal emargination at all and thus cannot be scored. Given that other individuals have some emargination that allow scoring this character (see Gaffney, 1972), we score this taxon as possessing a rounded crista supraoccipitalis.
- 23) Posterior thickening of parietal: 0 = absent, parietals thin out towards their posterior edge; 1 = present, parietals greatly thickened at their posterior edge.
- 24) Posterior extension of the crista supraoccipitalis: 0 = crista extends posterior to occipital condyle; 1 = crista reduced and does not extend posterior to occipital condyle.
- 25) Foramen preapalatinum: 0 = located within premaxillae; 1 = located within contact of premaxillae and vomer.
- 26) Posterior edge of vomer: 0 = posterior suture with pterygoids straight or concave; 1 = posterior suture with pterygoids pointed posteriorly or convex.
- 27) Foramen palatinum posterius: 0 = formed by pterygoid and palatine; 1 = formed entirely by palatine.
- 28) Midline contact of pterygoids (Gaffney and Meylan, 1988, C1.1; Brinkman and Nicholls, 1991, 9): 0 = absent; 1 = present, but small; 2 = present and large.
 Comments: The character states of this character form a morphocline and can thus be ordered in an analysis.
- 29) Pterygoid contact with basioccipital: 0 = poorly developed; 1 = well developed.
- 30) Epipterygoid (Gaffney and Meylan, 1988, C4.2): 0 = present; 1 = absent, or at least not apparent as separate ossification.
- 31) Basisphenoid size and shape (Brinkman and Nicholls, 1991, 14): 0 = rectangular and long; 1 = pentagonal; 2 = triangular.
 Comments: The three character states developed for this character do not form a logical morphocline and thus should not be run ordered in an analysis.
- 32) Contribution of opisthotic to stapedial foramen (Brinkman and Nicholls, 1991, 8): 0 = opisthotic excluded from stapedial foramen; 1 = opisthotic enters stapedial foramen.
- 33) Splenial (Gaffney and Meylan, 1988, C6.1): 0 = present and large; 1 = reduced in size; 2 = absent.
 Comments: The three character states developed for this character form a morphocline and thus can be run ordered in an analysis.
- 34) Tubercle on posterolateral edge of dentary: 0 = absent; 1 = present.
 Comments: This new character captures the presence of a distinct tubercle that is visible on the posterolaterally edge of the triturating surface of the dentary in a number of baenid turtles (see Fig. 5). Likely this tubercle serves at the attachment site of a muscle and may thus be size or age dependent. However, our review of lower jaw material indicates that this presence or absence of this tubercle is taxon specific instead.
- 35) Shape of the suture between the dentary and the surangular: 0 = strongly Z-shaped; 1 = straight, or mostly straight.
- 36) Scalloping of posterior rim of carapace: 0 = absent, posterior margin of carapace smooth; 1 = present, but light; 2 = present and very distinct.
 Comments: This character can be treated as a morphocline and may thus be run ordered in a phylogenetic analysis.
- 37) Fifth vertebral scute contributes to posterior margin of carapace: 0 = absent, only the marginals forms the posterior rim of the carapace; 1 = present.
- 38) Posterior margin of carapace: 0 = posterior margin rounded and convex; 1 = posterior margin flattened or concave.
- 39) Presence of carapacial fontanelles in fused or otherwise clearly adult shells: 0 = fenestrae are absent; 1 = fenestrae present between the costals and peripherals.
- 40) Supernumerary bone anterior to the first neural (i.e., preneural, Brinkman and Nicholls, 1991, 1): 0 = absent; 1 = present.
- 41) Number of peripherals (in part Gaffney and Meylan, 1988, C4.3): 0 = eleven pairs; 1 = twelve or more pairs.
- 42) Mesoplastra: 0 = present, in midline contact; 1 = present, but midline contact absent.
- 43) Cervical scutes (Gaffney and Meylan, 1988, C5.2; Brinkman and Nicholls, 1991, 6): 0 = always single; 1 = sometimes or always divided.
- 44) Vertebral shape: 0 = vertebrals wider than long; 1 = vertebrals longer than wide.
- 45) Nuchal scute (i.e., supernumerary scute anterior to the first vertebral and on top of the nuchal bone, Brinkman and Nicholls, 1991, 7): 0 = absent; 1 = present.
- 46) Anterior supernumerary pleural scute (i.e., supernumerary scute anterior

- to first pleural; Gaffney and Meylan, 1988, C5.3; Brinkman and Nicholls, 1991, 3): 0 = absent; 1 = present.
- 47) Posterior supernumerary pleural scute (i.e., supernumerary scute posterior to fourth pleural, Brinkman and Nicholls, 1991, 18): 0 = absent; 1 = present.
- 48) Supramarginal scutes (i.e., supernumerary scutes lateral to pleural series, Brinkman and Nicholls, 1991, 16): 0 = absent; 1 = present.
- 49) Position of marginal I: 0 = placed symmetrically over nuchal/peripheral I suture; 1 = more than 3/4 is position on peripheral I.
- 50) Anterior plastral lobe (Brinkman and Nicholls, 1991, 4): 0 = overall rectangular in outline, anterior rim broadly rounded; 1 = overall triangular, anterior rim tapered to a blunt point.
- 51) Epiplastral processes (i.e., cleithra): 0 = reduced but present; 1 = absent.
- 52) Gular scutes (i.e., the anterior most pair of scutes, in part Brinkman and Nicholls, 1991, 5): 0 = gulars as larger as extragulars (by surface area); 0 = gulars significantly smaller than extragulars, or even absent.
- 53) Medial contact of extragulars (in part Brinkman and Nicholls, 1991, 5): 0 = absent; 1 = present, posterior to the gulars.
- 54) Placement of anal scute: 0 = anal on xiphiplastron only; 1 = anal scute crosses hypo/xiphiplastral suture.

APPENDIX 3—Character-taxon matrix for the phylogenetic analysis performed in this study. Missing data are coded as “?”. Polymorphic character states are in parentheses.

	1	11111	11112	22222	22223	33333	33334	444	4	4	44445	5555	
	12345	67890	12345	67890	12345	67890	12345	67890	123	4	5	67890	1234
<i>Pleurosternon bullockii</i>	00000	00000	00000	00000	00000	00000	00?0?	00000	000	0	0	0000?	0???
<i>Glyptops plicatulus</i>	01000	00000	00000	00000	00000	00000	00?00	00000	000	0	0	0000?	0???
<i>Trinitichelys hiatti</i>	00000	01000	00010	00100	00001	002??	21???	???	00	0	0	0?000	1000
<i>Neurankylus exemiis</i>	?0???	???	???	00???	010??	???	21???	10000	000	0	0	00000	1000
<i>Hayemys latifrons</i>	100??	0???	00000	21100	100??	0121?	20???	???	???	?	?	???	???
<i>Plesiobaena antiqua</i>	10000	01111	01011	01010	10001	10211	10010	11110	100	0	0	00011	1111
<i>Boremys pulchra</i>	1100	0?10?	01011	01?00	1000?	00211	10100	21101	101	(01)	1	11100	1010
<i>Boremys grandis</i>	???	???	???	???	???	???	???	21101	101	0	1	11100	1010
<i>Eubaena cephalica</i>	11101	02100	01011	21000	10000	00211	10???	???	???	?	?	???	???
<i>Palatobaena cohen</i>	20000	12111	11221	11110	10001	10211	10011	11110	?00	0	0	00011	11?1
<i>Palatobaena bairdi</i>	20000	12111	11221	11210	11101	10211	10011	???	???	?	?	???	???
<i>Palatobaena gaffneyi</i>	20001	12111	11221	11110	11101	10111	10???	???	???	?	?	???	???
<i>Stygiochelys estesi</i>	10010	01110	11121	01100	10011	01111	11???	???	???	1	1	1?0?0	?11?
<i>Baena arenosa</i>	11010	01110	01?21	01201	01110	00211	11210	11100	111	1	0	10000	1111
<i>Chisternon undatum</i>	11010	01110	01121	01201	00110	01111	11200	11101	101	1	1	10000	1111
<i>Goleremys mckennai</i>	11001	01100	01021	11200	000?1	00211	1???	???	???	?	?	???	???