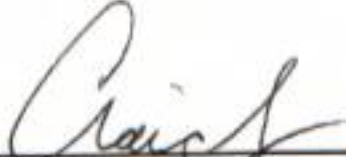
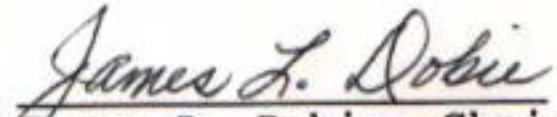


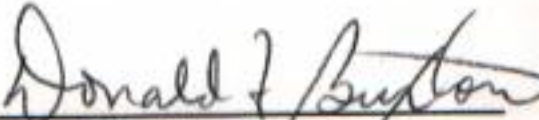
REDESCRIPTION OF THE PROTOSTEGID TURTLE  
*Calcarichelys gemma* ZANGERL, 1953  
AND SYSTEMATIC REVISION OF  
THE PROTOSTEGIDIAE  
USING CLADISTIC  
ANALYSIS


George Edward Hooks, III

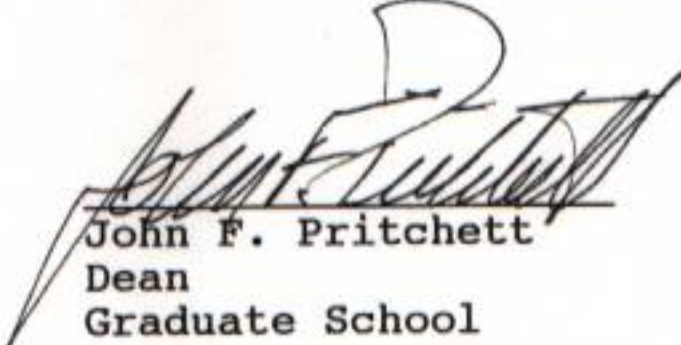
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Style manual or journal used Journal of Vertebrate  
Paleontology

Computer software used Word Perfect 5.2 for Windows

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THE PROTOSTEGIDAE

USING CLADISTIC

ANALYSIS

George Edward Hooks, III

A Thesis

Submitted to

the Graduate Faculty of

Auburn University

In Partial Fulfillment of the

Requirements for the

Degree of

Master of Science

Auburn, Alabama

March 17, 1995

REDESCRIPTION OF THE PROTOSTEGID TURTLE

CALCARICHELYS GEMMA ZANGERL, 1953

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George Edward Hooks, III  
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6-13-95  
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REDESCRIPTION OF THE PROTOSTEGID TURTLE

CALCARICHELYS GEMMA ZANGERL, 1953

George Edward Hooks III, son of George Edward Hooks Jr. and Margaret (Rayden) Hooks, was born in San Antonio, Texas on March 28, 1967. He graduated from high school at Morgan Academy in Selma, Alabama, in 1985. After receiving a Bachelor of Science Degree in Zoology from Auburn University in 1991, he entered George Edward Hooks, III as year.

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THESIS VITA TRACT

REDESCRIPTION OF THE PROTOSTEGID TURTLE

George Edward Hooks III, son of George Edward Hooks Jr.

*Calcarichelys gemma* SANGERL, 1953

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AND SYSTEMATIC REVISION OF

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THE PROTOSTEGIDAE

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George Edward Hooks, III

Master of Science, March 17, 1995

(B.S., Auburn University, 1991)

76 Typed Pages

Directed by James L. Doble

This thesis consists of two articles, each comprising a separate chapter. The first chapter is a redescription of the protostegid turtle *Calcarichelys gemma*. The redescription, based on a nearly complete specimen from the Mooreville Chalk of Alabama, reveals several previously unknown features of the species.

In the second chapter, cladistic analysis produces a phylogenetic system of classification for taxa within the family Protostegidae. Thirty-seven characters from the skull, carapace, plastron, and appendicular skeleton are analyzed for all species considered to be members of the

Protostegidae and for the outgroup taxa *Toxochelys*  
*latirostris*, *Caretta caretta*, and *Dermatochelys levi*. Since  
no characters separate *Anchylon nupel*, *Protostega dixie*, or  
*P. giffoni* from *P. giffoni* THESIS ABSTRACT  
designated REDESCRIPTION OF THE PROTOSTEGID TURTLE The  
consensus classification of CALCARICHELYS GEMMA ZANGERL, 1953 belongs in  
the *Dermatochelys* AND SYSTEMATIC REVISION OF Protostegidae, that  
*Claochelys lonstedii* THE PROTOSTEGIDAE protostegid, and  
that *Protostega eugenia* USING CLADISTIC be assigned to a new  
genus. The name *Zangerella* ANALYSIS *fordensis* is proposed as  
the replacement for *Protostega eugeniafordensis*.

George Edward Hooks, III

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Protostegidae and for the outgroup taxa Toxochelys latiremis, Caretta caretta, and Desmatochelys lowi. Since no characters separate Archelon copei, Protostega dixie, or P. potens from P. gigas, the former three taxa are designated as junior synonyms of Protostega gigas. The consensus cladogram indicates that Rhinochelys belongs in the Desmatochelyidae rather than in the Protostegidae, that Cimochelys benstedii is a chelosphargine protostegid, and that Protostega eaglefordensis should be assigned to a new genus. The name Zangerlonia eaglefordensis is proposed as the replacement for Protostega eaglefordensis.

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Chapter 1

Although considerable work was done on the protostegids during the century, little has been done

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## THESIS INTRODUCTION

The Protostegidae were Late Cretaceous marine turtles. Although considerable work was done on the protostegids during the first half of this century, little has been done since then to increase our knowledge of the family.

During the last four decades more protostegid specimens have been discovered and previously existing ones more adequately prepared for study. Also, the recent development of cladistic analysis has provided a tool which allows for better resolution of the phylogenetic relationships of the protostegids.

The first chapter of this study deals with the redescription of the protostegid Calcarichelys gemma. This redescription is based on a recently discovered specimen which is nearly complete. In the second chapter recent information on the protostegids is combined with previously existing data. Cladistic analysis is then performed on the data to produce a phylogenetic system of classification for the members of the Protostegidae.

ABSTRACT

Recently, a nearly complete skeleton of the  
chelonian protostegid **CHAPTER 1** *Calcarichelys gemma*  
Zangerl, **A REDESCRIPTION OF THE PROTOSTEGID TURTLE** Alabama.  
It is the most **CALCARICHELYS GEMMA** Zangerl, 1953 found, and  
includes portions of the carapace, plastron, appendicular  
skeleton, and the first known skull material for the  
species. **George Edward Hooks, III**  
Department of Zoology and Wildlife Science,  
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## ABSTRACT

Recently, a nearly complete skeleton of the chelosphargine protostegid turtle Calcarichelys gemma Zangerl, 1953 was found in the Mooreville Chalk of Alabama. It is the most complete specimen of C. gemma yet found, and includes portions of the carapace, plastron, appendicular skeleton, and the first known skull material for the species. P. gigas Cope (1872), and P. colius Hay (1908) were included in the protosteginae while Chelosphargis advena (Hay, 1908), and Calcarichelys gemma Zangerl (1953) comprised the chelospharginae.

Zangerl's (1953) description of Calcarichelys gemma is based primarily on Field Museum of Natural History (FMNH) specimen PR129, an incomplete specimen from the Mooreville Chalk of Montgomery Co., Alabama. The specimen consists of neurals two through four; peripherals four, five, and seven through eleven on the left side; three through seven and ten and eleven on the right side; the pygal; a portion of the suprapygal; costal fragments; right hypoplastron; a portion of the right xiphiplastron; and a coracoid. Zangerl also makes reference to FMNH PR152, consisting of the left third and fourth peripherals and fragments of the costals, and FMNH PR122, consisting of an isolated left fifth peripheral.

Recently, a nearly complete specimen of C. gemma (Red Mountain Museum specimen 3216) was found in the Mooreville Chalk of Greene Co., Alabama. Due to its well-preserved

INTRODUCTION

The most comprehensive study of the Protostegidae is by Zangerl (1953). He divided the family into two subfamilies, the Chelospharginae (the more primitive group) and the Protosteginae (the more derived group). Archelon copei (Wieland, 1909), A. ischyros Wieland (1896), Protostega dixie Zangerl (1953), P. eaglefordensis Zangerl (1953), P. gigas Cope (1872), and P. potens Hay (1908) were included in the protosteginae while Chelosphargis advena (Hay, 1908), and Calcarichelys gemma Zangerl (1953) comprised the chelospharginae.

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state, this specimen reveals characters previously unknown in Calcarichelys gemma.

Abbreviations -- FMNH = Field Museum of Natural History; RMM = Red Mountain Museum Collection; housed at Discovery 2000, Birmingham, Alabama.

Hypoplastron and hypoplastron roughly square in

outline with later **SYSTEMATIC PALEONTOLOGY**

approaching or making contact along midline and forming a

diamond-shaped **Order TESTUDINES Linnaeus, 1758**

Superfamily **CHELONIOIDEA Bauer, 1893**

Family **PROTOSTEGIDAE Cope, 1872**

Calcarichelys Zangerl, 1953

**Type Species -- Calcarichelys gemma Zangerl, 1953.**

**Revised Diagnosis --** Small chelosphargine (maximum known carapace length 25.3 cm). Triturating surface of premaxilla and maxilla with pronounced labial and lingual ridges. Lingual ridges extending further ventrally than labial ridges and divided by a sagittal groove. Floor of cavum cranii smooth, slightly concave. Nuchal with posterior processes extending along lateral sides of first neural. Seven neurals. Mid-dorsal keel composed of alternating, laterally compressed conical and saddle-shaped elements. Eight pairs of costals, extending distad for more than half the length of ribs. Last pair of costals meet

along midline. Distal end of ribs insert into pits on peripherals. Peripheral edge of carapace, from peripherals five to eleven, strongly serrate. One suprapygal present. Pygal plate narrow. Contact between last pair of peripherals on anteroventral surface of pygal. Epiplastra absent. Hyoplastron and hypoplastron roughly square in outline with lateral edges only slightly serrate, approaching or making contact along midline and forming a diamond-shaped central fontanelle. Scapular angle approximately  $110^\circ$ . Humerus with distally displaced radial process.

Calcarichelys gemma Zangerl, 1953

Holotype -- FMNH PR129, from the Mooreville Chalk, Montgomery County, Alabama.

Hypodigm -- FMNH PR129 (holotype), PR122, PR152; RMM 3164, 3216.

Distribution -- Central and Southeastern United States.

Stratigraphic Range -- Lower Coniacian - lower Campanian.

Diagnosis -- Same as for genus.

Description of New Material (RMM 3216)

Skull -- The skull (Fig. 1) is relatively elongate (maximum length, from anterior of premaxilla to posterior of

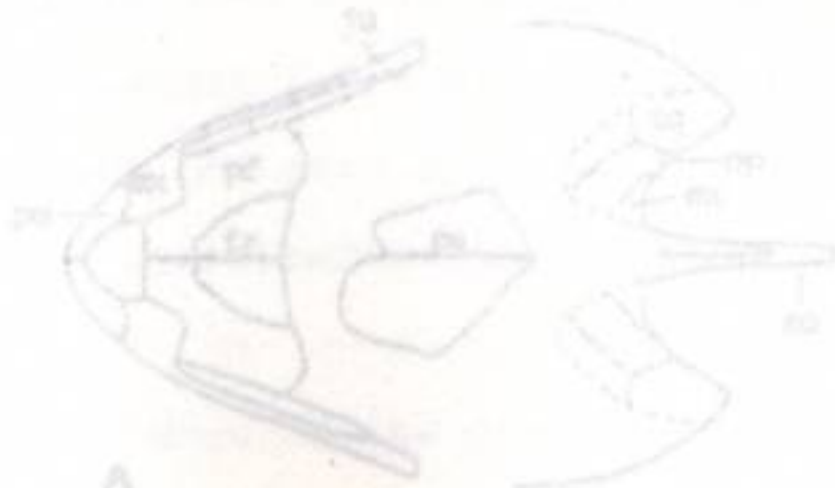
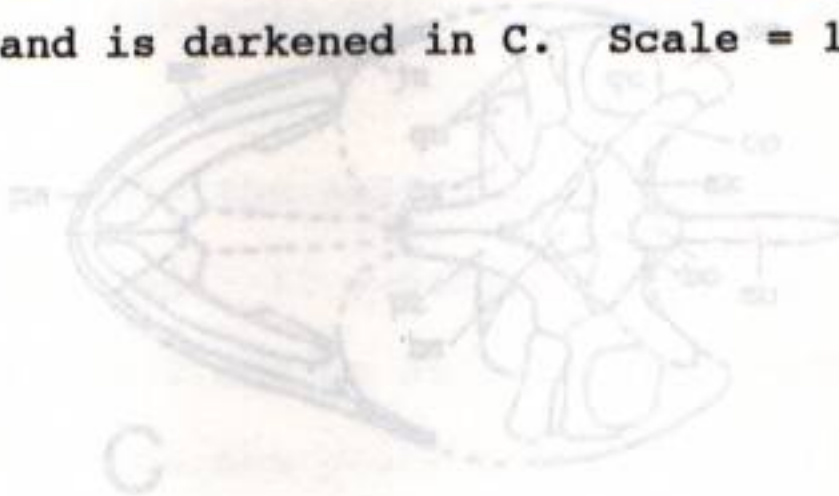
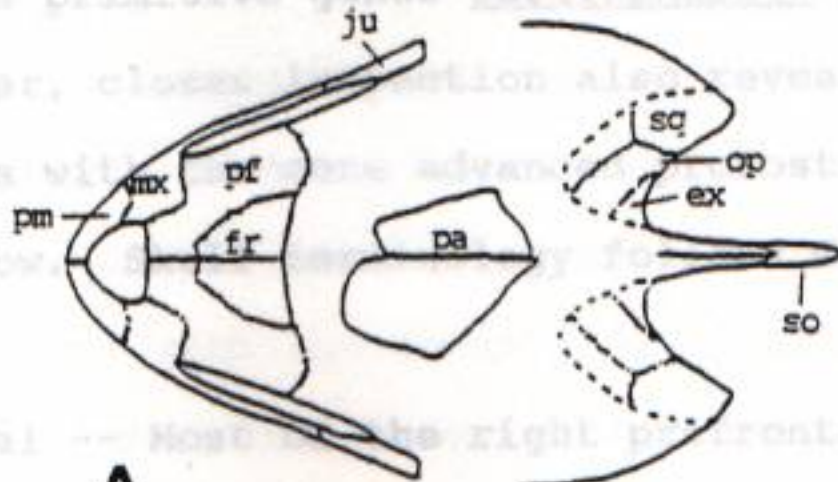


FIGURE 1. Calcarichelys gemma. Reconstruction of skull of RMM 3216. A, dorsal view; B, lateral view; C, ventral view. Abbreviations: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pf, prefrontal; pm, premaxilla; pr, prootic; pt, pterygoid; qu, quadrate; so, supraoccipital; sq, squamosal. The foramen posterius canalis caroticus internus is located at the anterior of the basisphenoid and is darkened in C. Scale = 1 cm.

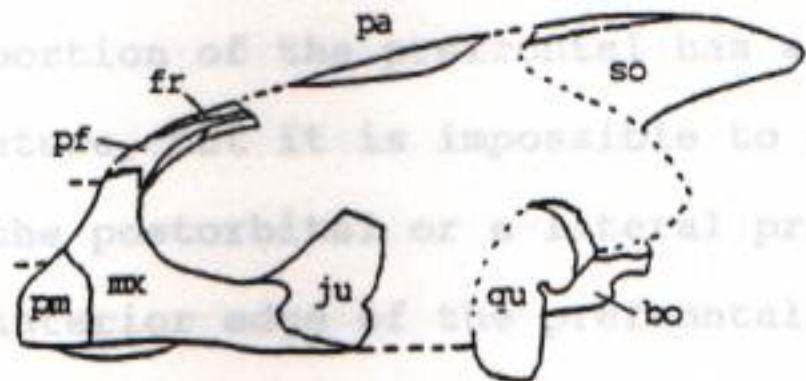




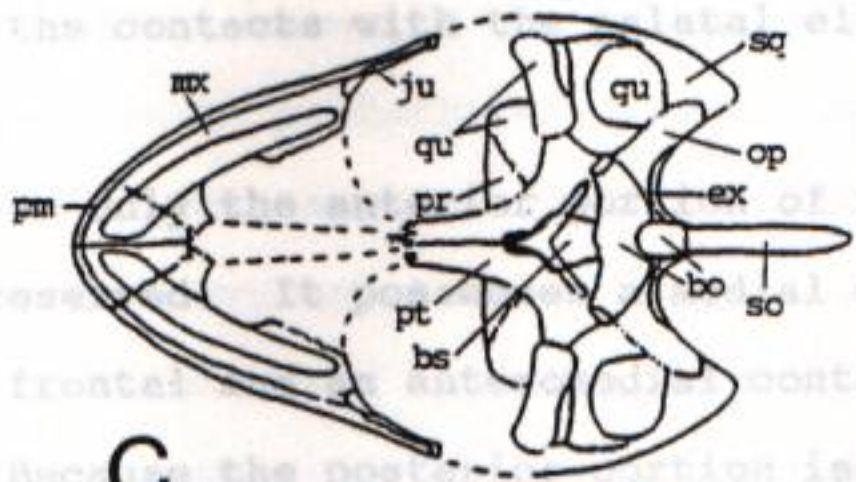
supraorbital 8.9 cm; maxilla width, across reconstructed squamosals, 4.9 cm) with large orbits and a blunt preorbital area as in the primitive genus *Chelopharyx* (Zangerl, 1953). However, close attention also reveals synapomorphies with more advanced stegids, as described below (see also Zangerl & Jeffrey (1972, 1979).



Prefrontal -- Most of the right prefrontal is intact. It contacts the maxilla anterolaterally, the opposing prefrontal anteromedially, and the frontal posteromedially. The posterior portion of the bone is distinct...



semicircular sulcus. It is impossible to determine if this met with the posterior or a lateral process of the frontal. The anterior end of the bone forms the dorsal border of the apertura narum externa. There are no nasals. The descending process of the prefrontal is present, but the contacts with lateral elements are not preserved.



Frontal -- The anterior portion of the right frontal is preserved. It is in contact with the opposing prefrontal anterolaterally and with the prefrontal. Because the posterior portion is missing, it is impossible to determine contacts with other bones or if a lateral process of the bone reaches the orbit. The sulcus olfactorius is preserved on the ventral surface of the bone.

supraoccipital 8.4 cm; maximum width, across reconstructed squamosals, 4.9 cm) with large orbits and a blunt preorbital area as in the primitive genus Chelosphargis (Zangerl, 1953). However, closer inspection also reveals sagittal synapomorphies with the more advanced protostegids, as described below. Skull terminology follows Gaffney (1972, 1979).

**Prefrontal** -- Most of the right prefrontal is intact. It contacts the maxilla anterolaterally, the opposing prefrontal anteromedially, and the frontal posteromedially. The posterior portion of the prefrontal has a distinct semicircular suture, but it is impossible to determine if this met with the postorbital or a lateral process of the frontal. The anterior edge of the prefrontal forms the dorsal border of the apertura narium externa. There are no nasals. The descending process of the prefrontal is present, but the contacts with the palatal elements are not preserved.

**Frontal** -- Only the anterior portion of the right frontal is preserved. It possesses a medial contact with the opposing frontal and an anteromedial contact with the prefrontal. Because the posterior portion is missing, it is impossible to determine contacts with other bones or if a lateral process of the bone reaches the orbit. The sulcus olfactorius is preserved on the ventral surface of the bone. The ventral surface (Fig. 1C) contains two deep

**Parietal** -- Portions of the left and right parietals are present. Dorsal portions of the processus inferior parietalis are preserved on both bones and outline the dorsal area of the cavum cranii. Other than the sagittal suture, no contacts of these bones are preserved.

**Jugal** -- Anterior portions of both jugals are present, exhibiting contact with the maxilla anteriorly and anteroventrally. A medial process, for contact with the palatine, is lacking.

**Quadratojugal** -- Although no portions of this bone remain, reconstruction of the skull indicates that it was smaller and formed less of the cheek margin than the jugal. Such quadratojugal reduction is typical of the protostegids.

**Squamosal** -- Sutures on the posterodorsal portion of the quadrate and on the dorsal portion of the processus paroccipitalis of the opisthotic are the only evidence of the occurrence of this bone.

**Postorbital** -- No postorbitals are present.

**Premaxilla** -- This specimen contains both premaxillae. Each bone shows the typical lateral contact with the maxilla and medial contact with the opposing premaxilla. The contacts with the vomer and the maxilla of the other side are unusual (see Maxilla below). On the right premaxilla three pits of unknown function are visible in the floor of the fossa nasalis. They do not extend to the ventral surface. The ventral surface (Fig. 1C) contains two deep

troughs extending onto the maxilla; one is between the lingual and labial ridges, while the second runs sagittally between the lingual ridges. These presumably accommodated opposing labial and sagittal ridges on the dentary as in Chelosphargis (Zangerl, 1953) and the desmatochelyid Rhinochelys (Collins, 1970).

**Maxilla** -- The entire left maxilla is preserved along with portions of the right. It contacts the premaxilla anteromedially; the prefrontal anterodorsally; the vomer, palatine, and opposing maxilla medially; and the jugal posterodorsally. Viewed ventrally, the area of contact with the vomer shows an unusual arrangement (Fig. 1C) in which the maxilla contacts the vomer, both premaxillae, and the other maxilla at the same point. Sutures present on the medial surface of both maxillae indicate that the vomer attached to these bones. In posterior view, these sutures slope ventromedially, crowding out the contact between the premaxilla and vomer. Even at its most dorsal point, the premaxilla-vomer contact is highly reduced, resulting in the vomer having a greater area of contact with the maxilla than with the premaxilla. As in Protostega gigas, the maxilla sends a posterior process below the ventral border of the jugal to a point approximately even with the posterior rim of the orbit. The same ridge and trough patterns seen on the ventral surface of the premaxilla extend onto the maxilla (see Premaxilla).

~~poss~~ Vomer -- The only evidence for the existence of this bone is the sutures on the premaxilla and maxilla, which indicate an unusual type of attachment (see Maxilla).

~~The~~ Palatine -- The palatines are not preserved.

~~Indic~~ Quadrate -- Both quadrates are present. As in all turtles, the quadrate contacts the prootic dorsomedially, the opisthotic posteriorly, the squamosal posterodorsally, and the pterygoid ventromedially. Assuming the presence of a quadratojugal (exhibited in all other members of Cheloniodea), the quadrate made contact with this bone along the anterior edge of the cavum tympani. The medial wall of the cavum tympani and the lateral wall of the cavum acoustico-jugulare are well preserved, with the latter exhibiting grooves forming the lateral walls of the canalis stapedio-temporalis and the canalis cavernosus. The foramen stapedio-temporale is located at the contact between the quadrate and the prootic, near where they meet the opisthotic. However, in this specimen the opisthotic does not contribute to the formation of the foramen. The incisura columellae auris is open posteroventrally.

~~this~~ Epipterygoid -- The portions of the skull needed to determine the presence of this bone are missing.

Pterygoids -- With the exception of missing portions of the crista pterygoidea, both pterygoids are intact. Viewed ventrally, they have the elongate, narrow shape, typical of the Protostegidae. The pterygoid contacts the palatine (and

possibly the vomer) anteriorly, the opposing pterygoid anteromedially, the basisphenoid posteromedially, the quadrate posterolaterally, and the prootic posterodorsally. The presence of a descending process on the parietal indicates a dorsal contact with that bone. However, due to the absence of the crista pterygoidea, the precise nature of this contact is uncertain. A posterior contact with the basioccipital is present, and its structure is unique to the protostegids (see Basioccipital). The canalis caroticus internus (c.c.i.) and associated canals are also of unique design and merit further discussion.

The foramen posterior canalis caroticus internus (f.p.c.c.i.) is located at the anteriormost contact between the pterygoid and basisphenoid (Fig. 1C). It is only separated from the other f.p.c.c.i. by a thin portion of the basisphenoid. Dorsal to the f.p.c.c.i., the c.c.i. merges with the c.c.i. from the other side to form a single common c.c.i. Thus, both internal carotids enter the cavum cranii through a single foramen, the foramen anterior canalis caroticus internus (f.a.c.c.i.) (Fig. 2). To my knowledge, this arrangement is unique to the protostegids (see Chapter 2).

Three other foramina are visible on the pterygoid. Two are located on the floor of the canalis cavernosus and another on the lateral surface of the bone (lateral foramen). Of the two foramina located in the canalis

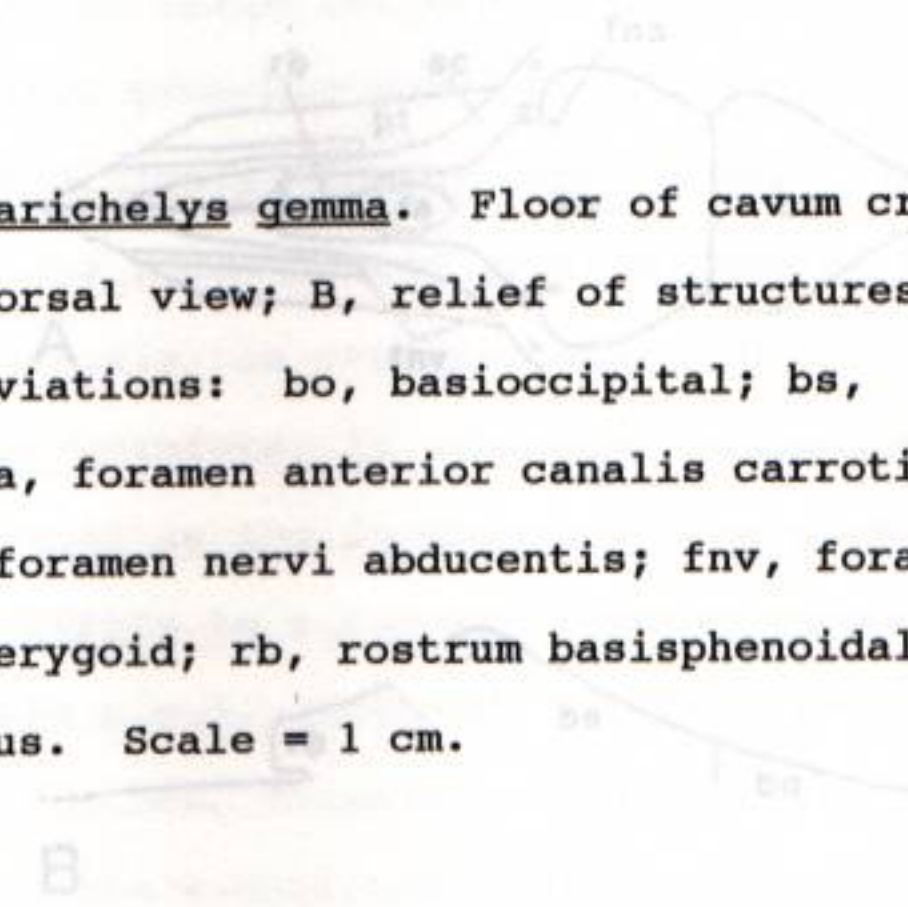
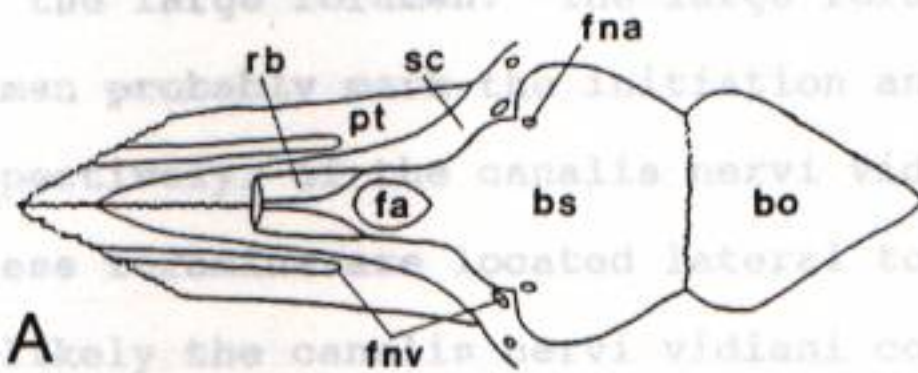


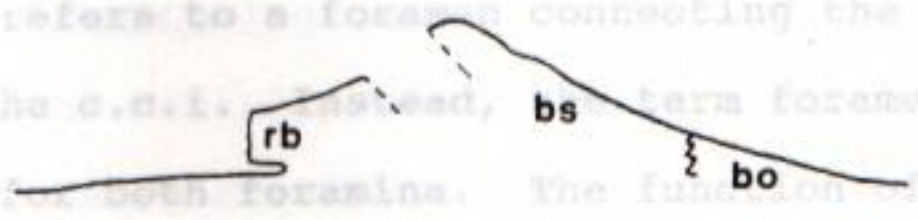
FIGURE 2. Calcarichelys gemma. Floor of cavum cranii of RMM 3216. A, dorsal view; B, relief of structures along midline. Abbreviations: bo, basioccipital; bs, basisphenoid; fa, foramen anterior canalis caroticus internus; fna, foramen nervi abducentis; fnv, foramen nervi vidiani; pt, pterygoid; rb, rostrum basisphenoidale; sc, sulcus cavernosus. Scale = 1 cm.

cavernosae, one is minuta (small foramen), and the canal leading from it slopes posteriorly. The other, larger foramen (large foramen) is situated anteromedially to the small foramen, with an anteriorly sloping canal. The lateral foramen is located lateral and slightly anterior to the f.a.c.i. It opens into a groove continuing anteriorly for the length of the pterygoid and is approximately the same diameter as the large foramen. The large foramen and



the lateral foramen probably has a similar origin and termination, respectively, to the canalis nervi vidiani. Since both of these foramina are located lateral to the c.c.i., it is unlikely that the canalis nervi vidiani connects

with the c.c.i. Therefore, it would be inaccurate to refer to the large foramen as the foramen pro cano nervi vidiani, since this term refers to a foramen connecting the cavernosa



cavernosae and the c.c.i. Instead, the term foramen nervi vidiani is used for both foramina. The function of the small foramen and the location of the canalis caroticus lateralis are unknown.

Supraoccipital -- Only the crista supraoccipitalis of the supraoccipital is preserved. Judging by the sutures on other bones, the supraoccipital contacts the parietals dorsally, the prootic anteroventrally, the opisthotic ventrally, and the exoccipital posteroventrally.

Exoccipital -- The right exoccipital is preserved. It contacts the supraoccipital dorsally, the opisthotic



cavernosus, one is minute (small foramen), and the canal leading from it slopes posteriorly. The other, larger foramen (large foramen) is situated anteromedially to the small foramen, with an anteriorly sloping canal. The lateral foramen is located lateral and slightly anterior to the f.a.c.c.i. It opens into a groove continuing anteriorly for the length of the pterygoid and is approximately the same diameter as the large foramen. The large foramen and the lateral foramen probably mark the initiation and termination, respectively, of the canalis nervi vidiani. Since both of these foramina are located lateral to the c.c.i., it is unlikely the canalis nervi vidiani connects with the c.c.i. Therefore, it would be inaccurate to refer to the large foramen as the foramen pro ramo nervi vidiani, since this term refers to a foramen connecting the canalis cavernosus and the c.c.i. Instead, the term foramen nervi vidiani is used for both foramina. The function of the small foramen and the location of the canalis caroticus lateralis are unknown.

**Supraoccipital** -- Only the crista supraoccipitalis of the supraoccipital is preserved. Judging by the sutures on other bones, the supraoccipital contacts the parietals dorsally, the prootic anteroventrally, the opisthotic ventrally, and the exoccipital posteroventrally.

**Exoccipital** -- The right exoccipital is preserved. It contacts the supraoccipital dorsally, the opisthotic

anterolaterally, the basioccipital ventromedially, and with contributes to the formation of the condylus occipitalis. An anterior process of the exoccipital also extends ventral to the opisthotic (see Opisthotic). The exoccipital does not contact the pterygoid.

**Basioccipital** -- The basioccipital is fully intact. It contacts the basisphenoid anteromedially, the pterygoids anterolaterally, the opisthotic and exoccipitals dorsolaterally, and contributes to the formation of the condylus occipitalis. The lateral portions of the basioccipital-pterygoid contact consist of an unusual arrangement in which smooth, hemispherical portions of the basisphenoid fit into opposing sockets on the pterygoids. This is similar to the condition found in Protostega gigas, except that in Calcarichelys gemma the sutures are maintained along the medial portion of the contact, whereas in P. gigas the sutures are lost (see Chapter 2). The dorsal surface of the basioccipital is smooth, slightly concave in lateral view, and lacks both a crista dorsalis basioccipitalis and a basis tuberculi basalis (Fig. 2).

**Prootic** -- Both prootics are present. The prootic contacts the parietals anterodorsally, the supraoccipital posterodorsally, the opisthotic posteriorly, the quadrate laterally, the pterygoid ventrally, and the basisphenoid ventromedially. Contributions to the processus trochlearis oticum and the foramen stapedio-temporale are made by both

the prootic and quadrate bones. Visible at the contact with the supraoccipital is the canalis semicircularis anterior.

**Opisthotic** -- Both opisthotics are preserved. The opisthotic contacts the prootic anteriorly, the quadrate anterolaterally, the supraoccipital dorsomedially, the exoccipital posteromedially, and the squamosal posterodorsally. The processus interfenestralis is present, but due to poor preservation of this area it is not possible to determine if it contacts the basioccipital. It is possible that the anterior extension of the exoccipital prevents opisthotic-basioccipital contact. The posterior portion of the processus paroccipitalis is flattened dorsoventrally and extends posterior to the quadrate. The canalis semicircularis posterior is located at the contact with the supraoccipital.

**Basisphenoid** -- Except for portions of the ventral surface, the basisphenoid is intact. It contacts the pterygoid anterolaterally, the prootic dorsolaterally, and the basioccipital posteriorly. The dorsal surface lacks a sella turcica, this structure having been replaced by the raised area surrounding the unified f.a.c.c.i. (Fig. 2, see also Pterygoid). The fused rostrum basisphenoidale is short and stout. Posterior to the dorsum sellae, the basisphenoid, in conjunction with the basioccipital, forms a smooth, slightly concave floor for the cavum cranii. The location of the canalis nervi abducentis is posterolateral

relative to that in modern cheloniids and is unknown in other protostegids. The ventral surface of the basisphenoid has a ridge running along each anterolateral edge. These ridges merge along the midline and continue anteriorly a short distance onto the thin bar of bone separating the two f.p.c.c.i. The ridges also continue posteriorly onto the pterygoid.

Carapace -- The carapace (Fig. 3) is almost complete. Missing are the 3rd neural, left 7th costal, the left 8th and 10th peripherals, and right 4th peripheral. The lateral portions of the nuchal are also missing, and the 1st and 2nd peripherals are fragmented to such a degree that it is not possible to reconstruct this portion of the shell. The morphology of the carapace agrees closely with the description by Zangerl (1953: fig. 56, 58), although there are some noteworthy differences (Fig. 3).

The preserved portion of the nuchal shows that it possessed a slightly raised area on its dorsal surface which contributed to the uneven keel continued posteriorly on the neurals. Posterior processes of the nuchal extend along the lateral margins of the 1st neural. In RMM 3216 the left process terminates just before reaching the 2nd neural, whereas the right process actually reaches the 2nd neural. A ventral process for articulation with the 8th cervical vertebra is present.

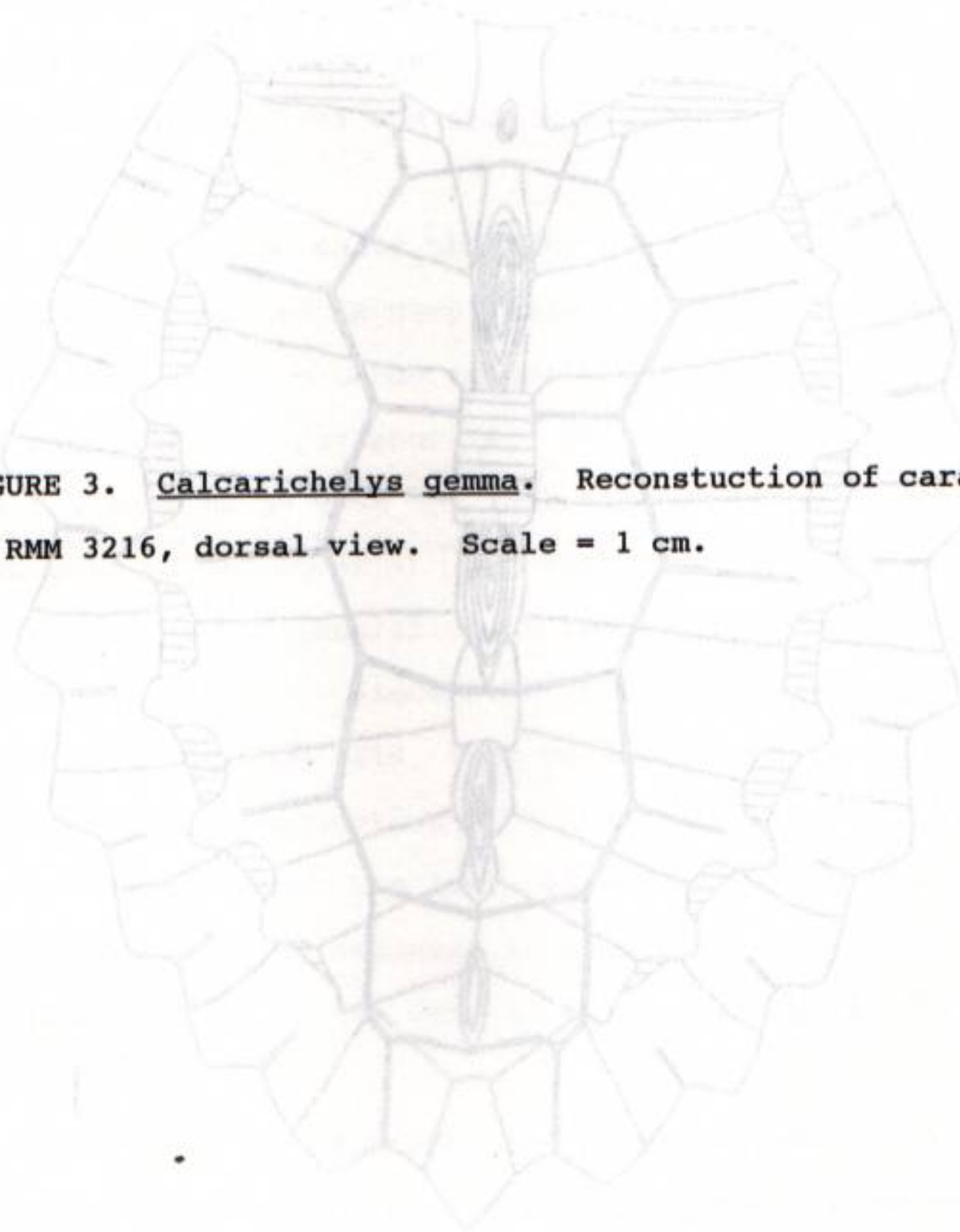
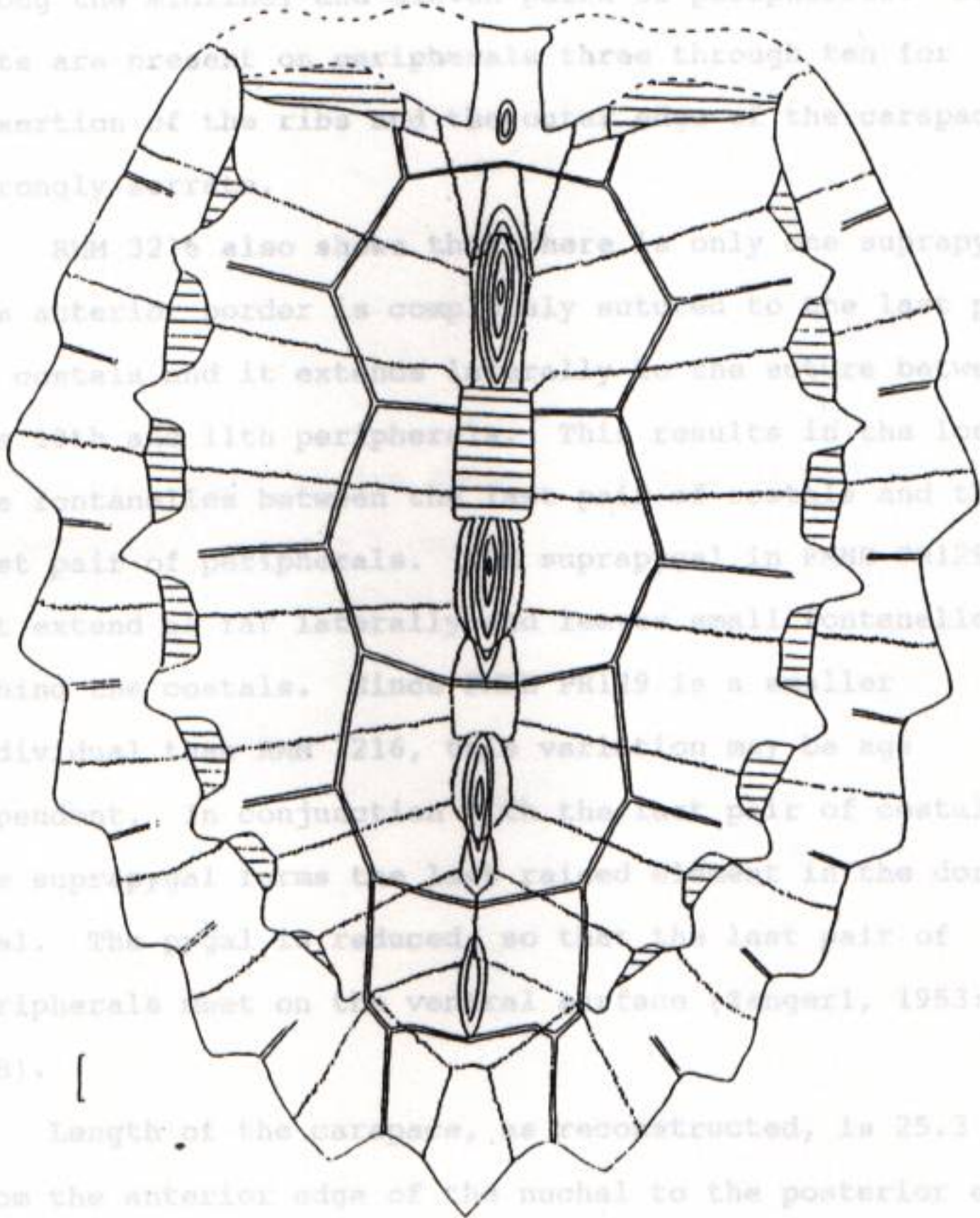


FIGURE 3. Calcarichelys gemma. Reconstuction of carapace of RMM 3216, dorsal view. Scale = 1 cm.

The material present shows that *Calcarichelys* possesses seven neurals, forming an uneven dorsal keel of alternating saddle-shaped and laterally compressed conical elements. There are eight pairs of costals, the last pair meeting

along the midline, and eleven pairs of peripherals. Deep pits are present on peripherals three through ten for insertion of the ribs. The interspace is strongly ...  
 ... also ... there ... only ... suprapygal.  
 Its anterior border is closely ... to the last pair of costals and it extends ... between the ... with peripherals. This results in the loss of the ... between ... and the last pair of peripherals. ... suprapygal in ... does not extend ... laterally ... small ... behind ... costals. ... is a ... individual ... 216, ... variation ... dependent ... conjunction ... the ... of costals, the suprapygal ... the dorsal keel. The ... so that the last pair of peripherals rest on the vertebral ... (Singer, 1953: fig. 56B).

Length of the carapace, as reconstructed, is 25.3 cm from the anterior edge of the nuchal to the posterior edge of the pygal. Maximum width, measured across the 6th peripherals, is 20.6 cm.



The material present shows that Calcarichelys possesses seven neurals, forming an uneven dorsal keel of alternating saddle-shaped and laterally compressed conical elements. There are eight pairs of costals, the last pair meeting along the midline, and eleven pairs of peripherals. Deep pits are present on peripherals three through ten for insertion of the ribs and the outer edge of the carapace is strongly serrate.

RMM 3216 also shows that there is only one suprapygal. Its anterior border is completely sutured to the last pair of costals and it extends laterally to the suture between the 10th and 11th peripherals. This results in the loss of the fontanelles between the last pair of costals and the last pair of peripherals. The suprapygal in FMNH PR129 does not extend as far laterally and leaves small fontanelles behind the costals. Since FMNH PR129 is a smaller individual than RMM 3216, this variation may be age dependent. In conjunction with the last pair of costals, the suprapygal forms the last raised element in the dorsal keel. The pygal is reduced, so that the last pair of peripherals meet on the ventral surface (Zangerl, 1953: fig. 56B).

Length of the carapace, as reconstructed, is 25.3 cm from the anterior edge of the nuchal to the posterior edge of the pygal. Maximum width, measured across the 6th peripherals, is 20.6 cm.

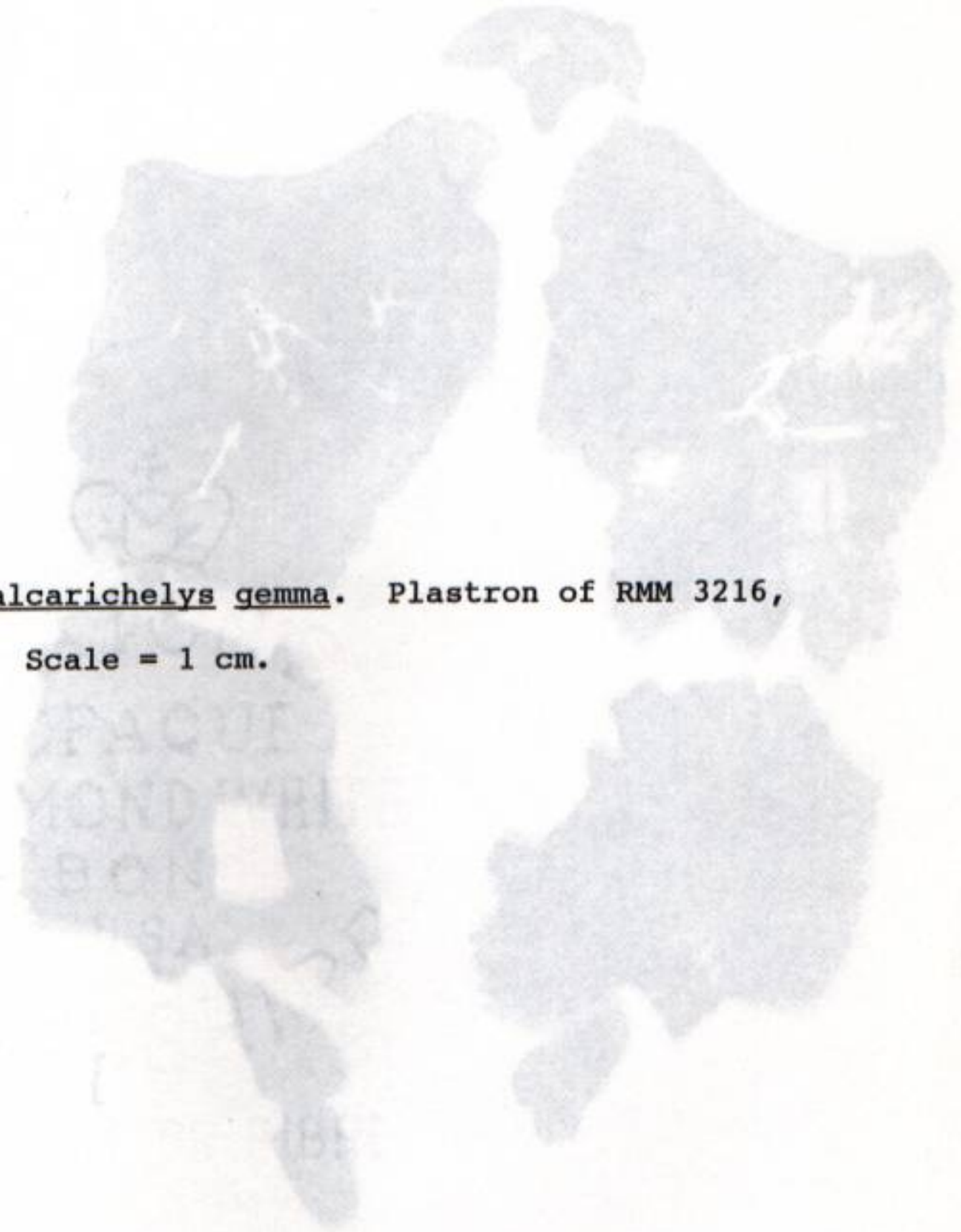


FIGURE 4. Calcarichelys gemma. Plastron of RMM 3216, dorsal view. Scale = 1 cm.



Plastron -- All of the plastral bones are well -

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Plastron -- All of the plastral bones are well preserved, except for the xiphiplastra which are missing significant portions (Fig. 4). The T-shaped entoplastron, diagnostic of the protostegids, is present, but the ends of the lateral and posterior processes are not. Since no epiplastra are present, they have either been dissociated from the skeleton or are absent in Calcarichelys: considering the fine state of preservation of the rest of the plastron, the latter conclusion is favored.

The hyoplastron and hypoplastron are roughly square in outline with the notable exception of excavations on the posteromedial side of the hyoplastron and the anteromedial side of the hypoplastron. These excavations form a diamond shaped fontanelle in the center of the plastron. The medial most portions of all four bones are missing, but it is clear that if they do not actually contact along the midline, they come to within a few millimeters of doing so. The lateral edges of these bones are relatively straight and only slightly serrate. The left hyoplastron and hypoplastron clearly show the wide suture joining these bones. Sufficient portions of the xiphiplastra are present to indicate they have a slightly sigmoidal shape.

Pectoral girdle and forelimbs -- The left scapula, both coracoids, the left ulna, and a possible ulnare are present, as are the proximal portion of the left humerus and the distal portion of a radius (Figs. 5 and 6).




FIGURE 5. Calcarichelys gemma. Appendicular skeleton of RMM 3216. Anterior, dorsal, and lateral views. A: left scapula, anterior view. B: coracoids, dorsal view. C: humerus, dorsal view. D: ulna, dorsal view. E: radius, distal portion. F: ulnare? G: pubic bones, dorsal view. H: ilia, lateral view. I: tibia, proximal portion. Scale = 1 cm.



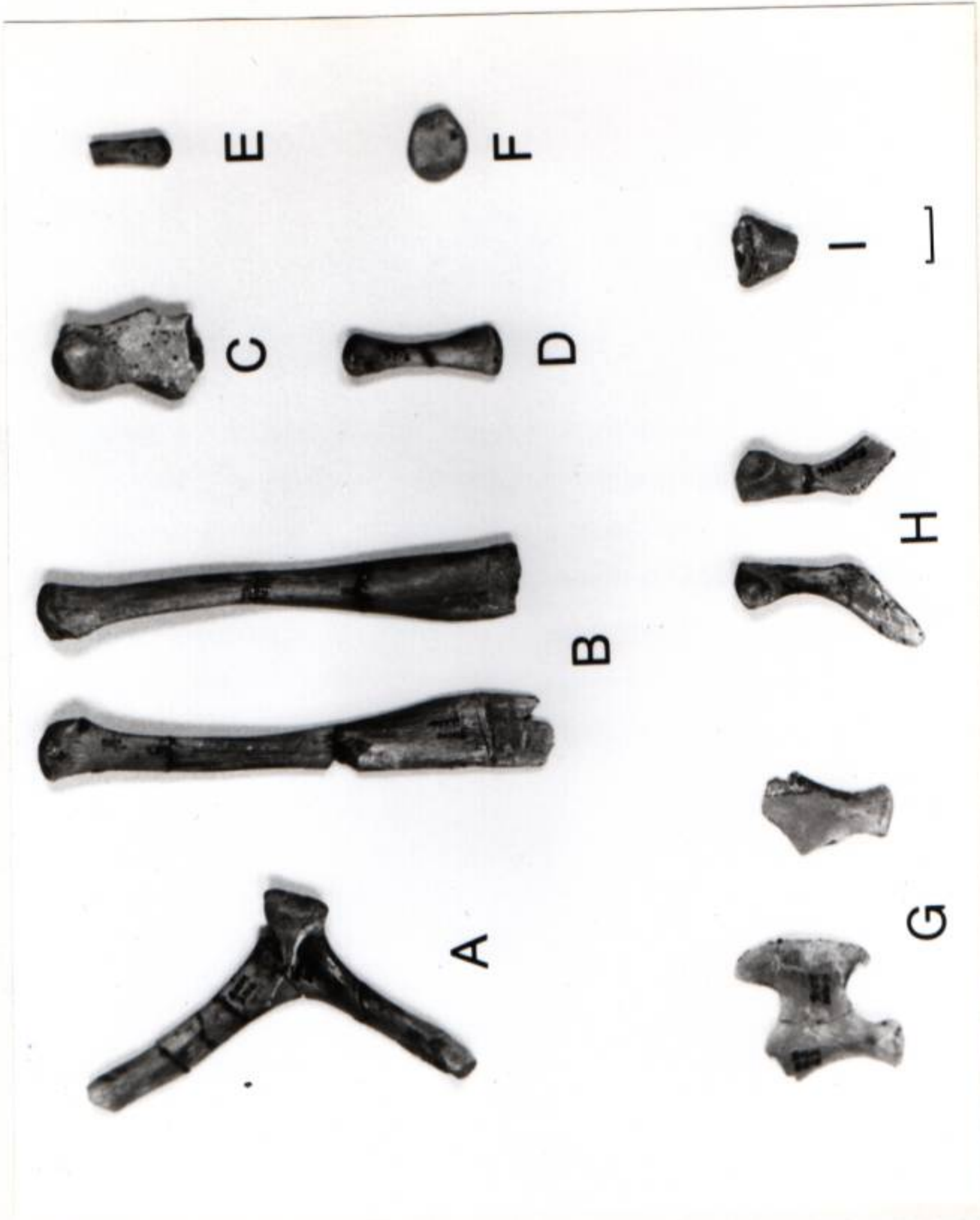
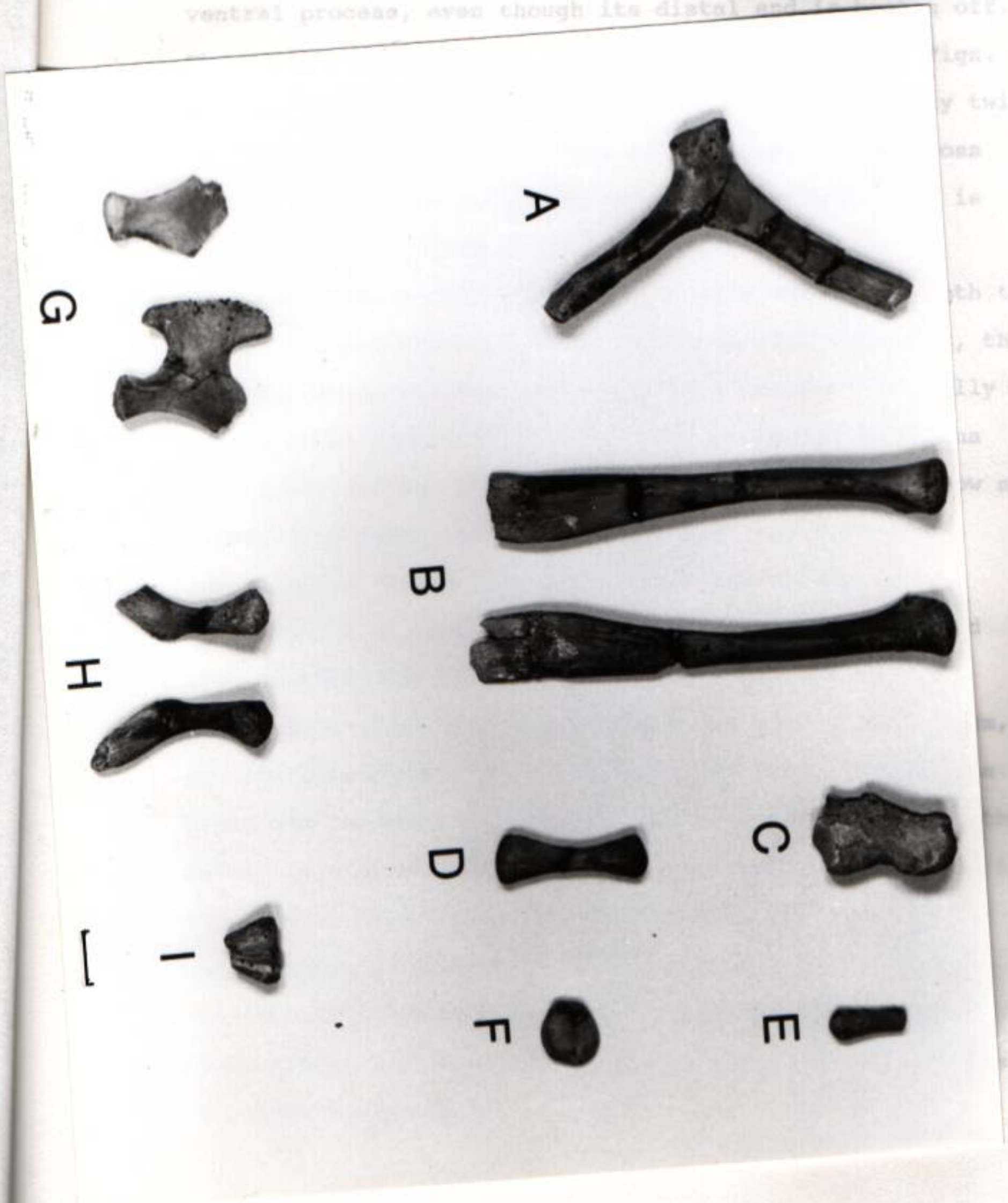


FIGURE 6. Calcarichelys gemma. Appendicular skeleton of RMM 3216. Posterior, ventral and medial views. A: left scapula, posterior view. B: coracoids, ventral view. C: humerus, ventral view. D: ulna, ventral view. E: radius, distal portion. F: ulnare? G: pubic bones, ventral view. H: ilia, medial view. I: tibia, proximal portion. E, F, and I in opposite view from Fig. 5. Scale = 1 cm.

The dorsal process of the scapula is longer than the ventral process, even though its distal end is broken off.



**Discus** The dorsal process of the scapula is longer than the ventral process, even though its distal end is broken off. The angle formed between the two processes is  $109^\circ$  (Figs. 5A, 6A). The coracoid (Figs. 5B, 6B) is approximately twice as long as the ventral process of the scapula. In cross section the coracoid is subtriangular at midshaft; it is also expanded and flattened at its distal end.

**Radius** The humerus (Figs. 5C, 6C) is badly weathered; both the distal end and the ulnar process are missing. However, the radial process is preserved, and it is displaced distally as in the other protostegids. The well preserved left ulna (Figs. 5D, 6D) and a possible ulnare (Figs. 5F, 6F) show no unusual features. Because the proximal portion of the radius (Figs. 5E, 6E) is missing, it is impossible to determine if it bent posteriorly as in the more advanced protostegids (see Chapter 2).

**Calcus** Pelvic girdle and hind limbs -- An entire left ilium, as well as portions of the right ilium, both pubes, and a tibia are preserved (Figs. 5G-I, 6G-I). No portions of the ischium are preserved, making it impossible to determine if a spur-like posterior process is present as in *P. eaglefordensis* (Zangerl, 1953).

**Basis** Vertebrae -- Portions of at least three cervical and seven dorsal vertebrae are present. The preserved cervical vertebrae are procoelus.

## Discussion

## LITERATURE CITED

Due to its excellent state of preservation, RMM 3216 adds greatly to our knowledge of Calcarichelys. Several systematically significant characters found in RMM 3216 are otherwise unknown in the Chelospharginae. These include the design of the lingual and labial ridges on the triturating surface of the upper jaw accompanying the sagittal crest on the mandible, the reduced quadratojugal, the narrow pterygoids, and the unusual contact between the pterygoid and basioccipital.

Despite the wealth of material present in this specimen, important missing portions of RMM 3216 include: the quadratojugal; the palatines, vomer and surrounding palatal area; the processus inferior parietalis; and elements of the front and hind limbs. Thus the morphological features of these skeletal elements remain unknown for Calcarichelys and the Chelospharginae.

Acknowledgments -- I wish to thank John Bolt and Steve McCarroll of the Field Museum of Natural History, James Lamb (formerly of Discovery 2000) and Susan Henson of Discovery 2000 for their assistance and the use of their collections; and James Dobie, Craig Guyer, David Schwimmer, and Donald Buxton, members of my Graduate Committee, for their assistance during this project and critical review of this manuscript.



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## ABSTRACT

Cladistic analysis was used to produce a phylogenetic system of classification within the family Protostegidae. **CHAPTER 2** SYSTEMATIC REVISION OF THE PROTOSTEGIDAE USING CLADISTIC ANALYSIS

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The former three taxa are considered junior synonyms of *Protostega*. The consensus cladogram indicated that *Rhinostegia* belongs in the Desmatostegidae rather than the Protostegidae, and that *Climacostoma* is a chelospherine protostegid. The cladogram also showed that *Protostega eaglefordensis* should be assigned to a new genus for which the name *Langeronia* is proposed.

## ABSTRACT

Cladistic analysis was used to produce a phylogenetic system of classification for species within the family the Protostegidae. Thirty-seven characters from the skull, carapace, plastron, and appendicular skeleton were analyzed for all species within the Protostegidae and the outgroups Toxochelys latiremis, Caretta caretta, and Desmatochelys lowi. No characters were found to separate Archelon copei, Protostega dixie, or P. potens from P. gigas. Therefore, the former three taxa are considered junior synonyms of Protostega gigas. The consensus cladogram indicated that Rhinochelys belongs in the Desmatochelyidae rather than the Protostegidae, and that Cimochelys benstedii is a chelosphargine protostegid. The cladogram also showed that Protostega eaglefordensis should be assigned to a new genus for which the name Zangerlonia is proposed.

Subsequent to Sanger's study, Collins (1970) placed the genus Rhinochelys Seeley (1869) in the Chelospharginae. She also suggested that shell materials assigned to Cimochelys benstedii (Nantall, 1841) were actually portions of Rhinochelys.

Sanger, and to a lesser extent, Collins, were confronted with a lack of well preserved specimens. Compounded with the questionable nature of some of the characters used in their classifications (to be described below), this has resulted in the generation of a highly

## INTRODUCTION

In 1871 Cope described the first protostegid material from the Niobrara Chalk of Kansas, to which he assigned the name Protostega gigas (Cope 1871, 1872a). He later placed it in a new family, the Protostegidae (Cope, 1872b). Since Cope's initial discovery, more protostegid material has been found and additional taxa added to the family. Zangerl (1953) made the most comprehensive study of the Protostegidae to date, dividing the family into the primitive Chelospharginae and the more derived Protosteginae. He included Chelosphargis advena (Hay, 1908) and Calcarichelys gemma Zangerl (1953) in the Chelospharginae. Protostega dixie Zangerl (1953), P. eaglefordensis Zangerl (1953), P. gigas Cope (1872a), P. potens Hay (1908), Archelon ischyros Wieland (1896), and A. copei (Wieland, 1909) were included in the Protosteginae. Subsequent to Zangerl's study, Collins (1970) placed the genus Rhinochelys Seeley (1869) in the Chelospharginae. She also suggested that shell materials assigned to Cimochelys benstedii (Mantell, 1841) were actually portions of Rhinochelys.

Zangerl, and to a lesser extent, Collins, were confronted with a lack of well preserved specimens. Compounded with the questionable nature of some of the characters used in their classifications (to be described below), this has resulted in the generation of a highly

uncertain classification of the protostegids. Recent discovery of additional specimens and better preparation of previously existing specimens has increased the amount of data available concerning the protostegids.

The purpose of this study is to review and identify problems in current protostegid taxonomy; find new characters while eliminating questionable ones from the current literature; and to utilize cladistic analysis on the remaining characters to produce a phylogenetic classification for the members of the Protostegidae.

Abbreviations -- ALAM = Alabama Museum of Natural History, University of Alabama; AMNH = American Museum of Natural History; AUMP = Auburn University Museum of Paleontology; BM(NH) = The Natural History Museum = British Museum (Natural History); FMNH = Field Museum of Natural History; KU(VP) = Museum of Natural History, University of Kansas; USNM = United States National Museum; RMM = Red Mountain Museum Collection, housed at Discovery 2000; SM = Sedgewick Museum, Cambridge; TMM = Texas Memorial Museum; YPM = Peabody Museum, Yale University.

*Desmatochelyidae* an invalid family. This transfer was based on limb characters from a supposed second specimen of *Desmatochelys* (FMNH PR385) consisting of a single postorbital bone and considerable portions of the postcranial skeleton.

Due to the SYSTEMATIC PALEONTOLOGY portions of each specimen, the only features linking the two specimens are similarities Order TESTUDINES Linnaeus, 1758, and Ichia. None of the Superfamily CHELONIOIDEA Bauer, 1893 rushing in both specimens. Zangerl and Sloan also noted differences between Family DESMATOCHELYIDAE Williston, 1898 or individual variation. Among these was the discrepancy between Revised Diagnosis -- Nasal bones present. Contact between parietal and squamosal absent. Primary palate. Foramen palatinum posterius present, open laterally in Rhinochelys. Medial process of jugal absent. Fused rostrum basisphenoidale. Small foramen caroticum laterale located on anterior of basisphenoid. Deep hemispherical pit in floor of cavum cranii posterior to the dorsum sellae.

Discussion -- Desmatochelyidae was originally established as a monogeneric family containing the type specimen of Desmatochelys lowi [KU(VP) 1200], represented by a well preserved skull and fragments of the postcranial skeleton (Williston, 1898). Later, transfer of D. lowi to the Cheloniidae (Zangerl and Sloan, 1960) rendered Desmatochelyidae an invalid family. This transfer was based on limb characters from a supposed second specimen of Desmatochelys (FMNH PR385) consisting of a single postorbital bone and considerable portions of the postcranial skeleton.

Due to the preservation of different portions of each specimen, the only features linking the two specimens are similarities between the postorbitals, humeri, and ischia. None of these bones are complete and free from crushing in both specimens. Zangerl and Sloan also noted differences between the two specimens which they attributed to crushing or individual variation. Among these was the discrepancy between the angle formed by the scapular processes. The angle is  $85^\circ$  in KU(VP) 1200 and, according to Zangerl and Sloan (1960),  $103^\circ$  in FMNH PR385.

My examination of the type specimen indicates that the amount of crushing was not sufficient to account for the discrepancy in scapular angles between the two specimens, and that the difference is of taxonomic significance. Considering these points, with the fact that Zangerl and Sloan relied on figures of the type (known to possess some errors), rather than first hand observations (Zangerl and Sloan, 1960); the evidence presented was not sufficient for identification of FMNH PR385 as Desmatochelys lowi. In fact, it is probably a form related to Corsochelys (pers. comm., K. Derstler) which was also described by Zangerl (1960). Because no basis exists for the transfer of Desmatochelys to the Cheloniidae, the family Desmatochelyidae is here retained.

He also noted that three of the type specimens came from the same locality and horizon and "the distinct

possibility of yet Rhinochelys Seeley, 1869 should be considered." In any event, it is clear that more work needs to be done.

Type Species -- Rhinochelys pulchriceps (Owen, 1851).

Revised Diagnosis -- Small desmatochelyid (maximum skull length approximately 65 mm). Quadratojugal reduced, crescent-shaped bone, forming less of cheek margin than jugal. Posterior palatine foramen open laterally. Basisphenoid without ridges on ventral surface. Mandible with sagittal ridge on triturating surface.

Discussion -- The taxonomic status of Rhinochelys has been quite variable. Relationships to the emydids (Seeley, 1869), pleurodires (Lydekker, 1889), desmatochelyids (Williston, 1898; Romer, 1956; Smith, 1989), and protostegids (Collins, 1970) have been proposed for the genus. As many as seven species of Rhinochelys have been described and an additional 15 named without descriptions (Seeley, 1869).

Collins (1970) attempted to bring order to this state of systematic chaos by using seven characters to differentiate four species of Rhinochelys: R. pulchriceps, R. elegans, R. cantabridgiensis, and R. amaberti. Four of these characters were measurement ratios or angle measurements. Smith (1989) noted, "the high degree of overlap in her species range results make her conclusions suspect..." He also noted that three of the type specimens came from the same locality and horizon and "the distinct



possibility of year groups of a single species should be considered." In any event, it is clear that more work needs to be done on the systematics of Rhinochelys.

Currently a point on brain case morphology in Rhinochelys can be clarified. Collins (1970, figs. 11, 12) bases her description of the brain case on SM B94606. This specimen is immediately suspect because it is several times larger than the largest known specimen of Rhinochelys. Examination of this specimen also reveals that, unlike Rhinochelys, it possesses a secondary palate. The erroneous assignment of this specimen has no bearing on Collins' classification, since she does not use brain case characters. Subsequent to her work, the brain cases of several Rhinochelys specimens have been prepared. These skulls, examined by Smith (1989) and me, provide the brain case characters for Rhinochelys used in this study.

Since, Rhinochelys pulchriceps, R. elegans, and R. cantabridgiensis exhibit the same character states for all characters used in this study, Rhinochelys is considered as monotypic. Cladistic analysis indicates that Rhinochelys is more closely related to Desmatochelys than to the protostegids (see Cladistic Analysis of the Protostegidae, Fig. 1). Therefore, Rhinochelys is included in the family Desmatochelyidae.

## Family PROTOSTEGIDAE Cope, 1872

Distribution -- Central and Eastern United States.

Stratigraphic Range -- Lower Albian - lower Maestrichtian.

Revised Diagnosis -- Medial process of jugal absent. Jugal forming more of cheek margin than quadratojugal. Foramen posterius canalis caroticus internus located at anterior of suture between pterygoid and basisphenoid. Single foramen anterior canalis caroticus internus present. Fused rostrum basisphenoidale. Anterolateral edge of basioccipital with hemispherical surfaces fitting into sockets on posterior of pterygoids. T-shaped entoplastron not sutured to other bones. Scapular angle wide ( $109^\circ$  in Chelosphargis advena to  $134^\circ$  in Protostega gigas). Radial process of humerus displaced distally.

Subfamily CHELOSPHARGINAE Zangerl, 1953

Revised Diagnosis -- Small protostegids (maximum carapace length approximately 0.5 m). Triturating surface of premaxilla and maxilla with pronounced labial and lingual ridges. Lingual ridges extending farther ventrally than the labial ridges and divided by a sagittal groove. Floor of cavum cranii smooth, slightly concave. Seven neurals. Costals extending more than half the length of the ribs in

adults. Last pair of costals meet along midline. Distal end of ribs insert into pits on peripherals. Hyoplastron and hypoplastron roughly square in outline with lateral edges only slightly serrate, approaching or making contact along midline and forming diamond-shaped central fontanelle. Scapular angle approximately  $110^\circ$ . Chapter 11: A redescription of the protostegid turtle *Calcarichelys gemma*, for more informs Calcarichelys Zangerl, 1953

Type Species -- Calcarichelys gemma Zangerl, 1953.

Diagnosis -- Nuchal with posterior processes extending along lateral sides of the first neural. Mid-dorsal keel composed of alternating laterally compressed conical and saddle-shaped elements. Peripheral edge of carapace, from peripherals five to eleven, strongly serrate. One last suprapygal present. Pygal plate narrow. Contact between last pair of peripherals on anteroventral surface of pygal. Epiplastra absent. *spheria advena* (Hay, 1908)

*Protostega advena* Hay, 1908

Calcarichelys gemma Zangerl, 1953

Holotype -- KU(VP) 1209, from the Niobrara Chalk of Kansas. Holotype -- FMNH PR129, from the Mooreville Chalk, Montgomery County, Alabama. (holotype), 1219, 1258; AMNH 1778. Hypodigm -- FMNH PR129 (holotype), PR122, PR152; RMM 3164, 3216.; RMM 7149; YPM 1258, 3601, 3603.

Distribution -- Central and Southeastern United States.

Stratigraphic Range -- Lower Coniacian - lower Campanian.

Diagnosis -- Same as for genus.

Discussion -- RMM 3216 provides new and important information on this species. See Chapter 1: A redescription of the protostegid turtle Calcarichelys gemma, for more information. Cincochelys beustadi (Mantell, 1841)

Diagnosis -- Chelosphargis Zangerl, 1953 Peripheral edge of carapace with only slight grooves where marginal scutes meet. Type Species -- Chelosphargis advena (Hay, 1908).  
 Diagnosis -- Frontals with lateral processes reaching rim of orbits. Neural keel low and even. Peripheral edge of carapace with only slight grooves where marginal scutes meet. One suprapygal present. Pygal wide, separating last pair of peripherals. Epiplastra present.

Chelosphargis advena (Hay, 1908)

Protostega advena Hay, 1908

Hypodigm -- BM(NH) 28706 (holotype), 29112, 36751.

Holotype -- KU(VP) 1209, from the Niobrara Chalk of Kansas. Stratigraphic Range -- Albian - Turonian.

Hypodigm -- KU(VP) 1209 (holotype), 1219, 1258; AMNH 1778; FMNH P27397, P27485, PR121, PR126, PR171, UR25, UR26, UR84, UR177; RMM 7149; YPM 1258, 3601, 3603.

Distribution -- Central and Southeastern United States.

Stratigraphic range -- Lower Coniacian - lower

Campanian.

Diagnosis -- Same as for genus.

posteriorly canalis caroticus internus present along

ventromedial edge Cimochelys Zangerl, 1960

costals present. Costal plates extending no more than half

the Type Species -- Cimochelys benstedii (Mantell, 1841)

separated by neural. Distal end of ribs fit into shallow

groove Diagnosis -- Neural keel low and even. Peripheral edge

of carapace with only slight grooves where marginal scutes

meet. Two suprapygals present. Hyoplastra and hypoplastra

sutured together along the midline. radius bent posteriorly.

Scapular angle  $>115^\circ$ .

Discus Cimochelys benstedii (Mantell, 1841)

diag Emys benstedii Mantell, 1841, only the reduced costals

and Chelone (Cimochelys) benstedii Owen, 1841

diag Chelone benstedii Owen, 1851 this species may show that

at least some of the remaining characters are not diagnostic

of the Holotype -- BM(NH) 28706,

Hypodigm -- BM(NH) 28706 (holotype), 39112, 36751.

Distribution -- Southeast England.

Stratigraphic Range -- Albian - Turonian.

Diagnosis -- Same as for genus.

Revised Diagnosis -- Premaxilla forming large down-

curved beak. Neural keel low and even, with sagittal neural

groove. Subfamily PROTOSTEGINAE Zangerl, 1953 low ridge.

Two plastrons present.

Revised Diagnosis -- Large protostegids (maximum carapace length 2.2 m). Groove leading to the foramen posterius canalis caroticus internus present along ventromedial edge of pterygoid. Nine neurals present. Nine costals present. Costal plates extending no more than half the length of ribs in adults. Last pair of costals separated by neural. Distal end of ribs fit into shallow grooves on ventral surface of peripherals. Single suprapygal present. Hyoplastron and hypoplastron stellate in outline, forming large central and smaller lateral fontanelles. Epiplastra absent. Radius bent posteriorly. Scapular angle  $>115^\circ$ .

Discussion -- Of the above characters, given as diagnostic for the Protosteginae, only the reduced costals and bent radius are actually known for Protostega eaglefordensis. Future finds of this species may show that at least some of the remaining characters are not diagnostic of the subfamily.

Archelon Wieland, 1896

Type Species -- Archelon ischyros Wieland, 1896.

Revised Diagnosis -- Premaxilla forming large down-curved beak. Neural keel low and even, with sagittal neural

groove. Radial process of humerus reduced to a low ridge.  
Two pisiforms present. May, 1908

*Protostega copei* Wieland, 1909

*Archelon* *Archelon ischyros* Wieland, 1896

*Protostega dixie* Zangari, 1953

Holotype -- YPM 3000, from the Pierre Shale of South  
Dakota. Holotype -- AMNH 1503, from the Niobrara Chalk of

Kansas. Hypodigm -- YPM 3000 (holotype), 1783; NMNH 13439.

Distribution -- Central and Eastern United States.

Stratigraphic range -- Lower Campanian - lower

Maestrichtian. LAM PV985.10.1; AUMP 412. *P. gigas*: AMNH

1503 Diagnosis -- Same as for genus. 1652. *P. potens*: AMNH  
180 (holotype).

Distribution -- *Protostega* Cope, 1872 Eastern United States.

Stratigraphic Range -- Lower Cretaceous - lower

Campanian. Type Species -- *Protostega gigas* Cope, 1872.

Revised Diagnosis -- Anterior tip of maxilla only  
slightly down-curved. Neural keel low and uneven, raised  
neurals alternating with saddle-shaped ones. Neural groove  
absent. *P. gigas*, and *P. potens*: division of the central  
plastral fontanelle by digitations of the hypoplastron,  
length of the hyo-hypoplastral suture, length of the  
anterolateral edge of the hypoplastron relative to the  
distance from the axial notch to the hyo-hypoplastral  
suture, width of the posterior lobe of the plastron relative  
to its length, and the angularity of the posterolateral edge

of the xiphiplastron. Protostega gigas Cope, 1872 were based on  
Protostega potens Hay, 1908 case of extension of the  
Protostega copei Wieland, 1909 expected that they would  
Archelon copei Zangerl, 1953 fact, examination of these  
Protostega dixie Zangerl, 1953 indicates individual  
variation in these species; hence it seems likely they would  
do as Holotype -- AMNH 1503, from the Niobrara Chalk of  
Kansas. observed protostegid specimens prohibits statistical  
analysis Hypodigm -- A. copei: YPM 1787 (holotype). P. dixie:  
FMNH P27314 (holotype), P27315, P27353, P27385, P27471,  
PR66, PR198; ALAM PV985.10.1; AUMP 412. P. gigas: AMNH  
1503 (holotype), 1502; NMNH 11651, 11652. P. potens: AMNH  
180 (holotype). relative to the orbits to distinguish  
between Distribution -- Central and Southeastern United States.  
turn Stratigraphic Range -- Lower Coniacian - lower tributed  
Campanian. usual variation. None of the specimens of P. dixie  
examined Diagnosis -- Same as for genus. complete premaxilla and  
maxilla Discussion -- Zangerl (1953) used differences in the  
following characters to separate Archelon copei, Protostega  
dixie, P. gigas, and P. potens: division of the central  
plastral fontanelle by digitations of the hypoplastron,  
length of the hyo-hypoplastral suture, length of the  
anterolateral edge of the hypoplastron relative to the  
distance from the axial notch to the hyo-hypoplastral  
suture, width of the posterior lobe of the plastron relative  
to its length, and the angularity of the posterolateral edge



of the xiphiplastron. Since these characters were based on measurements (indirectly in the case of extension of the plastral digitations), it is to be expected that they would exhibit individual variation. In fact, examination of these characters in modern marine turtles indicates individual variation in those species; hence it seems likely they would do so in protostegids. Unfortunately, the small number of well preserved protostegid specimens prohibits statistical analysis of these characters to determine if the variations they exhibit are significant. While the other measurements

Zangerl (1953, figs. 30, 31) also used differences in the amount of down-turning of the beak and the level of the tip of the beak relative to the orbits to distinguish between P. gigas and P. dixie. The differences in down turning of the beak are slight and might well be attributed to individual variation. None of the specimens of P. dixie examined by Zangerl possessed both a complete premaxilla and maxilla and all, including the P. gigas specimens, were affected by crushing. Thus, reconstructions of the anterior portion of the skull are inadequate for determination of these characters.

Wieland (1909) distinguished Protostega copei from P. gigas on the basis of the following characters: costals extending along proximal half of ribs, as apposed to extending along the proximal third in P. gigas; limb bones relatively short and small; and carapace relatively thick.

In fact only a few of the costal plates in A. copei come close to extending half the distance of the ribs and most extend much less (Wieland, 1909: fig. 2). The observed difference in extension of the costal plates between the two taxa is slight and attributable to individual variation.

Since Wieland gave no mathematical data to support his statement concerning limb size, I calculated the ratio of humerus length to carapace length for P. gigas (NMNH 11651) and P. copei (YMP 1787, type). The ratio is 0.27 for P. gigas and 0.21 for P. copei. While the other measurements were actually taken by me, the carapace length of P. copei was based on Wieland's estimation of 0.80 m for YPM 1787. It should be noted that in this specimen the pygal is missing and the precise placement of the suprapygal is uncertain, making the estimate of carapace length questionable. Even if Wieland's estimate for carapace length was correct, the lack of a suitable sample size of protostegid specimens prohibits determination of the significance of the differences illustrated by the taxa.

Moreover, due to the various amounts of crushing evident in all protostegid specimens, thickness of the carapace should not be used to differentiate taxa.

Transfer of Protostega copei to the genus Archelon by Zangerl (1953) was based on the presence of an even neural keel in NMNH 11649, a supposed specimen of P. copei. My examination of the neurals present in the type specimen (YPM

1787) revealed that it possesses an uneven keel as in P. gigas and does not belong in the genus Archelon. Since NMNH 11649 has a neural groove, it is most likely a specimen of a Archelon ischyros.

Considering the questionable nature of the above mentioned characters, Archelon copei, Protostega dixie, and P. potens should be considered junior synonyms of P. gigas.

protostegid, but it is impossible to say whether they are Zangerlonia, gen. nov. or to Archelon.

Since Protostega eaglefordensis possesses no

synap Type Species -- Protostega eaglefordensis Zangerl, with 1953.

Proto Diagnosis -- Bend in radius less pronounced than in its other protostegines. One pisiform present. Ischium with spur-like posterior process.

Etymology -- In honor of Dr. Rainer Zangerl.

indicates that it should be assigned to a new genus. The

name Zangerlonia eaglefordensis (Zangerl, 1953)

Protostega eaglefordensis Zangerl, 1953

eaglefordensis.

Holotype -- TMM 924, from the Eagleford Shale, Lake Waco Dam, McLennan County, Texas.

Distribution -- Eastern Texas.

Stratigraphic Range -- Upper Cenomanian - upper Turonian.

Discussion -- Zangerl (1953) tentatively referred TMM 924 to Protostega after making the following observations:

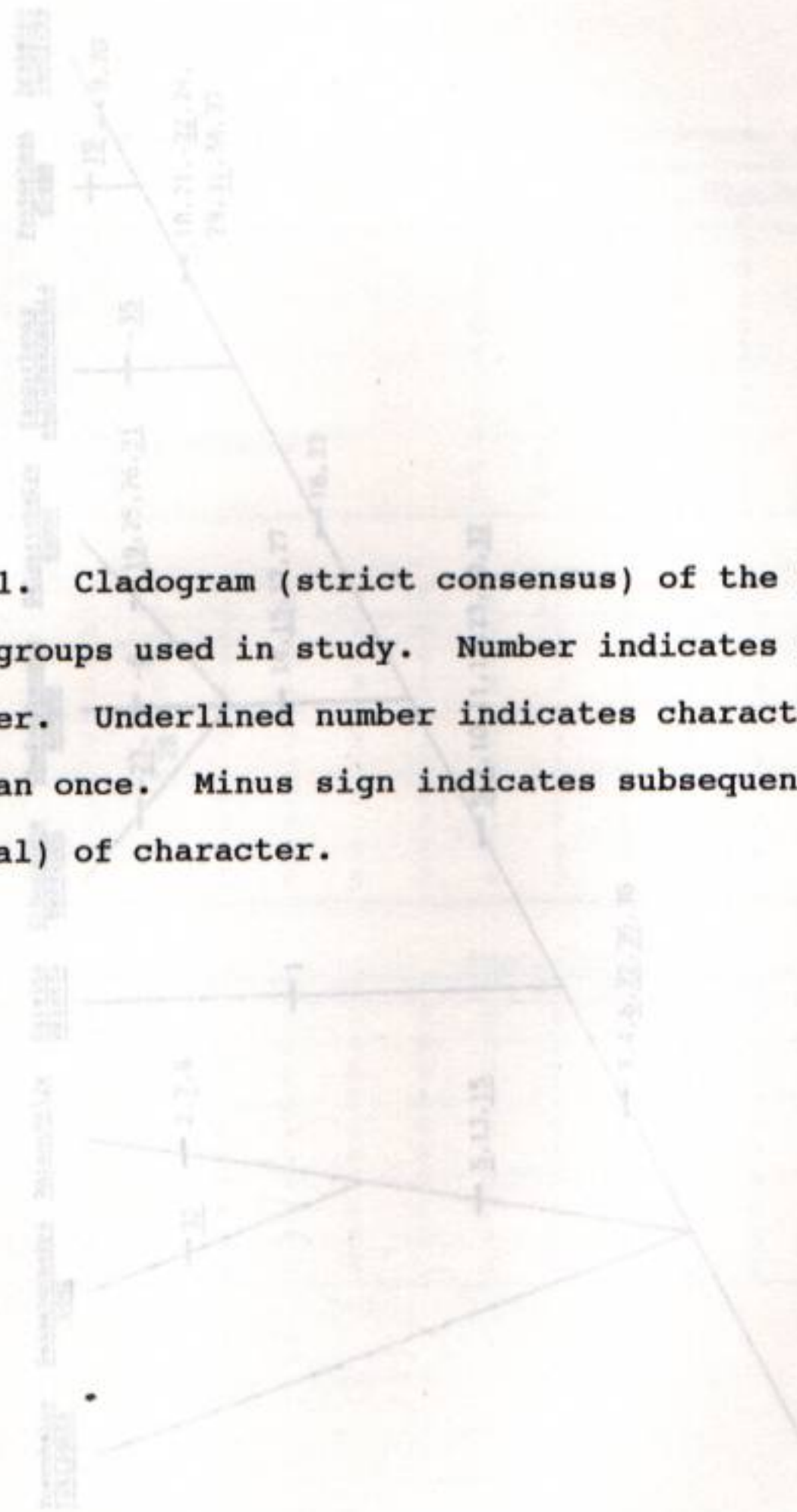
All parts preserved suggest at once that this is a large protostegid. But the critical elements that would permit a definite generic decision are unfortunately lacking. The limbs and girdles are more primitive than in any known large protostegid, but it is impossible to say whether they are closer to Protostega or to Archelon. Since Protostega eaglefordensis possesses no synapomorphies with P. gigas which are not also shared with Archelon ischyros (see Cladistic Analysis of the Protostegidae, Fig. 1, and Table 1), no basis exists for its assignment to the genus Protostega. This, in conjunction with the fact that P. eaglefordensis possesses characters separating it from Protostega gigas and Archelon ischyros, indicates that it should be assigned to a new genus. The name Zangerlonia eaglefordensis, in honor of Dr. Rainer Zangerl, is proposed as the replacement for Protostega eaglefordensis.

## CLADISTIC ANALYSIS OF THE PROTOSTEGIDAE

The Hennig 86 program was used to construct a cladogram containing all species within the Protostegidae as well as the outgroups Toxochelys latiremis, Caretta caretta, and Desmatochelys lowi (Fig. 1). Thirty-seven characters from the skull, carapace, plastron, and appendicular skeleton were used (Table 1). Three equally parsimonious trees of 47 steps were produced with consistency and retention indexes of 78 and 79 respectively. The strict consensus tree is shown in Figure 1.

FIGURE 1. Cladogram (strict consensus) of the Protostegidae and outgroups used in study. Number indicates presence of character. Underlined number indicates character occurs more than once. Minus sign indicates subsequent loss (reversal) of character.

FIGURE 1. Cladogram (strict consensus) of the Protostegidae and outgroups used in study. Number indicates presence of character. Underlined number indicates character occurs more than once. Minus sign indicates subsequent loss (reversal) of character.





## Explanation of Characters

For the characters in the following list used to construct the cladogram (Fig. 1), a reference indicating

Table 1. Character matrix used to construct cladogram in Fig. 1.

Taxa	Characters								
	1	2	3	4	5	6	7	8	9
<u>Toxochelys latiremis</u>	0	0	0	0	0	0	0	0	0
<u>Caretta caretta</u>	1	0	1	1	0	1	0	0	0
<u>Desmatochelys lowi</u>	0	0	0	0	1	0	0	0	0
<u>Rhinochelys</u>	0	1	0	0	1	0	1	1	0
<u>Chelosphargis advena</u>	0	?	?	1	1	0	?	?	0
<u>Calcarichelys gemma</u>	0	?	?	1	1	1	1	0	0
<u>Cimochelys benstedii</u>	?	?	?	?	?	?	?	?	?
<u>Zangerlonia eaglefordensis</u>	?	?	?	?	?	?	?	?	?
<u>Protostega gigas</u>	0	0	1	1	1	1	1	0	0
<u>Archelon ischyros</u>	0	0	1	1	1	1	1	0	1

1. Secondary palate present (Gaffney, 1971).

Taxa	Characters													
	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<u>T.l.</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>C.c.</u>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<u>D.l.</u>	0	0	0	1	0	1	?	?	?	?	0	0	?	1
<u>R.</u>	0	0	0	1	0	1	?	?	?	?	?	?	?	?
<u>C.a.</u>	?	1	?	0	1	1	0	1	0	0	0	0	1	1
<u>C.g.</u>	1	1	1	0	1	1	0	1	0	1	0	0	1	1
<u>C.b.</u>	?	?	?	?	?	?	0	1	0	0	0	0	1	0
<u>N.e.</u>	?	?	?	?	?	?	1	?	?	?	?	?	?	?
<u>P.g.</u>	1	1	1	0	0	0	1	0	1	1	0	1	0	1
<u>A.i.</u>	1	1	1	0	0	0	1	0	1	0	1	1	0	1

Taxa	Characters													
	24	25	26	27	28	29	30	31	32	33	34	35	36	37
<u>T.l.</u>	0	?	0	0	0	0	0	0	0	0	0	0	0	0
<u>C.c.</u>	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<u>D.l.</u>	0	0	0	0	?	0	?	?	1	0	?	0	0	0
<u>R.</u>	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>C.a.</u>	0	0	0	1	?	0	1	0	1	?	?	1	1	?
<u>C.g.</u>	0	1	1	1	?	0	1	1	1	?	?	?	1	0
<u>C.b.</u>	0	?	0	1	1	0	?	?	?	?	?	?	?	?
<u>N.e.</u>	?	?	?	?	?	?	?	?	1	1	0	0	?	?
<u>P.g.</u>	1	0	0	0	0	1	1	1	1	1	1	1	1	1
<u>A.i.</u>	1	0	0	0	0	1	1	1	1	1	1	1	1	1

5. Medial process of jugal absent (Gaffney, 1976).

6. Frontals do not extend to rim of orbit in dorsal view (Zangerl, 1953).



7. Jugal large, with ventral process extending posteriorly  
 Explanation of Characters margin than quadratojugal

For the characters in the following list used to construct the cladogram (Fig. 1), a reference indicating where more information on the character may be found follows the description. This reference is usually the first mention of the character in the literature, although not necessarily with reference to the protostegids. Unless otherwise stated, all characters were observed by me.

- basisphenoid-pterygoid contact (see Chapter 1). This
1. Secondary palate present (Zangerl, 1971). (RMM 3216),
  2. Foramen palatinum posterius open laterally (Collins, 1970). (YPM 1783). The f.p.c.c.i. is not visible in
  3. Foramen palatinum posterius absent (Gaffney, 1979).
  4. Nasal bones absent. Zangerl (1953) stated that one specimen of Chelosphargis advena (KU(VP) 1219) possesses nasals. The author was unable to examine the skull of this specimen because it is on extended loan overseas. However, a recently acquired skull of C. advena (RMM 7149, from the Mooreville Chalk) suggests
  12. that nasals are not present. capital with hemispherical
  5. Medial process of jugal absent (Gaffney, 1976). pterygoid
  6. Frontals do not extend to rim of orbit in dorsal view
  13. (Zangerl, 1953). cal pit in floor of cavum cranii posterior to the dorsum sellae (Smith, 1989).

7. Jugal large, with ventral process extending posteriorly to form more of cheek margin than quadratojugal (Gaffney and Meylan, 1988).
8. Quadratojugal reduced, crescent-shaped, forms anterior border of the cavum tympani (Collins, 1970).
9. Anterior of premaxillae forms robust, sharply down-curved beak (Wieland, 1909).
10. Foramen posterius canalis caroticus internus (f.p.c.c.i.) located at the anterior of the basisphenoid-pterygoid contact (see Chapter 1). This condition is known for Calcarichelys gemma (RMM 3216), Protostega gigas (AUMP 412, YPM 1787), and Archelon ischyros (YPM 1783). The f.p.c.c.i. is not visible in YPM 1783 due to poor preservation of the basicranium. However, the groove leading to it is preserved on the ventromedial edge of the left pterygoid.
11. Single foramen anterius canalis caroticus internus present (see Chapter 1). This condition is known for Chelosphargis advena (YPM 3603), Protostega gigas (AUMP 412), and Archelon ischyros (YPM 1783).
12. Anterolateral edge of basioccipital with hemispherical surfaces fitting into sockets on posterior of pterygoid (Fig. 2).
13. Deep, hemispherical pit in floor of cavum cranii posterior to the dorsum sellae (Smith, 1989).
14. None certain present.

14. Floor of cavum cranii smooth, slightly concave, lacking a crista dorsalis basioccipitalis and basis tuberculi basalis (see Chapter 1).
15. Triturating surface of premaxilla and maxilla with pronounced labial and lingual ridges. Lingual ridges extending farther ventrally than the labial ridge and divided by a sagittal groove (Collins, 1970). The sagittal groove presumably accommodates an opposing sagittal ridge on the mandible. Such a ridge is present in Rhinochelys (Collins, 1970) and Chelosphargis advena (Zangerl, 1953).
16. Costal plates extend less than one half the length of the ribs in adult. For this study, costal plate length is considered equivalent to the length of the suture between the costal being measured and the costal plate either anterior or posterior to it, whichever is longer. Rib length is measured from the midpoint of the suture between the costal and neural(s) to the distal end of the rib. Although the costals do not extend for one half the distance of the ribs in small specimens of Chelosphargis advena, in all of the larger (and presumably adult) specimens they extend for more than half the length of the ribs (Zangerl, 1953).
17. Seven neurals present (see Chapter 1).
18. Nine neurals present.

19. Neural keel uneven (Zangerl, 1953).
20. Sagittal neural groove present (Wieland, 1896).
21. Zangerl (1953) noted that in specimens of Protostega crushing caused cleavage of neurals along the sagittal plane. This cleavage produced furrows resembling the neural groove present in Archelon ischyros.
22. Examination of a specimen of Archelon ischyros, displayed in the Naturhistorisches Museum Wien in Vienna, Austria, indicates that the neural groove did not result from crushing (pers. comm., K. Derstler). I have examined the type of A. ischyros (YPM 3000) and agree with Dr. Derstler that the groove is a diagnostic feature of A. ischyros.
23. Nine pairs of costals present (Wieland, 1896).
24. Last pair of costals meet along midline (see Chapter 1).
25. Only one suprapygal present (see Chapter 1).
26. Distal end of ribs fit into shallow grooves on ventral surface of peripherals (Cope, 1872a).
27. Last pair of peripherals make sagittal contact in ventral view (Zangerl, 1953).
28. Peripheral edge of carapace strongly serrated (Zangerl, 1953).
29. Hyoplastron and hypoplastron roughly square in outline with lateral edges only slightly serrate, approaching

37. or making contact along midline and forming diamond-shaped central fontanelle (see Chapter 1).
28. Hyoplastron and hypoplastron sutured together along midline (Collins, 1970).
29. Hyoplastron and hypoplastron stellate in outline (Cope, 1872a).
30. Entoplastron T-shaped, not sutured to other bones (Wieland, 1898).
31. Epiplastra absent (Zangerl, 1953).
32. Radial process of humerus displaced distally compared to condition seen in Toxochelys and Caretta (Case, 1897). With the exception of Zangerlonia eaglefordensis, in which the radial process is closer to the head, the radial process is located near the midshaft of the humerus.
33. Proximal portion of radius bends posteriorly (Wieland, 1902).
34. Second pisiform present (pers. comm., K. Derstler). Dr. Derstler states that a second pisiform is present in the Vienna Archelon specimen and that the bone identified in Protostega gigas as a radiale? (Wieland, 1906: fig. 1) probably is a second pisiform.
35. Ischium lacks spur-like posterior process (Zangerl, 1953).
36. Angle formed by processes of scapula  $>100^\circ$  (Wieland, 1896).

37. Angle formed by processes of scapula  $>115^\circ$  (Wieland, 1896).

of the University of Texas at Austin, and M.L. Jeffreys of the Texas Memorial Museum for the use of their collections and the CONCLUSIONS extended during my

visit. Due to insufficient evidence linking a supposed second specimen of Desmatochelys (FMNH PR385) to the type, transfer of Desmatochelys lowi to the Cheloniidae (Zangerl, 1960) is unwarranted and the family Desmatochelyidae is retained.

Rhinochelys is more closely related to Desmatochelys than to the Protostegids and is included within the Desmatochelyidae as sister taxon to Desmatochelys.

Within the Protostegidae Calcarichelys gemma, Chelosphargis advena, and Cimochelys benstedii comprise the Chelospharginae, which is the sister group to all other protostegids. Protostega eaglefordensis is the sister taxon to the group comprised of Archelon ischyros and Protostega gigas and is placed in a new genus Zangerlonia.

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Robert Purdy and George Zug of the U.S. National Museum, Melissa Winans of the University of Texas at Austin, and M.L. Jeffreys of the Texas Memorial Museum for the use of their collections and the hospitality extended during my visits. Thanks to James Dobie, Craig Guyer, David ~~ley~~ from Schwimmer, and Donald Buxton for their assistance and critical review of this manuscript. Special thanks to James Dobie, Eugene Gaffney, and Kraig Derstler for their continuing advice through out this project and to my wife Christi for her support, assistance, and limitless patience during my travels. Funding for this project was provided by the Theodore Roosevelt Memorial Fund of the American Museum of Natural History and by a Collection Study Grant from the Field Museum of Natural History. pp. 323, 335 in P. V.

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adds greatly to our knowledge of Calcarichelys. Several systematically significant characters found in MN 3216 are otherwise unknown in the Chelospharginae. These include the design of the lingual and labial ridges on the triturating surface of the upper jaw accompanying the sagittal crest on the mandible, the reduced quadratojugal, the narrow pterygoide, and the unusual contact between the pterygoid and basioccipital.

Despite the wealth of material present in this specimen, important missing portions of MN 3216 include: the quadratojugal; the palatines, vomer and surrounding palatal area; the processus inferior parietalis; and elements of the front and hind limbs. Thus the morphological features of these skeletal elements remain unknown for Calcarichelys and the Chelospharginae.

Due to insufficient evidence linking a supposed second specimen of Desmatochelys (FMNH PR385) to the type, transfer of Desmatochelys lowi to the Cheloniidae (Sangerl, 1960) is unwarranted and the family Desmatochelyiidae is retained. Elphischelys is more closely related to Desmatochelys than to

the Protostegidae and is included within the Desmatochelyidae as sister taxon to Desmatochelys.

Within the Protostegidae

### THESIS CONCLUSION

Due to its excellent state of preservation, RMM 3216 adds greatly to our knowledge of Calcarichelys. Several systematically significant characters found in RMM 3216 are otherwise unknown in the Chelospharginae. These include the design of the lingual and labial ridges on the triturating surface of the upper jaw accompanying the sagittal crest on the mandible, the reduced quadratojugal, the narrow pterygoids, and the unusual contact between the pterygoid and basioccipital.

Despite the wealth of material present in this specimen, important missing portions of RMM 3216 include: the quadratojugal; the palatines, vomer and surrounding palatal area; the processus inferior parietalis; and elements of the front and hind limbs. Thus the morphological features of these skeletal elements remain unknown for Calcarichelys and the Chelospharginae.

Due to insufficient evidence linking a supposed second specimen of Desmatochelys (FMNH PR385) to the type, transfer of Desmatochelys lowi to the Cheloniidae (Zangerl, 1960) is unwarranted and the family Desmatochelyidae is retained. Rhinochelys is more closely related to Desmatochelys than to

the Protostegids and is included within the Desmatochelyidae as sister taxon to Desmatochelys.

Within the Protostegidae Calcarichelys gemma, Chelosphargis advena, and Cimochelys benstedii comprise the Chelospharginae, which is the sister group to all other protostegids. Protostega eaglefordensis is the sister taxon to the group comprised of Archelon ischyros and Protostega gigas and is placed in a new genus Zangerlonia.