Paludicola 5(4):111-124 June 2006

NICHOLLSEMYS BAIERI GEN. ET SP. NOV, A PRIMITIVE CHELONIOID TURTLE FROM THE LATE CAMPANIAN OF NORTH AMERICA

Donald Brinkman[1], Maggie Hart[2], Heather Jamniczky[3], and Matthew Colbert[4]

[1]Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta, T0J 0Y0, Canada, don.brinkman@gov.ab.ca.
[2]San Diego Natural History Museum, 1788 El Prado, San Diego, California, 92101, USA, mhart@sdnhm.org.
[3]University of Calgary, Department of Biological Sciences, 2500 University Drive NW, Calgary, Alberta, T2N 1N4, Canada, hajamnic@ucalgary.ca.
[4]University of Texas at Austin, High Resolution X-Ray Computed Tomography Laboratory, Jackson School of Geosciences, 1 University Station, C-1110, Austin, Texas 78712-0254, U.S.A., colbert@mail.utexas.edu.

ABSTRACT

We describe *Nichollsemys baieri* gen. et sp. nov., a primitive non-protostegid chelonioid turtle from the late Campanian Bearpaw Formation of Alberta, Canada, and DeGrey member of the Pierre Shale of South Dakota, USA. Known only from skull morphology, *Nichollsemys baieri* is phylogenetically intermediate between *Toxochelys* Cope, 1873, and *Ctenochelys* Zangerl, 1953. It is similar to *Toxochelys* and primitive with respect to *Ctenochelys* in the presence of a narrow triturating surface that does not incorporate the vomer, a large foramen palatinum posterius, and a well-developed processus pterygoideus externus on the pterygoid. It is derived relative to *Toxochelys* in features of the braincase, including the presence of a reduced area of exposure of the basisphenoid on the ventral surface of the braincase, a mid-ventral ridge on the palate extending between the basisphenoid and vomer, a rod-like rostrum basisphenoidale, a mid-line ridge extending from the foramen anterior canalis carotici interni to the dorsum sellae. It also differs in that the foramen caroticum laterale is larger in diameter than the foramen anterior canalis carotici interni.

INTRODUCTION

Chelonioid turtles are important members of many marine vertebrate assemblages from the Western Interior Seaway and taxa from this region have been central to interpretations of the origin and early diversification of the family. The primitive chelonioid *Toxochelys* is of particular relevance to these questions because of the presence of primitive features of the braincase and forelimbs. In recent cladistic analyses, it, along with *Ctenochelys* and related taxa, has been interpreted as a primitive member of the cheloniidae (Hirayama 1994, 1998; Parham and Fastovsky, 1997; Lynch and Parham, 2003), although a recent analysis has argued that it is a stem taxon intermediate between continental testudines and derived pelagic chelonioids (Kear and Lee, 2006). Because of the uncertain phylogenetic relationships of these taxa, they will be referred to here as primitive non-protostegid chelonioids.

Although primitive non-protostegid chelonioid turtles are widespread in the Western Interior Seaway of North America, the stratigraphic distribution of this group of turtles is patchy. They are diverse in the Smoky Hill Chalk Member of the Niobrara Formation of Kansas and the Mooreville Chalk of Alabama, both of Santonian to Early Campanian age (Zangerl, 1953: Everhart, 2005). A low diversity assemblage from the Sharon Springs and Pembina members of the Pierre Shale provides further data on early Campanian members of the group (Zangerl, 1953; Nicholls et al., 1990; Hart, 2004a, b). In contrast, the late Campanian record is very limited. One shell-based taxon, *Toxochelys weeksi* Collins, 1951, was erected on the basis of a carapace from the Ripley Formation of Tennessee. This formation has been considered to be Maastrichtian in age but was most recently reinterpreted as late Campanian (Cobban and Kennedy, 1993). Three shell based taxa, *Toxochelys barberi* Schmidt, 1944, *Prionchelys nauta* Zangerl, 1953, and *Catapleura arkansaw* Schmidt, 1944, have been named on the basis of specimens from the late Campanian-earliest Maastrichtian Marlbrook Marl (Bottjer, 1985). A well preserved, small shell from the late Campanian Bearpaw Formation of Alberta, Canada, was referred to *Lophochelys niobrarae* Zangerl, 1953 (Nicholls et al., 1990), and isolated shell elements from the Lethbridge Coal Zone, a unit at the top of the Dinosaur Park

Formation that is transitional between fluvial and marine environments, have also been referred to this taxon (Eberth and Brinkman, 1997). In addition, Brinkman (2005) reported on the occurrence of a marine turtle in the Lethbridge Coal Zone and, on the basis of an isolated maxilla that showed the presence of an extensive secondary palate, referred this turtle to the durophagous cheloniid *Euclastes*. Thus the new primitive non-protostegid chelonioid from the late Campanian of Alberta and South Dakota is the first from this time period to be represented by well preserved skulls, and thus adds to our understanding of the marine turtles of this age and the succession of chelonioid turtles through the Late Cretaceous of North America.

Brinkman (2000) referred the skulls from the Bearpaw Formation described here to the shell-based taxon *Lophochelys* Zangerl, 1953 because this taxon is present in the Bearpaw Formation (Nicholls et al., 1990) and because an independent assessment of the phylogenetic position of *Lophochelys* and of the Bearpaw skulls concluded that they occupy a similar phylogenetic position. However, the validity of *Lophochelys* is uncertain because it may include juvenile individuals of a number of different primitive chelonioids (Hirayama, 1994, 1997). Referral of the chelonioid skulls from the Bearpaw Formation to *Lophochleys* is further questioned by the subsequent discovery of a marine turtle carapace of moderate size that lacks diagnostic features of the shell of *Lophochelys*. This specimen (TMP 2001.26.3) indicates that a second, larger, marine turtle is present in the Bearpaw Formation. Because previous referrals of cranial material to shell-based taxa have often proved problematic (Parham, 2005) and because it is likely that the shells of closely related cheloniids are highly conservative while the skulls are distinct (Gaffney and Meylan, 1988; Moody, 1984), care is warranted in suggesting such isolated skull-isolate shell associations. Thus, in the absence of direct association of cranial and shell material, we establish a new taxon, *Nichollsemys baieri* gen. et sp. nov., for the skulls, although we recognize that this taxon may ultimately prove to be a junior synonym of one of the contemporaneous shell-based taxa.

Nomenclature of *Toxochelys*--Because the skulls described here are similar to those of species of *Toxochelys*, nomenclatural questions discussed by Nicholls (1988) are raised. *Toxochelys latiremis* Cope, 1873, was erected on the basis of a lower jaw. Later, Cope (1877) referred two skulls from the Niobrara Formation of Kansas to this species, and subsequent interpretations of the anatomy and relationships of the species were based primarily on the well-preserved Niobrara Formation specimens (eg. Hay, 1896, 1905, 1908; Zangerl, 1953; Nicholls, 1988). Complete skulls of a primitive non-protostegid chelonioid from the Pierre Shale were first attributed to the genus *Porthochelys* Williston, 1901, as the species *P. browni* Hay, 1905. Zangerl (1953) transferred this species to *Toxochelys,* restricted *T. latiremis* to the specimens from the Niobrara Formation, and erected the species *T. moorevillensis* Zangerl, 1953 for the *Toxochelys* species that occurs in the Mooreville Chalk of Alabama. However, as observed by Ren Hirayama in a memo left with the specimen, the nature of the matrix adhering to the type specimen of *T. latiremis* indicates that it is from the Pierre Shale. Thus, if the species present in the Pierre Shale and Niobrara formations differ, the name *T. latiremis* should apply also to the specimens from the Pierre Shale. Schultze et al. (1985) accepted this interpretation and concluded that the species name with priority for the Niobrara *Toxochelys* is *T. brachyrhinus* Case, 1898. Nicholls (1988) agreed that the name *T. latiremis* should apply to the Pierre Shale species of *Toxochelys*, but did not distinguish between the Pierre Shale species and the Niobrara species. However, we feel that the species of *Toxochelys* that occur in the Niobrara and Sharon Springs Member of the Pierre Shale are distinct, differing in that the Sharon Springs species has a constriction of the snout, a hooked beak of the mandible, a reduced degree of temporal emargination, more strongly developed labial and lingual ridges on the dentary, and reaches a larger adult size (Hart, 2004a). Furthermore, cheloniid skulls from the Sharon Springs Member of the Pierre Shale fall into two distinct size classes. While these may represent growth stages in a single species (Hart, 2004b), it raises the possibility that more than one taxon is present in this assemblage and it is uncertain whether an isolated dentary is sufficient to distinguish between these taxa or not. Thus we feel that a revision of the species-level taxonomy of *Toxochelys* is required before the nomenclatural questions can be fully resolved. Pending such a study, we avoid using binomial names when referring to the *Toxochelys* species found in the Sharon Springs Member of the Pierre Shale and the Niobrara Formation, referring to them instead as the Sharon Springs *Toxochelys* species and the Niobrara *Toxochelys* species, respectively. No questions have been raised regarding the validity of *T. moorevillensis*, so that species will be referred to by its binomial attribute.

Methods—Mechanical preparation revealed the external anatomy of the skull. To retrieve otherwise inaccessible data regarding the internal anatomy, specimen TMP 97.99.1 was subjected to high-resolution x-ray computed tomography (CT) at the High Resolution X-Ray Computed Tomography Laboratory at the University of Texas at Austin. The specimen was scanned in the transverse plane, with a slice thickness of 0.25 mm and an inter-slice spacing of 0.25 mm, for a total of 317 slices.

Since *Nichollsemys baieri* is represented only by skull material, comparisons were limited to those primitive non-protostegid chelonioids represented by skulls: *Porthochelys laticeps* Williston, 1901, *Toxochelys moorevillensis*, the Niobrara *Toxochelys* species, the Sharon Springs *Toxochelys* species, and species of *Ctenochelys* Zangerl, 1953. In most cases, comparisons are based on observations of original specimens by at least one author as well as on published descriptions. Comparisons with the Niobrara *Toxochelys* species are based primarily on ROM 28563. Comparisons with *Toxochelys moorvillensis* are based on FMNH PR219. Comparisons with the Sharon Springs *Toxochelys* species are based on material in the collections of the South Dakota School of Mines, Rapid City, South Dakota. Comparisons with *Porthochelys laticeps* and *Ctenochelys* are based on published descriptions only, particularly those of Williston (1901), Hay (1908), and Zangerl (1953). For features of the basicranial region, comparisons were limited to the Niobrara *Toxochelys* species and *T. moorevillensis* due to the preservation state of specimens. Where features could not be determined in the Sharon Springs *Toxochelys* species, it was assumed to be similar to the earlier.

Nichollsemys baieri was incorporated into the data matrix of Kear and Lee (2006), and a phylogenetic analysis was conducted using PAUP* v. 4.08d81 (Swofford, 2002). The analysis was performed using a heuristic search employing 1000 random-addition replicates, and bootstrap values were calculated over 1000 replicates. Multi-state characters were left unordered, yielding a single most parsimonious tree of 231 steps.

In the discussion of the relationships of *Nichollsemys baieri* relative to other chelonioids, stem-based definitions of higher taxonomic categories are used.

Institutional Abbreviations—TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; FMNH, Field Museum of Natural History, Chicago, Illinois; ROM, Royal Ontario Museum, Toronto, Ontario; SDSM, South Dakota School of Mines, Rapid City, South Dakota.

SYSTEMATIC PALEONTOLOGY

Order TESTUDINES Batsch, 1788
Superfamily CHELONIOIDEA Baur, 1893
Nichollsemys new genus

Etymology—Named in honor of Elizabeth Nicholls, in recognition of her contributions to the study of vertebrates in general and her work on marine turtles from the late Campanian Bearpaw Formation of southern Alberta in particular.

Type species—*Nichollsemys baieri* sp. nov.

Diagnosis—As for the type and only known species, presented below.

Nichollsemys baieri new species

Etymology—Named for Ron Baier, of Taber, Alberta, who found the type specimen and donated it to the Royal Tyrrell Museum of Palaeontology.

Holotype—TMP 97.99.1, skull with lower jaws preserved in a concretionary nodule.

Type Locality—The type specimen was found in glacial till exposed along Chin Coulee, south of Taber, Alberta (Figure 1) (UTM coordinates are: 12:315200; 5494000, datum: NAD27). Although the Foremost Formation forms the bedrock in this area, concretionary nodules containing invertebrates typical of the Bearpaw Formation are present in the till deposit. Thus the specimen is most likely derived from the Bearpaw Formation.

Referred Specimens—TMP 2000.55.1: skull in nodule, Bearpaw Formation, St. Mary's River, South of Lethbridge, Alberta (Figure 1); TMP 2000.53.2: otic capsule with partial quadrate, Bearpaw Formation, East of Manyberries, Alberta; SDSM 76193: skull with lower jaws preserved in a nodule, DeGrey Member of the middle Pierre Shale, Hyde County, South Dakota. Much of the skull roof and orbital area are missing in the latter specimen, but the remainder of the skull exhibits exceptional preservation.

Stratigraphic Distribution—Both the Bearpaw Formation and the DeGrey Member of the Pierre Shale are late Campanian in age. The base of the Bearpaw Formation has been radiometrically dated to 74.8 Ma (Eberth, 2005). A bentonite near the top of the formation in central Alberta has been dated at 73.2 Ma, although magnetostratigraphic evidence indicates that, in southern Alberta, the Bearpaw Formation extends to the Campanian/Maastrichtian boundary (Lerbekmo and Braman, 2002). The top of the DeGrey Member of the Pierre Shale has been interpreted as representing the maximum transgression stage of the Bearpaw Sea, and a radiometric date of 74.58 Ma has been obtained from the underlying Crow Creek Member (Hanczaryk, 2004). Thus the stratigraphic distribution of *Nichollsemys baieri* can be constrained to between 74.8 Ma (the base of the Bearpaw Formation) and 70.6 Ma (the Campanian/Maastrichtian boundary). The Sharon Springs and Pembina members of the Pierre Shale are of early to middle Campanian age (Dyman et al, 1994). A bentonite at the base of the Sharon Springs member of the Pierre Shale has been dated at approximately 80 Ma (Obradovich, 1993). Thus the Sharon Springs

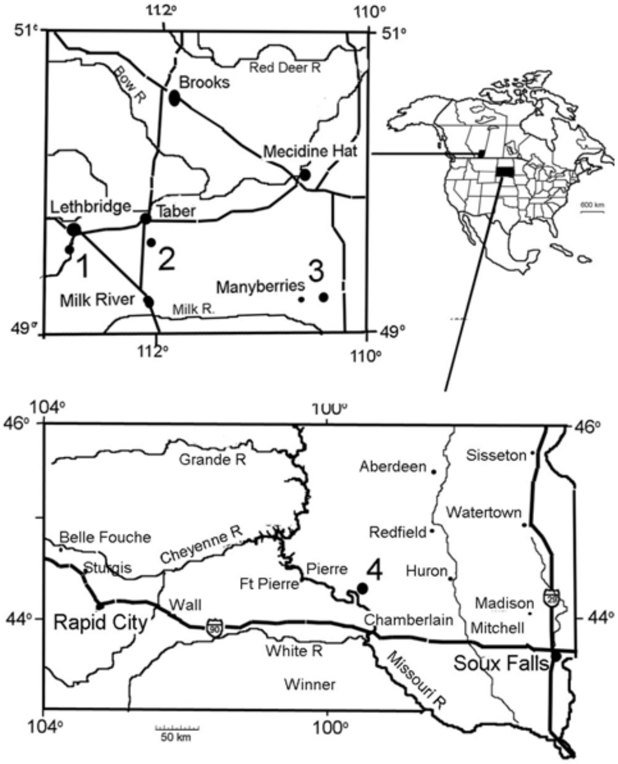

FIGURE 1. Map showing the localities of specimens of *Nichollsemys baieri*. 1) locality of TMP 2000.55.1; 2) locality of TMP 97.99.1; 3) locality of TMP 2000.53.2; 4) locality of SDSM 76193.

species of *Toxochelys* is approximately five million years older than *Nichollsemys baieri*.

Diagnosis—A primitive non-protostegid chelonioid similar to *Toxochelys* in that: a secondary palate is absent, the foramen palatinum posterius is large, the triturating surfaces are narrow but different from *Toxochelys* in the reduced exposure of the basisphenoid on the ventral surface of the palate, the presence of a mid-ventral ridge on the palate extending between the basisphenoid and vomer, the foramen anterior canalis carotici interni is separated by a thin bar of bone, the canalis caroticus internus joins the sulcus cavernosus, and the foramen caroticum laterale is larger than the foramen anterior canalis carotici interni. *Nichollsemys* differs from *Ctenochelys* in the presence of relatively narrower triturating surfaces that do not include the vomer and a larger foramen palatinum posterius. *Nichollsemys* differs also from *Porthochelys* in exhibiting a relatively narrower skull that is more triangular-shaped in dorsal view and in the small exposure of the basisphenoid on the ventral surface of the palate.

Description—In dorsal view (Figure 2A, 3A, 4A), the skull of *Nichollsemys baieri* is triangular with gently rounded cheek regions tapering to a blunt snout. No constriction of the snout is present. The orbits are large and face strongly dorsally. The posterior edge of the skull roof is not fully preserved in specimen TMP 97.99.1, but in TMP 2000.55.1 (Figure 3A) no posterior emargination is present. Measurements of the specimen TMP 97.77.1, which exhibits very little deformation from crushing, are shown in Table 1.

In lateral view, specimen TMP 97.99.1 (Figure 2C), shows that the skull of *Nichollsemys baieri* is moderately deep and has a well-developed cheek emargination. These proportions differ very little from the proportions of the skull of the Niobrara *Toxochelys* species as reconstructed by Zangerl (1953).

The skull roof bones are ornamented by striae radiating outwards from their centers of ossification. No sulci are present on the dermal bones.

TABLE 1. Measurements of the skull of *Nichollsemys baieri*.

	TMP 97.99.1	TMP 2000.55.1
Length from basioccipital to premaxilla:	11.4 cm	10.1 cm
Width across quadrates:	9.8 cm	8.0 cm
Depth at level of quadrates:	7.1 cm	--
Intraorbital width:	2.0 cm	1.9 cm
Length of orbit:	3.6 cm	3.8 cm

The sutures delineating the bones of the skull roof are clear (Figs. 2, 3, 4). Nasals are absent, in contrast to *Toxochelys* and *Porthochelys*. The prefrontals extend between the maxillae to form the dorsal margin of the external narial opening. The frontals have a V-shaped anterior edge that separates the posterior ends of the prefrontals. The anterior halves of the opposing prefrontals meet medially anterior to the frontals. The orbital margins of the prefrontal and frontal are subequal in length. The suture between the parietal and frontal is located immediately posterior to the posterior edge of the orbit. The squamosals project only a small distance posterior to the otic capsule. Dorsally, the squamosal contacts the quadratojugal, postorbital, and parietal. The postorbital is a large, plate-like element forming the dorso-lateral portion of the skull roof. Compared to the Niobrara *Toxochelys* species, the jugal has a large plate-like portion that covers the ventral half of the cheek region, and the quadratojugal has a reduced area of exposure laterally between the quadrate and jugal (Figs. 2C, 4C). The squamosal is

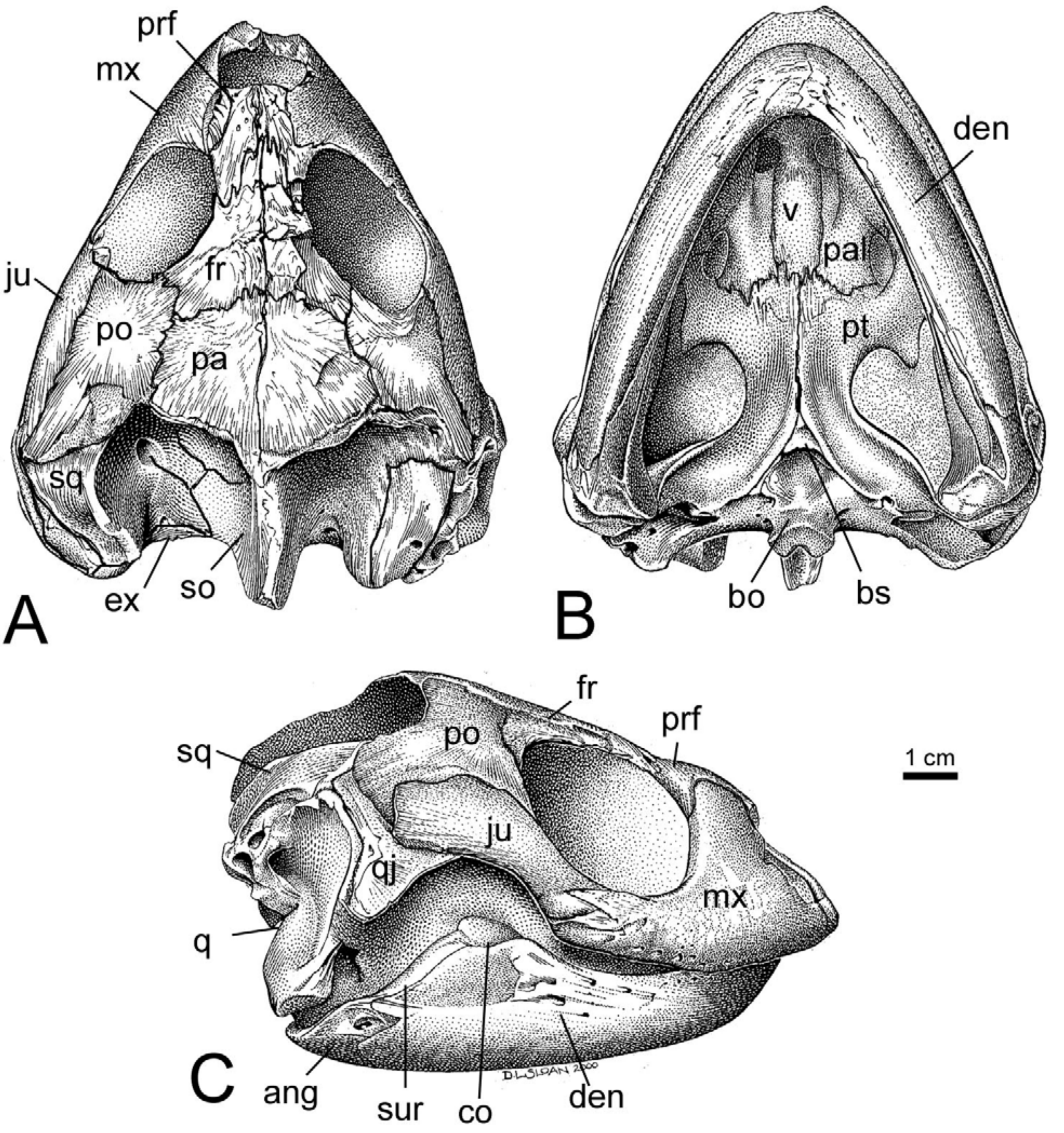

FIGURE 2. *Nichollsemys baieri* gen. et sp. nov. Specimen TMP 97.99.1, in: **A**, dorsal, **B**, ventral, and **C**, lateral views. **Abbreviations**: **ang**, angular; **bo**, basioccipital; **bs**, basisphenoid; **co**, coronoid; **den**, dentary; **ex**, exoccipital; **fr**, frontal; **ju**, jugal; **mx**, maxilla; **pa**, parietal; **pal**, palatine; **po**, postorbital; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **so**, supraoccipital; **sqm**, squamosal; **sur**, surangular; **v**, vomer.

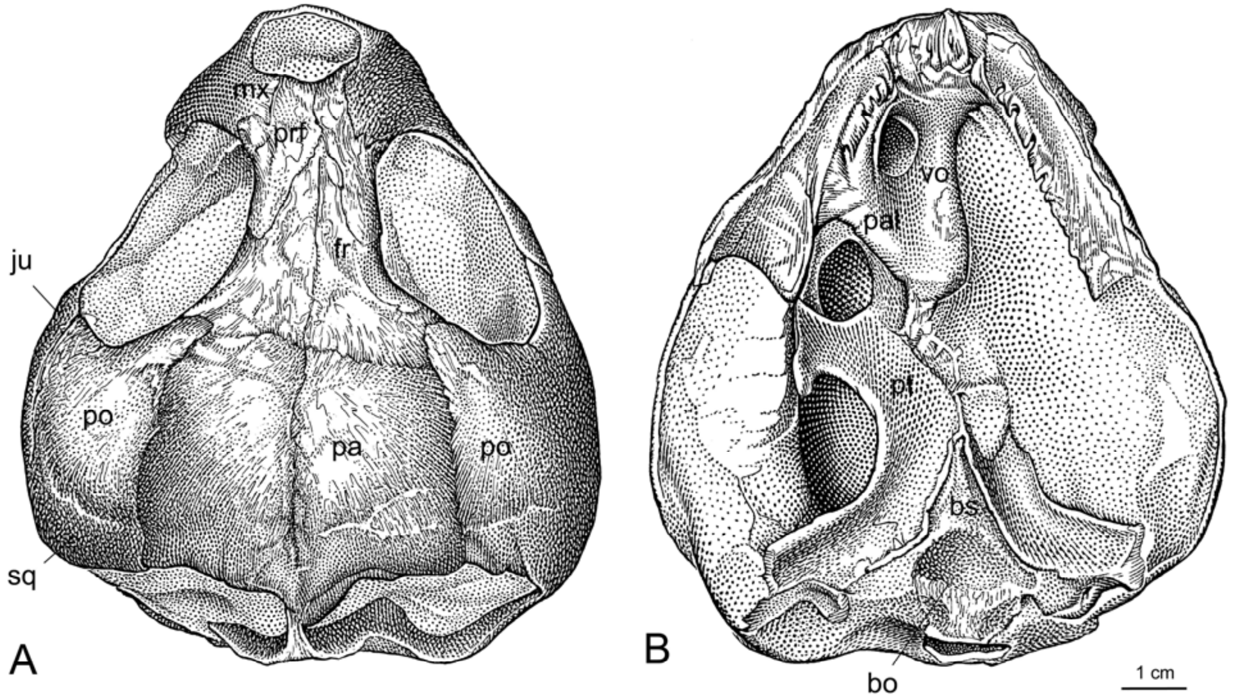

FIGURE 3. *Nichollsemys baieri* gen. et sp. nov. Specimen TMP 2000.55.1 in: **A**, dorsal, and **B**, ventral views. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **fr**, frontal; **ju**, jugal; **mx**, maxilla; **pa**, parietal; **pal**, palatine; **po**, postorbital; **prf**, prefrontal; **pt**, pterygoid; **vo**, vomer.

displaced and it is uncertain whether or not the squamosal contacted the postorbital. The supraoccipital has a narrow exposure on the skull roof in the form of the dorsal edge of the supraoccipital crest. Its ventral edge is flattened, a feature that Parham and Stidham (1999) noted was typical of primitive cheloniids. In all available specimens, the supraoccipital crest is short, barely extending posterior to the squamosal, although it is not possible to exclude the possibility that this is a result of incomplete preservation.

The palate of *Nichollsemys baieri* (Figure 2B, 3B, 4B) is similar to that of *Toxochelys* in that the triturating surface is narrow, a secondary palate is absent, a well-developed foramen palatinum posterius is present, and a distinct processus pterygoideus externus is present. Although a secondary palate is absent, CT scan slices show that the primary palate is highly arched (Figure 5A). The medial edge of the triturating surface in *Nichollsemys baieri* forms a low, rugose ridge. The anterior and medial portion of this ridge is formed by the palatines and the posterior portion is formed by the pterygoid. The vomer does not contribute to the triturating surface.

The internal narial openings are located far anteriorly. They are bordered by the vomer and palatine. The vomer forms a broad, rounded ridge between the narial openings. Posteriorly, the vomer contacts the pterygoids and inserts between the palatines. The foramen palatinum posterius is bordered by the palatine, pterygoid, and maxilla, and is located entirely medial to the triturating surface of the maxilla. This configuration differs from the condition observed in primitive eucryptodires, such as *Ordosemys* Brinkman, 1993, where the foramen extends posterior to the triturating surface (Brinkman and Wu, 1999). The foramen palatinum posterius is similar in size to that of *Toxochelys* and *Porthochelys* and is much larger than in *Ctenochelys*. As in *Toxochelys* and *Porthochelys*, *Nichollsemys baieri* has a well-developed processus pterygoideus externus on the pterygoids. The pterygoids are constricted between the processus pterygoideus externus and the quadrate articular surfaces so the palate in this region is very narrow. The basisphenoid is largely covered by the pterygoids, reducing its ventral exposure to a V-shaped crest. A mid-ventral ridge leads from the anterior end of this V-shaped crest to the vomer. Specimens of

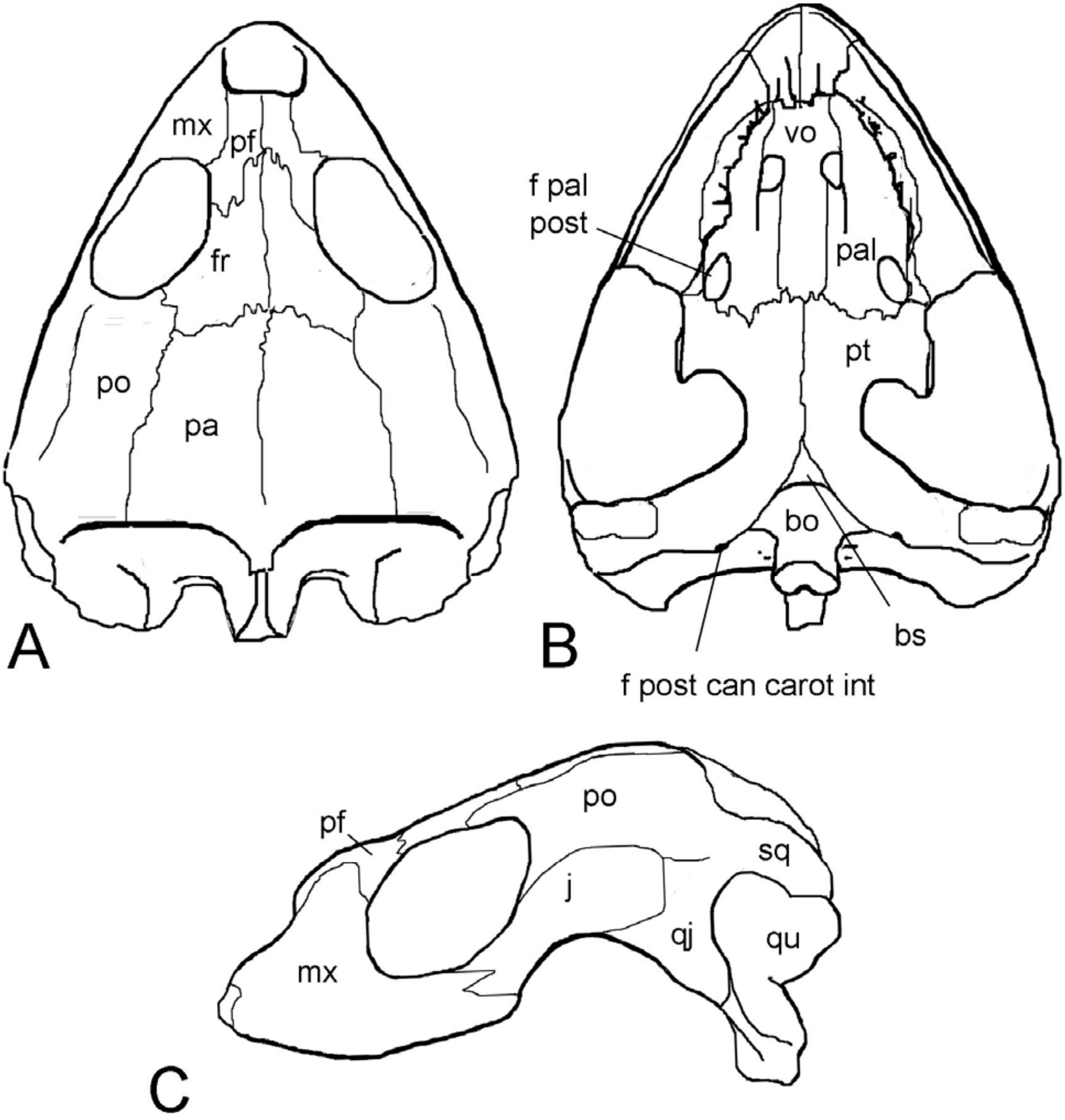

FIGURE 4. Reconstruction of the skull of *Nichollsemys baieri* in A) dorsal view, B) palatal view, and C) lateral view. Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **f pal post**, foramen palatinum posterior; **f post can carot int**, foramen posterior canalis caroticus internus; **fr**, frontal; **j**, jugal; **mx**, maxilla; **pa**, parietal; **pal**, palatine; **po**, postorbital; **pf**, prefrontal; **pt**, pterygoid; qj, quadratojugal; qu, quadrate; sq, squamosal; **vo**, vomer.

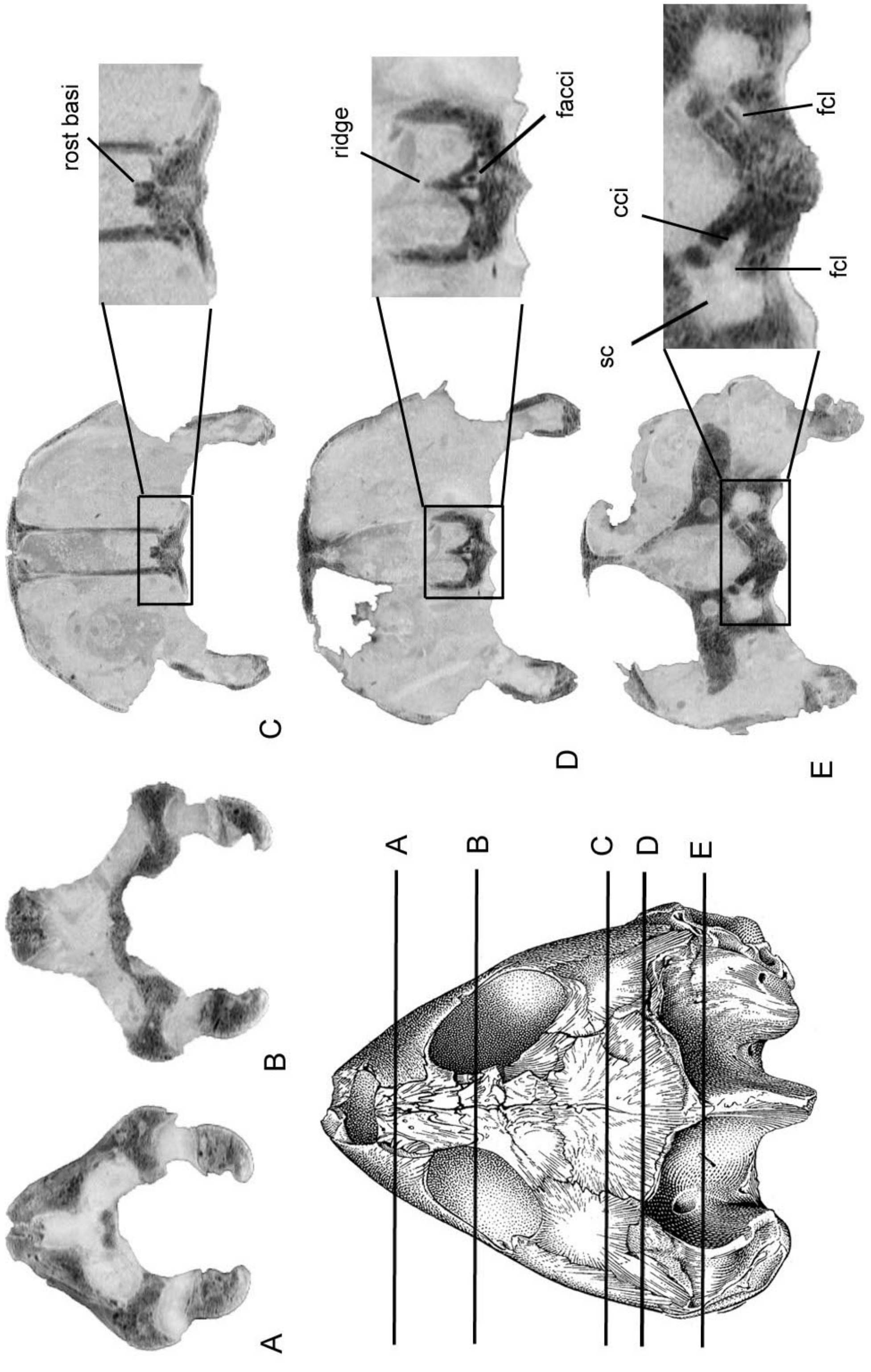

FIGURE 5. Transverse sections of the skull of *Nichollsemys baieri* from CT scans. **A**, cross section of anterior end of triturating surface of dentary; **B**, cross section mid-way along triturating surface of dentary; **C**, section through the rostrum basisphenoidale; **D**, section through the basisphenoid showing the anterior end of the canalis caroticus internus and the mid-line ridge extending between the foramina anterior canalis carotici interni and the dorsum sellae; and **E**, section showing the junction between the canalis caroticus internus and the sulcus cavernosus. **Abbreviations**: **cci**, canalis caroticus internus; **facci**, foramen anterior canalis carotici interni; **fcl**, foramen caroticum laterale; **ridge**, mid-line ridge extending between foramen anterior canalis carotici interni and dorsum sellae; **rost basi**, rostrum basisphenoidale; **sc**, sulcus cavernosus.

Niobrara *Toxochelys* species differ in having a larger area of exposure of the basisphenoid and lacking a mid-ventral ridge. Instead, a large flat area is present along the midline between the ventral crest of the basioccipital and the vomer in the Niobrara species, as seen in *Toxochelys moorevillensis* Zangerl, 1953. A mid-ventral ridge is variably developed in specimens of the Sharon Springs *Toxochelys* species. This ridge has been observed on seven of the ten skulls of this taxon that preserve this region but it does not always reach the vomer.

Only a small portion of the braincase is exposed, but many features of its internal and external morphology can be interpreted from CT scans of TMP 97.99.1. The supraoccipital forms the roof of the braincase, articulating with the exoccipital and prootic bones. The exoccipitals articulate with the basioccipital, supraoccipital, and opisthotic bones. They form two-thirds of the occipital condyle and are separated in the midline by the basioccipital, which forms the lower third of the occipital condyle and is exposed dorsally between the exoccipitals for its entire length. Internally, a distinctive, oblong-shaped basis tuberculi basalis is present, flanked by deep sulci on both sides. The basis tuberculi basalis of *Nichollsemys baieri* is larger and slightly broader than that of *Toxochelys moorevillensis*. A moderately developed midline crest, the crista dorsalis basioccipitalis (crista basioccipitalis of Zangerl [1953]) extends posterior from the basis tuberculi basalis along the dorsal midline of the basioccipital. A weakly developed crest, the crista basisphenoidalis of Zangerl (1953), extends anteriorly on the basisphenoid from the basis tuberculi basalis to the dorsum sellae.

In CT scans, the basisphenoid can be seen to contact the basioccipital by way of a large flat surface, although the suture between the two bones is difficult to distinguish in ventral view. Internally, the basisphenoid has a long, raised, rod-like rostrum basisphenoidale (Figure 5A). Because a long rod-like rostrum basisphenoidale is absent in *Toxochelys* (Hirayama, 1994), this feature unites *Nichollsemsy baieri* with *Ctenochelys* and cheloniids. However, in contrast to the condition in *Ctenochelys* and derived cheloniids, *Nichollsemys* displays a suture between the two halves of the rostrum basisphenoidale. As in other cheloniids, the dorsum sellae is high, and does not conceal the posterior portion of the sella turcica. In *Toxochelys moorevillensis,* the space between the foramen anterior canalis carotici interni is flat (Zangerl, 1953, pl. 9 B), whereas a midline ridge extends from the foramen to the dorsum sellae in derived cheloniids (Zangerl, 1953, pl. 9A). *Nichollsemys* resembles derived cheloniids in having a midline ridge in this position. A processus clinoideus is present on both sides of the dorsum sellae in *Nichollsemys*, with a distinct foramen nervi abducentis below each process.

The internal carotid artery enters the skull via the foramen posterior canalis carotici interni, formed entirely by the pterygoid. The canalis caroticus internus runs anteriorly and medially along the basisphenoid – pterygoid suture and eventually contacts the sulcus cavernosus (Figure 5E). In extant cheloniids, the internal carotid artery enters the sulcus cavernosus through a foramen formed by the contact between the canal and the sulcus cavernosus. The palatine artery extends forwards in a groove at the base of the sulcus cavernosus, whereas the medial branch of the internal carotid artery passes through the basisphenoid into the dorsum sellae, exiting through the foramina anterior canalis caroticus internus. In derived cheloniids, the palatine artery is larger in diameter than the medial branch of the internal carotic artery. In *Nichollsemys*, the canalis caroticus internus is reduced to a foramen between the canalis caroticus internus and the sulcus cavernosus. The diameter of this foramen gives an indication of the diameter of palatine artery. This foramen is larger than the diameter of the medial branch of the canalis caroticus internus (Figure 5E). Thus, in this feature, *Nichollsemys baieri* is more similar to derived cheloniids than to *Toxochelys*. A short section of the canalis caroticus internus continues forward from the foramen caroticum laterale through the basisphenoid to emerge onto the floor of the braincase through the foramen anterior canalis carotici interni. The two foramina anterior canalis carotici interni are separated by a thin bar, as in *Ctenochelys* and more derived cheloniids (Figure 5D). In *Toxochelys*, the bar of bone separating them is wider.

The lower jaw is preserved in TMP 97.99.1 (Figure 2C, 5A-B) and SDSM 76193. The proportions of the lower jaw are similar to those of *Toxochelys* in that the symphysis is narrow, the posterior end of the dentary is relatively shallow, and the coronoid process is located at two-thirds the length of the mandible posterior from the anterior edge. The triturating surface, seen in cross section in CT scans, is relatively narrow and flat and lacks distinct lingual and labial ridges (Figure 5A-B). The lateral surface of the postdentary region has an enlarged, deep concavity for the adductor muscles. The coronoid and surangular are visible on the lateral surface of the lower jaw posterior and dorsal to the dentary. An attachment site for the mandibular depressor muscle, which occurs on a posteromedial process of the articular in *Toxochelys*, is absent in both TMP 97.99.1 and SDSM 76193.

DISCUSSION

Nichollsemys baieri is similar to the primitive non-protostegid chelonioids *Toxochelys*, *Porthochelys*, and *Ctenochelys* in the absence of an extensive secondary palate, in the presence of a foramen palatinum posterius, and the presence of a processus pterygoideus externus, all primitive chelonioid features. The skull of *Nichollsemys baieri* is similar to that of *Toxochelys* and *Porthochelys* and different from that of *Ctenochelys* in the larger size of the foramen palatinum posterius and in the narrower triturating surface to which the vomer does not participate. The bones of the skull roof in *Nichollsemys baieri* differ from *Toxochelys* in the absence of nasals and in the presence of a relatively larger jugal that approaches the quadrate more closely. *Nichollsemys baieri* presents a mosaic arrangement of those features that differentiate the Niobrara and Sharon Springs species of *Toxochelys*. *Nichollsemys baieri* is similar to the Niobrara species in the absence of a constriction of the snout and in the indistinct lingual and labial ridges on the dentary, but the presence of an extensively developed skull roof in *Nichollsemys baieri* is similar to the Sharon Springs species.

The phylogenetic position of *Nichollsemys baieri* relative to *Toxochelys moorevillensis,* the Niobrara *Toxochelys* species*,* and *Ctenochelys* is documented by features of the braincase. In *Nichollsemys* and *Ctenochelys,* the area of exposure of the basisphenoid on the ventral surface of the braincase is much smaller than in *Toxochelys*. Also, a mid-ventral ridge extends between the basisphenoid and vomer in *Nichollsemys*, in contrast to the condition in *Toxochelys moorevillensis* and the Niobrara *Toxochelys* species, which have a flat ventral surface; as noted above, the Sharon Springs *Toxochelys* species is variable in this feature. *Toxochelys* is primitive in the absence of a rod-like rostrum basisphenoidale, a canalis caroticus internus that does not join the sulcus cavernosus. In *Ctenochelys,* as in derived cheloniids, a rod-like rostrum basisphenoidale is present, and the canalis caroticus internus joins the sulcus cavernosus. *Nichollsemys baieri* is similar to *Ctenochelys* and derived cheloniids in these features of the braincase demonstrating that, despite the general similarities to *Toxochelys* in skull shape and development of the triturating surfaces, *Nichollsemys baieri* is relatively more derived.

The relative size of the canalis caroticus lateralis and the medial branch of the canalis caroticus internus also provides information on the phylogenetic relationships of these taxa. In *Toxochelys*, the canalis caroticus lateralis is much smaller in diameter than the canalis caroticus internus, while in *Nichollsemys baieri* the canalis caroticus lateralis is slightly larger. The presence of a small canalis caroticus lateralis has been considered primitive for cheloniids because this condition is present in chelydrids, testudinoids and baenids (Zangerl, 1953; Gaffney, 1975). However, the polarity of these character-states in eucryptodires has been reinterpreted on the basis of the presence of equally sized canals in primitive eucryptodires from Asia, such as *Ordosemys* and *Sinemys* (Brinkman and Nicholls, 1993; Brinkman and Peng, 1993; Brinkman and Wu, 1999), as well as other primitive cryptodires such as *Kallokibotion* (Gaffney and Meylan, 1992). Thus, in the presence of a canalis caroticus lateralis smaller in diameter than the medial branch of the canalis caroticus internus, the basicranial region of *Toxochelys* can be interpreted as autapomorphic for that genus, while that of *Nichollsemys*, which has canals of equal size, can be interpreted as retaining the primitive eucryptodirian condition.

This presence of a chelonioid that is similar to *Toxochelys* in the development of the palate and triturating surface but derived in features of the braincase is of interest in view of a recent cladistic analysis which places *Toxochelys, Ctenochelys*, and their close relatives outside a clade including cheloniids, protostegids and dermochelyids (Kear and Lee, 2006). Although this placement of *Toxochelys* had been suggested earlier on the basis of features of the braincase (Gaffney and Meylan, 1988), subsequent studies included *Toxochelys* and *Ctenochelys* within the Cheloniidae (Hirayama 1994, 1998; Parham and Fastovsky, 1997; Lynch and Parham, 2003). Since the characters that support this revised placement of *Toxochelys* and *Ctenochelys* are features of the forelimb, which is not known in *Nichollsemys*, it is not possible to use the apomorphies that Kear and Lee (2006) identified to evaluate whether it should be placed within the *Toxochelys-Ctenochelys* clade or within the cheloniid clade. A cladistic analysis based on the character matrix used by Kear and Lee (2006) was undertaken. The codings for the characters of *Nichollsemys* are shown in Appendix 1. This analysis placed *Nichollsemys* as the sister to *Ctenochelys*, with *Toxochelys* as the sister taxon to those two, in a tree that is 213 steps long, two steps longer than that of Kear and Lee (2006). However, in a bootstrap analysis with 1000 replicates, several clades, including *Nichollsemys-Ctenochelys*, collapse due to support below 50%. Data on the postcranial skeleton, particularly the structure of the forelimbs, could easily alter the position of *Nichollsemys* relative to *Ctenochelys* and the Cheloniidae, and in the absence of these data, the relationships indicated by this cladistic analysis are best considered tentative.

The occurrence of *Nichollsemys baieri* in both the Bearpaw Formation of southern Alberta and the DeGrey Member of the Pierre Shale of South Dakota

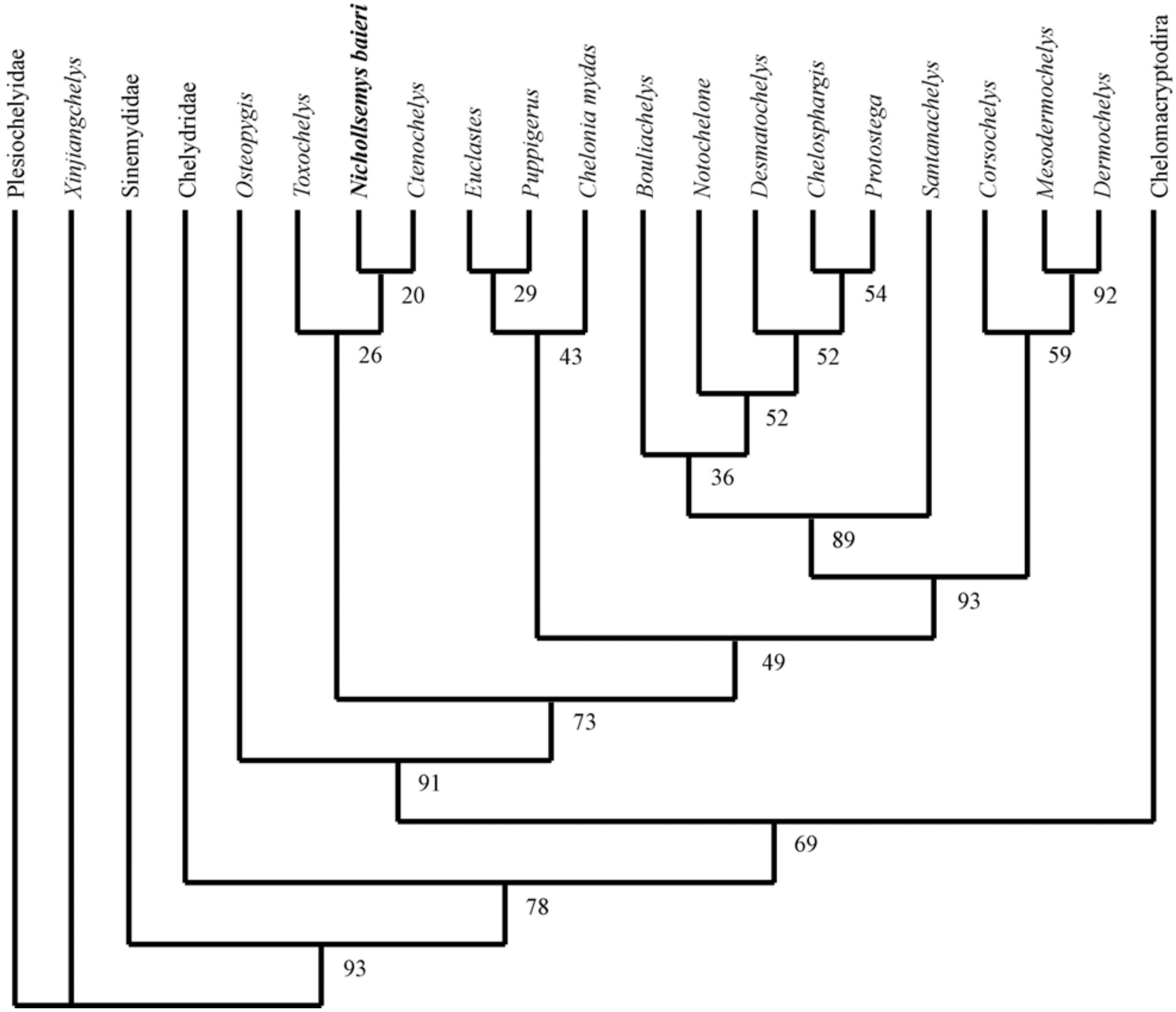

FIGURE 6. Cladogram showing the interrelationships of primitive non-protostegid chelonioids. Cranial apomorphies supporting the clades shown in this cladogram are: 1) the presence of an incipient secondary palate involving the palatines; an apertura narium interna entirely formed by the palatines and vomer; and the presence of a v-shaped crest on the ventral surface of the basisphenoid; 2) , area of exposure of the basisphenoid on the ventral surface of the braincase reduced; a mid-ventral ridge on the palate extends between the basisphenoid and vomer; a rod-like rostrum basisphenoidale present; foramen anterior canalis carotici interni separated by thin bar of bone; a mid-line ridge extends from the foramen anterior canalis carotici interni to the dorsum sellae; and foramen caroticum laterale equal to or larger in diameter than the foramen anterior canalis carotici interni; 3) triturating surface involving vomer in addition to palatines; foramen palatinum posterius reduced; and processus pterygoideus externus reduced; 4) foramen palatinum posterius absent. Numbers refer to bootstrap values at each node. Tree length = 213 steps; RI = 0.73; CI = 0.55.

indicates that it was widespread in the northern reaches of the Western Interior Seaway during the late Campanian (Figure 1). The cheloniids from the Bearpaw and underlying Dinosaur Park formations represent the northern-most occurrence of this family in the late Campanian along the Western Interior Seaway. This range is thought to closely approximate the original limit of their distribution, because marine turtles are rare in these formations. The limited occurrence of cheloniids in southern Alberta is consistent with the culmination of a trend of latitudinal reduction in diversity and abundance of marine turtles in Late Cretaceous marine reptile assemblages from south to north (Nicholls and Russell, 1990). Because the northern limit of extant cheloniid distribution is controlled by temperature (Schwartz, 1978), it is likely that climate was also the controlling factor limiting the distribution of marine turtles in the late Campanian.

ACKNOWLEDGMENTS

We would like to thank R. Baier, who found the type specimen and donated it to the Royal Tyrrell Museum, M. Getty, who prepared the type specimen, and D. L. Sloan, who illustrated the two specimens from the Bearpaw Formation. In part this paper includes the results of a Master's thesis completed by M. Hart at the South Dakota School of Mines and Technology. Maggie Hart would like to thank her advisor, J. Martin, and colleagues at the South Dakota School of Mines and Technology for help while completing her thesis. Pat Holroyd, Gene Gaffney, Howard Hutchison, Ren Hirayama, Jim Parham, and François Therrien read earlier drafts of this paper. Their time and efforts are greatly appreciated.

LITERATURE CITED

Batsch, A. J. G. C. 1788. Versuch einer Anleitung, zur Kennnish und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena, 528 pp.

Baur, G. Notes on the classification of the Cryptodira. American Naturalist 27:672-675.

Bottjer, D. J. 1985. Trace fossils and paleoenvironments of two Arkansas Upper Cretaceous discontinuity surfaces. Journal of Paleontology 59: 282-298.

Brinkman, D. B. 1993. *Ordosemys leios*, n.gen., n.sp. a new turtle from the Early Cretaceous of the Ordos Basin, Inner Mongolia. Canadian Journal of Earth Sciences 30:2128-2138.

Brinkman, D. B. 2000. A primitive cheloniid from the Campanian (Late Cretaceous) of Alberta, Canada. Journal of Vertebrate Paleontology 20(3, Supplement):31A.

Brinkman, D. B. 2005. A vertebrate assemblage from the marine shales of the Lethbridge Coal Zone. Pp 486-500 in P. J. Currie and E. B. Koppelhus (eds.) Dinosaur Provincial Park, A spectacular ancient ecosystem revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Brinkman, D. B., and E. L. Nicholls. 1993. The skull of *Neurankylus eximius* (Testudines: Baenidae) and a reinterpretation of the relationships of this taxon. Journal of Vertebrate Paleontology 13: 273-281.

Brinkman, D. B., and J. –h. Peng. 1993. New material of *Sinemys* (Testudines, Sinemydidae) from the Early Cretaceous of China. Canadian Journal of Earth Sciences 30: 2139-2152.

Brinkman, D. B., and X. C. Wu. 1999. The skull of *Ordosemys*, an Early Cretaceous turtle from Inner Mongolia, People's Republic of China, and the interrelationships of Eucryptodira (Chelonia, Cryptodira). Paludicola 2:134-147.

Case, E. C. 1898. *Toxochelys*. University of Kansas Geological Survey 4:370-385.

Cobban, W. J., and W. J. Kennedy. 1993. Upper Cretaceous ammonites from the Coon Creek Tongue of the Ripley Formation at its type locality in McNarry County, Tennessee. U. S. Geological Survey Bulletin 2073: B1-B12.

Collins, R. E. L. 1951. A new turtle, *Toxochelys weeksi*, from the Upper Cretaceous of west Tennessee. Journal of the Tennessee Academy of Science 26:262-269.

Cope, E. D. 1873. *Toxochelys latiremis*. Proceedings of the Academy of Natural Sciences, Philadelphia 1873:10.

Cope, E. D. 1877. *Toxochelys latiremis*. Proceedings of the American Philosophical Society 1877:176

Dyman, T. S., W. A. Cobban, J. E. Fox, R. H. Hammond, D. J. Nichols, W. J. Perry, jr. K. W. Porter, D. D. Rice, D. R. Stterholm, G. W. Shurr, R. G Tysdal, J. C. Haley, and E. B. Campen. 1994. Cretaceous rocks from southwestern Montana to southwestern Minnesota, northern Rocky Mountains, and Great Plains region. Geological Society of America Special Paper 287: 5-26.

Eberth, D. A. 2005. The Geology. Pp 54-87 in P. J. Currie and E. B. Koppelhus (eds.) Dinosaur Provincial Park, A spectacular ancient ecosystem revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Eberth, D. A., and D. B. Brinkman. 1997. Paleoecology of an estuarine, incised-valley fill in the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) of southern Alberta, Canada. Palaios 12: 43-58.

Everhart, M. J. 2005. Oceans of Kansas, A natural history of the Western Interior Sea. Indiana University Press, Bloomington and Indianapolis, Indiana.

Gaffney, E. S. 1975. A phylogeny and classification of the higher categories of turtles. Bulletin of the American Museum of Natural History 147: 241-320.

Gaffney, E. S., and P. A. Meylan. 1988. A phylogeny of turtles. Pp 157-219 in M. J. Benton (ed.) The phylogeny and classification of the tetrapods; Volume 1, Amphibians, Reptiles, Birds. Systematics Association Special Volume 35A. Clarendon Press, Oxford.

Gaffney, E. W., and P. A. Meylan. 1992. The Transylvanian turtle *Kallokibotion*, a primitive cryptodire of Cretaceous age. American Museum Novitates 3040: 1-37.

Hanczaryk, P. A. 2004. Stratigraphy and paleoecology of the Middle Pierre Shale along the Missouri River (Central South Dakota. Geological Society of America, Rocky Mountain Section, Abstracts with Programs 36: 67-68.

Hart, M. M. 2004a. *Toxochelys*: Taxonomic Comparison and Stratigraphic Distribution During the Campanian Lower Pierre Shale of South Dakota. M.S. thesis, South Dakota School of Mines and Technology, Rapid City, South Dakota, 109 pp.

Hart, M. M. 2004b. Size variation in cranial morphology of Late Cretaceous *Toxochelys* (Testudines Cheloniidae) of South Dakota. Geological Society of America Abstracts with Programs, Rocky Mountain and Cordilleran Sections 36: 80.

Hay O. P. 1896. On the skeleton of *Toxochelys latiremis*. Field Museum, Zoological Series 1:101-106.

Hay, O. P. 1905. A revision of the species of the family of fossil turtles called Toxochelyidae, with descriptions of two new species of *Toxochelys* and a new species of *Porthochelys*. Bulletin of the American Museum of Natural History 21:177-185.

Hay, O. P. 1908. Fossil Turtles of North America. Carnegie Institution of Washington, Washington, D. C., 568 pp.

Hirayama, R. 1994. Phylogenetic systematics of chelonioid sea turtles. The Island Arc 3:270-284.

Hirayama, R. 1997. Distribution and diversity of Cretaceous chelonioids. Pp. 225-241 in J. M. Callaway and E. L. Nicholls (eds.) Ancient Marine Reptiles. Academic Press, San Diego, California.

Hirayama, R. 1998. Oldest known sea turtle. Nature 392:705-708.

Kear, B. P., and M. S. Y. Lee. 2006. A primitive protostegid from Australia and early sea turtle evolution. Biology Letters 2:116-119.

Lerbekmo, J. F., and D. R. Braman. 2002. Magnetostratigraphic and biostratigraphic correlation of late Campanian and Maastrichtian marine and continental strata from the Red Deer Valley to the Cypress Hills, Alberta, Canada. Canadian Journal of Earth Sciences 39:539-557.

Lynch, S. C., and J. F. Parham. 2003. The first report of hard-shelled sea turtles (Cheloniidae sensu lato) from the Miocene of California, including a new species (*Euclastes hutchisoni*) with unusually plesiomorphic characters. PaleoBios 23: 21-25.

Moody, R. T. J. 1984. The relative importance of cranial/post cranial characters in the classification of sea turtles. Studia Geologica Salmanticensia, vol especial 1 (Studia Palaeocheloniologica I): 205-213.

Nicholls, E. L. 1988. New material of *Toxochelys latiremis* Cope, and a revision of the genus *Toxochelys* (Testudines, Chelonioidea). Journal of Vertebrate Paleontology 8:181-187.

Nicholls, E. L. T. T. Tokaryk, and L. V. Hills. 1990. Cretaceous marine turtles from the Western Interior seaway of Canada. Canadian Journal of Earth Sciences 27:1288-1298.

Nicholls E. L., and A. P. Russell. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 79:149-169.

Obradovich, J. 1993. A Cretaceous time scale. Pp.379-396 in Caldwell, W.G.E., and Kauffman, E. (eds.) Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Parham, J. F. 2005. A reassessment of the referral of sea turtle skulls to the genus *Osteopygis* (Late Cretaceous, New Jersey, USA). Journal of Vertebrate Paleontology 25: 71-77.

Parham, J. F., and D. E. Fastovsky. 1997. The phylogeny of cheloniid sea turtles revisited. Chelonian Conservation and Biology 2: 548-554.

Parham, J. F., and T. A. Stidham. 1999. Late Cretaceous sea turtles from the Chico Formation of California. PaleoBios 19:1-7.

Schmidt, K. P. 1944. Two new thalassemyd turtles from the Cretaceous of Arkansas. Geological Series of the Field Museum of Natural History 8: 63-74.

Schultze, H.-P., L. Hunt, J. Chorn, and A.M. Neuner. 1985. Type and figured specimens of fossil vertebrates in the collection of the University of Kansas Museum of Natural History. Part II. Fossil amphibians and reptiles. University of Kansas, Museum of Natural History, Miscellaneous Publication 77:1-66.

Schwartz, F. J. 1978. Behavioral and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina. Florida Marine Research Publication 33: 16-18.

Swofford, D. L. 2002. Phylogenetic analysis using parsimony (* and other methods). Sinauer Associates, Sunderland MA.

Williston, S. W. 1901. A new turtle from the Kansas Cretaceous. Transactions of the Kansas Academy of Science 18:195-199.

Zangerl, R. 1953. The vertebrate fauna of the Selma Formation of Alabama. Part 4. The turtles of the Family Toxochelyidae. Fieldiana, Geology Memoirs 3:137-277.

APPENDIX 1

Coding of characters in *Nichollsemys* used in the cladistic analysis of primitive non-protostegid chelonioids. The character states recognized in this analysis and codings for the remaining taxa included in the analysis are from Kear and Lee (2006).

Nichollsemys: 0110100000 0101100100 0010000?12 1111111000 0101?????? ?????????? ?????????? ?????????? ?????????? ?????????? ????