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CRANIAL ANATOMY AND PHYLOGENETIC PLACEMENT OF THE ENIGMATIC TURTLE *COMPSEMYS VICTA* LEIDY, 1856

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ABSTRACT—The skull of the enigmatic turtle *Compsemys victa* Leidy, 1856 is described. A number of unique characteristics are apparent, including the extremely thick nature of all cranial bones, the presence of rod-like epipterygoids, placement of the foramen posterius canalis carotici interni halfway along the contact between the pterygoid and basisphenoid, lack of cheek emarginations, and the reduction of the size of the cavum tympani relative to the orbit. Two differing global turtle analyses and one paracryptodiran analysis were performed to determine the phylogenetic placement of *C. victa*. Both global analyses converged by placing *C. victa* within Paracryptodira, herein defined as the most inclusive clade that includes *Pleurosternon bullockii* and *Baena arenosa*, but no species of living turtle, whereas the paracryptodiran analysis places *C. victa* outside of Baenoidea, herein defined as the least inclusive clade that contains *P. bullockii* and *B. arenosa*. Although a number of similarities are apparent between *C. victa* and the uncommon, extant testudinoid *Platysternon megacephalum*, the available data indicate that these similarities are convergent, likely due to their carnivorous diet. Taphonomic evidence reveals that basal paracryptodires, including *C. victa*, preferred slow moving or ponded water environments. The riverine habitat preference of baenoids must therefore be derived.

INTRODUCTION

COMPSEMYS VICTA Leidy, 1856 is a relatively common, yet poorly known fossil turtle from the Campanian to early Paleocene of North America (Gaffney, 1972; Hutchison et al., 1998; Brinkman and Rodriguez de la Rosa, 2006). Leidy (1856) described the first remains of *C. victa* based on a shell fragment with characteristic ornamentation from the Late Cretaceous Hell Creek Formation of North Dakota. Subsequent scientists named at least seven species that were at one time referred to *Compsemys*. “*Compsemys*” *plicatulus* Cope, 1877 was attributed to *Glyptops* Marsh, 1890 by Hay (1908). Of the remaining species, four (*Compsemys vafer* Hay, 1910; *C. parva* Hay, 1910; *C. puercensis* Gilmore, 1919; and *C. torreonensis* Gilmore, 1919) are from the Paleocene of New Mexico and were provisionally synonymized with *C. victa* by Gaffney (1972) based on the similar sculpture pattern and the lack of unique diagnostic characters. We herein add to this list of synonyms “*Glyptops*” *depressus* Hay, 1908 from the Late Cretaceous or Paleocene of Colorado and *Compsemys obscurus* (Leidy, 1856) from the Hell Creek Formation of North Dakota.

As is typical for fossil turtles, shell fragments of *Compsemys victa* are relatively abundant, whereas skull elements are quite rare. Hutchison and Holroyd (2003) presented the first *C. victa* skull material in their summary of turtles from the Denver Basin. However, while they briefly discussed and figured one of two available skulls, they did not illustrate this specimen in detail or explicitly analyze the phylogenetic placement of *C. victa*.

Over the last 150 years ideas regarding the phylogenetic placement of *Compsemys victa* have changed markedly. Hay (1908) tentatively recognized two species of *Compsemys* and regarded them as belonging to Dermatemydidae based on the presence of inframarginal scutes and the putative lack of mesoplastra. However, based on more complete material that showed the presence of mesoplastra, Hay (1910) placed *Compsemys* in Baenidae. Gilmore (1919) noted similarities

between species placed in *Glyptops*, *Neurankylus*, and *Compsemys*, in particular the shell sculpture, and united them under Pleurosternidae. Gaffney (1972) placed *Compsemys victa* within Baenidae based on the presence of a medial contact between the mesoplastra, a character that he notes as being plesiomorphic for turtles. Hutchison and Holroyd (2003) noted a list of similarities between *Compsemys victa* and pleurosternids and placed it once again within Pleurosternidae. None of these studies utilized cladistic methods and so it remains unclear if the characters used represent synapomorphies or symplesiomorphies. To date the placement of *C. victa* within Paracryptodira has not been tested in a global analysis.

The purpose of this manuscript is 1) to describe and illustrate a skull of *C. victa*; 2) to determine the phylogenetic placement of *C. victa* by placing it in the global cladistic matrices of Gaffney et al. (2007) and Joyce (2007); 3) to further investigate the placement of *C. victa* within Paracryptodira by including it in an analysis that incorporates all currently accepted species of paracryptodiran turtles; 4) to explicitly summarize the known geographic and temporal distribution of *C. victa*; and 5) create phylogenetic definitions for Pleurosternidae, Baenidae, Baenoidea, and Paracryptodira. The taxonomic nomenclature used herein follows Joyce et al. (2004) as applied to the phylogeny of Joyce (2007).

Institutional abbreviations.—NMMNHS, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; SMP VP, State Museum of Pennsylvania Vertebrate Paleontology Collection, Harrisburg, Pennsylvania, U.S.A.; UCM, University of Colorado, Boulder, Colorado, U.S.A.; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, U.S.A.; USNM, National Museum of Natural History, Washington DC, U.S.A.; UW, University of Wyoming Geological Museum, Laramie, Wyoming, U.S.A.; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788

PARACRYPTODIRA Gaffney, 1975

COMPSEMYS Leidy, 1856*Type species.*—*Compsemys victa* Leidy, 1856.

Comments.—All North American fossil turtle material referable to *Compsemys* is herein placed in a single taxon, *Compsemys victa*. Fragmentary material from the Paleocene of France was referred to *Compsemys* by de Broin (1977) but this identification was later questioned by Gaffney and Meylan (1992). All relevant specimens remain unfigured and undescribed and we therefore cannot independently assess the phylogenetic affinities of this material. More recently, Joyce et al. (in press) noted similarities between the Early Cretaceous English taxa '*Helochelydra*' *bakewelli* (Mantell, 1833), '*Helochelydra*' *anglica* (Lydekker, 1889), and *C. victa* and therefore removed them from the Solemydidae and tentatively affiliated them with *Compsemys*. Given the strong faunal ties between western Europe and North America in the Mesozoic, it is not surprising that material found on one continent resembles material from the other. However, as all European material referred to *Compsemys* is highly fragmentary, it is questionable if their phylogenetic affinities will be resolved with more confidence in the near future.

COMPSEMYS VICTA Leidy, 1856*Compsemys* (orig. *Emys*) *obscurus* (Leidy, 1856)*Glyptops depressus* Hay, 1908*Compsemys vafer* Hay, 1910*Compsemys parva* Hay, 1910*Compsemys puercensis* Gilmore, 1919*Compsemys torrejonensis* Gilmore, 1919

Figures 1, 2

Type specimen.—USNM 960.

Type locality.—Long Lake, North Dakota (Hay, 1908, p. 233). Long Lake is located approximately 30 miles southeast of Bismarck, North Dakota.

Type horizon.—Probable Laramie age (Hay, 1908, p. 233). As noted by Gaffney (1972) this horizon is most likely late Cretaceous. The shallow water marine Fox Hills Formation and the overlying Hell Creek Formation are exposed around Long Lake (Bluemle, 1977). Given that there are only a few vertebrate fossils known from the Fox Hills Formation and that the holotype is preserved much like fossils from the Hell Creek Formation, we are confident in constraining the provenance of this fossil to the Hell Creek Formation.

Referred material and distribution.—Only those materials are listed herein that were published with museum numbers or which are known to us by museum specimens: Campanian, Cerro del Pueblo Formation, Mexico (see materials listed in Brinkman and Rodriguez de la Rosa, 2006); Campanian, Kaiparowits Formation, Utah (UMNH 16982); Campanian, Kirtland and Fruitland Formations, New Mexico (SMP VP 2201, NMMNHS 22741 and 40512); Maastrichtian, Hell Creek Formation, Montana and North Dakota (USNM 960, holotype of *C. victa*; also see material listed in Gaffney, 1972; Hutchison and Archibald, 1986; Holroyd and Hutchison,

2002; YPM 57251, 57260, 57283, 57305, 57315, 57355); Maastrichtian, Scollard Formation, Alberta (TMP 2002.71.64; also see materials listed in Brinkman, 2003a); Maastrichtian, Ojo Alamo (Naashoibito Member), New Mexico (SMP VP 2527, SMP VP 2590); Maastrichtian and Puercan, Denver Basin, Colorado (see material listed in Hutchison and Holroyd, 2003; USNM 5731, holotype of *Glyptops depressus*); Puercan, Fort Union Formation, Montana (see materials listed in Hutchison and Archibald, 1986; YPM 57550, 57551, 57552, 57553); Puercan, various basins and formation, Wyoming (see materials listed by Bartels, 1980; UW 25290); Puercan, Fort Union Formation, Montana (YPM57550, YPM57551, YPM57552, YPM57553); Puercan and Torrejonian, Nacimiento Formation, New Mexico (see specimens listed in Gaffney, 1972; NMMNHS 21602); Torrejonian, Tongue River Formation, Wyoming (see specimen listed by Estes, 1976; YPM PU 20581). For summary, see Figure 3.

Diagnosis.—Placed along the phylogenetic stem of Paracryptodira by nasals that prevent frontals from entering narial opening; no medial contact of the prefrontals; foramen posterius canalis carotici interni located halfway along contact between pterygoid and basisphenoid; posterior plastral thickening medial to the bridge.

Autapomorphies include: no cheek emargination; rectangular quadratojugal; quadratojugal extends ventrally to a level even with mandibular condyles of quadrate, covering up these condyles; postorbital contributes to rim of cavum tympani; cavum tympani diameter less than diameter of orbit; mesoplastra unusually large and with broad midline contact; first peripherals meet medially in front of nuchal, preventing the nuchal from being exposed along the anterior margin of carapace; deep xiphoplastral notch present, varying from U-shaped to V-shaped; sinuous midline sulcus on plastron.

Associating skulls and shells.—While the skull and lower jaws (UCM 49223) described herein were not found associated with a shell, they can be confidently assigned to *C. victa* based on the distinctive sculpturing that the skull (UCM 49223) has in common with all referred shell materials listed above, including the type (USNM 960). In addition, Hutchison and Holroyd (2003) examined UCM 49223 as well as a *C. victa* shell associated with a skull (UCMP 131103) and identified UCM 49223 as belonging to *C. victa*.

PHYLOGENETIC NOMENCLATURE

We herein explicitly follow the phylogenetic nomenclature for turtles that was developed and justified by Joyce et al. (2004). This type of nomenclature differs from traditional, Linnaean nomenclature primarily by applying rank-free taxon names to clades and by determining the content of a clade by reference to a phylogeny. The nomenclatural system of Joyce et al. (2004) only provides names for the primary clades of extant turtles. Various authors have therefore formulated names for groups of fossil turtles (e.g., Adocusia Danilov and Parham, 2006; Palatochelydia Joyce and Lyson, 2010; Plastomenidae Joyce and Lyson, 2011). To allow us to better

FIGURE 1—*Compsemys victa*, skull (UCM 49223), from the Denver Formation of Colorado. 1, dorsal view (left, photograph; right, line drawing); 2, anterior view (top, photograph; bottom, line drawing); 3, ventral view (left, photograph; right, line drawing); 4, posterior view (top, photograph; bottom, line drawing); 5, right lateral view (left, photograph; right, line drawing); 6, left lateral view (left, photograph; right, line drawing). Shaded regions represent missing or crushed portions of the skull. Abbreviations: bo=basioccipital; bs=basisphenoid; epi=epipterygoid; fpcci=foramen posterius canalis carotici interni; fpp=foramen palatine posterius; 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.

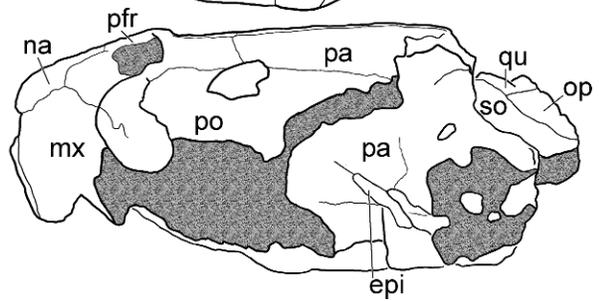
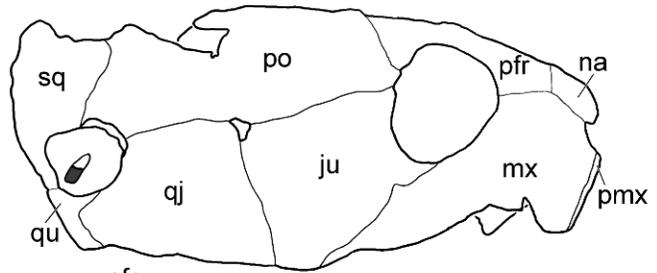
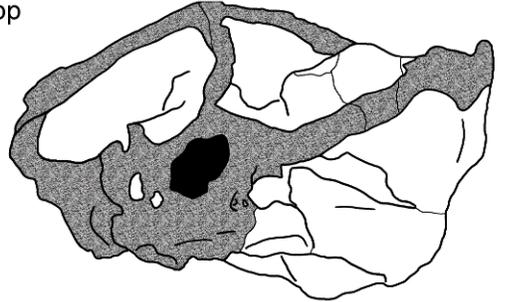
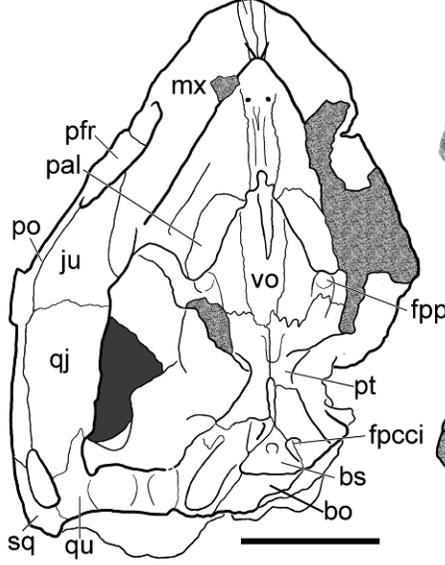
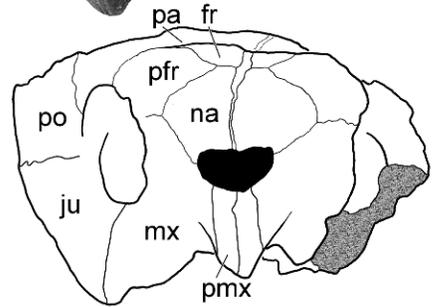
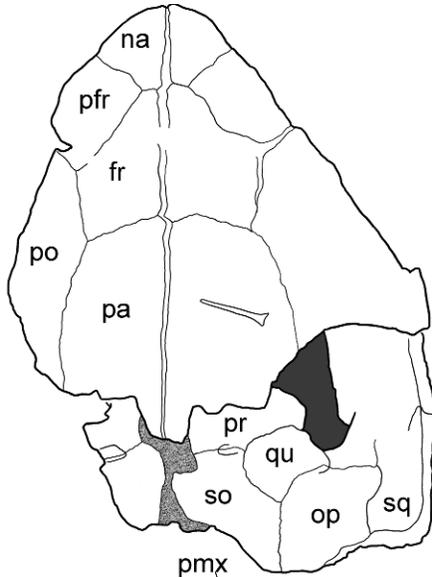
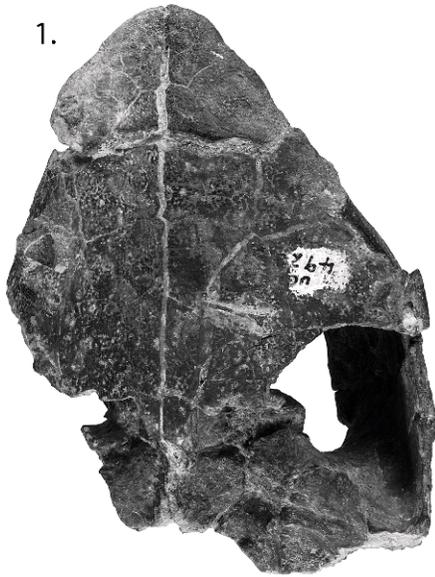




FIGURE 2—Ventral stereophotograph of *Compssemys victa* (UCM 49223) from the Denver Formation of Colorado.

communicate the results of our phylogenetic analysis, we herein develop a series of phylogenetic definitions for the four most important paracryptodiran clades.

BAENIDAE, Cope 1882, converted clade name

Definition.—“Baenidae” refers to the most inclusive clade containing *Baena arenosa* Leidy, 1870 but not *Pleurosternon* (orig. *Platemys*) *bullockii* Owen, 1842 or any species of Recent turtle.

Currently hypothesized content.—*Arundelemys dardeni* Lipka et al., 2006, *Trinitichelys hiatti* Gaffney, 1972, *Neurankylus eximius* Lambe, 1902, *Hayemys latifrons* Hay, 1908, “*Denazinemys*” *ornata* (Gilmore, 1935), *Stygiochelys estesi* Gaffney and Hiatt, 1971, *Baena arenosa*, *Chisternon undatum* (Leidy, 1872), *Eubaena cephalica* Hay, 1904, *Denazinemys nodosa* (Gilmore, 1916), *Boremys pulchra* (Lambe, 1906), *Boremys grandis* Gilmore, 1935, *Plesiobaena antiqua* (Lambe, 1902), *Peckemys brinkman* Lyson and Joyce, 2009b, *Cedrobaena putorius* (Gaffney, 1972), *Gamerabaena sonsalla* Lyson and Joyce, 2010, *Palatobaena cohen* Lyson and Joyce, 2009a, *Palatobaena gaffneyi* Archibald and Hutchison, 1979, *Palatobaena bairdi* Gaffney, 1972.

Diagnostic characters.—Lingual ridge developed anteriorly only; deep temporal emargination (i.e., no parietal/squamosal contact) present; parietal overhang on top of supraoccipital and epiplastral processes absent, strongly developed axillary buttress present that extends onto costals; strongly developed inguinal buttress.

Discussion.—The term Baenidae was originally coined by Cope (1882), but the exact composition of his taxon is somewhat unclear, beyond the fact that it does not include Pleurosternidae. The composition of Baenidae of later authors is rather similar to the current usage, but occasionally includes taxa currently excluded, such as the enigmatic *Naomichelys speciosa* (Hay, 1908) or Meiolaniidae (Williams, 1950). The phylogenetic relationship of *Neurankylus eximius* relative to more ‘classic’ baenids such as *Baena arenosa* remained unclear for a long time and various classifications included (e.g., Hay, 1908; Gaffney, 1972) or excluded that taxon (e.g., Williams, 1950) from Baenidae. However, numerous phylogenetic analyses (e.g., Brinkman and Nicholls, 1993; Joyce, 2007; Lyson and Joyce, 2009a, 2009b, 2010) have more recently established a

close relationship between these taxa. In our opinion, it appears that Baenidae is not conceptualized as a group of turtles with specific characters but rather as all turtles more closely related to *Baena arenosa* than to *Pleurosternon bullockii*. We therefore capture this usage with our phylogenetic definition.

PLEUROSTERNIDAE, Cope 1868, converted clade name

Definition.—“Pleurosternidae” refers to the most inclusive clade containing *Pleurosternon* (orig. *Platemys*) *bullockii* Owen, 1842 but not *Baena arenosa* Leidy, 1870 or any species of Recent turtle.

Currently hypothesized content.—*Dorsetochelys delairi* Evans and Kemp, 1976 *Glyptops plicatulus*, *Pleurosternon bullockii*.

Diagnostic characters.—Oblong skull shape (length is significantly greater than maximum width); rectangular basisphenoid; anterior plastral lobe larger than posterior plastral lobe.

Discussion.—Similar to Baenidae, the term Pleurosternidae was coined by Cope (1868), but its original composition is unclear, beyond the exclusion of Baenidae. Various taxa were at one time included in Pleurosternidae that are currently thought to be more distantly related, such as *Helochelys danubina* Meyer, 1855 (Hay, 1908) or *Kallokibotion bajazidi* (Williams, 1950). Only after the discovery and description of cranial material (Evans and Kemp, 1975; Gaffney, 1979a) did it become apparent that the North American taxon *Glyptops plicatulus* is indeed closely related with the European *Pleurosternon bullockii*. This clade consisting of *Glyptops plicatulus* and *Pleurosternon bullockii* was briefly referred to as Glyptopsidae Marsh, 1890 (e.g., Gaffney, 1975; Mlynarski, 1976) but for the last 30 years this clade has been consistently referred to as Pleurosternidae (e.g., Gaffney, 1984, 1996; Gaffney et al., 1991, 2007; Hirayama et al., 2000; Joyce, 2007). Most fossil turtle paleontologists likely conceptualize Pleurosternidae as all taxa closer to *Pleurosternon bullockii* than any baenid and therefore we capture that usage with our phylogenetic definition.

BAENOIDEA, Williams, 1950, converted clade name

Definition.—“Baenoidea” refers to the clade originating from the most recent common ancestor of *Pleurosternon* (orig.

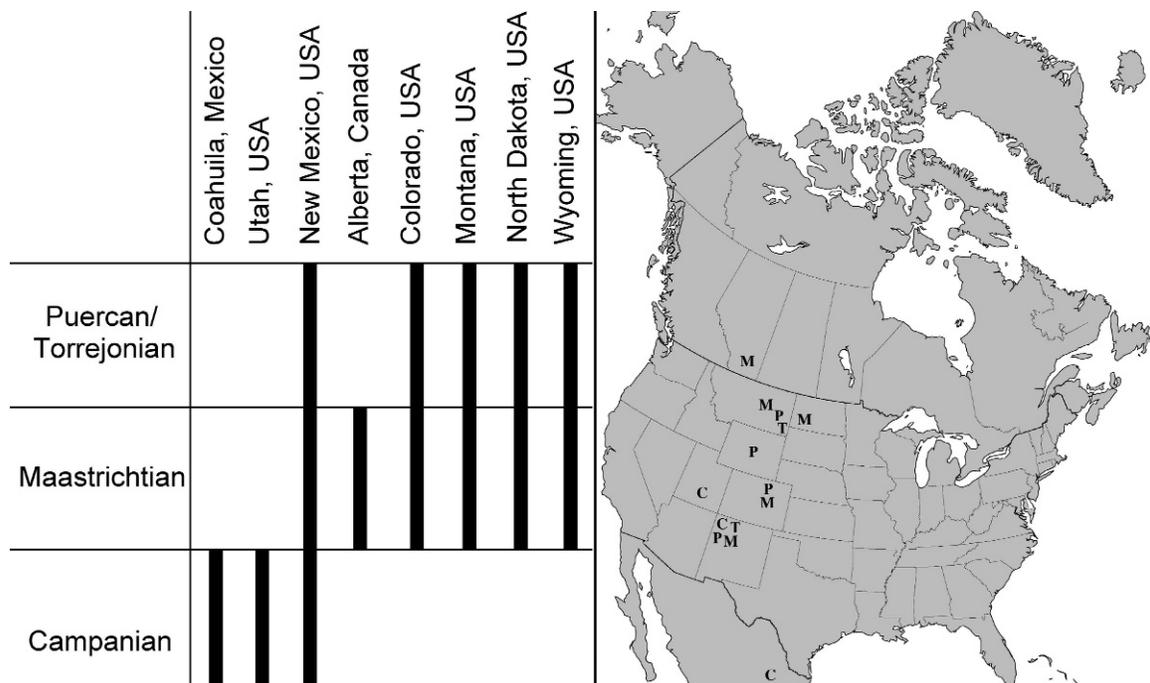


FIGURE 3—Stratigraphic range diagram (left) and map of North America (right) illustrating the current known stratigraphic (Campanian–C, Maastrichtian–M, and Puercan–P/Torrejonian–T) and geographic (Canada, Mexico, and the United States) distribution of *Compssemys victa*.

Platemys bullockii Owen, 1842 and *Baena arenosa* Leidy, 1870 and may not include any species of Recent turtle.

Currently hypothesized content.—By definition, all of Baenidae and Pleurosternidae (see above).

Diagnostic characters.—Jugal process contributes to the posterior most portion of labial ridge; deep cheek emargination reaches at least ventral margin of orbit.

Discussion.—The term Baenoidea was originally coined by Williams (1950) for the clade consisting of Baenidae and Meiolaniidae. Gaffney (1972) used the same term to unite Baenidae and Pleurosternidae, but that usage was eventually lost in favor of the term Paracryptodira. Given that we herein tie Paracryptodira to the stem group of Baenoidea (see below), the clade consisting of Baenidae and Pleurosternidae lacks a name. We therefore resurrect the term Baenoidea, as used by Gaffney (1972), for that clade.

PARACRYPTODIRA, Gaffney, 1975, converted clade name

Definition.—“Paracryptodira” refers to the most inclusive clade containing *Pleurosternon* (orig. *Platemys*) *bullockii* Owen, 1842 and *Baena arenosa* Leidy, 1870 but not any species of Recent turtle.

Currently hypothesized content.—*Dinochelys whitei* Gaffney, 1979a, *Compssemys victa*, *Uluops uluops* Bakker, 1990, and all of Baenidae and Pleurosternidae (see above).

Diagnostic characters.—Canalis caroticus internus located halfway along suture between pterygoid and basisphenoid; interpterygoid vacuity absent; distinct thickening of plastron medial to inguinal buttress.

Discussion.—The term Paracryptodira was originally coined by Gaffney (1975) for the clade of turtles diagnosed by the presence of a single foramen for the canalis caroticus internus that is positioned midway along the basisphenoid-ptyergoid suture. As originally conceived, Paracryptodira included Baenidae, Pleurosternidae, and *Kallokibotion bajazidi* (Gaffney, 1975). A reanalysis of the skull of *K. bajazidi* has since shown that this taxon does not reveal the true paracryptodiran

condition (Gaffney and Meylan, 1992) and the vast majority of phylogenetic analyses have demonstrated that *K. bajazidi* is not closely related with true paracryptodires (e.g., Gaffney, 1996; Gaffney et al., 2007; Hirayama et al., 2000; Joyce, 2007), with exception of the recent phylogenetic analysis Gaffney et al. (2007), which placed this taxon as sister to Baenidae + Pleurosternidae. Until recently, the clade diagnosed by the paracryptodiran carotid condition, the clade formed by Baenidae + Pleurosternidae, and the stem clade of Baenidae + Pleurosternidae were equivalent in composition, but addition of new taxa necessitated a choice of which of the three clades should be given the name Paracryptodira. No clear precedence is apparent. For instance, Lipka et al. (2006) refer all taxa closer to Baenidae and Pleurosternidae than any living turtle to the Paracryptodira, whereas Joyce (2007) uses this name to refer to the clade formed by Baenidae + Pleurosternidae. Given that one of the analyses presented herein reveals a number of ‘classic’ paracryptodires are placed outside of Baenoidea, we feel that stability is best served by tying the name Paracryptodira to the stem group of Baenoidea.

DESCRIPTION

Skull.—The skull is mostly complete and uncrushed (Fig. 1). The posterior portion of the dorsal skull roof and the left cheek region are missing due to erosion. All parts of the skull are notably robust. For instance, the thickness of the parietals is approximately 4 mm, while in all baenids, except *Neurankylus eximius* and *Chisternon undatum*, the parietals are approximately 1 mm thick. This does not appear to be an artifact of size, as *Palatobaena cohen* is as large or larger than *C. victa*, *N. eximius*, and *C. undatum*, but nevertheless has thinner parietals. The same trend appears to apply to all other dermal roofing bones, as well as the elements of the palate. The skull is oblong and sub-triangular in shape, similar to that of *Arundelemys dardeni*. The extent of the upper temporal emargination cannot be determined. Unlike baenids and other paracryptodires, there is no cheek emargination. The orbits

are large and are oriented vertically. The distance between the orbits is large as in *A. dardeni*, but unlike *Glyptops plicatulus* Cope, 1877 and *Pleurosternon bullockii* Owen, 1842. The dermal skull bones have a distinct, finely beaded and ridged texturing, similar to the texturing found on the shell, a character also found in the shells and/or skulls of *G. plicatulus*, *P. bullockii*, *A. dardeni*, and *Uluops uluops*. The cavum tympani is greatly reduced in size, smaller than the diameter of the orbit, and similar to that of the extant *Platysternon megacephalum* Gray, 1831. The incisura columellae auris is loosely enclosed dorsolaterally and likely includes the Eustachian tube, much as in *Cedrobaena putorius*, *Meiolania platyceps* Owen, 1886, and various pleurodires (Joyce, 2007). The external narial opening is heart shaped and notably small, smaller than that found in the similar sized *A. dardeni* (Lipka et al., 2006).

Nasals.—The nasals are large blocky elements that prevent the frontals from entering the narial opening, similar to other basal paracryptodires (Gaffney, 1979a; Brinkman et al., 2000; Lipka et al., 2006; Lyson and Joyce, 2009b). In dorsal view, the nasals taper posteriorly and, unlike other paracryptodires, form a straight contact with the frontals. Posterolaterally, the nasals contact the prefrontals and anteroventrally they contact the dorsally expanded maxilla anterior to the orbit. The nasals extend as far anteriorly as the underlying premaxillae. The anterior portions of the nasals roll ventrally around the nasal capsule before terminating along the external narial opening. This rolled portion of the nasals forms a small part of the anterior portion of the face in anterior view, unlike other paracryptodires, which have straight nasals that end sharply at the external narial opening.

Prefrontals.—The prefrontals are large elements. The dorsal plate-like portion of the prefrontal forms a large portion of the dorsal skull roof, larger than in any other paracryptodire. However, like paracryptodires, the prefrontals do not contact one another medially. In dorsal view the dorsal plate is diamond shaped and contacts the nasal anteromedially, the frontal posteromedially, and the postorbital posteriorly. The large dorsal exposure of the prefrontals and the prefrontal/postorbital contact prevents the frontals from entering the orbital margin. As in cryptodires (Gaffney, 1979b), the descending process is well developed, broadly forms the anterior orbit wall, contacts the maxilla laterally, and presumably contacts the palatine and vomer ventrally, although the latter could not be confidently determined from either the specimen or the CT data of the skull.

Frontals.—The dorsal exposure of the frontals is greater than that of the nasals and prefrontals, but smaller than that of the postorbitals and parietals. The frontals extend posteriorly just beyond the posterior extent of the orbit. The posterior portion of the frontal is squarish whereas the anterior portion tapers anteriorly. Combined, the frontals are hexagonal in shape. The frontals are fully contained within the dorsal skull roof and do not enter the orbits or external narial opening. The frontals broadly contact the nasals anteriorly, the prefrontals anterolaterally, the postorbitals laterally, the parietals posteriorly, and another medially. Unlike baenids, but similar to pleurosternids, the frontals do not contact the dorsal process of the maxillae.

Parietals.—The posterior portion of the parietals is missing and their posterior extent and contacts thus cannot be determined. What remains of the parietals are rectangular in shape with parallel lateral margins. The parietals contact the frontals anteriorly, postorbitals laterally, what remains of the supraoccipital posteroventrally, and another medially. Like

the other dermal roofing bones, the parietals are very thick compared to those of other turtles, approximately 4 mm thick along their fractured posterior edge. The descending process of the parietal extends ventrally and contacts the epipterygoid posteroventrally and the pterygoid anteroventrally. As in most other turtles, a small portion of the descending process of the parietal participates in the anterodorsal portion of the trigeminal foramen.

Jugal.—The jugals are large sub-triangular elements that form a large portion of the cheek region. In lateral view, the jugal widely enters the orbital margin anteriorly and forms the posteroventral floor of the orbit. A similar condition is found in *G. plicatulus*, *P. bullockii*, and *A. dardeni*, but is widely present among other turtles (Gaffney, 1979b). The jugal forms an oblique contact with the maxilla anteroventrally, contributes to the ventral margin of the skull posterior to the labial ridge of the triturating surface, forms a straight posterior contact with the quadratojugal, and forms a straight dorsal contact with the postorbital. The medial process of the jugal contacts the pterygoid and palatine just posterior to the triturating surface.

Quadratojugal.—Unlike other paracryptodires, which have a distinctly C-shaped quadratojugal, the quadratojugal of *C. victa* is a large rectangle. Due to the lack of cheek emargination, the ventral margin of the quadratojugal is at the same level as the mandibular condyle of the quadrate. Posteroventrally the quadratojugal almost contacts the mandibular condyle and covers up most of the quadrate in lateral view, unlike most other turtles. The quadratojugal forms a broad contact with the jugal anteriorly, the postorbital dorsally, and the quadrate posteroventrally, and forms the anterior rim of the cavum tympani.

Squamosal.—Only a small portion of the right squamosal is preserved. As in other turtles, it is situated in the posterolateral portion of the skull and caps the underlying antrum postoticum and quadrate. In lateral view, a descending process of the squamosal clearly contacts an ascending process of the quadrate to loosely enclose the incisura columellae auris and, presumably, the Eustachian tube. A similar condition is found in *C. putorius*, *M. platyceps*, and various pleurodires (Gaffney, 1979b; Joyce, 2007; Lyson and Joyce, 2009b). The only other preserved contact of the squamosal is its anterior contact with the postorbital and a medial contact with the paroccipital process of the opisthotic. The antrum postoticum extends into the squamosal, but given the massive nature of the squamosal, the antrum is only minimally developed. The squamosal forms the posterodorsal portion of the rim of the cavum tympani.

Postorbital.—The postorbital is a broad element on the dorsolateral portion of the skull. Anteriorly, it narrowly enters the orbit margin. The posterior portion of the postorbitals is fractured and their posterior extent cannot be determined. The postorbital contacts the prefrontal anteromedially, which prevents the frontals from entering the orbit margin. Laterally, the postorbital contacts the frontal and the parietal. Unlike any other paracryptodire, except *C. undatum*, a small portion of the postorbital contributes to the anterior rim of the cavum tympanum.

Premaxilla.—The premaxillae are paired structures that are narrowly exposed below the external nares. The premaxillae form a pronounced median hook (or tooth), as in *Dinochelys whitei* and *G. plicatulus*. In palatal view, a deep pit is apparent between the anterior portions of the premaxillae just posterior to the labial margin. We speculate that this pit likely accommodated a median tooth of the dentary. The labial ridge of the premaxilla is wedge shaped.

Maxilla.—In lateral view, the maxilla forms a broad, posteriorly tapering bar below the orbit. The ascending process of the maxilla forms the anterior rim of the orbit, part of the lateral rim of the external nares, and contacts the nasal and prefrontal dorsally, but not the frontal as in most derived baenids (Gaffney, 1979b; Lyson and Joyce, 2009a). The maxilla forms much of the ventral rim of the orbit and broadly contacts the jugal posterodorsally. The left maxilla is broken and, like the other bones in the skull, is very thick in cross section. The labial ridge is very thick and forms a rounded wedge. A very low lingual ridge is developed that runs along the posterior half of the palate and is situated just lateral to the maxillary palatine suture. The triturating surface is quite broad and includes significant portions that are formed by the palatine and vomer (Figs. 1, 2). The anterior portion of the maxillae extends medially to contact the vomer and forms a small secondary palate that floors the narial passage. The portion of the triturating surface that is formed by the palate is slightly lower in palatal view than the rest of the triturating surface and has a rough surface. In palatal view, the maxilla contacts the premaxilla anteriorly, the vomer anteromedially, and the palatine posteromedially.

Vomer.—Similar to all crown turtles, the vomer is single (Figs. 1, 2). The vomer is a remarkably large and narrow element. The anterior half is at a level even with the maxillae and helps form the secondary palate. Two distinct but fine ridges run lengthwise along the vomerine portion of the secondary palate. We speculate that these ridges were too fine to perform a masticatory function but rather may have helped anchor the ramphotheca. The internal choanae are located halfway along the length of the vomer and delineate the transition from the anterior, palatal half of the vomer and the posterior, choanal half. The posterior half of the vomer reaches posteriorly to contact the pterygoids and fully divides the palatines along straight and parallel anteroposterior sutures. A distinct median ridge runs along the anterior half of the choanal portion of the vomer and subdivides the narial passage in this region. The vomer contacts the premaxillae anteriorly, maxilla anterolaterally, palatine posterolaterally, pterygoid posteriorly, and the prefrontal anterodorsally.

Palatine.—The palatine forms a large portion of the palate and forms the posteromedial part of the triturating surface, as in *A. dardeni* and *D. whitei* (Figs. 1, 2). This palatal portion of the palatine has a notably rough surface relative to the rest of the palate and, in palatal view, appears to be sitting lower (more dorsal) than the remaining portions of the palate. The palatal portion of the palatine broadly contacts the maxillae laterally. The foramen palatinum posterior is a large foramen and oriented obliquely from anterodorsal to posteroventral just below the palatal portion of the palatine. As a result, this foramen is somewhat obscured in palatal view. The majority of the foramen palatinum posterior is formed by the palatine, but the posterior rim is formed by the pterygoid, as in most paracryptodires. The medial portion of the palatine roofs the narial passage and broadly contacts the vomer medially.

Quadrate.—The quadrate is a stout bone that forms the posteroventrolateral portion of the skull. The mandibular condyle is at a level even with the lower temporal margin, unlike the condition found in most other turtles. The quadrate forms the roughly circular cavum tympani, but only forms the posteroventral rim of that structure. The quadrate does not surround the anterior opening of the antrum postoticum. The cavum tympani opens laterally and, unlike most cryptodires but similar to *Platysternon megacephalum*, its diameter is smaller than the diameter of the orbit. Due to a surficial

contact of the quadrate with the squamosal, the incisura columella auris is enclosed and likely includes the Eustachian tube as well, much as in some other paracryptodires, pleurodires, and *Meiolania platyceps*. The incisura columellae auris itself is a relatively narrow slit. No stapes is preserved. The greater portion of the processus trochlearis oticum is formed by the quadrate and the break on the left side of the skull clearly reveals that the otic region is greatly thickened. In lateral view, the quadrate contacts the quadratojugal and postorbital anterior to the cavum tympani and the squamosal dorsal to and posterior to the cavum. Within the temporal cavity, the quadrate contacts the prootic anteromedially, the supraoccipital posteromedially, the opisthotic posteriorly, and the squamosal posterolaterally.

Pterygoid.—As in all cryptodires and paracryptodires, the pterygoids are enlarged and reach the posterior margin of the skull (Figs. 1, 2). The processus pterygoideus externus is damaged on both sides. Similar to *A. dardeni*, but unlike *G. plicatulus* and *P. bullockii*, the pterygoids form a broad contact with one another. The pterygoid contacts the vomer and palatine anteriorly, the basioccipital and basisphenoid posteromedially, the quadrate ventrolaterally, and the prootic, parietal, and epipterygoid dorsally. Similar to *G. plicatulus* and *P. bullockii*, but unlike baenids and *A. dardeni*, the pterygoid has a very narrow anterolateral contact with the maxilla. The pterygoids form an extremely narrow waist halfway along their length. As in baenids and pleurosternids, the foramen posterior canalis carotici interni is located midway along the length of the basisphenoid and pterygoid suture. The foramen palatinum posterius is formed by the pterygoid and palatine. Posteriorly each pterygoid forms a deep groove that runs parallel to the suture with the basisphenoid and basioccipital.

Epipterygoid.—As in *G. plicatulus*, *P. bullockii*, *U. uluops*, and *A. dardeni*, but unlike most baenids, which fuse the epipterygoid to the parietal (Gaffney, 1979b; Brinkman, 2003b), a relatively large, oblong epipterygoid is present anterior to the trigeminal foramen. Similar to basal turtles, but unlike cryptodires, this element is not flat, but rod-shaped (Sterli and Joyce, 2007).

Supraoccipital.—Much of the supraoccipital is missing due to erosion and a potential dorsal exposure of the supraoccipital on the skull roof cannot be determined. The supraoccipital contacts the prootic anteriorly, the quadrate anterolaterally, and the opisthotic laterally. The foramen magnum is not preserved and so it is unclear which elements contributed to its formation.

Exoccipital.—Unfortunately, most of the exoccipital is either missing or crushed. However, it is apparent that two pairs of foramina jugulare anterior pierce the exoccipital to enter the cavum cranii.

Basioccipital.—The basioccipital is rectangular and is situated posterior to the basisphenoid and posteromedial to the posterior process of the pterygoid. The posterior portion of the basioccipital is missing due to erosion and the contacts cannot be determined in this view.

Prootic.—The prootic forms the anterior portion of the bony inner ear. Similar to the condition found in cryptodires, the prootic contributes to the formation of the processus trochlearis oticum and the break to the skull on the left side reveals a thickening to the anterior otic chamber. The processus trochlearis oticum is also partly formed by the quadrate. The prootic, quadrate, and opisthotic form the stapedia foramen. Similar to baenids and pleurodires, the diameter of the stapedia foramen is much larger than the

foramen canalis carotici interni (Gaffney, 1979b). The prootic forms a large portion of the trigeminal foramen. It contacts the parietal anterodorsally, the supraoccipital posterodorsally, the quadrate laterally, and the pterygoid ventrally.

Opisthotic.—The opisthotic is excluded from the foramen stapedio-temporale due to the contact of the supraoccipital with the quadrate. Like other turtles the opisthotic forms the posterior portion of the bony inner ear.

Basisphenoid.—The basisphenoid is a small triangular bone. It is smaller than in any other paracryptodire. The basisphenoid contacts the pterygoids anteriorly and forms a straight contact with the basioccipital posteriorly. A sharp pit is present near the apex of the basisphenoid and may have served as a muscle attachment site.

PHYLOGENETIC ANALYSIS

Given that the phylogenetic placement of *Compsemys victa* has never been assessed within an explicit phylogenetic analysis, two maximum parsimony analyses were performed using the independent global matrices of Gaffney et al. (2007) and Joyce (2007). Both matrices were left unaltered, with exception of the addition of *C. victa* (see Appendix 1 for character coding for this taxon and Appendix 2 for the list of *C. victa* specimens used for the scoring). The expanded matrix of Gaffney et al. (2007) includes 111 osteological characters and 29 taxa, including 28 ingroup taxa. All characters were run unordered and all characters were left unweighted. The augmented Joyce (2007) matrix includes 136 osteological characters and 69 taxa, including 68 ingroup taxa. Following Joyce (2007), 17 characters were considered morphoclines and were ordered (7, 24, 27, 33, 35, 54, 60, 61, 65, 66, 68, 71, 85, 98, 120, 134, 135). The remaining characters were run unordered and all characters were left unweighted. For both analyses, a maximum parsimony analysis was performed on the dataset using PAUP 4.0b10 (Swofford, 2001). "Synapsida/Diapsida" was specified as the outgroup taxa for the Gaffney et al. (2007) matrix and 'hypothetical ancestor' for the Joyce (2007) matrix. Given the large size of the matrices and in order to more confidently obtain the shortest tree(s), the parsimony ratchet method (Nixon, 1999) was used, with 20% of the characters perturbed and 200 iterations. Five independent parsimony ratchet searches were performed and the shortest trees resulting from these independent searches were combined and filtered to eliminate duplicate trees and only the shortest trees were kept. These trees were used as the starting point for a heuristic search using the tree-bisection-reconnection algorithm. Minimum branch lengths were set to collapse. Support for each node was measured by calculating the bootstrap frequencies (Felsenstein, 1985), with 1,000 bootstrap replicates and 100 random sequence addition replicates. Bootstrap frequencies greater than 70% are considered strong support (Hillis and Bull, 1993).

The expanded matrices of Gaffney et al. (2007) and Joyce (2007) confirmed previous non-cladistic hypotheses (e.g., Gaffney, 1972; Hutchison and Holroyd, 2003) in that *C. victa* is placed within Paracryptodira (Fig. 4A, 4B). The Joyce (2007) analysis resulted in eighteen trees with a tree length of 374 steps (CI=0.4545; RI=0.8079; RC=0.3672). The 50% majority rule tree places *C. victa* in a basal polytomy with Baenidae, Pleurosternidae, and *D. dalairi* (Fig. 4A). The Gaffney et al. (2007) analysis, by contrast, resulted in two most parsimonious trees with a tree length of 235 (CI=0.5447; RI=0.7242; RC=0.3945). The strict consensus tree places *C. victa* as sister to Pleurosternidae (Fig. 4B).

To further test the phylogenetic position of *C. victa*, this taxon was then placed in the first phylogenetic analysis that includes all turtles thought to possess the paracryptodiran carotid condition. *Desmemys bertelsmanni* Wegner, 1911 has been hypothesized to be a paracryptodire (e.g., Brinkman et al., 2000), but was not included in the analysis because the type material has been lost over the course of the last 100 years and therefore cannot be reexamined. The matrix of Lyson and Joyce (2009b) forms the basis of this analysis, but two additional outgroup taxa were added: *Proganochelys quenstedti* Baur, 1887 (as described by Gaffney, 1990) and *Kayentachelys aprix* Gaffney et al., 1987 (as described by Sterli and Joyce, 2007; Gaffney and Jenkins, 2010; and personal observation of postcranial material). The list of ingroup taxa was expanded through the addition of *Denazinemys nodosa*, "*Denazinemys*" *ornata*, *Compsemys victa*, *Arundelemys dardeni*, *Dinochelys whitei*, *Dorsetochelys delairi*, and *Uluops uluops*. To allow for greater resolution, 35 osteological characters were added to the analysis and are listed in Appendix 3. A total of 107 osteological characters and 27 taxa, including 25 ingroup taxa, were analyzed. Nine characters were considered to represent morphoclines and were run ordered (1, 7, 14, 16, 18, 28, 33, 36, 70). The remaining characters were run unordered and all characters were left unweighted. The complete matrix can be found in Appendix 4. *Proganochelys quenstedti* and *Kayentachelys aprix* were specified as the outgroup taxa, and a parsimony ratchet method with the same parameters as outlined above was used. Support for each node was measured by calculating Bremer support values (Bremer, 1994) and bootstrap frequencies (Felsenstein, 1985), with 10,000 bootstrap replicates and 100 random sequence addition replicates. Bootstrap frequencies greater than 70% are considered strong support (Hillis and Bull, 1993).

The analysis resulted in eight most parsimonious trees with a tree length of 247 (CI=0.4899; RI=7296; RC=0.3574). The outcome of this analysis generally supports previous notions regarding the evolution of paracryptodiran turtles (Fig. 4C). However, this analysis regards *A. dardeni* as the basal most baenid, not as the basal most paracryptodire as in Lipka et al. (2006). Character support for this hypothesis includes: no parietal/squamosal contact, lack of parietal overhang over the supraoccipital, and reduced size of the canalis caroticus lateralis relative to the canalis caroticus internus. Bootstrap support for this placement is less than 50%, but has a high Bremer support of 5 (Fig. 4). Besides the addition of *A. dardeni* to Baenidae, the composition of Baenidae is as originally suggested by Gaffney (1972). In addition, the baenid genus "*Denazinemys*" is not regarded as a monophyletic taxon. Contrary to Joyce (2007), *Dorsetochelys delairi* is placed within Pleurosternidae and *Dinochelys whitei* is placed for the first time outside of Pleurosternidae and Baenoidea (Brinkman et al., 2000; Joyce, 2007). *Uluops uluops* is placed in a polytomy with Pleurosternidae and Baenidae. *Compsemys victa* is regarded as a stem baenoid. The lack of extant taxa in this analysis does not allow strict application of the herein proposed phylogenetic definition of Paracryptodira. However, given that the ingroup enjoys very high bootstrap support (98%) and the fact that the previous two analyses recover a monophyletic Paracryptodira, we are confident that this clade is monophyletic relative to crown Testudines.

DISCUSSION

Both the skull and shell of *Compsemys victa* possess an unusual combination of characters (see diagnosis in System-

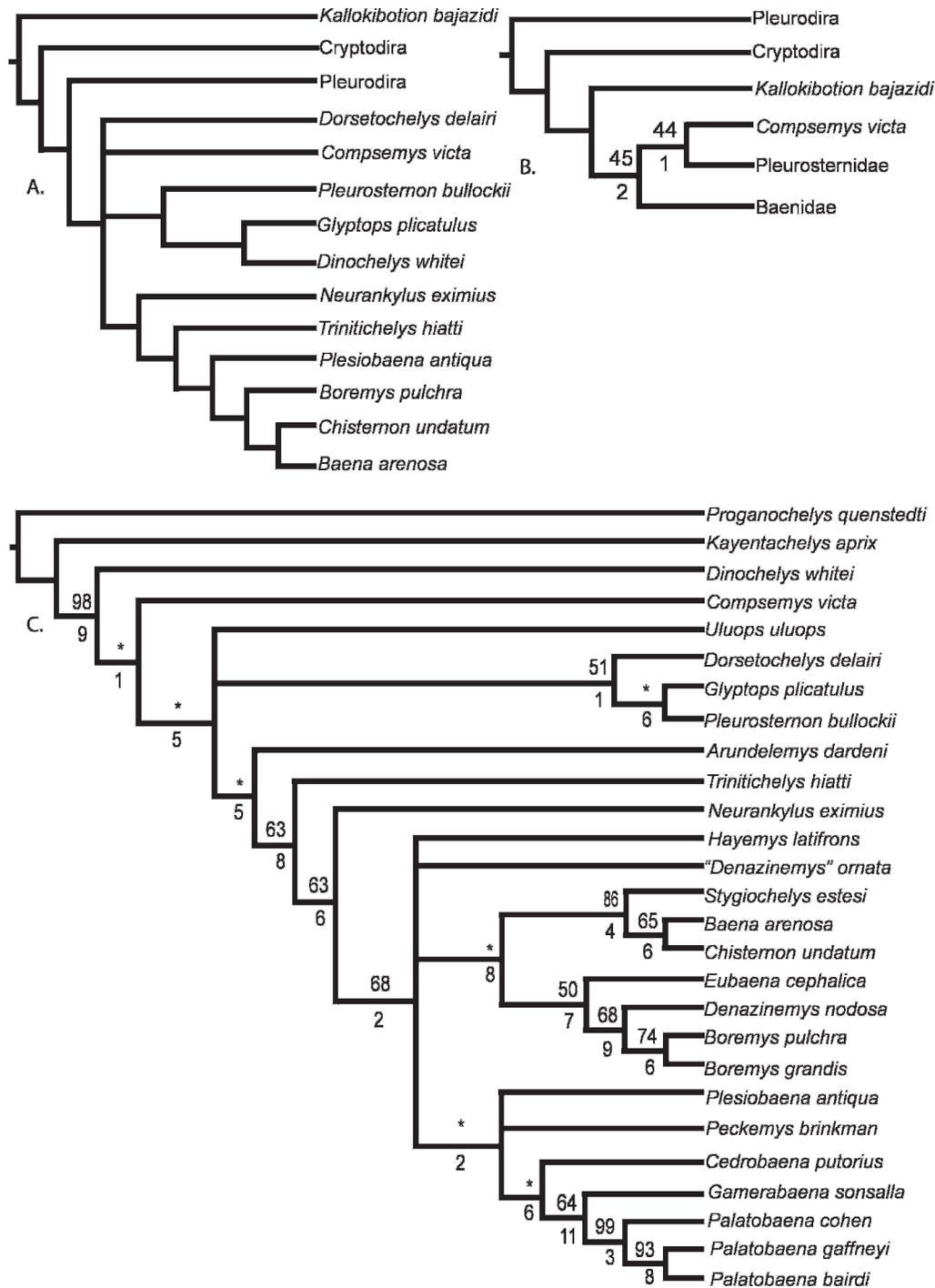


FIGURE 4—Phylogenetic hypotheses for the placement of *Compsemys victa*: A, 50% majority rule tree of the augmented Joyce (2007) matrix places *C. victa* in a polytomy with *Dorsetochelys delairi* and Baenidae; B, strict consensus tree of two MPTs from the augmented Gaffney et al. (2007) matrix places *C. victa* as a sister to Pleurosternidae; C, strict consensus tree of eight MPTs when all paracryptodires are analyzed in a phylogenetic analysis. Support for each node is measured using bootstrap frequency (top) and Bremer support for each clade (bottom).

atic Paleontology) and this enigmatic turtle thus has been allied with a number of clades (Hay, 1908, 1910; Gilmore, 1919; Gaffney, 1972; Hutchison and Holroyd, 2003). However, the phylogenetic placement of *C. victa* has never been explicitly tested in a cladistic framework. The two independent global matrices of Gaffney et al. (2007) and Joyce (2007) place *C. victa* within Paracryptodira, but relegate *C. victa* to different positions within this clade. Joyce's (2007) matrix places *C. victa* in a polytomy with *D. delairi*, Pleurosternidae,

and Baenidae (Fig. 4A). In contrast, Gaffney et al.'s (2007) matrix places *C. victa* as sister to Pleurosternidae (Fig. 4B) or, using the newly phylogenetic taxonomic proposed herein, within Pleurosternidae. The paracryptodiran matrix developed herein places *C. victa* along the stem of Baenoidea, more derived than *Dinochelys whitei* but basal to a polytomy made up of *U. uluops*, Pleurosternidae, and Baenidae (Fig. 4C).

The three phylogenetic analyses conducted herein firmly place *C. victa* within Paracryptodira, but the placement of *C.*

victa within Baenoidea is more tentative. The presence of numerous symplesiomorphies found in *C. victa*, such as the elongate rod-shaped epipterygoid, lack of the extreme axillary and inguinal buttresses, and the lack of a thickening of the plastron between the axillary buttresses, at the very least indicate that this taxon is not a derived baenid (i.e., within the clade formed by *N. eximius* and Baenodds). The incomplete nature of most known basal stem baenoids, however, makes it difficult to distinguish between all other hypotheses. For instance, *D. whitei* is only known from shell material and a fragmentary skull whereas *U. uluops* is known from an isolated skull. We nevertheless give the most weight to the results of the paracryptodiran analysis developed herein and interpret *C. victa* as a stem baenoid, because this matrix specifically utilizes all variation seen within paracryptodiran and thus likely better reflects the intrarelationships of this group compared to the more global matrices of Joyce (2007) and Gaffney et al. (2007).

The placement of *C. victa* in a basal position within Paracryptodira implies a minimum ghost range for that taxon of 70 Ma that extends from the Tithonian to the Campanian. However, given that the shell sculpturing of the most common Morrison Formation turtle, *G. plicatulus*, is virtually identical with that of *C. victa*, it is entirely plausible that many shell fragments attributed to *G. plicatulus* in particular, or *Glyptops* in general, may actually belong to *C. victa*. This hypothesis will be tested by the discovery of more Morrison Formation skull and shell material.

The phylogenetic placement of *A. dardeni* as the basal most baenid is novel for this taxon. *Arundelemys dardeni* is the oldest known baenid (late Albian to early Aptian) and the only known baenid from the East Coast of North America. *Arundelemys dardeni* shares a number of characters with the late Aptian baenid *Trinitichelys hiatti* from Texas, including upturned nasals, deep temporal and cheek emargination, a finely sculptured skull, and a square snout. Although no shell material has of yet been referred to *A. dardeni*, the Arundel Formation of Maryland has produced a number of shell fragments that were referred to *Glyptops* based on similarities to the sculpturing of the shell (see Lipka et al., 2006). Though speculative, it appears plausible that this material actually belongs to *A. dardeni*, and that “glyptopsid” sculpturing is primitive for Baenoidea in general.

In overall appearance, the number of convergent similarities between the big-headed turtle *Platysternon megacephalum* (recently placed as sister to Emydidae within Testudinoidea by Parham et al., 2006 and Barley et al., 2010) and *C. victa* is striking. The skulls are similar in relevant size and shape, as well as in the possession of hooked premaxillae and small cavum tympani and the lack of cheek emarginations. *Platysternon megacephalum* possesses a number of characters not found in *C. victa*: a quadratojugal and maxilla contact, a jugal that does not enter the orbital margin, absence of nasals, internal carotids that exit via foramina situated at the posterior end of the pterygoids, and the absence of mesoplastra and extragular scutes. The combined morphological evidence clearly demonstrates that these two taxa are not closely related. All similarities must therefore be interpreted as convergence due to similar environmental demands. *Platysternon megacephalum* is perhaps one of the strangest turtles alive, in that it lives in cool, tropical mountain streams, tenaciously climbs through its rocky habitat, and patiently waits for the opportunity to snap after a fish with an open mouth (Ernst and Barbour, 1989). Although it may be tempting to draw numerous parallels between these two taxa, we think that the large-sized head and well-developed premaxillary beak simply indicate that *C. victa* was likely largely carnivorous.

Compsemys victa has been interpreted as inhabiting slow moving water environments based on the fine grained lithology in which it is most commonly preserved (Hutchison and Holroyd, 2003). Personal observations (TRL) of *C. victa* material collected in the Hell Creek Formation of southwestern North Dakota and eastern Montana is congruent with this idea and we agree that *C. victa* likely inhabited slow moving water environments. Interestingly, the quarries from which much of the *D. whitei*, *U. uluops*, and *G. plicatulus* material was recovered (Dry Mesa Quarry, Breakfast Bench Quarry, and Quarry Nine, respectively) are thought to represent low energy pond or swamp environments as well (Richmond and Morris, 1998; Foster, 2003; Carrano and Velez-Juarbe, 2006), indicating that this is the original paleoecology for North American paracryptodires. The basal baenids *A. dardeni* and *T. hiatti*, each only known from a single specimen, were both found in claystone, which is indicative of a slow moving water environment (Lipka et al., 2006; TRL, personal observation). *Neurankylus eximius* appears to be found in both claystones and mudstones, while baenodds are almost exclusively found in sandstones (Hutchison and Holroyd, 2003; TRL, personal observation). The paleoecological transition within Paracryptodira from low energy ponded environments to higher energy stream environments therefore took place near the Baenodda node.

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