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A Redescription of the Cretaceous Marine Turtle Ctenochelys acris Zangerl, 1953 and A Systematic Revision of the 'Toxochelyid'-Grade Taxa Using Cladistic Analysis

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A REDESCRIPTION OF THE CRETACEOUS MARINE TURTLE *CTENOCHELYS ACRIS* ZANGERL, 1953 AND A SYSTEMATIC REVISION OF THE 'TOXOCHELYID'-GRADE TAXA USING CLADISTIC ANALYSIS

by

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A THESIS

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2015

A REDESCRIPTION OF THE CRETACEOUS MARINE TURTLE *CTENOCHELYS ACRIS* ZANGERL, 1953 AND A SYSTEMATIC REVISION OF THE ‘TOXOCHELYID’-GRADE TAXA USING CLADISTIC ANALYSIS

ANDREW DOUGLAS GENTRY

BIOLOGY

ABSTRACT

Within this thesis are two separate articles, each representing a distinct chapter. The first chapter is a redescription of the ‘toxochelyid’-grade marine turtle *Ctenochelys acris* Zangerl, 1953. This redescription, based on several nearly complete specimens from the early Campanian Mooreville Chalk of Alabama, reveals multiple previously undescribed autapomorphic characteristics of this species and contributes significantly to our understanding of ‘toxochelyid’ alpha taxonomy.

The second chapter is comprised entirely of the results of multiple cladistic analyses of the ‘toxochelyid’-grade taxa that produce a hypothesized phylogenetic system of classification for this clade. 108 characters from the cranium, carapace, plastron, and appendicular skeleton were coded for three of the best described species considered ‘toxochelyid’-grade [*Toxochelys latiremis* Cope, 1873; *Ctenochelys stenoporus* (Hay, 1905); *Ctenochelys acris* Zangerl, 1953] (Hirayama, 1997), and for the outgroup taxa *Plesiochelys etalloni* Gaffney, 1975; *Xinjiangchelys wusu* (Rabi et al., 2013); *Ordosemys brinkmania* (Danilov and Parham, 2007); *Pacifichelys urbinai* Parham and Pyenson, 2010; *Chelydra serpentina* Linneaus, 1758; *Kinosternon flavescens* Agassiz, 1857; *Chelonia mydas* Linneaus, 1758; *Dermochelys coriacea* Vandelli, 1761; *Puppigerus camperi* (Gray, 1831); *Santanachelys gaffneyi* Hirayama, 1998; *Protostega gigas* Cope,

1872; *Calcarichelys gemma*, Zangerl, 1953; *Corsochelys haliniches* Zangerl, 1960; *Desmatochelys lowii* Williston, 1894; and a hypothetical primitive taxon.

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THESIS INTRODUCTION

Marine turtles are flagship species for conservation, but the modern species (7 spp.) represent only a fraction of their total diversity (Zangerl, 1953; Hirayama, 1997). Marine turtles [chelonioids] are the longest living marine tetrapod lineage with a fossil history extending back more than 100 million years. During the Mesozoic, there may have been as many as a dozen genera of chelonioid occupying a broad range of ecological niches from shallow, coastal estuaries to the open ocean (Zangerl, 1953; Joyce, 2007; Parham and Pyenson, 2010; Lapparent de Broin, 2013). As a result of their overall diversity and rich fossil record, the phylogenetics of marine turtles has been a productive field of study for paleontologists and evolutionary biologists for more than a century (Cope, 1873; Hay, 1908; Zangerl, 1953; Gaffney and Meylan, 1988; Hirayama, 1997; Joyce, 2007; Parham and Pyenson, 2010; Anquetin, 2012; Lapparent de Broin, 2013).

Once thought to have an ancestry leading back to the Cretaceous ‘protostegids’, which include the well-known genera *Archelon* and *Protostega*, recent paleontological studies suggest that ‘protostegids’ do not share a marine ancestor with extant species (Joyce, 2007; Joyce, 2013; Parham et al., 2014). Coupled with the exclusion of ‘protostegids’ from the chelonioid lineage, genetic data obtained from modern turtle fauna have placed chelonioids as a sister group to the chelydroids [chelydrids (i.e. snapping turtles) and kinosternoids (i.e. mud and river turtles)] which together form the newly created clade Americhelydia (Joyce et al., 2013; Crawford et al., 2014). This clade is named for the shared origin of these three lineages in the Americas following the high latitude dispersal of durocryptodires from Eurasia during the mid-Cretaceous (Crawford et al., 2014). This molecular evidence supports the claim that the three Americhelydian clades share a common ancestor in the Cretaceous of North America (Crawford et al., 2014). Several taxa have been proposed as stem-durocryptodires, including the macrobaenids (Parham, 2005), sinemydids (Crawford et al., 2014) and the xinjuangchelyids (Rabi, 2013) but this does not resolve the gap at the stem of Americhelydia.

Another group, referred to ambiguously as the 'toxochelyids' fits both the spacial and temporal confinements of the molecular phylogeny, but unfortunately is perhaps the poorest known North American clade of Cretaceous turtles. This diverse group of marine turtles can be found in the Aptian-Maastrichtian marine deposits of South Dakota, Kansas, Arkansas, New Jersey and much of the southeastern United States (Zangerl, 1953; Baird, 1964; Nicholls and Russell, 1990; Hirayama, 1997; Carrino, 2007; Matzke, 2009; Ikejiri et al., 2013). Several studies have identified the 'toxochelyids' as perhaps the earliest definitive chelonioids [i.e stem-chelonioids](Joyce, 2007; Joyce et al., 2013) and yet much of our current understanding of these fossil turtles comes from a single monograph of the 'toxochelyids' of Alabama published more than 60 years ago (Zangerl, 1953). Since the early 1950's, this clade of turtles has gone largely unstudied primarily due to the poor preservation of the type material, the limited number of specimens available for study and the general lack of diagnostic characters that can be used to differentiate the members of this group (Zangerl, 1953; Nicholls, 1988; Parham and Pyenson, 2010; Joyce et al., 2013).

As a result, the phylogenetic placement of 'toxochelyids' as either stem-cheloniids or stem-chelonioids remains in question, as does the identity of the common ancestor of the extant Americhelydian lineages. These questions can only be resolved with a formal re-description of the ‘toxochelyid’-grade taxa and the subsequent inclusion of these taxa into a global phylogenetic analysis constrained by an established molecular topology (Joyce, 2007; Parham and Pyenson, 2010; Joyce, 2013; Crawford et al., 2014). As a first step in this process, ‘toxochelyid’ material from the Cretaceous of Alabama identified as *Ctenochelys acris* is herein formally redescribed with a special emphasis on phylogenetically useful characteristics. In the second chapter, these characters are integrated into a novel character state matrix and cladistic analysis is performed to establish a phylogenetic system of classification for a number of ‘toxochelyid’-grade taxa.

Chapter 1

A REDESCRIPTION OF THE CRETACEOUS MARINE TURTLE *CTENOCHELYS ACRIS* ZANGERL, 1953

by

ANDREW DOUGLAS GENTRY

In preparation for *The Journal of Systematic Palaeontology*

Format adapted for thesis

ABSTRACT -- Recently, several nearly complete specimens of the ‘toxochelyid’-grade marine turtle *Ctenochelys acris* Zangerl, 1953 were identified within the collections at McWane Science Center in Birmingham, Alabama and The University of Alabama Museum of Natural History in Tuscaloosa. The specimens were originally collected from the early Campanian Mooreville Chalk of Alabama and represent the most complete remains yet known for this species. The largest individual (MSC 35085) consists of portions of the carapace, plastron and appendicular skeleton. Separate referred specimens include the first adult cranium, endoskeleton, limb elements, and the first juvenile cranial material described for *C. acris*. These specimens allow for a more detailed osteological description of the species than has previously been possible along with the determination of novel apomorphic characters for the genus.

INTRODUCTION

Marine turtle taxa traditionally referred to as ‘toxochelyids’ have undergone a rather tumultuous taxonomic history. Cope (1873) described the first material belonging to this clade from the Campanian Sharon Springs Member of the Pierre Shale in western Kansas and referred it to the newly created genus *Toxochelys,* formed from the Greek root ‘toxo-‘ meaning ‘bow’ and ‘-chelys’, turtle (Cope, 1872; Nicholls, 1988). Since that time, the ‘toxochelyids’ have grown into a much larger group consisting of six genera and more than a dozen recognized species (Hirayama, 1997). The most comprehensive study of these animals was performed by Zangerl (1953) and focused primarily on the ‘toxochelyids’ from the early Campanian Mooreville Chalk of Alabama (Figs. 2 and 3). Zangerl subdivided the ‘toxochelyids’ into two groups: the Lophochelyinae (the more derived group) and the relatively primitive Toxochelyinae based on the presence (derived) or absence (primitive) of a prominent mid-sagittal keel along the dorsal face of the carapace, often consisting of both neural and epineural ossifications.

The most well-known representative of the Toxochelyinae is *Toxochelys latiremis,* previously known from the Cretaceous outcrops of Kansas and South Dakota (Zangerl, 1953; Nicholls, 1988). This enigmatic species of primitive marine turtle is separated from other ‘toxochelyids’ by the retention of minimal plastral and costal fontanelles in adult forms, a moderately sized foramen caroticum laterale and a poorly developed secondary palate (Zangerl, 1953; Nicholls, 1988; Matzke, 2009). The primitive characteristics of the cranium of *T. latiremis* have been described by Matzke (2009) however, save the disarticulated slab specimen described by Nicholls (1988), all of the specimens used in Matzke’s descriptions are isolated crania lacking associated post-cranial material. This does not entirely preclude this material from phylogenetic analyses but characters taken from these specimens should be treated with caution. While many researchers consider *T. latiremis* to be the earliest definitive cheloniid (Joyce, 2013; Parham and Pyenson, 2010), due to its odd mixture of primitive and derived characters, questions remain as to the phylogenetic placement of this taxon (Fig. 1) as either a stem-cheloniid (Hirayama, 1998; Lapparent de Broin, 2013) or a stem-chelonioid (Gaffney and Meylan, 1988; Moody, 1997; Parham and Pyenson, 2010).

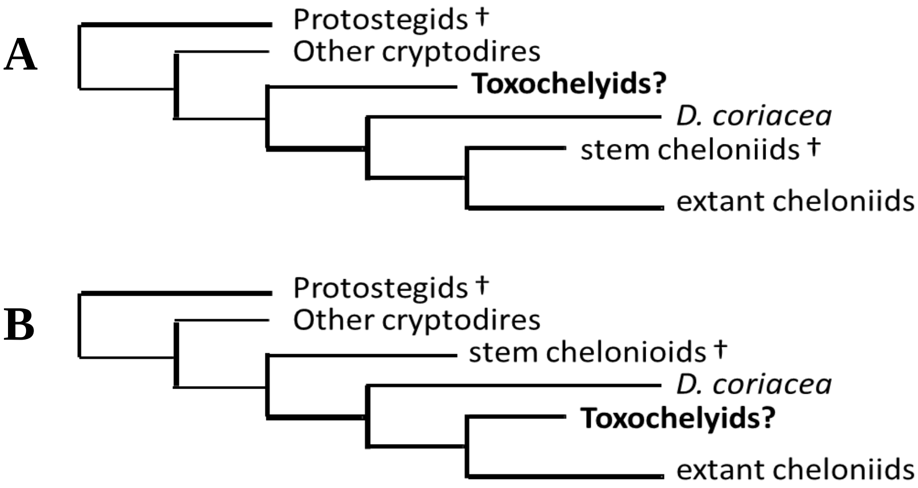

FIGURE 1 -- Example cladogram showing the 'toxochelyid'-grade taxa as either (A) stem chelonioids or (B) stem cheloniids.

The other members of the Toxochelyinae include the less common *Toxochelys moorevillensis* Zangerl, 1953 and *Thinochelys lapisossea* Zangerl, 1953 both known exclusively from the Mooreville Chalk of Alabama (Zangerl, 1953; Hirayama, 1997). To date, the only known specimens of these two taxa lack associated cranial and post-cranial elements, resulting in their exclusion from all existing cladistic studies (i.e. Gaffney and Meylan, 1988; Kear and Lee, 2006; Anquetin, 2011; Lapparent de Broin, 2013). It has also been suggested that another Cretaceous marine turtle genus, *Porthochelys*, may form a monophyletic grouping with *Toxochelys* and *Thinochelys* based on the presence of a broad cervical scute on the dorsal surface of the nuchal plate (Hirayama, 1997). However, due to a lack of figured material for these genera, this issue remains unresolved.

Far less is known of the more derived Lophochelyinae ‘toxochelyids’ with only one well described representative species, *Ctenochelys stenoporus* Hay, 1905 (Matzke, 2007). The exact evolutionary relationships of *Ctenochelys stenoporus* remain unknown but this species is hypothesized to be a sister taxon to *Toxochelys* and more closely related to extant cheloniids than other genera of ‘toxochelyids’ (Hirayama, 1997; Joyce, 2004; Parham and Pyenson, 2010). Several species of *Ctenochelys* were described by Zangerl (1953) but due to the partial nature of many of the holotypes and their subsequent incomplete descriptions, all *Ctenochelys* species were later synonymized, resulting in a monotypic genus containing the single species *Ctenochelys stenoporus* (Hirayama, 1997).

One of the more fragmentary holotypes of *Ctenochelys* described by Zangerl (1953) was that of *Ctenochelys acris* Zangerl, 1953. Zangerl’s (1953) description of this species was based largely on specimen FMNH P27354 from the Mooreville Chalk in Dallas County, Alabama which is currently housed in the Field Museum of Natural History in Chicago. This specimen consists of portions of the nuchal, peripherals 1, 2, 4-6 of the left side (in dorsal view), peripherals 3, 7, (8 or 9?) of the right side, a partial costal, the central portion of the left hyoplastron, a preneural, and 3 anterior neurals with an associated epineural between neural 1 and 2. Zangerl (1953) also references FMNH PR153 which consists of only a few isolated posterior peripherals and PR62, which is two posterior peripherals (10 and 11?) and a partial xiphiplastra. The only other referred specimen, FMNH P27356, includes a partial plastron, two peripherals, and an isolated neural, however, these elements are morphologically indistinguishable from those of *C. stenoporus* (Hay, 1905; Zangerl, 1953; Matzke, 2007).

Recently, a nearly complete specimen of a Cretaceous marine turtle from the Mooreville Chalk of Greene County, Alabama (Fig. 2) was identified in the collections at McWane Science Center (MSC 35085) in Birmingham, Alabama. This specimen possesses features identical to those figured in Zangerl, 1953 for *Ctenochelys acris* and, due to its nearly complete nature and exquisite preservation, reveals previously unknown characteristics for this species. These newly discovered characters assist in differentiating *C. acris* from the better known *C. stenoporus,* as well as, other panchelonioid taxa. Two other specimens identified as *C. acris* in the MSC collections represent the first examples of juvenile material and also of associated cranial and appendicular elements for this species, allowing for more thorough analyses of the Lophochelyinae and their phylogenetic placement within Cryptodira.

Geologic Setting

The *Ctenochelys acris* specimens referenced herein were collected from Mooreville Chalk deposits at site AGr-3 in Greene County, Alabama (Fig. 2). The Mooreville Chalk is diachronous, with surface exposures ranging in age from latest Santonian in the central portion of the state to early Campanian at the western edge of Alabama (Mancini et al., 1995) (Fig. 3). Cretaceous nanofossils from the Mooreville Chalk of Greene County indicate a biostratigraphic age for the deposits at site AGr-3 of between 83 Mya and 83.5 Mya (Liu, 2009). The Mooreville Chalk is notable for the common occurrence of the remains of extinct marine reptiles such as pliosaurs and mosasaurs, as well as, numerous sharks, fish and turtles (Zangerl, 1953a; Russell, 1970; Campagalio et al., 2013; Ikejiri et al., 2013). Fossil deposition is thought to have occurred in a shallow marine environment under dysoxic conditions (Kiernan, 2002).

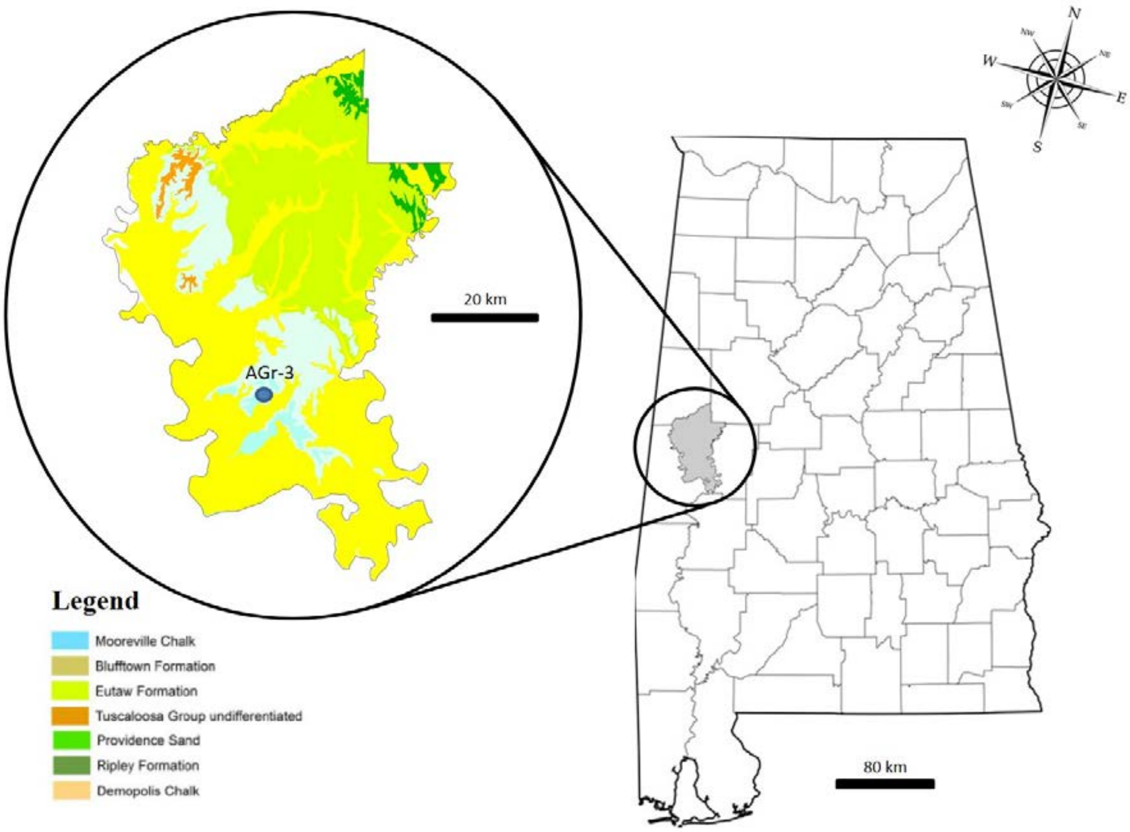

FIGURE 2 -- Map of Alabama showing the surface stratigraphy of Greene County.

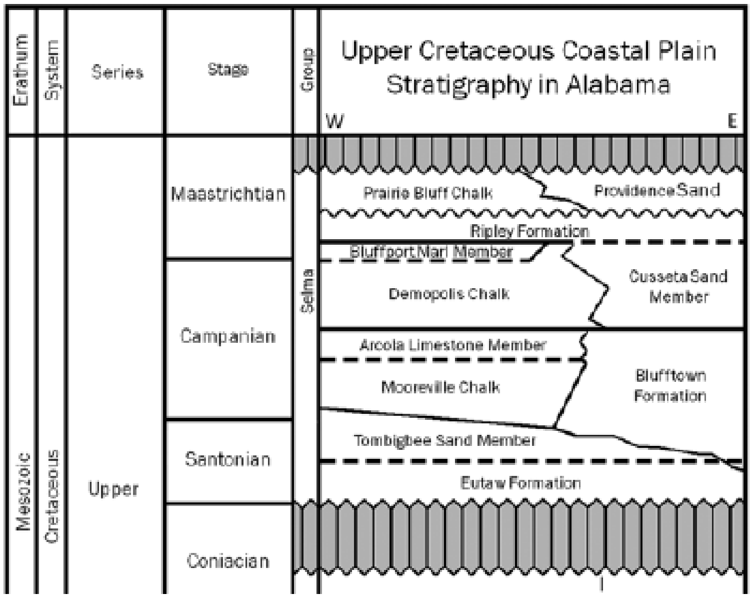

FIGURE 3 -- Correlation chart of the Cretaceous strata of Alabama. Gray shading indicates unconformities. Modified from Cicimurri and Ebersole, 2014.

MATERIALS AND METHODS

Ctenochelys acris specimens used for this study were housed in the collections at McWane Science Center in Birmingham, AL. Specimens were measured to the nearest millimeter using digital calipers and photographs were taken using a Canon A630, 8.0 megapixel digital camera. Figures were created using Adobe Photoshop© 2014. Anatomical terminology follows Gaffney (1972).

Institutional abbreviations. **--** **ALMNH**, Alabama Museum of Natural History, Tuscaloosa, AL; **AMNH**, American Museum of Natural History, New York, NY; **ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia, PA; **ChM**, Charleston Museum, Charleston, SC; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MH**, Naturhistorisches Museum, Basel, Switzerland; **MSC**, McWane Science Center, Birmingham, AL; **NJSM**, New Jersey State Museum, Trenton, NJ; **PMOL**, Paleontology Museum of Liaoning, Shenyang, Xinjiang Autonomous Province; **RMM**, former Red Mountain Museum, Birmingham, AL (collections now at MSC); **SM**, Solothurn Museum, Solothurn, Switzerland; **UNMSM**, Universidad Nacional Mayor de San Marcos, Lima, Peru; **USNM**, National Museum of Natural History, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Testudines Batsch, 1788

Cryptodira Cope, 1868

Americhelydia Joyce et al., 2013

Panchelonioidea Joyce, Parham and Gauthier, 2004

Ctenochelys Zangerl, 1953

Synonymies. **--** See Zangerl (1953) and Hirayama (1997).

*Type Species****.*** -- *Ctenochelys stenoporus* (Hay, 1905).

Generic Diagnosis. -- Testudines because of its shell. Differentiated from "macrobaenid"-grade durocryptodires by the retention of developed costal and plastral fontanelles in adult forms. Diagnosed from stem-cheloniids such as *Euclastes* (Cope, 1867) by a deeply concave nuchal emargination and a lack of a hyoplastral buttress inserted into the second peripheral. Diagnosed from pandermochelyids such as *Corsochelys* Zangerl, 1960 by the presence of an acute neural carina and a lack of carapacial surface sculpturing. Diagnosed as panchelonioid by the presence of a raised articulation for the neural spine of the eighth cervical vertebra on the visceral surface of the nuchal, elongate epiplastra, and forelimbs developed into modest paddles. Moderately sized Lophochelyinae (Maximum carapace length - MCL = approx. 120 cm).

Can be diagnosed as *Ctenochelys* by the following combination of characters found in both juvenile and adult specimens of the genus (Zangerl, 1953; Matzke, 2007; USNM 357166; RMM 3050; MSC 35085): Medially expanded triturating surfaces of the maxillae and dentary with pronounced labial and tomial ridges; anteroventral portion of the vomer narrow and rugose; triturating surface involving significant contributions from the ventral portion of the palatines; the presence of epineural ossifications between neurals 2-3, 4-5, and 6-7; peripherals with a moderately serrated lateral edge; well-developed plastral and costal fontanelles retained even in large adult individuals.

Ctenochelys acris Zangerl, 1953

Holotype. **--** FMNH PR13245, partial nuchal, left anterior peripherals 1, 2 , 4-6, right anterior peripherals 3, 7, (8 or 9?), several costal fragments, bridge of the left hyoplastron, preneural, and three anterior neurals.

Type Stratum and Locality. **--** Mooreville Chalk, Selma Group, early Campanian. Moore Brothers Farm, Harrell Station area, Dallas County, Alabama (Fig. 3).

Proposed Paratype. -- MSC 35085 - - partial nuchal, a nearly complete peripheral series, pygal, pelvic girdle, both scapulae, coracoids, left hyo- and hypoplastron, left epiplastra, partial right epiplastra, both xiphiplastra, two cervical vertebrae, right tibia and fibula, carpal and metacarpal elements, and numerous costal fragments from the Mooreville Chalk, Greene County, Alabama (Fig. 2).

Referred Material. -- RMM6157 – nearly complete cranium, lower jaw, scapula, neural series, three posterior peripherals, three cervical vertebra, hyoids; RMM3050 – nearly complete juvenile cranium.

Revised Diagnosis. -- Differentiated from *Ctenochelys stenoporus* by the presence of a prominent lingual ridge of the dentary, peripheral serrations located at or near the lateral midpoint of the corresponding peripheral, posterior peripherals 8-10 as wide as long, width of pterygoid bridge equal to length of median pterygoid suture, and a lack of vomer-palatine contact anterior to the internal naris. Nasals absent; strong posterior temporal emargination with dorsally visible *processus trochlearis*; moderately wide pterygoid bridge with midsagittal ridge along anteroventral portion diminished or absent; posteromedially expanded maxillary triturating surface; deeply ventrodorsally pitted triturating surface of the premaxillae; distinct, ventrally oriented ridge along the posterolateral margin of ventral surface of the premaxillae; well-developed secondary palate entirely excluding the maxillae from the tomial ridge of the upper triturating surface; widest point of the lower triturating surface at the mandibular symphysis; significant contribution of the frontal to the orbital margin; prominent neural keel; slender, elongated epiplastra; diminished plastral fontanelle relative to *C. stenoporus*; mediolateral expansion of posterior peripherals and pygal; carapace with elongate general outline and bluntly pointed posterior end; lateral most point of peripherals 6-11 located at or near the midpoint sulcus; peripherals 6-11 pentagonal with concave lateral margins anterior to the furrow point; peripherals 10 and 11 appearing as nearly equilateral pentagons in dorsal or ventral aspect; oblique sutural contact between peripherals 10 and 11; scapular angle approximately 110°; distal end of tibia possessing distinct lateral and medial facets divided by a saddle-like groove.

DESCRIPTION OF NEW MATERIAL

(MSC 35085; RMM 6157; RMM 3050)

Anatomical abbreviations. **-- ani**, apertura narium interna; **bo**, basioccipital; **bsp**, basisphenoid; **btb**, basis tuberculi basalis; **cci**, canalis caroticus internus; **cdbo**, crista dorsalis basioccipitalis; **den**, dentary; **ex**, exoccipital; **facci**, foramen anterior carotici interni; **fpp**, foramen praepalatinum; **fr**, frontal; **fil**, facet for ilium; **fon**, foramen orbitonasale; **fpp**, foramen palatinum posterius; **fst**, foramen stapedio-temporale; **mx**, maxilla; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **pm**, premaxilla; **po,** postorbital; **pr**, prootic; **pt**, pterygoid; **qu**, quadrate; **rbs**, rostrum basisphenoidale; **so**, supraoccipital; **sq**, squamosal; **vo**, vomer.

Cranium. -- The cranium (Figs. 4-8) is broadly pointed anteriorly with the largest specimen, RMM 6157, having a maximum length from the anterior margin of the premaxillae to the posterior of the supraoccipital of 201.0 mm and a width of 130.0 mm.

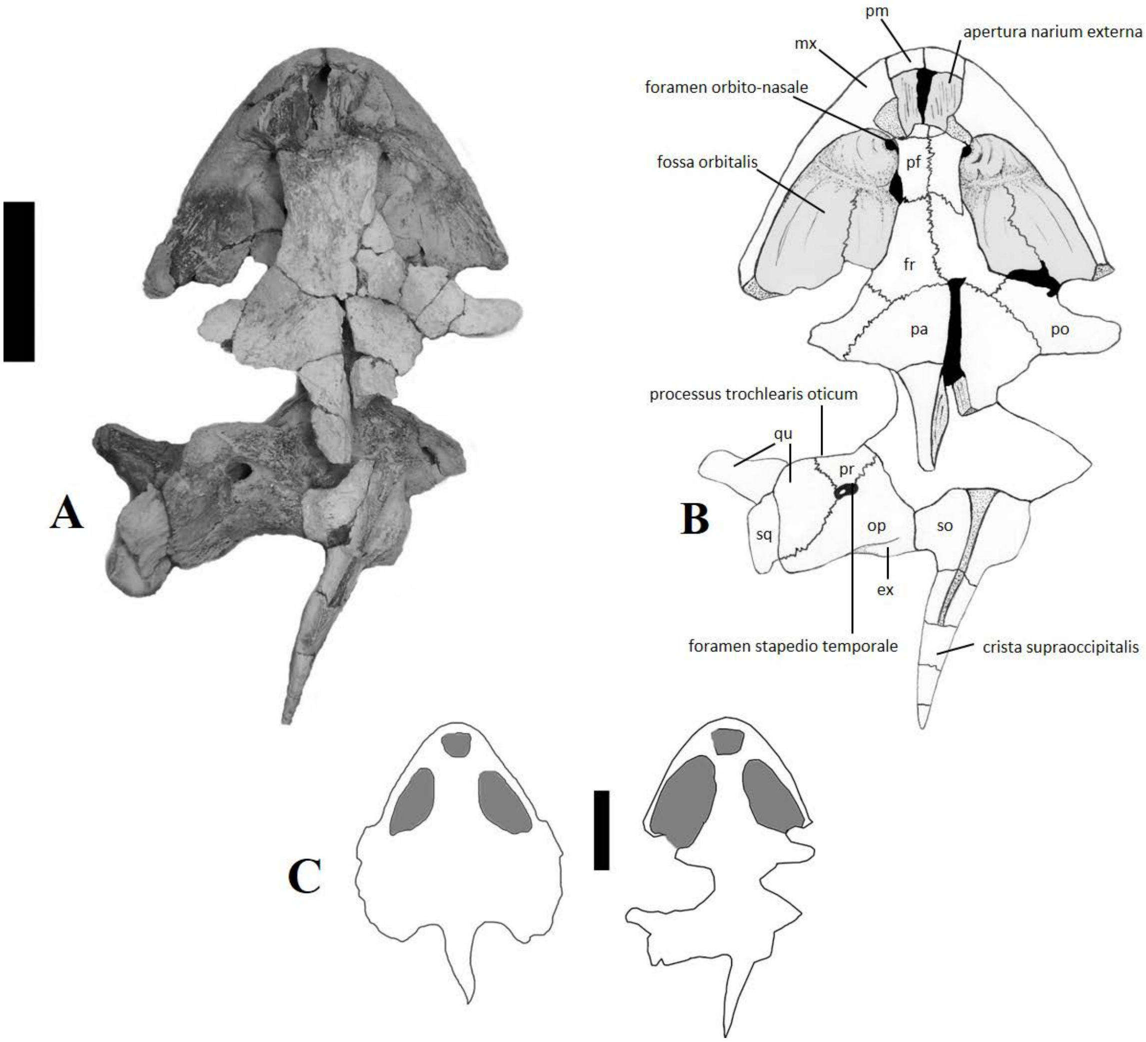

FIGURE 4 -- *Ctenochelys acris*, RMM 6157. A, B - Dorsal view of the cranium. Dorsal surface of pterygoid and braincase present but not illustrated; (See: Fig. 6A, B). C – Orbital size comparison between *C. stenoporus* (left) and *C. acris* (right). Abbreviations: **ex**, exoccipital; **fr**, frontal; **mx**, maxilla; **op**, opisthotic; **pa**, parietal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pr**, prootic; **qu**, quadrate; **so**, supraoccipital. Scale bars = 5.0 cm.

(Width is estimated as twice the distance from the medial prefrontal contact to the lateral edge of the quadrate). The smaller individual, RMM 3050, is approximately 97.0 mm long and 71.0 mm wide. Large, dorsolaterally facing orbits typical of panchelonioids present in both crania with those of the larger RMM 6157 measuring 52.0 mm long and 37.0 mm wide (Fig. 4) while the orbits of the smaller RMM 3050 measure 25.0 mm long by 11.0 mm wide. The orbits of *C. acris* are proportionally larger than the orbits of even the largest described adult specimen of *C. stenoporus* (USNM 391920) possibly indicative of a species endemic to the murky estuaries of the Mississippi Embayment rather than the more pelagic *C. stenoporus* (Fig. 4C).

Dermal Roof Elements

Prefrontal. -- The nasals are absent in both juvenile and adult individuals. The prefrontals are generally rectangular in dorsal view with a flat dorsal surface and triangular cross section. The prefrontals are excluded from the apertura narium externa with the posterior margin of the narial opening formed by the short, median suture of the maxillae (Figs. 4, 7). The prefrontals are sutured medially and posteriorly join with the triangular suture of the frontals. Laterally, the contribution to the fossa orbitalis by the prefrontals is nearly equivalent to that of the frontals in both juvenile (RMM 3050) and adult (RMM 6157) individuals. The ventrally descending portion of the prefrontal contacts the maxilla and vomer anteriorly but the remainder of this area is either missing or too poorly preserved to determine the extent of any additional contact with the palatal elements.

Frontal. -- The frontals contact the prefrontals, parietal and postorbitals. Anteriorly situated between the posterior processes of the prefrontals, each frontal forms an obtuse

‘L’ which extends posterolaterally to the anterior suture of the parietal. The median suture of the frontals is slightly offset to the left of the median suture of the prefrontals in both adults and juveniles resulting in a slightly wider right frontal (Figs. 4, 8). Laterally the frontal forms the posteromedial border of the fossa orbitalis and posterolaterally, the bluntly triangular suture of the frontal contacts the postorbital. The contribution of the frontal to the orbital rim is always significantly larger than that of the prefrontal, even in juveniles.

Parietal. -- The parietals are the largest of the dermal roof elements and comprise the majority of the dorsal surface of the cranium. Only the anteromedial portions of the parietals are preserved in both RMM 6157 and RMM 3050 with the median parietal suture preserved posteriorly 47.0 mm in RMM 6157 and 33.0 mm in RMM 3050. Though incompletely preserved, the dorsal portions of the processus inferior parietalis are visible in lateral profile. Most of the foramen interorbitale is preserved in RMM 6157 though due to dorsoventral compression, the exact metrics of this feature cannot be accurately determined. The broad, anteriorly convex suture of the parietal forms most of the posterior margin of the frontals and continues posterolaterally to form the medial border of the postorbitals. At the anterodorsal end of the squamosal, two small fragments can be observed in RMM 6157 that presumably represent the posterolateral most portions of both the left and right parietal. The posterolateral margin of the parietal is formed by the sutural contact with the anteromedial edge of the prootic.

Jugal. -- Anterior portions of both jugals are present only in RMM 6157 but lack the entirety of the posterior processes to the quadratojugals. The jugals contact the maxillae anteriorly and anteroventrally. The jugal extends anteriorly nearly half the length of the orbit and is suturally contacted along the entire posterior margin of the maxillae. Medioventrally, the jugal contacts the anterolateral corner of the processus pterygoideus externus as in *Ctenochelys stenoporus* (Matzke, 2007)

Quadratojugal. -- A small fragment preserved on the anterior portion of left squamosal of RMM 6157 can clearly be identified as the processus trochlearis oticum portion of the left quadratojugal. Anterior to the foramen stapedio-temporale, the quadratojugal contacts the lateral edge of the prootic. The posterior margin of the quadratojugal is bound medially by the opisthotic and laterally by the squamosal.

Squamosal. -- The posteromedial portion of the left squamosal is preserved in RMM 6157 and is suturally connected to the lateral margin of the quadratojugal. Though incompletely preserved, it appears the posterolateral edge of the temporal emargination is formed entirely by the squamosal as in *C. stenoporus* and extant cheloniids (Matzke, 2007).

Postorbital. -- The anteromedial portions of the postorbitals are present in both RMM 6157 and RMM 3050 but since neither possess an intact postorbital, it is impossible to determine the contribution of the postorbital to the temporal emargination, however, based on the reconstructions (Figs. 4, 7) it can be reasonably assumed to represent the majority of the anterolateral margin. The postorbital contacts the frontal and parietal anteriorly and extends posterolaterally to join with the anterior edge of the quadrate.

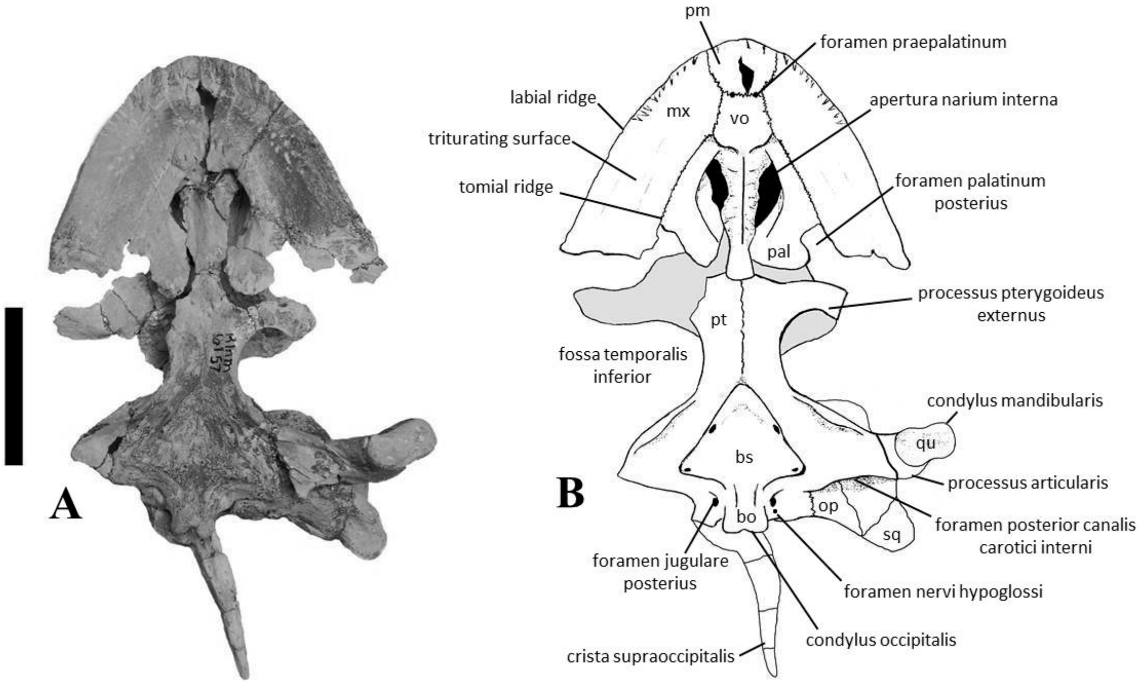

FIGURE 5 -- *Ctenochelys acris*, RMM 6157. Ventral view of the cranium. Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **mx**, maxilla; **op**, opisthotic; **pal**, palatine; **pm**, premaxilla; **pt**, pterygoid; **qu**, quadrate; **sq**, squamosal; **vo**, vomer. Scale bar = 5.0 cm.

Palatal elements

Premaxilla. -- The premaxillae are preserved in both RMM 3050 and RMM 6157. In dorsal view, the premaxillae form the anterior margin of the apertura narium externa. Ventrally, the premaxillae exhibit the deep concavity immediately posterior to the labial ridge seen in both adults and juveniles of *Ctenochelys stenoporus* (Zangerl, 1953; Matzke, 2007). The premaxillae are bordered laterally by the maxillae and posteriorly by the vomer. The width of the premaxillae is roughly equivalent to the width of the triturating surface of the maxillae. The labial ridge of both the maxillae and premaxillae are marked by distinct parallel notches formed by the worn medial surfaces of the lateral most nutrient foramina of the upper triturating surface.

Maxilla. -- Both maxillae are preserved in RMM 6157. RMM 3050 lacks only the posterior half of the right maxilla. The maxilla articulates with the premaxilla and vomer anteriorly, the palatine medially and posteriorly with the jugal. The anterior most section of the pterygoids is incompletely preserved in both specimens making it difficult to determine the nature or extent of a sutural connection between the maxilla and pterygoids but given the apparent size of the foramen palatinum posterius, any maxilla-pterygoid contact would have been limited to the anterolateral most corner of the processus pterygoideus externus. Dorsally, the maxilla-prefrontal suture runs from the anterior margin of the orbit anteromedially to the posterior margin of the external naris. Unlike *Ctenochelys stenoporus*, the ventrally concave triturating surface of the maxilla does not increase in width moving posteriorly but instead remains wide throughout (Figs. 5, 8). This is true for both juveniles and adults of this species as indicated by the constant width of the maxillary triturating surfaces of both RMM 3050 and RMM 6157.

Vomer. -- The vomer is elongate with moderately broadened anterior and posterior ends. The anterior portion of the vomer is broad with parallel rugosities partially overlapping the anteroventral edge of both the left and right palatine immediately posterior to the sutural contact between the vomer, maxillae, and premaxillae. The anterior contact with the premaxilla is equal in length to the lateral contacts with either the left or right maxilla. The anteroventral section of the vomer contributes to the upper triturating surface and increases in width during development (Figs. 5, 8) as in *C. stenoporus* (Matzke, 2007). The posteroventral portion of the vomer is not as significantly keeled as in adult specimens of *C. stenoporus* (USNM 391920; Zangerl, 1953; Matzke, 2007). The anteroventral section of the vomer is strongly keeled and is triangular in cross-section, similar to the condition seen in *C. stenoporus* but unlike *C. stenoporus*, this crest ends approximately 11 mm anterior of the vomer-pterygoid suture. A distinct mid-sagittal keel runs along the ventral face of the vomer posteriorly along the midline and diminishes gradually with the posterior third of the vomer being almost entirely flat. The vomer-pterygoid contact extends beyond the anterior margin of the pterygoids and overlaps the pterygoids posteroventrally.

Palatine. -- The palatines are preserved in both specimens. The palatine is suturally connected with the vomer, maxilla and pterygoid. Anteriorly, the palatine is separated from the premaxilla by the anterior portion of the vomer. Ventrolaterally, the palatine is sutured to the maxilla forming the medial 25% of the upper triturating surface. The proportional palatine contribution to the upper palate remains somewhat constant during maturation unlike the incipient development of a secondary palate observed in *C. stenoporus* (Zangerl, 1953; Matzke, 2007). The ontogenetic expansion of the upper triturating surface and secondary palate observed in *Ctenochelys stenoporus* are not present in *C. acris.* The juvenile cranium (RMM 3050) shows a similarly proportioned contribution from the palatines and vomer to the upper triturating surface as can be seen in the much larger adult specimen, RMM 6157 (Figs. 5, 8).

The dorsal process of the palatine forms nearly the entire aperture narium interna which is clearly visible in ventral and dorsal aspect. Dorsally, the palatine expands laterally to overlap the anteromedial portion of the corresponding maxilla and forms the posterodorsal margin of the foramen orbito-nasale. In contrast with juveniles of *C.*

stenoporus, the well-developed secondary palate of *C. acris* overlaps the foramen orbito-nasale in ventral view again illustrating the presence of a secondary palate early in development. Posterior to the palatine-maxilla suture, the palatines extend dorsomedially to contact the posterolateral margin of the vomer and the anteromedial margin of the pterygoid. In the adult cranium (RMM 6157) the dorsomedial process of the palatine is separated from the jugal by the foramen palatinum posterius. The posterior expansion of the palatine-maxilla suture has shifted the position of this foramen posteriorly relative to its position in other panchelonioids such as *C. stenoporus* or *Toxochelys latiremis* (Zangerl, 1953; Matzke, 2007; Matzke, 2009). This has resulted in the anterior margin of the foramen palatinum posterius being in line with the posterior margin of the maxillary triturating surface (Fig. 5).

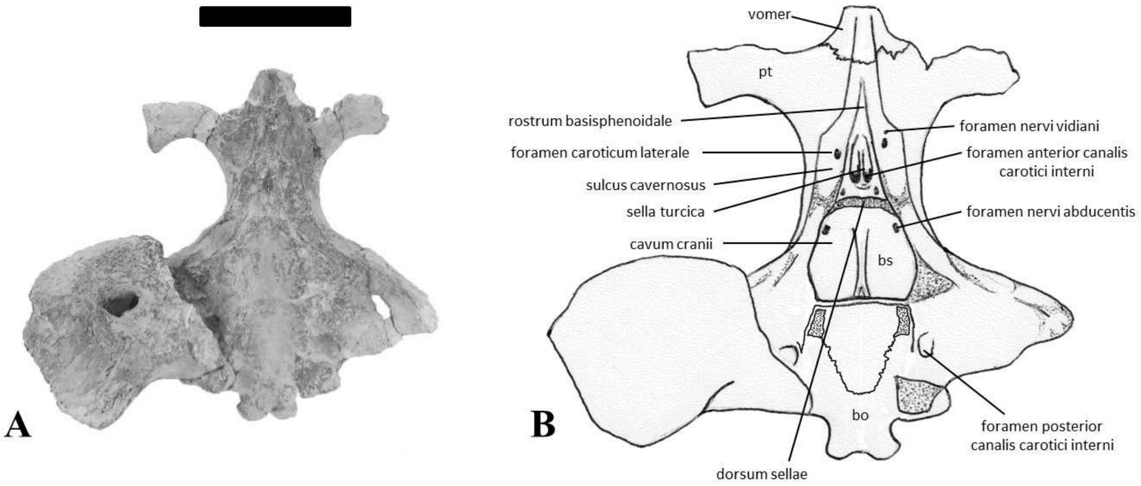

FIGURE 6 -- *Ctenochelys acris*, RMM 6157. Dorsal view of the cranium with dermal roof elements removed to illustrate the features of the basicranium. Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **pt**, pterygoid. Scale bar = 5.0 cm.

Palatoquadrate elements (Quadrate, Pterygoid, Basisphenoid, Basioccipital)

Quadrate. -- Only the left quadrate of RMM 6157 is preserved. The quadrate contacts the squamosal posterodorsally, the prootic dorsomedially, the pterygoid ventromedially and the opisthotic posteromedially. A fragment of bone sutured to the anterolateral facet of the quadrate is almost certainly the posterolateral most portion of the quadratojugal (Figs. 4, 5). The dorsal surface of the quadrate is badly worn and approximately equivalent to the combined exposed dorsal surfaces of the prootic and opisthotic. Anterodorsally, the quadrate forms the lateral third of the processus trochlearis oticum and the lateral margin of the foramen stapedio-temporale. Though extensive wear to the dorsal surface elements surrounding the foramen may have distorted the general outline, the foramen stapedio temporale is approximately 6 mm in length and 8 mm wide. In medial view, the paths of the canalis stapedio-temporalis and canalis cavernosus can be seen running posterodorsally from the incisura columella auris. The condylus mandibularis is only slightly dorsolaterally oriented and is divided into nearly equal medial and lateral halves by a shallow midsagittal groove.

Pterygoid. -- Only the pterygoids of the adult specimen (RMM 6157) are preserved. The pterygoids are medially sutured to one another, posterodorsally to the prootic, posteroventrally to the quadrate, posteriorly to the basioccipital and basisphenoid, and dorsally with the parietal. The pterygoids are moderately broad and at their narrowest point are still equal to 40% of the overall width. The dorsal surface of the pterygoid is very similar in arrangement to *Ctenochelys stenoporus* (Matzke, 2007; USNM 357166) and *Chelydra serpentina* (Gaffney, 1972; AMNH 107386). The epipterygoids are incompletely preserved but appear to have overlapped the mediolateral third of the pterygoid laterally from the anterior portion of the sulcus cavernosus. A prominent ridge runs posteriorly from the pterygoid-vomer contact to the anterior margin of the rod-like rostrum basisphenoidale. The path of the vena capitis lateralis (sulcus cavernosus) runs posteriorly along the lateral margin of the pterygoid. The sulcus cavernosus is bordered medially and laterally by distinct ridges and is posteromedially enclosed by the medial dorsal process of the pterygoid and the prootic. The position of the foramen palatinum posterius entirely excludes the pterygoids from contact with the maxillae, however, small sutural contacts present on the anterolateral corner of the processus pterygoideus externus are presumably indicative of contact between each pterygoid and the anteroventral process of the corresponding jugal (Fig. 5).

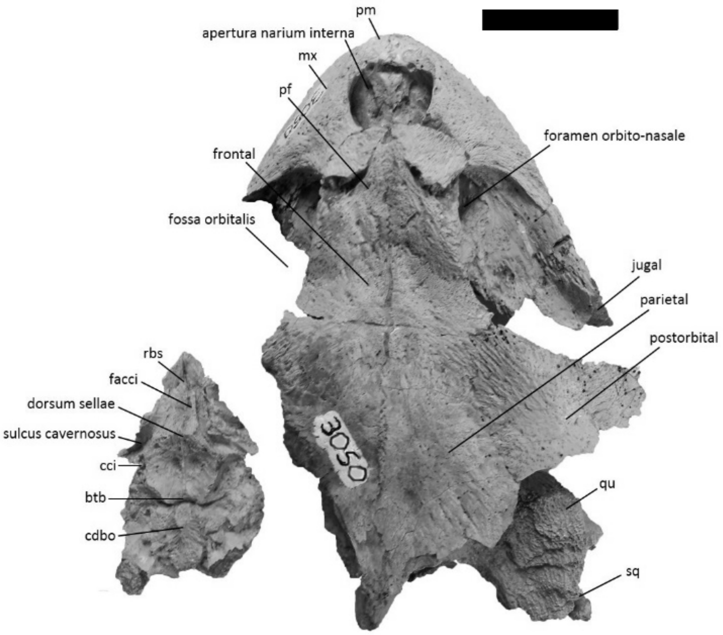

FIGURE 7 -- *Ctenochelys acris*, RMM 3050. Dorsal view of cranial elements including dorsal aspect of braincase. Abbreviations: **btb**, basis tuberculi basalis; **cci**, canalis caroticus internus; **cdbo**, crista dorsalis basioccipitalis; **facci**, foramen carotici interni; **mx**, maxilla; **pf**, prefrontal; **pm**, premaxilla; **qu**, quadrate; **rbs**, rostrum basisphenoidale; **sq**, squamosal. Scale bar = 2.0 cm.

In both specimens (RMM 6157 and RMM 3050), the two foramina anterior canalis carotici interni are located immediately anterior to the anteriormost pterygoid-basisphenoid contact and posteromedially from the much smaller foramen caroticum laterale. The foramina anterior canalis carotici interni are very close together and separated by only a 0.5 mm thick anterior projection of the basisphenoid. Ventrally, a slight ridge runs posteriorly along the median suture of the pterygoids from the pterygoid-vomer contact to the anterior margin of the basisphenoid. It should be noted that the features of tjnhe pterygoids of RMM 6157 and RMM 3050 are, again, virtually indistinguishable from the analogous features described by Matzke (2009) from an isolated cranium assigned to *Toxochelys moorevillensis* (FMNH PR219). Considering the lack of associated post-cranial material with FMNH PR 219 and the incomplete nature of the specimen, it is probable that the material described by Matzke belongs to *C. acris.*

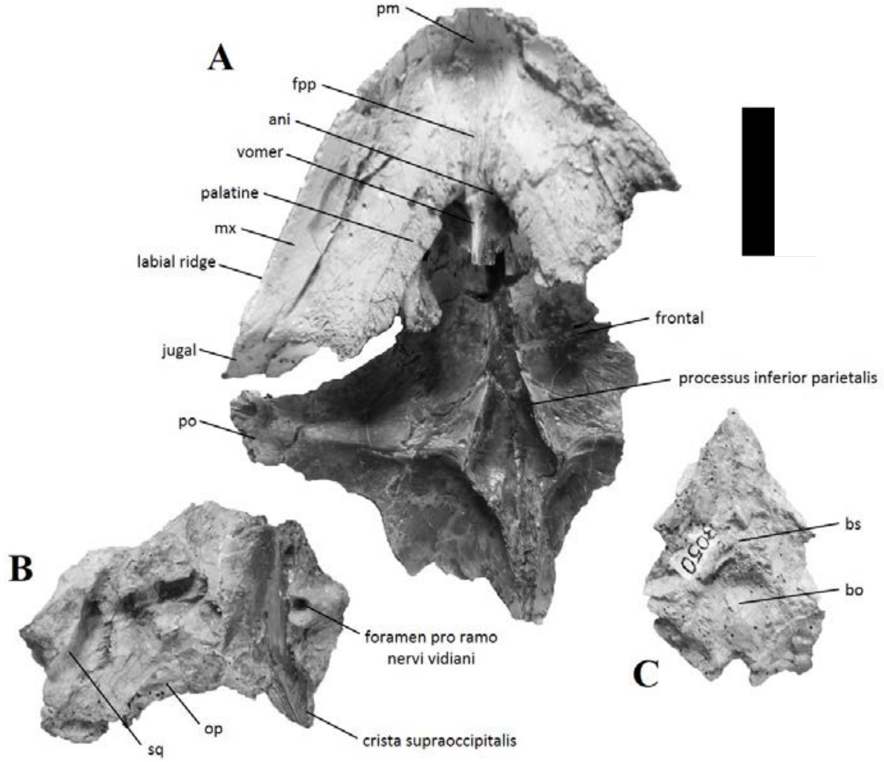

FIGURE 8 -- *Ctenochelys acris*, RMM 3050. Ventral view of disarticulated cranial elements showing the detail of the parietal contribution to the braincase. Abbreviations: **ani**, apertura narium interna; **bo**, basioccipital; **bs**, basisphenoid; **fpp**, foramen praepalatinum; **mx**, maxilla; **op**, opisthotic; **pm**, premaxilla; **po**, postorbital; **sq**, squamosal. Scale bar = 2.0 cm.

Braincase elements

Supraoccipital. -- The supraoccipital of RMM 6157 is well preserved lacking only the dorsal expansion of the crista supraoccipitalis (Figs. 4, 5). The supraoccipital contacts the prootic anterolaterally, the parietal anterodorsally, and the opisthotic posteriorly. At 81.0 mm long, the supraoccipital of RMM 6157 would not have extended much beyond the posterior margin of the occipital condyle. Anteroventrally, the supraoccipital forms the dorsal roof of the foramen magnum which has been slightly deformed as a result of dorsoventral compression.

Exoccipital. -- The articulated left exoccipital and the disarticulated right exoccipital of RMM 6157 are preserved. In posterior view, the exoccipitals are medially sutured together forming the dorsal two thirds of the condylus occipitalis. Dorsomedially the exoccipital participates in forming the lateral wall of the foramen magnum along with the ventrolateral process of the supraoccipital. Also in posterior view, the foramen nervi hypoglossi are visible and accompanied laterally by the significantly larger foramen jugulare posterius. As is the case for *Ctenochelys stenoporus* (USNM 357166) a ventrally oriented crest-like protrusion from the posterolateral section of the exoccipital contributes to the fenestra postotica but in *C. acris* (RMM 6157, RMM 3050) this contribution is limited to the medial third of the opening. In contrast with juvenile specimens of *C. stenoporus* (USNM 357166) the ventromedial process of the exoccipital is well developed in juveniles of *C. acris* and extends medially over the posterior part of the floor of the foramen magnum.

Prootic. -- The medial portion of the left prootic of RMM 6157 and the intact right prootic of RMM 3050 are preserved. The prootic contacts the quadrate laterally and the opisthotic posteriorly. Due to the incomplete preservation, the nature and extent of the medial sutures of the prootic cannot be accurately determined. Anteriorly, the prootic forms a much larger percentage of the processus trochlearis oticum than the quadrate and laterally forms the medial margin of the foramen stapedio-temporale.

Opisthotic. -- The lateral portion of the left opisthotic of RMM 6157 and the intact right opisthotic of RMM 3050 are preserved. The position and contacts of the opisthotic are typically pan-chelonioid with the opisthotic contacting the squamosal posterolaterally, the quadrate anterolaterally, the prootic anteriorly, the supraoccipital medially, and the exoccipital posteromedially. Though poorly preserved, it appears that in both the juvenile and adult specimens, that the medial expansion of the exoccipital entirely excludes the opisthotic from contacting the basioccipital posteroventrally, as seen in *Toxochelys latiremis* (Matzke, 2009)

Basisphenoid. -- The basisphenoid is preserved intact in both the adult (RMM 6157) and juvenile specimens (RMM 3050) and in both specimens, the basicranium has become disarticulated from the associated dermal roofing elements allowing for a detailed comparison of the dorsal surface of the cavum cranii. In ventral view, the basisphenoid forms an anteriorly oriented triangle situated between the posterolateral processes of the pterygoids. A prominent V-shaped crest can be seen on the anteroventral surface of the basisphenoid with each branch sutured the medial margin of each pterygoid. Posterior to the V-shaped crest, the basisphenoid forms a posteriorly open concavity divided by a prominent sagittal ridge. The basisphenoid is more acutely angled anteriorly in the juvenile specimen and appears to expand laterally during development, resulting in a much broader basisphenoid in adult specimens. Unlike *Toxochelys latiremis*, the basisphenoid of *C. acris* is considerably shorter than the median pterygoid suture (Figs. 5, 6, 8C).

The dorsal surface of the basisphenoid is visible in both specimens and is divided into distinct anterior and posterior portions by a low dorsum sellae posterior to the foramen anterior canalis carotici interni. The fused trabeculae of the rostrum basisphenoidale form a rod-like structure which in RMM 6157, extends anteriorly nearly to the level of the posteromedial vomer-pterygoid contact. The sella turcica is more pronounced in the juvenile cranium and runs posteriorly along the dorsal midline of the basisphenoid from the posterior margin of the paired foramen anterior canalis carotici interni to the anterior margin of the cavum cranii. The cavum cranii is moderately concave and is divided into equal left and right halves by the crista dorsalis basisphenoidalis and in the adult specimen, diminishes in height anteriorly until disappearing at the level of the foramen nervi abducentis as in juvenile specimens of *C. stenoporus*. However, in the juvenile cranium of *C. acris*, the crista dorsalis basisphenoidalis runs the length of the cavum cranii from the dorsum sella to the basis tuberculi basalis where it joins with the crista dorsalis basioccipitalis. The foramina nervi abducentis are located near the anterolateral corners of the cavum cranii similar to their position in *Chelydra serpentina.* It should be noted that the relative size, shape and location of the basicranial features of the adult specimen of *C. acris* are indistinguishable from the features of the isolated cranium figured by Matzke (2009) referred to as *Toxochelys moorevillensis* (FMNH PR 219).

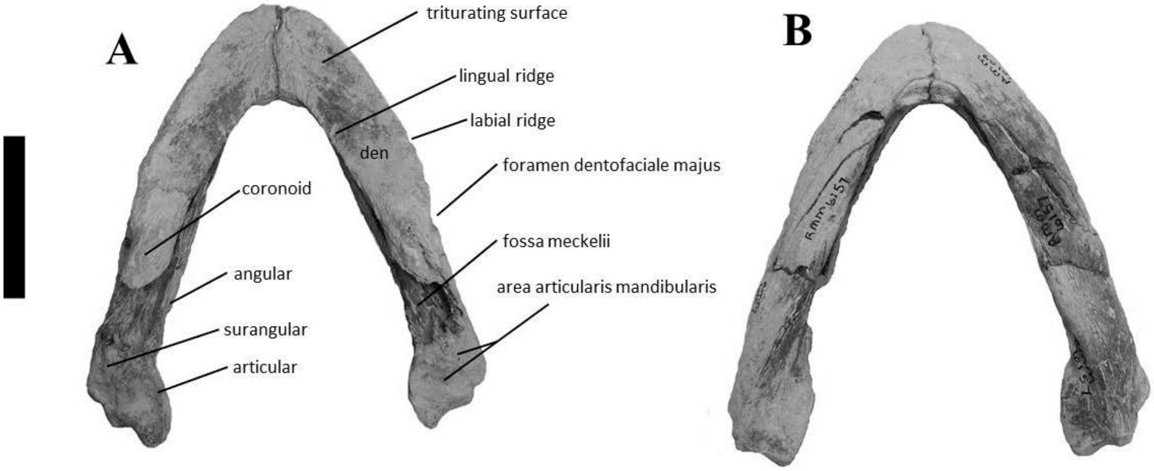

FIGURE 9 -- *Ctenochelys acris*, RMM 6157. Dorsal (A) and ventral (B) view of the lower jaw. Abbreviations: **den**, dentary. Scale bar = 5.0 cm.

Lower jaw. -- The lower jaw is preserved only in the adult specimen (RMM 6157). Dorsally, the dentaries are sutured at the symphysis which forms a moderate ridge bordered laterally by slight depressions on the triturating surface of each dentary (Fig. 9A). The widest portion of the triturating surface is located at the symphysis as in *Ctenochelys stenoporus* but unlike *C. stenoporus*, the width of the triturating surface is not drastically diminished posteriorly. Anteriorly, the dentaries form a bluntly rounded point and in lateral view, the anterior tip turns dorsally creating a small hook (Fig. 9).

The distinct labial ridge of the dentary lies just above the level of the triturating surface and is marked by the same parallel notches found on the labial ridge of the maxillae and premaxillae of both RMM 6157 and RMM 3050. In lateral view, the pronounced foramen dentofaciale majus is located immediately anterior to the dentary-coronoid suture. The posteriorly oriented groove associated with the foramen dentofacial majus continues posteriorly to form the ventral margin of the attachment zone for the M. adductor mandibulae externus. Also laterally visible are the foramina nervi auriculotemporalis which are located on the posterolateral portion of the surangular between the area articularis mandibularis and the posterior process of the angular. The posteriorly expanded lower triturating surface overlaps the anteroventral portions of the lower jaw in dorsal view, just as in adult specimens of *C. stenoporus*, but the lower triturating surface of *C. acris* is not as significantly diminished posteriorly.

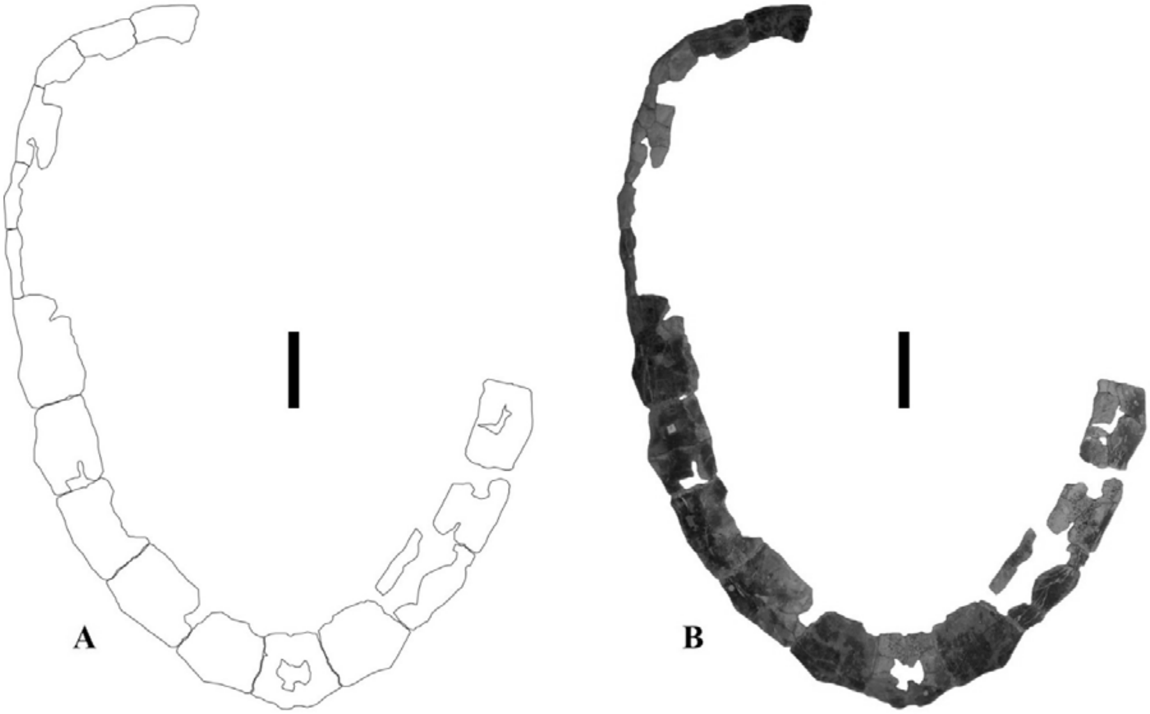

FIGURE 10 -- *Ctenochelys acris,* MSC 35085. Carapace in dorsal view. Scale bar = 10 cm.

Post-Cranial Material

Carapace. -- Much of the carapace of MSC 35085 is preserved as are several peripherals of RMM 6157. Strongly cordiform in general outline, the carapace of *C. acris* is much longer than wide (Fig. 10). At its midline, the carapace of MSC 35085 is 98.0 cm long and 77.0 cm wide across the 6th peripherals. The conformation of the carapace is typical of Lophochelyine ‘toxochelyids’ and is comprised of a nuchal, one preneural, eight neurals, two suprapygals, four epineurals, a pygal and 11 peripherals. Matzke (2007) notes in his description of a juvenile *C. stenoporus* the presence of 12 peripherals, however, upon examination of USNM 357166 figured by Matzke, only 11 peripherals are visible on each side of the carapace. The nuchal emargination of *C. acris* is more acutely angled than in *C. stenoporus* and receives minimal contributions from the first peripherals.

One of the more distinctive features of the carapace is the presence of acute serrations located at or near the intersection of the marginal scute sulci and the lateral margin of the associated peripheral (Fig. 10). Peripherals 8-11 are proportionally much wider than those of adult specimens of *C. stenoporus* with the 11th peripheral forming a nearly equilateral pentagon. The posterolateral corners of the pygal possess lateral projections which notch into the posteromedial edge of both the left and right 11th peripheral (Fig. 10). Perhaps the most striking carapacial difference between these two closely related taxa is the location of the lateral serrations of the posterior peripherals. In adult specimens of *C. stenoporus*, peripherals 9-11 are not significantly wider than peripherals 6-8 and the anterolateral margin of the peripheral is always laterally convex. The posterolaterally oriented peripheral scute sulci divide the peripherals of *C. stenoporus* into almost equal posterior and anterior halves and with the lateral serration of each peripheral always being anterior to the point at which the scute sulci contacts the lateral margin of the peripheral (Zangerl, 1953; Hirayama, 1997; Matzke, 2007). This is not the case for *C. acris* and on the 10th and 11th peripherals, the scute sulci intersects the lateral margin of the peripheral at the lateral most point of the serration. Rather than forming a moderate concavity at the mediolateral peripheral margin, the serrations of the posterior peripherals form a sharp, triangular projection and in the case of the 11th peripheral, the lateral most point of the serration is at the peripheral midline which results in peripheral 11 being roughly pentagonal (Fig. 10). There is no evidence to support this being an ontogenetic artefact, as similarly sized specimens of *C. stenoporus* exhibit posterior peripherals typical for the species (Zangerl, 1953).

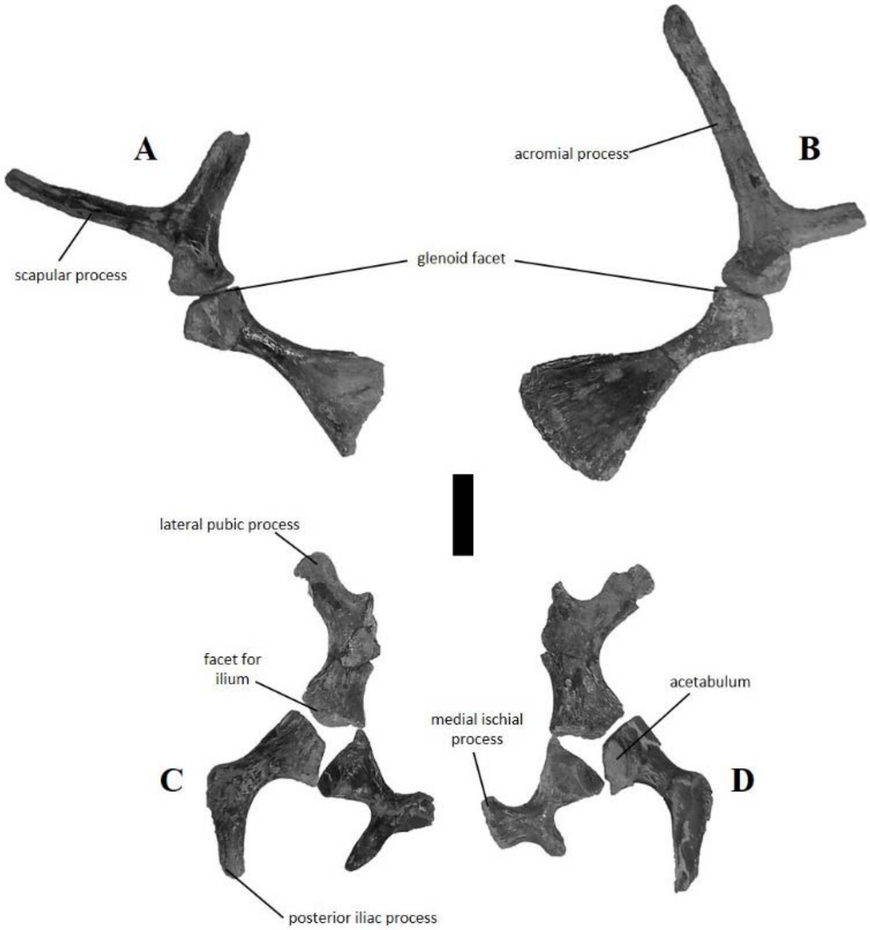

FIGURE 11 -- *Ctenochelys acris*, MSC 35085. (A-B) dorsal views of (A) left and (B) right scapula and coracoid. (C-D) dorsal view of (C) left and (D) right pubis, ilium and ischium. Scale bar = 5.0 cm.

Shoulder girdle. -- Both scapulae of specimen MSC 35085 and the left scapula of RMM 6157 are preserved (Fig. 11A-B). The acromial process is much longer than the scapular process with the two enclosing an angle of approximately 110 degrees. The left and right coracoids of MSC 35085 are preserved with the left lacking the medial half of the dorsal plate. The completely preserved right coracoid is 151 mm long with a broad dorsal plate 88 mm wide. There are well-developed glenoid and scapular facets on the head of the coracoid with the latter being the slightly larger of the two.

Pelvic girdle. -- MSC 35085 possesses a nearly intact pelvic girdle which represents the first known pelvic material for this species (Fig. 11C-D). The medial process of both the left and right pubis are incomplete, however, the medial process of the pubis appears to have been nearly twice the width of the lateral process. Given the incomplete nature of both medial processes, it is impossible to determine whether the lateral processes extended further anteriorly. The ischia are suturally connected by a well-developed medial process. The length of posterior iliac process is equal to or greater than length of iliac shaft. Other metrics and the general arrangement of pelvic elements are typical for the genus (Zangerl, 1953; Matzke, 2007).

FIGURE 12 -- *Ctenochelys acris*, MSC 35085. Tibia (A, D) and fibula (B, C) in dorsal (A, B) and ventral (C, D) aspects. Scale bar = 5.0 cm.

Limb elements. The right tibia and fibula of MSC 35085 are preserved along with a number of tarsal and metatarsal elements (Fig. 12). This specimen represents only the second known ‘toxochelyid’ hind limb and is more completely preserved than the *Toxochelys moorevillensis* material described by Zangerl (1953; FMNH PR 136). The chelydrid affinities of the ‘toxochelyid’ hind limb noted by Zangerl in the limb material of the primitive *Toxochelys* are also apparent in *C. acris.* The distal articular surface of the tibia is divided into medial and lateral facets by a deep, saddle-shaped groove as in *Chelydra* while extant cheloniids such as *Lepidochelys* and *Chelonia* lack any indication of such a division. The lengths of the tibia and fibula relative to the estimated overall length of the adult individual of *C. acris* (MSC 35085) are indicative of well-developed hind limbs and chelydrid locomotion involving all four limbs (Zangerl, 1953; Zug, 1971). A flared ridge runs anteromedially along the lateral edge of the distal end of the fibula beginning at the distal articular surface and terminating near the narrowest point of the fibular diaphysis, essentially as in *Chelydra.*

Several large fragments of the proximal tarsal elements such as the fibulare, intermedium, centrale, and tibiale are preserved but have become worn and disarticulated, preventing precise reconstruction of their position within the pes. However, the arrangement of tarsal elements appears to have been quite similar the Eubaenid pes figured by Case (1939) from the Cretaceous of Montana with the only notable exception being the large articulation with the first metatarsal on the distal facet of the intermedium. The fifth tarsal is marked by a large, fan-shaped process which carries a distinct articulation site on its posterolateral edge for the proximal phalange of the fifth digit. The first metatarsal is broad and dorsoventrally flattened while the third through fifth metatarsal appear to have been slender and elongate. The two preserved distal phalanges are curved and bluntly pointed but their relative position within the pes is doubtful.

Vertebrae. -- The remains of two cervical vertebrae are preserved, both from the larger of the two adult specimens (Fig. 13). The seventh cervical vertebra has suffered from severe dorsoventral compression making any estimates as to the height of the neural arch impossible. Both centra are approximately 25.0 mm long and nearly 15.0 mm tall. A distinct ventral keel is present on both vertebrae as is common for other species of panchelonioid (Zangerl, 1953; Matzke, 2007). Both vertebrae are procoelous.

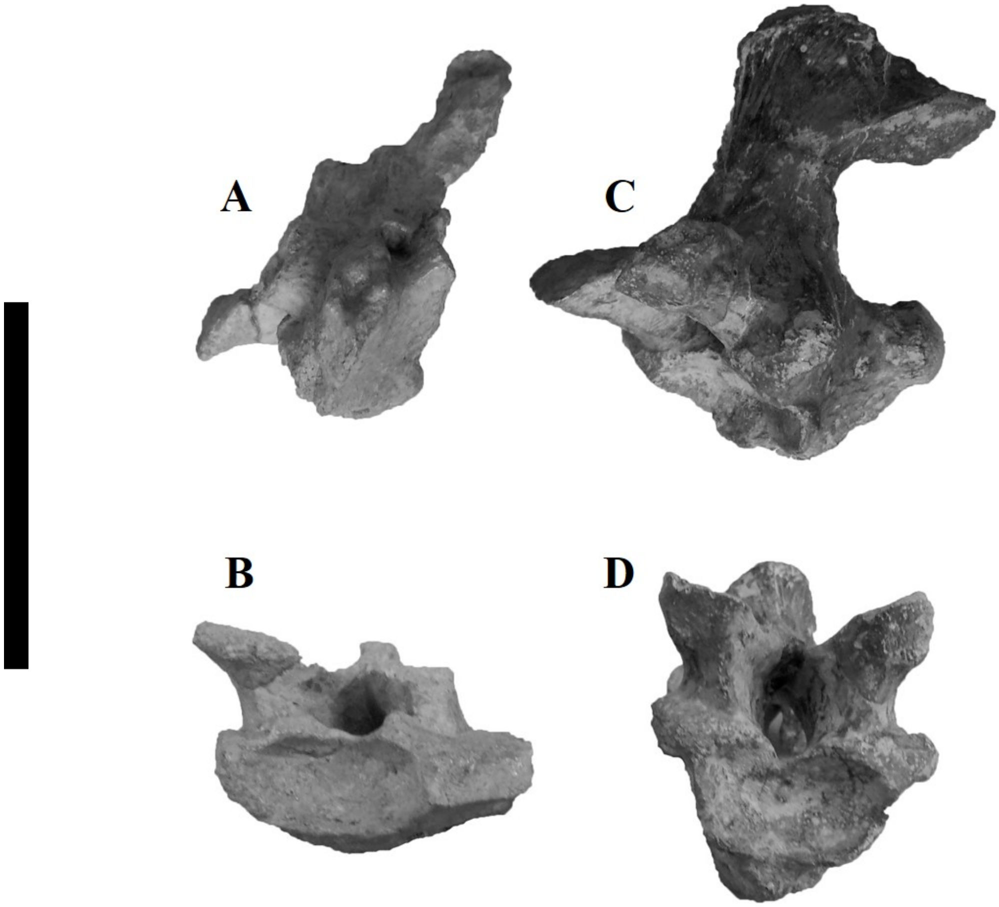

FIGURE 13 -- *Ctenochelys acris*, MSC 35085. Cervical vertebrae 7 (A, B) and 8 (C, D) in left lateral (A, C) and anterior view (C, D). Scale bar = 5.0 cm.

Plastron. -- Epiplastra are narrow and elongate running posterolaterally nearly the entire length of the medial process of the hypoplastron (Fig. 14). A significantly reduced central fontanelle between the hyo- and hypoplastron is present as a result of the increased width of the hyo-hypoplastral bridge. The plastron is much wider than long in all examined specimens with an estimated plastral index between 50 and 60.

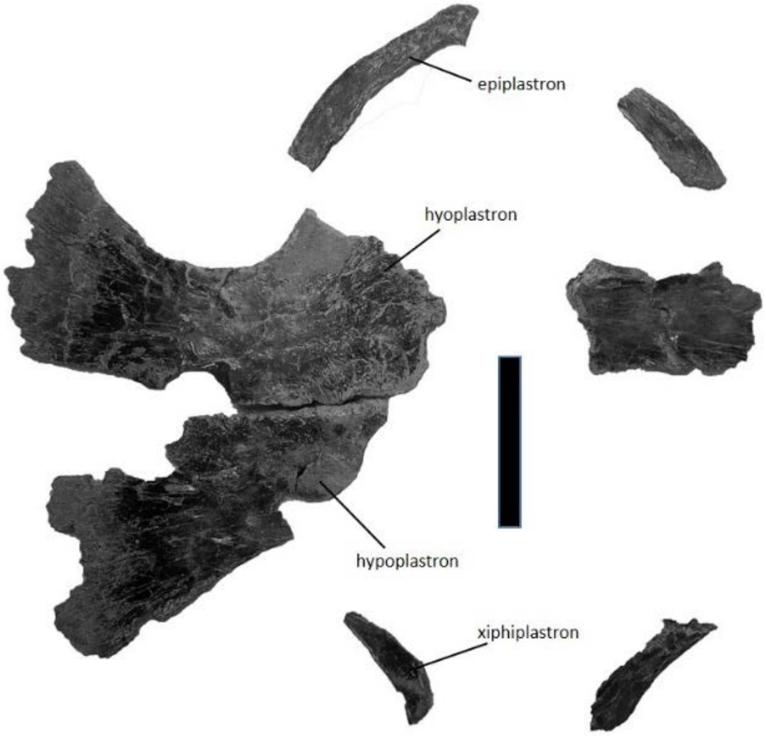

FIGURE 14 -- *Ctenochelys acris*, MSC 35085. Ventral view of plastral elements. Scale bar = 10 cm.

DISCUSSION

The cranial and endoskeletal elements of *C. acris* appear to possess an intermediate suite of characters between *Chelydra* and *Chelonia* while also exhibiting typical ‘toxochelyid’ morphology. The poorly developed flipper elements, heavily ossified carapace and nearly dorsally facing orbits of *C. acris* are evidence that this species occupied a niche very different from its more pelagic relative, *C. stenoporus,* and lived primarily along the bottom of the shallow, coastal waters within the Mississippi Embayment. Easily differentiated from the more common *C. stenoporus* by its unique carapacial serrations and large orbits, the limited distribution of *Ctenochelys acris* supports the paleobiogeographic scenario of Cretaceous Western Interior Seaway (W.I.S.) proposed by Nicholls and Russell (1990) which divides the W.I.S. into northern and southern subprovinces during the Cretaceous via the existence of a partial geographical barrier between the southern border of present-day Kansas and the northern border of Texas.

The lack of ontogenetic development of the secondary palate of *C. acris* implies a possible shift from a shearing to a crushing ectomorph within *Ctenochelys* during the early Campanian. The contemporaneous presence of both species within the Mooreville Chalk of Alabama provides evidence in support of a speciation event within an already durophagous (shearing/crushing) lineage as seen in the Miocene genera *Pacifichelys* and extant carettines (Parham and Pyenson, 2010). Coeval with this proposed speciation is the Cretaceous origin of sea grass (Parham and Pyenson, 2010) which would have certainly opened novel feeding niches and played a role in facilitating the evolution of distinct cranial characteristics and perhaps ultimately, speciation. This would serve as yet another example of a unique durophagous feeding ecology and the resulting associated cranial characteristics evolving independently in closely related sea turtle lineages. However, the stratigraphic distribution of *C. stenoporus* extends into the latter half of the Santonian while *C. acris* is known exclusively from early Campanian deposits (Zangerl, 1953; Matzke, 2007; Joyce et al., 2013). This temporal distribution implies the evolution of a crushing ecomorpholgy from within a lineage clearly suited for a shearing feeding ecology. The high number of specimens previously identified as *C. stenoporus* recovered from the Mooreville Chalk relative to the rare occurrence of *C. acris* may imply that with the evolution of sea grass, the well-suited *C. stenoporus* was able to more effectively utilize the area in and around the Mississippi Embayment than the benthic molluscivore, *C. acris*. However, given the previous lack of diagnostic characters for *C. acris*, the seeming rarity of referred specimens for this species may simply be an artefact of misidentification.

CONCLUSION

Based on the wealth of evidence provided by newly identified specimens of the Cretaceous panchelonioid species *Ctenochelys acris* (MSC 35085, RMM 6157, RMM 3050), the synonymy of this taxon with *Ctenochelys stenoporus* argued for by Hirayama (1997) is not supported here. *Ctenochelys stenoporus* was a more pelagic marine turtle with a nearly cosmopolitan distribution and a diet consisting primarily of vegetation while *C. acris* was a bottom-feeder within the warm, shallow waters of the Mississippi Embayment. This provides evidence for the independent evolution of distinct feeding ecomorphologies within a single sea turtle lineage. The limb and endoskeletal material of *Ctenochelys acris* possess a distinct blend of cheloniid and chelydrid features shared by other panchelonioid taxa which lends support to the hypothetical placement of certain ‘toxochelyid’-grade taxa as panchelonioids. This issue can only be resolved through further study of ‘toxochelyid’ alpha taxonomy and the inclusion of additional ‘toxochelyid’ taxa into global, species- level cladistic analyses.

Chapter 2

A SYSTEMATIC REVISION OF THE ‘TOXOCHELYID’-GRADE TAXA USING CLADISTIC ANALYSIS

by

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ABSTRACT -- Using parsimoniously informative phylogenetic characters recorded using established scoring protocols for fossil taxa, cladistic analysis is performed on a variety of fossil and extant Cryptodiran turtle species to ascertain their evolutionary interrelationships. The resulting phylogeny indicates a separation of *Toxochelys* and *Ctenochelys* into separate clades with the more derived *Ctenochelys* being placed within the crown group Panchelonioidea and *Toxochelys* positioned at the stem of Panchelonioidea as a basal representative of Americhelydia. This arrangement excludes the possibility of these taxa being placed as a single terminal node in any subsequent phylogenetic analyses and helps to resolve the placement of these taxa within Cryptodira.

INTRODUCTION

The characters used in the construction of the phylogenetic matrix for this study were based primarily on those of Lapparent de Broin (2013) and Anquetin (2011) which were themselves taken from the analyses performed by Kear and Lee (2006) and Hirayama (1994, 1998). The Lapparent de Broin (2013) matrix is useful for the study of Chelonioidea as it includes a number of characters necessary to distinguish clades within the chelonioids and panchelonioids. Anquetin (2011) uses similar a similar suite of characters but includes a number of features pertaining to stem Testudine taxa which are beyond the scope of this study. However, Anquetin follows the recommendation of Joyce (2007) and Parham and Pyenson (2010) in limiting terminal operational taxonomic units (OTU’s) to single species in order to lessen the potential for chimeric taxa. For these reasons, the present study uses a blend of characters from both the Anquetin and Lapparent de Broin matrices along with several novel characters and reduces all included taxa to species level OTU’s.

MATERIALS AND METHODS

The following data matrix consists of 108 cranial and post-cranial characters scored for 18 taxa, including 14 fossil and 4 living species of turtle. The matrix was assembled in Morphobank ™ with all characters unordered and equally weighted. Parsimony analyses were performed using PAUP*4.0a (Swofford, 2002). The data matrix was analyzed using the branch-and-bound search method with branches set to collapse if their minimum length was 0.

In an effort to reduce the risk of chimeric scoring, the binary character states in the present study are based primarily on the holotype material for each of the listed fossil species when possible. Several holotypes (e.g. *Toxochelys latiremis, Ctenochelys acris*) are so partial in nature that an accurate phylogenetic placement is unfeasible and so have been supplemented with referred material (for specimens used in codings, see "Full Matrix and Referenced Material" below). Several characters were taken from the matrix constructed by Parham and Pyenson (2010) which pertain to diagnostic carapacial features of stem cheloniids. Character 88 was added as a novel character for this study to assist in differentiating the Lophochelyinae from "protostegid" grade taxa also possessing keeled neurals.

Character list

1. Cranial scute sulci on dermal roofing elements. 0: present; 1: absent (Lapparent de Broin (2013) ch.1).

2. Nasals. 0: present; 1: absent (Lapparent de Broin (2013) ch.2; Anquetin (2011) ch.1).

3. Medial contact of prefrontals on the dorsal cranial surface. 0: not meeting medially; 1: meeting medially (Lapparent de Broin (2013) ch.3; Anquetin (2011) ch.5). Modified from Lapparent de Broin (2013) to include additional specifications regarding the nature of the prefrontal contact as noted by Anquetin (2011). Lapparent de Broin (2013) codes *Corsochelys haliniches* as unknown for this character presumably due to the absence of the anterior most portion of the cranium in the described material for this species (Zangerl, 1960). However, the relative position of the frontals with the other preserved dermal roof elements of the cranium and the extent of their dorsomedial suture with one another are indicative of dorsomedially sutured prefrontals and therefore, *C. haliniches* is coded in the present analysis as 3/1.

4. Prefrontal-Postorbital contact. 0: present; 1: absent (Lapparent de Broin (2013) ch.4). Lapparent de Broin (2013) reports this character state as 4/0 for *Corsochelys haliniches* but the figured cranial material (Zangerl, 1960; pp. 287 Fig. 126) clearly shows a preserved right frontal which contributes to the medial portion of orbital rim. This contribution of the frontal to the fossa orbitalis would certainly prevent the prefrontal from contacting the postorbital, though neither the postorbitals nor prefrontals are preserved in the type specimen. For this reason, this *C. haliniches* is coded here as 4/1. The cranial material of *Calcarichelys gemma* (RMM 3216) lacks preserved postorbitals, however, the position of the prefrontals and their relative position to the frontals and the preserved portion of the parietal indicates the presence of sutural contact between the prefrontal and postorbital (Hooks, 1995; Fig. 1, pp. 8).

5. Dorsal prefrontal exposure. 0: present; 1: absent or near absent (Anquetin (2011) ch.9). This character was included in the present matrix to increase the resolution between chelonioids and baenids as noted by Anquetin (2011). The binary coding arrangement for this character is favorable over the multistate coding employed by Joyce (2007) to avoid *a priori* homology assumptions (Anquetin, 2011).

6. Orbit orientation. 0: faces laterally; 1: faces dorsolaterally (Lapparent de Broin (2013) ch.5). Lapparent de Broin (2013) coded this character for *Xinjuangchelys* as ‘0’, however, the cranial material of *Xinjuangchelys wusu* figured by Rabi et al. (2013) clearly exhibits dorsolaterally facing orbits in spite of the oblique, dorsoventral compression suffered by many of the specimens. Therefore, this character scoring is changed from 6/0 to 6/1 in the present study.

7. Frontal contribution to the orbit. 0: absent, contact between prefrontal and postorbital; 1: present (Anquetin (2011) ch.13). See Character 4 for a discussion of the coding of this character for *Calcarichelys gemma.* The polymorphic scoring for *Kinosternon flavescens* was based on the observation made by Knauss (2014) of a *K. flavescens* specimen, FMNH 6849, on which the left frontal contributes to the orbit while the right frontal does not.

8. *Processus inferior parietalis*. 0: narrow anteroposteriorly; 1: wide anteroposteriorly (Lapparent de Broin (2013) ch.6).

9. Parietal-Squamosal contact. 0: present; 1: absent (Lapparent de Broin (2013) ch.7; Anquetin (2011) ch.16).

10. Posterior temporal emargination. 0: weak, *processus trochlearis oticus* more than 50% concealed in dorsal view, generally *foramen stapedio-temporale* concealed; 1:

strong, more than 50% of *processus trochlearis oticus* exposed in dorsal view, generally *foramen stapedio-temporale* visible. (Modified from Lapparent de Broin (2013) ch. 8).

11. Ouadratojugal excluded from lateral emargination. 0: no; 1: yes by jugal-quadrate contact or by maxillary-quadrate contact (Lapparent de Broin (2013) ch.9).

12. Medial process of jugal visible in ventral view in the fossa temporalis inferior. 0: present, strongly developed; 1: weakly developed or absent (Lapparent de Broin (2013) ch.10).

13. Jugal-Pterygoid contact. 0: present; 1: absent (Lapparent de Broin (2013) ch.11).

14. Ventral cheek concavity along the ventral margin of the jugal-quadratojugal. 0: absent or indistinct (shallow concavity); 1: deep or at least distinct (Modified from Lapparent de Broin (2013) ch. 12).

15. Premaxilla. 0: not hooked; 1: hooked (Lapparent de Broin (2013) ch.13).

16. *Foramen praepalatinum.* 0: present; 1: absent (Lapparent de Broin (2013) ch. 14). The tentative recoding of *Toxochelys* from ‘absent’ to ‘present’ in Lapparent de Broin (2013) is supported here by personal examination of cranial material of both *T. latiremis* and *T. moorevillensis* from the Mooreville Chalk of Alabama, both of which clearly show the presence of developed *foramina praepalatinum*.

17. Upper triturating surface. 0: not involving palatine; 1: involving palatine (Lapparent de Broin (2013) ch.15)

18. Upper triturating surface. 0: without contribution from the vomer; 1: with contribution from the vomer (Lapparent de Broin (2013) ch.16).

19. Vomers. 0: not developed into narrow sagittal pillar in ventral view; 1: developed into narrow sagittal pillar (Modified from Lapparent de Broin (2013) ch.17). The scoring of ‘0’ for *Ctenochelys stenoporus* by Lapparent de Broin (2013) is not supported here. Upon examination of the *C. stenoporus* cranial material figured by Zangerl (1953) previously referred to as the type specimen of *Toxochelys elkader*, AMNH 6137, it is evident that the vomer has been medially compressed by the dorsomedial expansion of the palatines and has become an elongate pillar-like structure, similar to the condition seen in stem-cheloniids such as *Euclastes* and *Osteopygis* (Parham, 2005).

20. Vomer-Palatine contact anterior to internal naris (*apertura narium interna).* 0: absent; 1: present (Lapparent de Broin (2013) ch.18)

21. Lingual ridge of maxilla. 0: absent or weakly developed; 1: strongly developed (Lapparent de Broin (2013) ch.19). Parham and Pyenson (2010) note that this character may be ontogenetically variable in *Pacifichelys urbinai* but code the character as ‘0’. This coding is supported here by comparison with the sharply defined lingual ridges on the maxillae of *Ctenochelys acris* and *Chelydra serpentina.*

22. Palatines and Vomer-Pterygoid contact. 0: palatines not meeting medially, vomer contacting pterygoid; 1: palatines meeting medially, vomer not contacting pterygoid (Lapparent de Broin (2013) ch.20). The illustrations of the cranial material of *Pacifichelys urbinai* provided by Parham and Pyenson (2010) present an interesting arrangement of this character (Fig. 5, pp. 238). USNM 1447 (holotype) appears to show a palatine-vomer state similar to *Chelydra serpentina* (Gaffney, 1972) while USNM 1448 (paratype) clearly shows a palatine-pterygoid contact along the entire anterior margin of the pterygoid. As a result of this variation and the incomplete preservation of the holotype and referred specimens, the character is coded here as ‘unknown’ rather than polymorphic.

23. *Foramen palatinum posterius.* 0: fully enclosed within palatal bones; 1: open posterolaterally, but anteriorly forms embayment in palate; 2: absent (Lapparent de Broin (2013) ch.21). The unordered, multistate arrangement for this character from Lapparent de Broin (2013) is used here rather than the binary arrangement of Anquetin (2011) since the limited taxonomic scope of the taxa included in the current analysis (lack of basal stem-Testudines) prevent the need for congruence testing of this character.

24. *Processus pterygoideus externus.* 0: with vertical flange or small projection; 1: totally lacking vertical flange (Lapparent de Broin (2013) ch.22).

25. Pterygoids. 0: without median ventral ridge; 1: with median ventral ridge (Lapparent de Broin (2013) ch.23).

26. Pterygoids. 0: do not form part of the mandibular condyle; 1: form part of the mandibular condyle (Lapparent de Broin (2013) ch.24).

27. Pterygoids. 0: at least moderately wide; 1: narrow bar (Lapparent de Broin (2013) ch.25). Personal observation of Cretaceous panchelonioid material has led to the conclusion that this may be an ontogenetically variable character in a number of species. In this study, the definition is revised to consider this factor. ‘Wide’ is now a minimal pterygoid width equal to 50% or more of the distance between the lateral most point of the left and right *processus pterygoideus externus* and ‘narrow’ is considered any minimal pterygoid width less than 50% of this measurement.

28. *Processus trochlearis oticus.* 0: with significant contribution from the quadrate; 1: with marginal to no contribution from the quadrate. (Lapparent de Broin (2013) ch.26).

29. *Crista supraoccipitalis.* 0: small, not greatly extending beyond occipital condyle; 1: large, greatly extending beyond occipital condyle (Lapparent de Broin (2013) ch.27). All observed specimens of *C. acris* lack the posterior portions of the dermal roof of the cranium preventing a completely accurate assessment of the extent of the occipital condyle. However, RMM 6157 possesses an intact crista supraoccipitalis that extends 23.0 mm beyond the posterior margin of the squamosal and is coded herein as 29/1.

30. *Foramina anterior canalis carotici interni.* 0: widely separated; 1: close together or fused (Lapparent de Broin (2013) ch.28).

31. Internal carotid artery (posterior to junction with palatine artery). 0: not embedded in braincase elements or partially embedded; 1: fully embedded (Modified from Lapparent de Broin (2013) ch.29). The coding strategy for this character is altered from the multistate coding of Lapparent de Broin (2013) and reconstructed here as a binary character.

32. Ventral surface of basisphenoid. 0: without V-shaped crest; 1: with V-shaped crest (Lapparent de Broin (2013) ch.30).

33. Posterolateral pterygoid articulations with basisphenoid in ventral view. 0: no posterolateral pterygoid projections; 1: pterygoid posterolateral projections inducing a V-shaped basisphenoid (Lapparent de Broin (2013) ch.31). Lapparent de Broin (2013) codes the primitive state for this character in *Toxochelys latiremis* but examination of the *T. latiremis* cranial material figured by Matzke (2009) show a distinctly triangular basisphenoid in ventral view as a result of the posterolateral processes of the pterygoids. The coding for *Toxochelys latiremis* is herein adjusted to reflect this observation from ‘0’ to ‘1’.

34. *Dorsum sellae.* 0: low, not extending dorsally beyond the level of the rostrum basisphenoidale; 1: high (Lapparent de Broin (2013) ch.32). This character is in need of revision to include additional relative spacial qualities.

35. *Rostrum basisphenoidale.* 0: wide, trabeculae separate; 1: trabeculae approximated or fused in a rod-like structure (Lapparent de Broin (2013) ch.33). Lapparent de Broin (2013) codes this character as being polymorphic [01] within the plesiochelyidae, however, when reduced to the single species *Plesiochelys etalloni*, the specimen figured by Gaffney (1975; SM 135) clearly shows a rod-like rostrum basisphenoidale and is herein coded as 35/1.

36. *Rostrum basisphenoidale.* 0: prominent; 1: reduced (Lapparent de Broin (2013) ch.34). The examined specimen of *Calcarichelys gemma* (RMM 3216) possesses a distinct rostrum basisphenoidale, however, the process is much less developed than in other protostegid taxa (i.e. *Protostega gigas*) and much more prominent than in several panchelonioid taxa. *Calcarichelys gemma* is coded herein as ‘36/0’ but future phylogenetic analyses of cryptodires should consider a revision of this character to include the gradient of possible states.

37. Junction of palatine artery and internal carotid artery. 0: not enclosed in bone; 1: enclosed in bone (Lapparent de Broin (2013) ch.35).

38. *Foramen caroticum laterale.* 0: not larger than the *foramen anterius canalis carotici interni*; 1: larger (Lapparent de Broin (2013) ch.36). The figured basicranium of *Calcarichelys gemma* (Hooks, 1995; Fig. 2, pp. 15) show the presence of foramina located laterally from the rostrum basisphenoidale on the dorsal surface of the pterygoid and are labeled as ‘foramen nervi vidiani’, presumably referring to the foramen pro ramo nervi vidiani. These foramina are, in fact, the foramen caroticum laterale which are roughly the same diameter as the adjacent foramen canalus carotici interni and are recorded here as ‘38/0’.

39. *Foramen caroticum laterale.* 0: not confluent with the *canalis cavernosus;* 1: confluent (Lapparent de Broin (2013) ch.37).

40. Mandible. 0: with narrow triturating surface, symphysis less than 1/3 of jaw length; 1: with broad triturating surface, symphysis greater than 1/3 of jaw length (Modified from Lapparent de Broin (2013) ch.38). Danilov and Parham (2007) note that the morphology of the lower jaw of *Ordosemys brinkmania* is indiscernible, however, the figured specimen IVPP V4074.8 shows a clear enough aspect of the lower jaw to determine an approximate width of the symphyseal portion for the purposes of this study and is coded here as ‘40/0’.

41. Dentary. 0: not hooked; 1: hooked (Lapparent de Broin (2013) ch.39).

42. Symphyseal ridge of dentary. 0: absent or diminished, not being exposed in lateral view; 1: present and greatly developed, being exposed laterally (Modified from Lapparent de Broin (2013) ch.40). For the purposes of the present study, the binary arrangement of this character is preferable to the multistate alternative used by Lapparent de Broin (2013) simply due to the lack of variation of this character within many cryptodire species (personal observation; Zangerl, 1953; Matzke, 2007; Anquetin, 2011). This character is employed here to increase the resolution between clades of panchelonioids. Juvenile *Ctenochelys stenoporus* specimens exhibit a prominent symphyseal ridge visible in lateral view extending dorsally above the level of the labial margin of the dentary, as in adults of the same species. Inversely, specimens of *Ctenochelys acris* and *Toxochelys latiremis* possess no such symphyseal ridge in either juveniles or adults (RMM 6157; Matzke, 2009).

43. Lingual ridge of dentary. 0: prominent; 1: weak or absent (Lapparent de Broin (2013) ch.41).

44. Dentary expanded posteriorly, almost reaching articular surface. 0: no; 1: yes (Lapparent de Broin (2013) ch.42).

45. Splenial. 0: present; 1: absent (Lapparent de Broin (2013) ch.43).

46. Transverse process of cervicals. 0: double; 1: single (Lapparent de Broin (2013) ch.44).

47. Shape of central articulation of posterior cervicals. 0: as high as wide; 1: much wider than high (Lapparent de Broin (2013) ch.45). The interpretation of this character from fossil taxa should be treated with caution as many specimens have undergone some degree of dorsoventral compression which has the potential to greatly alter the shape of vertebral centra.

48. Strongly developed ventral keel on posterior cervical centra. 0: absent; 1: present (Lapparent de Broin (2013) ch.46; Anquetin (2011) ch.143).

49. Amphicoelous cervical central articulations. 0: present; 1: absent (Modified from Lapparent de Broin (2013) ch.47).

50. Biconvex centrum of anterior cervicals. 0: absent; 1: present (Lapparent de Broin (2013) ch.48).

51. Biconvex anterior cervical centrum. 0: on 2nd or 3rd cervical; 1: on 4th cervical (Lapparent de Broin (2013) ch.49).

52. 8th cervical. 0: amphicoelous; 1: procoelous; 2: biconvex; 3: opistocoelous (Lapparent de Broin (2013) ch.50).

53. 8th cervical centrum. 0: not shorter than the 7th; 1: shorter than the 7th (Lapparent de Broin (2013) ch.51; Anquetin (2011) ch.144).

54. Double cervical articulation between 7th and 8th cervicals. 0: absent; 1: present (Lapparent de Broin (2013) ch.52).

55. 1st thoracic vertebra, anterior articulation. 0: facing anteriorly; 1: facing ventrally or anteroventrally (Lapparent de Broin (2013) ch.53).

56. 1st thoracic rib. 0: long, distal end extending to lateral margin of first costal; 1: short, distal end does not extend beyond nuchal (Lapparent de Broin (2013) ch.54).

57. 10th thoracic rib. 0: contacting 8th costal; 1: ends freely (Lapparent de Broin (2013) ch.55).

58. Chevrons. 0: present; 1: absent (Lapparent de Broin (2013) ch.56).

59. Anterior facet of caudals. 0: amphicoelous; 1: procoelous (Lapparent de Broin (2013) ch.57).

60. Posterior facet of caudals. 0: amphicoelous; 1: opisthocoelous or procoelous (Lapparent de Broin (2013) ch.58). Given the complexity of the evolutionary history of caudal articulation among testudines as first noted by Joyce (2007) and subsequently by Anquetin (2011), the overly simplified binary arrangement of this character as proposed by Sterli (2008) is preferred over the multistate coding of Lapparent de Broin (2013), pending further revision of this character.

61. Coracoid. 0: shorter than humerus; 1: at least as long as humerus (Lapparent de Broin (2013) ch.59).

62. Scapular angle, between scapular prong and acromion. 0: less than or equal to 100 degrees; 1: from ca. 100 degrees or more (Modified from Lapparent de Broin (2013) ch.60).

63. Lateral process of pubis (pectineal process). 0: small, not extending anteriorly beyond level of medial portion of pubis; 1: large, extending anteriorly beyond level of medial portion of the pubis (Lapparent de Broin (2013) ch.61).

64. Thyroid fenestra. 0: small to moderately developed and subdivided by pubis-ischium contact; 1: large and single (Lapparent de Broin (2013) ch.62).

65. Lateral process of ischium or metischial process. 0: prominent, at least as long as acetabular process of ischium; 1: small but distinct process; 2: rudimentary or lost (Lapparent de Broin (2013) ch.63).

66. Large pelvis approaching coracoid. 0: no; 1: yes (Lapparent de Broin (2013) ch.64).

67. Humerus. 0: shorter than femur; 1: longer than femur (Lapparent de Broin (2013) ch.65).

68. Lateral process of humerus. 0: abuts *caput humeri*; 1: slightly separated from *caput humeri*; 2: distal from *caput humeri*, located at middle of humeral shaft (Modified from Lapparent de Broin (2013) ch.66).

69. Proximal articular surface of humerus. 0: with shoulder on preaxial side, upturned; 1: without shoulder, not upturned (Lapparent de Broin (2013) ch.67).

70. Scar for *M. latissimus dorsi* and *M. teres major*. 0: located anterior to humeral shaft; 1: located at middle of shaft (Lapparent de Broin (2013) ch.68).

71. Lateral process of humerus V-shaped. 0: no; 1: yes (Lapparent de Broin (2013) ch.69).

72. Expansion of lateral process of humerus limited to anterodorsal surface of the humeral diaphysis. 0: no, expands onto posteroventral surface; 1: yes (Modified from Lapparent de Broin (2013) ch.70).

73. Medial concavity of lateral process of humerus. 0: absent; 1: present (Lapparent de Broin (2013) ch.71).

74. Prominent anterior projection of lateral process of humerus. 0: absent; 1: present (Lapparent de Broin (2013) ch.72).

75. Ulna-radius contact through rugosity and ridge. 0: absent; 1: present (Lapparent de Broin (2013) ch.73).

76. Radius curves towards anterior. 0: no; 1: yes (Lapparent de Broin (2013) ch.74).

77. Carpal and tarsal elements. 0: not flattened; 1: flattened (Lapparent de Broin (2013) ch.75).

78. 3rd to 5th digits modified into paddle with rigid articulations. 0: no; 1: yes (Lapparent de Broin (2013) ch.76).

79. 1st and 2nd digits modified into paddle with rigid articulations. 0: no; 1: yes (Lapparent de Broin (2013) ch.77). This character is scored as ‘0’ for *Ctenochelys* in Lapparent de Broin (2013) despite there currently being no figured manus material for this genus. The only described flipper element from a ‘toxochelyid’-grade species is the material figured by Zangerl (1953; Fig. 70, p. 167; CNHM=FMNH PR123) which was questionably assigned to *Toxochelys moorevillensis*. Until more complete specimens are described in detail, the scoring of this character for *Ctenochelys stenoporus* is changed to ‘?’ or unknown.

80. Femoral trochanters. 0: distinct and separated from one another; 1: indistinct and connected by bony ridge (Lapparent de Broin (2013) ch.78).

81. Scute sulci on carapace. 0: prominent; 1: absent or poorly developed (Lapparent de Broin (2013) ch.79).

82. Irregularly textured carapacial elements. 0: absent; 1: present (Parham and Pyenson (2010) ch.34). This character is taken from the matrix of Parham and Pyenson (2010) and is herein modified to represent an unambiguous synapomorphy of stem-dermochelyoids such as *Corsochelys haliniches* which exhibit moderate carapacial 'erosions' as noted by Zangerl (1953) in the form of collapsed epithelial bone over large vascular inervations. This is not homologous with the textured carapacial elements found in members of Trionychidae or the Lophochelyinae genus *Peritresius*.

83. Posterior nuchal fontanelles. 0: absent; 1: present (Lapparent de Broin (2013) ch.80).

84. Cervical scute. 0: overlying less than half the width of nuchal; 1: overlying more than half the width of nuchal (Lapparent de Broin (2013) ch.81).

85. Raised pedestal on the visceral surface of the nuchal for articulation with the neural spine of the 8th cervical vertebra. 0: absent; 1: present (Anquetin (2011) ch.90). Anquetin (2011) notes that the stem turtles (e.g. *Proganochelys*) and panchelonioids are the only groups that possess a raised vertebral articulation on the ventral surface of the nuchal but that these two characters are not homologous and should be coded separately. Though an accurate assessment, stem turtles such as *Proganochelys* are outside the scope of the present study and the character is used in the current analysis only to help increase the resolution between panchelonioids and the clade formed by baenids and non-marine cryptodires. This character is an unambiguous synapomorphy of panchelonioids and is therefore coded as a single character. It should be noted, however, that other than the Cretaceous 'toxochelyid'-grade taxa, the only species included in this study that possesses a homologous nuchal rugosity is the stem-cheloniid *Pacifichelys urbinai* from the Miocene of Peru (Parham and Pyenson, 2010).

86. 1st vertebral. 0: not reaching second peripheral; 1: reaching 2nd peripheral (Lapparent de Broin (2013) ch.82). The scoring of *Ctenochelys stenoporus* as ‘unknown’ for this character in Lapparent de Broin (2013) is herein altered to reflect the information derived from the juvenile *C. stenoporus* figured by Matzke (2007), USNM 357166. Though there may be a degree of unconsidered ontogenetic variation of this character in using a juvenile specimen, considering that USNM 357166 is the most complete *C. stenoporus* known to date and that larger individuals appear to exhibit a similar condition, *C. stenoporus* is tentatively scored as ‘86/0’ pending the description of more complete adult specimens.

87. Thick neurals with median keel. 0: no; 1: yes (Lapparent de Broin (2013) ch.83).

88. Epineural ossifications. 0: absent; 1: present (Gentry (2015) Novel character).

89. Neural number. 0: eight or less; 1: nine; 2: ten or more (Lapparent de Broin (2013) ch.84). For all included taxa, the presence of a preneural is counted as an additional neural (i.e. *Ctenochelys stenoporus*).

90. Neural shape. 0: mostly hexagonal with short anterolateral or posterolateral sides; 1: mostly rectangular (Modified from Lapparent de Broin (2013) ch.85). Lapparent de Broin coded an unordered multistate character for neural shape (0: mostly hexagonal, not equilateral; 1: mostly hexagonal and equilateral; 2: mostly rectangular) but within the context of the present study, neurals being primarily equilateral hexagons are not found in any of the included taxa and are therefore uninformative.

91. Neural reduction. 0: all neurals present; 1: 7th and 8th neurals reduced or lost; 2: all neurals lost (Lapparent de Broin (2013) ch.86).

92. Suprapygals. 0: 1st suprapygal moderately large; 1: 1st suprapygal absent or much smaller than 2nd (Lapparent de Broin (2013) ch.87). As described by Hooks (1995), *Calcarichelys gemma* possesses only a single suprapygal, herein coded as ‘92/1’.

93. Costal ossification reduction. 0: absent, costals fully or almost fully ossified, costal fontanelles small or absent; 1: present, costals ossified only two thirds or less of the rib length in adult individuals; 2: costals absent (Modified from Lapparent de Broin (2013) ch.88; Anquetin (2011) ch.101).

94. 9th costal plate. 0: present; 1: absent (Lapparent de Broin (2013) ch.89).

95. Plastral scute sulci. 0: present; 1: absent or rudimentary (Lapparent de Broin (2013) ch.90).

96. Axillary buttress. 0: only reaching peripheral; 1: reaching past peripheral, onto 1st costal (Lapparent de Broin (2013) ch.91).

97. Inguinal buttress. 0: only reaching peripheral; 1: reaching past peripheral, onto 5th or 6th costals (Lapparent de Broin (2013) ch.92).

98. Femoroanal sulcus. 0: not reaching hypoplastron. 1: reaching hypoplastron (Lapparent de Broin (2013) ch.93).

99. Plastral index. 0: larger than 100; 1: between 100 and 60; 2: lower than 60 (Lapparent de Broin (2013) ch.94).

100. Plastron. 0: not star-shaped; 1: star-shaped (Lapparent de Broin (2013) ch.95).

101. Plastral fontanelles between hyo- and hypoplastra. 0: absent; 1: smaller than hyo- or hypoplastron; 2: at least as large as hyo- or hypoplastron (Lapparent de Broin (2013) ch.96).

102. Epiplastra. 0: broad throughout; 1: narrow (Modified from Lapparent de Broin (2013) ch.97).

103. Entoplastron tightly sutured with hyoplastron. 0: yes; 1: no (Lapparent de Broin (2013) ch.98). As noted by Joyce (2007), the absence of an entoplastron is unambiguous synapomorphy of a clade including *Kinsternon flavescens*. This taxon is therefore coded as inapplicable or '-' for characters 103-105.

104. Epi- and entoplastron. 0: separate; 1: fused (Lapparent de Broin (2013) ch.99). Though the entoplastron is unknown for *Ctenochelys acris*, MSC 35085 has an intact right epiplastron possessing a deep sulcus along its anteromedial margin seemingly indicative of sutural contact between the epi- and entoplastron. For this reason, *Ctenochelys acris* is coded herein as '104/1'

105. Entoplastron. 0: without elongate lateral wing; 1: with elongate lateral wing (Lapparent de Broin (2013) ch.100).

106. Xiphiplastra. 0: as wide or wider than epiplastron; 1: narrower than epiplastron (Modified from Lapparent de Broin (2013) ch.101).

107. Medial contact of xiphiplastra. 0: sutured along its entire edge; 1: reduced or lost (Lapparent de Broin (2013) ch.102).

108. Short xiphiplastra with lateral curvature. 0: absent; 1: present (Lapparent de Broin (2013) ch.103).

Full Matrix and Referenced Material

(108 Characters / 18 taxa)

1) Hypothetical primitive taxon

000000000000000000000000000000000000000000000000000000000000000000000000
000000000000000000000000000000000000

2) *Plesiochelys etalloni* Gaffney, 1975 (Scorings of Lapparent de Broin, 2013 and Anquetin, 2011; *MH* 435, SM 135, SM 136)

001101111101110000001110000000100100110000100010000000000?00000100?00000
000000000000000000000101100000000000

3) *Xinjiangchelys wusu* Rabi et al., 2013 (PMOL-SGP A0100-1, PMOL-SGP A0100-2, PMOL-SGP A0100-3)

00110111?10??00???1??010??001?100???0??0000??10000100000011000100000000000
0000000000001000000100011000000000

4) *Ordosemys brinkmania* Danilov and Parham, 2007 (IVPP V4074.4, IVPP V4074.8, IVPP V4074.14-18)

1001001??10?01000?1000?00?0?0?0110??00?000???????????????????????????????????
???0000010001000100011011010000

5) *Chelydra serpentina* Linneaus, 1758 (Scorings of Lapparent de Broin, 2013 and Anquetin, 2011; Gaffney, 1972; AMNH 5305, AMNH 67015, AMNH 107386)

01100101110001000000000000000101000001000001011111111111000110000000000000000000000000000000000100012011100100

6) *Toxochelys latiremis* Cope, 1873 (Scorings of Lapparent de Broin, 2013 and Anquetin, 2011; Zangerl, 1953; Matzke, 2009; AMNH 2362, YPM 3602, ROM 28563)

?1110110010001001001000000001111110010000110111111111101??111100100110000001011000011100010001 1?00?2011100100

7) *Ctenochelys stenoporus* (Hay, 1905) (Scoring of Lapparent de Broin, 2013; Zangerl, 1953; Matzke, 2007; KU (VP) 1205, USNM 391920, USNM 357166)

?111011000000101111100001000111111101000011011111111001101111001001100000010110000111011110011000002011100110

8) *Ctenochelys acris* Zangerl, 1953 (MSC 35085, RMM 6157, RMM 3050)

?1110110??????00111000001010111111101010000010111????????11?10101??????????111?00101?11000011000??01111????

9) *Pacifichelys urbinai* Parham and Pyenson, 2010 (UNMSM 1447-1453)

?110000??00??10?11110?2100000??11?10???1?0?????1111?????????11?????00?01??11????00011???????1???????????????

10) *Kinosternon flavescens* Agassiz, 1857 (Scorings of Knauss, 2014, Anquetin, 2011; Joyce, 2007)

?11000011000001011100000000010101001001010001111110110111011000010000001
00010000000001000011010000?000---000

11) *Puppigerus camperi* Gray, 1831 (Scoring of Lapparent de Broin, 2013; Moody, 1974; IRSNB 1687/R.4, IRSNB IG8402/R.17)

0111001000000001111100201000111111011010110111111111110111110110121010
00101111000000000100001000?1011100100

12) *Chelonia mydas* Linneaus, 1758 (Scorings of Lapparent de Broin, 2013 and Anquetin, 2011; Hirth, 1997; MSC Reg. 353)

0111001000000001111100201000111111011100100111111111110111110110121110
001011110001010010001100010011100110

13) *Desmatochelys lowii* Williston, 1894 (Scorings of Lapparent de Broin, 2013 and Anquetin, 2011; Zangerl and Sloan, 1960; KU (VP) 1200; FMNH PR385)

0001001011?110010100111001111100011010000110110011010001???111010121001
10011111000101000101111100?0021101?1?

14) *Santanachelys gaffneyi* Hirayama, 1998 (Scoring of Lapparent de Broin, 2013; THUg1386)

00010010101110011000011001001100011010000110110011010000?11?1110?0121001
0001110?00010010010111000?0011101100

15) *Calcarichelys gemma* Zangerl, 1953 (Hooks, 1998; FMNH PR129, RMM 3216)

?110000??0?0100?????1??1?0101111011001??????111???????????11?????1??1?001?????0001?010000101100??01?1?10?0

16) *Protostega gigas* (Cope, 1872) (Scoring of Lapparent de Broin, 2013; Cope, 1875; Zangerl, 1953b; AMNH FR1503; FMNH P27314)

111000000011101101?011210111110001101000001011001101000101111110111211011001111100?0?10110120100?0111111111

17) *Corsochelys haliniches* Zangerl, 1960 (Scoring of Lapparent de Broin, 2013; FMNH PR 249)

1?110?1011011?????????00000111001?1110??????10000???00?????1100?01210?0000011?11000?100010011100?002110?110

18) *Dermochelys coriacea* Vandelli, 1761 (Scorings of Lapparent de Broin, 2013; Aquetin, 2011; Gaffney, 1979)

11100000000111111100021000001100111111010111110111100000111111010131100 0100111110--------2-2-1---002110-110

Cladograms

Many phylogenetic analyses which incorporate ‘toxochelyid’-grade taxa routinely group *Toxochelys* and *Ctenochelys* as a single terminal node at the base of Chelonioidea (Hirayama, 1994, 1998; Joyce, 2007; Joyce, 2013) while others place them as separate nodes on either the stem of Cheloniidae or Chelonioidea (Kear and Lee, 2006; Parham and Pyenson, 2010; Anquetin, 2011). The unconstrained, morphology based phylogenies produced for this study place *Toxochelys* apart from *Ctenochelys* as separate, monophyletic clades at the stem of Panchelonioidea (Joyce et al., 2004) within the crown group Americhelydia (Fig. 2-1). A morphology based phylogenetic pattern supports one of the two proposed placements of panchelonioids proposed by Parham and Pyenson (2010) though in order to further support or refute this arrangement on a broader scale, a larger matrix than the one employed in the current study containing additional fossil and extant taxa will be needed along with additional molecular and temporal constraints (Joyce, 2013; Crawford et al., 2014).

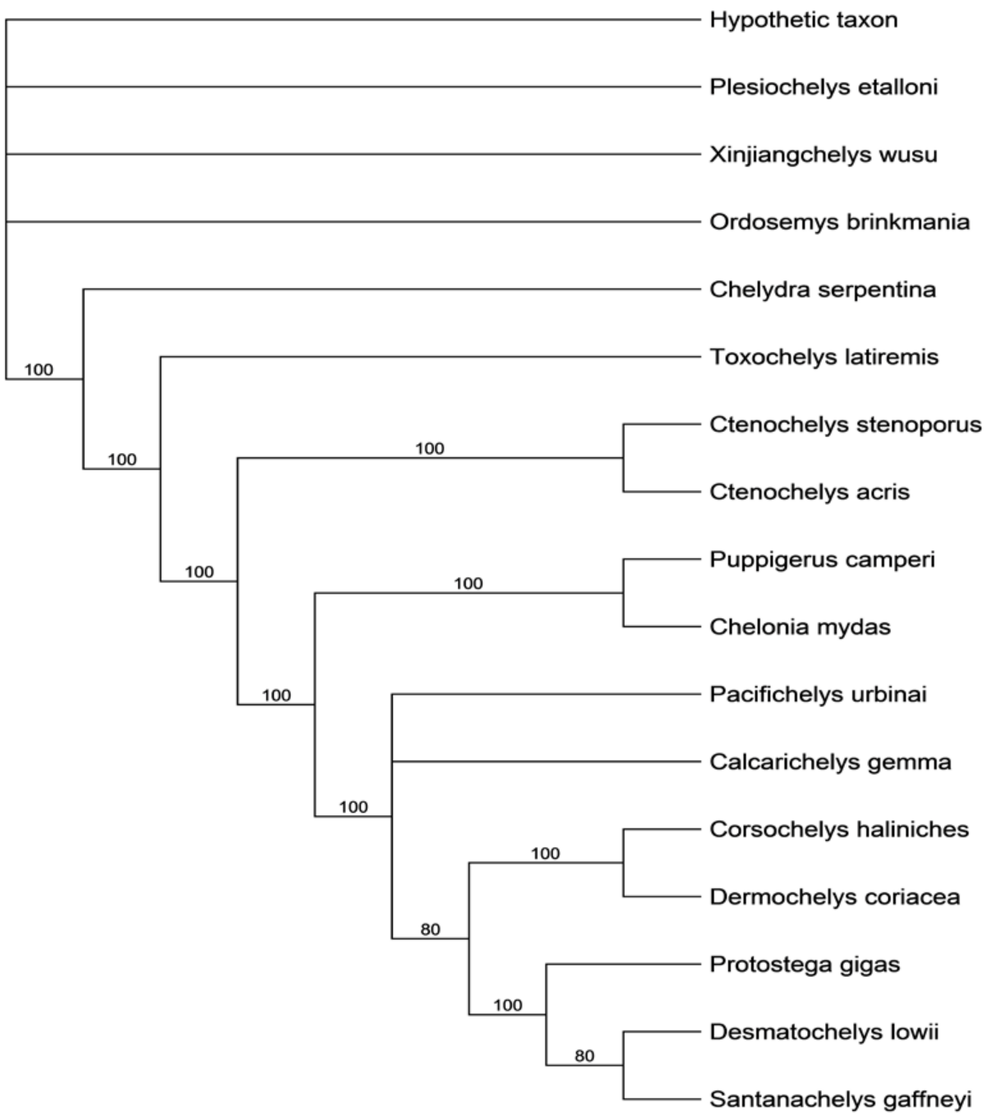

FIGURE 2.1 -- (Tree length = 246 steps; CI = .4472; RI = .6012) Morphology based, majority-rule consensus tree with bootstrap values showing the hypothesized, unconstrained phylogenetic interrelationships of numerous extinct cryptodire taxa. Protostegids are grouped morphologically within Dermochelyidae, however, this phylogeny does not reflect temporal distribution and merely illustrates the high number of symplesiomorphic characters shared by advanced chelonioids and the Protostegidae. *Calcarichelys gemma* is tentatively placed outside of Protostegidae though the character scorings for this taxon were limited by the partial nature of the available material.

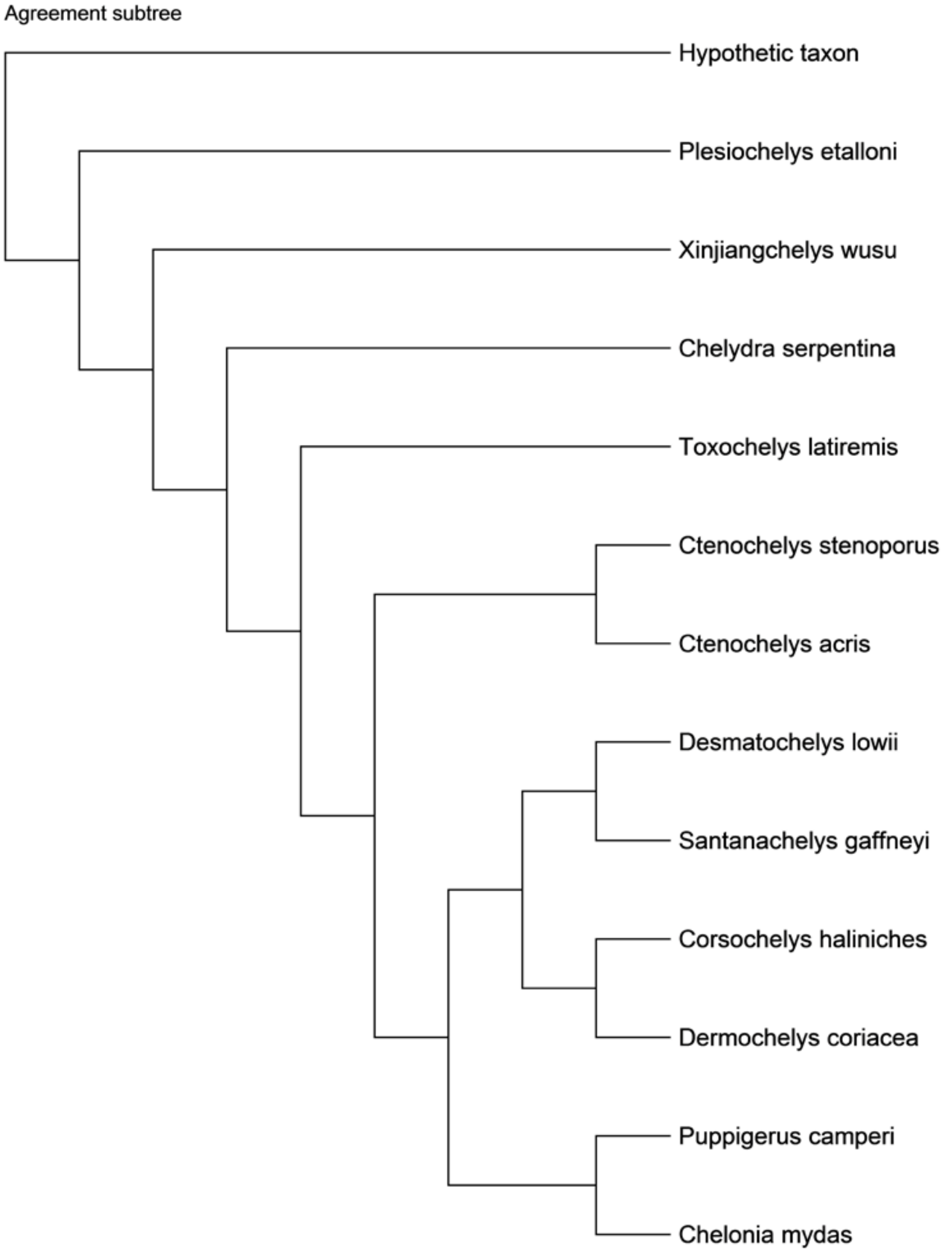

FIGURE 2.2 – Cladogram (agreement subtree) illustrating the phylogenetic interrelationships of a number of the Cryptodire taxa used in this study.

SYSTEMATIC PALEONTOLOGY

Testudines Batsch, 1788
Cryptodira Cope, 1868
Americhelydia Joyce et al., 2013
Toxochelys Cope, 1873
Toxochelys latiremis (Cope, 1873)

Synonymies: *T. serrifer* Cope, 1875; *T. brachyrhinus* Case, 1898; *Porthochelys browni* Hay, 1905; *Phyllemys barberi* Schmidt, 1944; *T. weeksi* Collins, 1951; *Lophochelys niobrarae* Zangerl, 1953.

Testudines Batsch, 1788
Cryptodira Cope, 1868
Americhelydia Joyce et al., 2013
Panchelonioidea Joyce, Parham and Gauthier, 2004
Ctenochelys Zangerl, 1953
Ctenochelys stenoporus (Hay, 1905)

Synonymies: *Toxochelys procax* Hay, 1905; *T. elkader* Hay, 1908; *Lophochelys natarix* Zangerl, 1953; *L. venatrix* Zangerl, 1953; *Ctenochelys tenuitesta* Zangerl, 1953.

Testudines Batsch, 1788
Cryptodira Cope, 1868
Americhelydia Joyce et al., 2013
Panchelonioidea Joyce, Parham and Gauthier, 2004
Ctenochelys Zangerl, 1953
Ctenochelys acris (Zangerl, 1953)

CONCLUSION

The *Ctenochelys* clade is distinguished phylogenetically from *Toxochelys latiremis* by the presence of a strongly keeled neural series (87/1), intermediate epineural ossifications (88/1), and a reduced femoroanal sulcus (98/0). *Ctenochelys acris* is differentiated from *C. stenoporus* by the following phylogenetically informative autapomorphic characters: a lack of vomer-palatine contact anterior to the internal naris (20/0), comparatively reduced minimal pterygoid width (27/1), diminished symphyseal ridge on the dorsal surface of the dentary (42/0), prominent lingual ridge of the dentary (43/0), and a heightened degree of connectivity between the epi- and entoplastron (104/1).

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THESIS CONCLUSION

The taxonomic validity of *Ctenochelys acris* is supported by morphology based phylogenetic analysis of numerous panchelonioid specimens. *Toxochelys* and *Ctenochelys* are hereby placed into two separate clades with *Toxochelys* placed within total group Americhelydia or stem-panchelonioids, while *Ctenochelys* is placed within the crown group Panchelonioidea. The family name 'Toxochelyidae' is hereafter considered invalid as a monophyletic clade. The term 'toxochelyid' should only be used to refer to the members of the paraphyletic grouping of the *Toxochelys* and *Ctenochelys* clades pending a formal taxonomic revision of these and other genera previously identified as 'toxochelyids' and their inclusion in a global phylogenetic analysis.

LITERATURE CITED

Agassiz, L. 1857. Contributions to the Natural History of the United States of America. First monograph, vol. I and II. Little, Brown and Company, Boston; Trubner and Company, London.

Anquetin, J. 2011. Reassessment of the phylogenetic interrelationships of basal turtles (Testudinata). Journal of Systematic Palaeontology, DOI:10.1080/14772019.2011.558928.

Ciampagalio, C. et al. 2013. A note on Late Cretaceous fish taxa recovered from stream gravels at site AGr-43 in Greene County, Alabama. Bulletin of the Alabama Museum of Natural History, vol. 1, no. 31, pp. 84-97.

Case, E. 1939. A nearly complete turtle skeleton from the Upper Cretaceous of Montana. Contrib. Mus. Paleont., Univ. Michigan, vol. 6, no. 1, pp. 1-19.

Cicimurri, D. and Ebersole, J. 2014. Late Cretaceous chimaeroids (Chondricthyes: Holocephali) from Alabama, USA. PaleoBios, vol. 31(2): pp. 1-14.

Cope, E. 1867. On *Euclastes*, a genus of extinct Cheloniidae. Proceedings of the Academy of Natural Science, Philadelphia vol. 1867: p. 41.

-------- 1872. Description of *Plesiosaurus gulo* and of the turtle afterwards named *Toxochelys latiremis*. Proceedings of the Academy of Natural Sciences in Philadelphia, vol. 1872: pp. 127-129.

-------- 1873. *Toxochelys latiremis*. Proceedings of the Academy of Natural Sciences in Philadelphia, vol. 1873: p. 10.

-------- 1875. The Vertebrata of the Cretaceous Formations of the West. Rep. U.S. Geol. Surv. Territ. Rep. vol. 2: pp. 1-303.

Crawford, N. et al. 2014. A phylogenomic analysis of turtles. Mol. Phylogenet. Evol., http://dx.doi.org/10.1016/ j.ympev.2014.10.021

Danilov, I. and Parham, J. 2007. The type series of '*Sinemys' wuerhoensis*, a problematic turtle from the Lower Cretaceous of China, includes at least three taxa. Paleontology, vol. 50, part 2: pp. 431-444.

Gaffney, E. 1972. An illustrated glossary of turtle skull nomenclature. American Museum Novitates, vol. 2486, pp. 1-33.

Gaffney, E. and Meylan, P. 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 No. 35A. Clarendon Press, Oxford.

Gray, J. 1831. *Synopsis Reptilium*: or short descriptions of the species of reptiles. Part I: Cataphracta, Tortoises, Crocodiles and Enaliosaurians. London. viii + 85 pp., 11 pls.

Hay, O. 1905. On the group of fossil turtles known as the Amphichelydia, with remarks on the origins and relationships of the suborder, superfamilies and families of Testudines. Bulletin of the American Museum of Natural History, vol. 21, pp. 137-175.

-------- 1908. The fossil turtles of North America. Carnegie Institution of Washington, Publication, vol. 75, pp. 1-568.

Hirayama, W. 1994. Phylogenetic systematic of chelonioid turtles. The Island Arc, vol. 3, pp. 270-284.

-------- 1997. Distribution and diversity of Cretaceous chelonioids. pp. 225-241. In: Callaway, J. and Nicholls, E. (eds.): Ancient marine reptiles. Academic Press, San Diego: 501 pp.

-------- 1998. Oldest known sea turtle. Nature, vol. 392, pp. 705-708.

Hirth, H. 1997. Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaues, 1758). Biological Report to the U.S. Fish and Wildlife Service, vol. 97, no. 1: 88 pp.

Hooks, E. 1995. Redescription of the protostegid turtle *Calcarichelys gemma* Zangerl, 1953 and systematic revision of the protostegidae using cladistic analysis. Thesis submitted to the graduate faculty of Auburn University in partial fulfillment of the requirements for the degree of Master of Science. pp. 76.

Ikejiri, T. 2013. An overview of Late Cretaceous vertebrates from Alabama. Bulletin of the Alabama Museum of Natural History, vol. 31: pp. 46-71.

Joyce, W. 2007. Phylogenetic relationships of Mesozoic turtles. Bulletin of the Peabody Museum of Natural History, vol. 48: pp. 3-102.

Joyce, W. et al. 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. Journal of Paleontology, vol. 87 no. 4: pp. 612-634.

Kear, B. and Lee, M. 2006. A primitive protostegid from Australia and early sea turtle evolution. Biology Letters, vol. 2, pp. 116-119.

Kiernan, C. 2002. Stratigraphic distribution and habitat segregation of mosasaurs in the Upper Cretaceous of western and central Alabama, with an historical review of Alabama mosasaur discoveries. Journal of Vertebrate Paleontology, vol. 22: pp. 91-103.

Knauss, G. 2014. A morphological description of *Baptemys wyomingensis* and an analysis of its phylogenetic relationship within Kinosternoidea. A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Geoscience in the Graduate College of The University of Iowa, 181 pp.

Lapparent de Broin, F. 2013. A strange new chelonioid turtle from the latest Cretaceous phosphates of Morocco. Comptes Rendus Palevol, vol. 13 (2): pp. 87-95.

Linneaus, C. 1758. Systema naturae, 10th ed. Stockholm, vol. 1, 824 pp.

Liu, K. 2009. Oxygen and carbon isotope analysis of the Mooreville Chalk and Late Santonian-Early Campanian sea level and sea surface temperature changes, northeastern Gulf of Mexico, U.S.A. Cretaceous Research, vol. 30 no. 2009: pp. 980-990.

Mancini, E. et al. 1995. Upper Cretaceous sequence stratigraphy of the Mississippi-Alabama area. Gulf Coast Association of Geological Societies Transactions, vol. 45: pp. 377-384.

Matzke, A. 2007. An almost complete juvenile specimen of the cheloniid turtle *Ctenochelys stenoporus* (Hay, 1905) from the Upper Cretaceous Niobrara Formation of Kansas, USA. Palaeontology, vol. 50, Part 3, pp. 669-691

-------- 2009. Osteology of the skull of *Toxochelys* (Testudines, Chelonioidea). Palaeontographica Abt. A, vol. 288, pp. 93-150.

Moody, R. 1974. The taxonomy and morphology of *Puppigerus camperi* an Eocene sea turtle from northern Europe. Bulletin of the British Museum (Natural History) Geology, vol. 25: pp. 155-186.

Nicholls, E. 1988. New material of *Toxochelys latiremis* Cope, and a revision of the genus *Toxochelys* (Testudines: Chelonioidea). Journal of Vertebrate Paleontology, vol. 8 (2): pp. 181-187.

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

Parham, J. and Pyenson, N. 2010. New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. Journal of Paleontology, vol. 84 (2): pp. 231-247.

Parham, J. et al. 2014. A sea turle skull from the Cretaceous of Chile with comments on the taxonomy and biogeography of *Euclastes* (formerly *Osteopygis*). Cretaceous Research, vol. 49: pp. 181-189.

Parham, J. 2005. A reassessment of the referral of sea turtle skulls to the genus *Osteopygis* (Late Cretaceous, New Jersey, USA). Journal of Vertebrate Paleontology, vol. 25 (1): pp. 71-77.

Russell, D. 1970. The vertebrate fauna of the Selma Formation of Alabama. Part VII. The mosasaurs. Fieldiana Geology Memoirs, no. 3, vol. 7: pp. 365-380.

Swofford, D. 2002. PAUP* Phylogenetic Analysis using Parsimony (and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts. pp. 142.

Vandelli, D. 1761. Epistola de holothurio, et testudine coriacea ad celeberrimum Carolum Linnaeum equitem naturae curiosum Dioscoridem II. Conzatti, Padua. 72 pp.

Williston, S. 1898. Turtles. Introduction, and *Desmatochelys*. Univ. Geol. Surv. Kansas, vol. 4: pp. 349-387.

Zangerl, R. 1953a. The vertebrate fauna of the Selma formation of Alabama. Part III: The turtles of the family Protostegidae. Fieldiana: Geol. Mem., vol. 3, no. 3, pp. 61-133.

-------- 1953b. The vertebrate fauna of the Selma Formation of Alabama. Part IV: The turtles of the family Toxochelyidae. Fieldiana: Geol. Mem., vol. 3, no. 4, pp. 134-277.

-------- 1960. The vertebrate fauna of the Selma Formation of Alabama. Part V: an advanced cheloniid sea turtle. Fieldiana: Geol. Mem., vol. 3, no. 5, pp. 279-312, pls. 30-33.

Zangerl, R. and Sloan, R. 1960. A new specimen of *Desmatochelys lowi* Williston. A primitive cheloniid sea turtle from the Cretaceous of South Dakota. Fieldiana: Geol., vol. 14, no. 2, pp. 7-40.

Zug, G. 1971. Bouyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles. Misc. Publ., Mus. Zool., Univ. Michigan, no. 142, pp. 1-98.