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### Permalink

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### Journal

PaleoBios, 33(0)

### ISSN

0031-0298

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### Publication Date

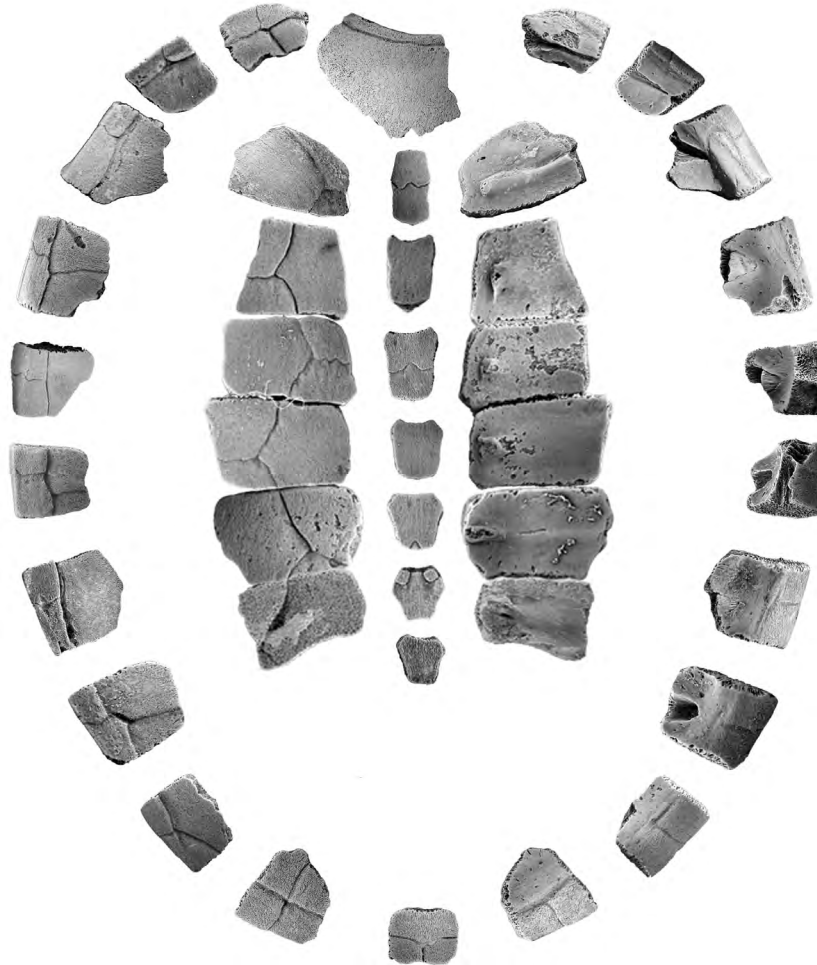
2016-04-13

Peer reviewed

# *PaleoBios*

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Don Brinkman, Martha Carolina Aguillon-Martinez, J. Howard Hutchison, and Caleb M. Brown (2016). *Yelmochelys rosarioae* gen. et sp. nov., a stem kinosternid (Testudines; Kinosternidae) from the Late Cretaceous of Coahuila, Mexico.

**Cover photo:** Composite reconstruction of carapace of *Yelmochelys rosarioae* gen. et sp. nov. in exploded view. The peripherals and neurals on the left and right sides are the same specimens only flipped.

**Citation:** Brinkman, D., Aguillon-Martinez, M. C., Hutchison, J. H., & Brown, C. M. 2016. *Yelmochelys rosarioae* gen. et sp. nov., a stem kinosternid (Testudines; Kinosternidae) from the Late Cretaceous of Coahuila, Mexico. *PaleoBios*, 33. ucmp\_paleobios\_30601.

## *Yelmochelys rosarioae* gen. et sp. nov., a stem kinosternid (Testudines; Kinosternidae) from the Late Cretaceous of Coahuila, Mexico

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A small smooth-shelled kinosternoid from the late Campanian Cerro del Pueblo Formation and the early Maastrichtian Canyon del Tule Formation of Coahuila, Mexico that is abundantly represented by isolated elements is described as *Yelmochelys rosarioae* gen. et sp. nov. A phylogenetic analysis concludes that *Y. rosarioae* is a representative of the stem lineage of the Kinosternidae. Inclusion of *Y. rosarioae* in Kinosternidae is supported by presence of a groove for the musk duct, the loss of the eleventh peripheral and twelfth marginal, reduced articulation between the plastron and carapace, and diamond-shaped vertebral scales. A basal position within Kinosternidae is indicated by the presence of distinct abdominal scales that meet at the midline and the presence of a relatively long costiform processes. The inclusion of *Y. rosarioae* in Kinosternidae supports the hypothesis that Kinosternidae and Dermatemydidae had diverged by the Late Campanian.

**Keywords:** Kinosternidae, *Yelmochelys rosarioae*, Cerro del Pueblo Formation, Cretaceous, Mexico

### INTRODUCTION

Kinosternoidea [Gaffney and Meylan, 1988](#), represented today by the Kinosternidae [Baur, 1893](#) (the mud and musk turtles) and Dermatemydidae [Gray, 1870](#) (the Mesoamerican river turtle), and the Chelydridae [Gray, 1831](#) are two groups of eucryptodire turtles that are thought to have originated in North America in the Late Cretaceous ([Hutchison 2000](#)). Kinosternoids, unlike chelydrids which were also endemic to North America during the Cretaceous, did not spread into Europe or Asia in the Cenozoic. Although kinosternoids have been aligned with the trionychoids based on morphological evidence, recent molecular data has indicated that they are more closely related to the Chelydridae ([Near et al. 2005](#), [Parham et al. 2006](#), [Barley et al. 2010](#), [Crawford et al. 2015](#)). This relationship was accepted by [Knauss et al. \(2011\)](#) in their recent analysis of kinosternoid interrelationships. While a sister-group relationship between these two groups of eucryptodires is biogeographically satisfying since both groups first occur in North America, it challenges the morphological basis for our understanding of higher-level interrelationships of eucryptodiran turtles. A better understanding of the fossil record of early members of these

groups is therefore necessary to more fully understand the evolutionary changes that occurred during the origin and early diversification of Kinosternoidea.

Kinosternoids first occur in the Campanian Kaiparowits Formation of Utah ([Hutchison et al. 1998](#), [Eaton et al. 1999](#), [Hutchison 2000](#), [Hutchison et al. 2013](#)) where they are represented by an unnamed small-bodied taxon with a smooth shell referred to as “the smooth-shelled kinosternoid.” This kinosternoid was first recognized by [Hutchison and Archibald \(1986\)](#) based on material from the Hell Creek Formation (Maastrichtian). Subsequently, it has been reported from the Campanian of Utah ([Hutchison et al. 2013](#)), New Mexico ([Sullivan et al. 2013](#)), and Mexico ([Rodriguez de la Rosa and Cevallos-Ferriz 1998](#), [Brinkman and Rodriguez de la Rosa 2006](#)). [Hutchison and Archibald \(1986\)](#) initially included this taxon in the family Kinosternidae. Later, [Hutchison \(1991\)](#) noted that its affinities remained to be demonstrated and referred to it as kinosternid-like. [Brinkman and Rodriguez de la Rosa \(2006\)](#) recognized that kinosternid features are present but felt that additional data was required before it could be confidently included in that family. If correctly included in Kinosternidae it would be the earliest member of the clade because the family is not otherwise documented in the fossil record until the lower

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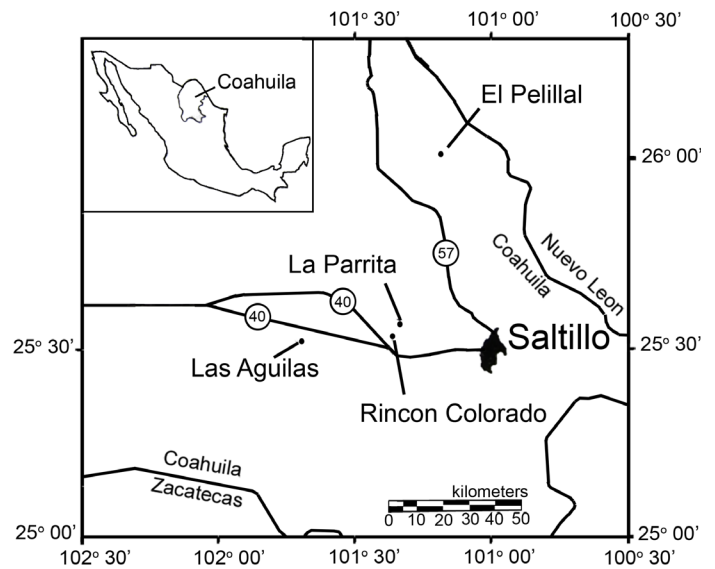
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Eocene, where it is represented by two taxa, *Xenochelys* Hutchison, 1991 and *Baltemys* Hutchison, 1991. Hutchison (1991) concluded that Kinosternidae had a long history prior to the Eocene because his phylogenetic analysis indicated that *Baltemys* is a sister-taxon to Kinosterninae Baur, 1893, a clade that includes the extant genera *Sternotherus* Gray, 1825 and *Kinosternon* Spix, 1824. In a subsequent analysis of kinosternoid interrelationships by Knauss et al. (2011), both *Baltemys* and *Xenochelys* were retrieved within crown Kinosternidae along the stem of the Kinosterninae. These results imply that Kinosterninae and Staurotypinae Baur, 1893, the kinosternid subfamily that includes the extant genera *Staurotypus* Wagler, 1830 and *Claudius* Cope, 1865, had already diverged by the early Eocene. In addition, Knauss et al. (2011) concluded that Kinosternidae and Dermatemydidae had diverged by the Campanian. *Hoplochelys* Hay, 1908, which first occurs in the late Campanian Cerro del Pueblo Formation of Mexico (Brinkman and Rodriguez de la Rosa 2006), was located in their analysis on the phylogenetic stem of the extant *Dermatemys* Gray, 1847, an idea supported by recent molecular divergence estimations (Joyce et al. 2013, Warnock et al. 2015). However, one analysis in the most recent study of the interrelationships of Dermatemydidae (Bourque et al. 2014) suggests *Hoplochelys* was more closely related to the Kinosternidae than to the Dermatemydidae, although this difference may be a result of use of different outgroups in their analysis.

In this paper, the small smooth-shelled kinosternoid from the late Campanian Cerro del Pueblo Formation and early Maastrichtian Cañon del Tule Formation of Coahuila, Mexico, is described as *Yelmochelys rosarioae* gen. et sp. nov. Brinkman, Aguillon-Martinez, Hutchison and Brown. Although the only articulated specimens that have been recovered are a partial plastron and a few conjoined peripherals, well-preserved isolated elements are common. Most elements of the shell are represented by multiple specimens, allowing a composite reconstruction of the carapace to be assembled. A phylogenetic analysis of the relationships of *Yelmochelys* is undertaken to evaluate its position relative to other kinosternoids.

## GEOLOGY

A small, smooth-shelled kinosternoid was first reported in the Late Cretaceous of Mexico by Rodriguez de la Rosa and Cevallos-Ferriz (1998) on the basis of material from the El Pelillal locality in the Parras Basin (Fig. 1). Because of the lithological and faunal similarities with the Cerro del Pueblo Formation of the Rincon Colorado area in the Parras Basin, they interpreted the El Pelillal locality as being within the Cerro del Pueblo Formation. However, subsequent work



**Figure 1.** Map showing the localities from which elements of *Yelmochelys rosarioae* were collected. Inset shows the position of Coahuila in Mexico.

demonstrated that the locality is in the younger Cañon del Tule Formation, which is lower Maastrichtian in age (Aguillon-Martinez 2010). Although the Cañon del Tule Formation is typically marine, non-marine intervals are present in the El Pelillal area. These represent tongues from the laterally equivalent non-marine Muerto Formation that extends into the northern-most portion of the Parras Basin. The El Pelillal locality is located in one of these non-marine intervals.

The presence of the small, smooth-shelled kinosternoid in the late Campanian Cerro del Pueblo Formation was documented by Brinkman and Rodriguez de la Rosa (2006). The Cerro del Pueblo Formation was deposited in a shallow marine to a fully non-marine environment (Kirkland et al. 2000, Eberth et al. 2004). The small, smooth-shelled kinosternoid is particularly abundant in the upper fully non-marine portion of the formation. The Cerro del Pueblo Formation is dated by both biostratigraphic and magnetostratigraphic data. *Inoceramus vanuxemi* Meek and Hayden, 1860, a middle to late Campanian index fossil (Kauffman et al. 1993), is locally abundant in the Cerro del Pueblo Formation (Kirkland et al. 2000). Magnetostratigraphic studies concluded that the Cerro del Pueblo Formation was deposited in magnetochron zones 32n.3r-32n.2n (Eberth et al. 2004). This interval is interpreted as late Campanian in age (Lerbekmo and Braman 2002), further constraining the age of the formation.

## MATERIALS AND METHODS

This study is based on approximately 500 isolated elements from the Cerro del Pueblo Formation and 17 elements from the Cañon del Tule Formation. The specimens from the Cerro

del Pueblo Formation were surface collected from four vertebrate microfossil localities in the County of General Cepeda. Three of these localities are in the Ejido of La Parrita. The fourth is the Las Aguilas locality in the Ejido of Porvenir de Jalpa (Fig. 1). The specimens from the Cañon del Tule Formation were surface collected from the El Pelillal locality.

While plastron elements are easily identifiable, the identification of individual neurals, peripherals, and costals presents challenges. To differentiate these elements, each of 125 elements was photographed in multiple views. To highlight surface relief, the specimens were dusted with ammonium chloride before being photographed. The photographs were then placed into morphological groups based on features such as shape, proportions, and position of sulci on the element. The identity of each morphological group was determined through comparison with the shell of extant kinosternids and through the recognition of serial patterns of change in morphology along the shell.

To visualize the general size and shape of the carapace, a composite reconstruction of the shell was undertaken using isolated elements. Elements of approximate equivalent size were selected and put in relative position on a clay base. The width was constrained by the width of the plastron. The curvature of the preserved portions of the costals and the peripherals provide a minimum degree of vaulting of the shell. This reconstruction formed the basis for the illustration of the carapace presented in Figure 8.

A general phenetic similarity between *Yelmochelys rosarioae* and members of the Kinosternidae has long been recognized. To evaluate whether or not *Y. rosarioae* is a stem kinosternid or better interpreted as a basal kinosternoid that independently evolved a small body size, a phylogenetic analysis was undertaken. The data matrix presented by Knauss et al. (2011) was used as a basis for this analysis, with the inclusion of *Y. rosarioae* as an operational taxonomic unit (OTU). The final matrix consisted of 16 OTUs and 48 morphological characters (Appendix 1), including both extinct and extant taxa (Appendix 2). *Yelmochelys rosarioae* was coded for 28 out of the 48 characters (60.4%). The parsimony analysis was run in PAUP\*4.0 beta 10 (Swofford 2002) using the Branch-and-Bound search option, and *Chelydra serpentina* (Linnaeus, 1758) and *Macrochelys temminckii* (Troost, 1835) specified as the outgroup. All characters were given equal weight, and following Knauss et al. (2011) eight of the characters were run ordered (4, 10, 23, 30, 35, 41, 46, 47). To determine relative clade support a bootstrap analyses (10,000 replicates) was performed. Bremer support values were also obtained using TNT (Goloboff et al. 2008).

**Anatomical Abbreviations**—Carapacial bones (upper case) and scales (lower case) are denoted by a letter and

position number (e.g., C2); C - costal, N- neural plus number, P- peripheral plus number, m- marginal plus number (e.g., m4), p- pleural plus number, v-vertebral.

**Institutional Abbreviations**—CPC, Colección Paleontológica de Coahuila (Paleontological Collection of Coahuila) Saltillo, Coahuila Mexico.

#### SYSTEMATIC PALEONTOLOGY

Order: TESTUDINATA Klein, 1760

Suborder: CRYPTODIRA Cope, 1868

Family: KINOSTERNIDAE Baur, 1893

*YELMOCHELYS* gen. nov.

*Yelmochelys rosarioae* sp. nov.

Figs. 2-9

**Diagnosis**—Carapace small, with smooth shell, the maximum estimated length is 10 cm. Cervical scale thin and wide, extending the width of the nuchal. Vertebral scales hexagonal to diamond-shaped; first vertebral scale wide; third vertebral scale extending onto neural six; vertebral scales two, three, and four with small anterior projection at the midline; midline projection of fourth vertebral scale extending from sixth onto the fifth neural. Eight neurals, ten pairs of peripherals, and 11 pairs of marginals present; nuchal with costiform process extending across P1 to posterior edge of P2; groove for musk duct present on P3; plastron with narrow bridge, hypoplastron extending to middle of P4 and hypoplastron extending to posterior edge of P6; posterior lobe of plastron broad, without caudal notch and without femoral cusp on lateral edge; gular scale extending onto anterior end of entoplastron; abdominal scales meeting at the midline; the humeral scale covering the area between the gular and abdominal scales; two inframarginal scales present.

**Holotype**—CPC 278 (Fig. 9A-C): a partial plastron, including the entoplastron, partial hyo- and hypoplastra, and complete xiphiplastra. The plastron has folded over on itself at the suture between the hyo- and hypoplastron so the visceral surfaces of these elements face each other. The lateral edge of the plastral bridges is missing on both sides.

**Type locality**—Turtle Heaven Locality, Ejido of La Parrita (UTM coordinates: 14R:264481; 2826989, WGS 84). The Turtle Heaven Locality is in the upper Cerro del Pueblo Formation and was deposited in a fully non-marine environment (see Geology above).

**Referred material**—elements that were photographed and used in documenting variation in the individual elements are listed here.

NAP Locality, Ejido of La Parrita, upper non-marine beds in the Cerro del Pueblo Formation (UTM coordinates: 14R:63920; 2826778, WGS84): CPC 292, pygal (Figs. 5K, 7); CPC 293, pygal; CPC 327, neural 5 (Figs. 3E; 7); CPC 328,

neural 6 (Figs. 3F; 7); CPC 338, peripheral 2 (Figs. 5B; 7); CPC 329, neural 3; CPC 330, neural 3; CPC 331, neural 6; CPC 353, hyoplastron; CPC 376, costal 1.

Theropod Locality, Ejido of La Parrita, upper non-marine beds in the Cerro del Pueblo Formation (UTM coordinates: 14R:263854; 2826840, WGS84): CPC 282, costal 3-4 (Fig. 7); CPC 333, neural 3; CPC 334, neural 5; CPC 335, neural 5; CPC 336 (Figs. 3D; 7), neural 4; CPC 346, peripheral 8 (Figs. 5H, 7); CPC 377, costal 1; CPC 388, costal 5; CPC 402, hyoplastron; CPC 411, costal 3; CPC 412, costal 4.

Turtle Heaven Locality, Ejido of La Parrita, upper non-marine beds in the Cerro del Pueblo Formation (UTM coordinates: 14R:264481; 2826989, WGS 84): CPC 279, costal 1; CPC 280, costal 1; CPC 284, costal 6 (Fig. 7); CPC 285, costal 6; CPC 286, unidentified costal; CPC 287, costal 6; CPC 288, costal 6 (Fig. 4F); CPC 289, costal 3; CPC 290, costal 6; CPC 900, neural 1 (Figs. 3A, 7); CPC 291, conjoined neural 7 and 8 (Fig. 3H); CPC 321, neural 2 (Figs. 3B, 7); CPC 322, neural 3 (Figs. 3C, 7); CPC 323, neural 3; CPC 325, neural 4; CPC 326, neural 6; CPC 332, neural 7 (Figs. 3G, 7); CPC 337, peripheral 1 (Figs. 5A, 7); CPC 342, peripheral 6 (Figs. 5D, 7); CPC 343, peripheral 6; CPC 344, conjoined peripheral 5 and 6 (Fig. 5L); CPC 347, peripheral 9; CPC 348, peripheral 10 (Figs. 5J, 7); CPC 349, peripheral 10; CPC 356, peripheral 3; CPC 358, peripheral 7 (Figs. 5G, 7); CPC 359, peripheral 2; CPC 361, peripheral 2; CPC 899, peripheral 3 (Figs. 5C, 7); CPC 898, peripherals 6-7 preserved in articulation (Fig. 5M); CPC 369, peripheral 8; CPC 370,

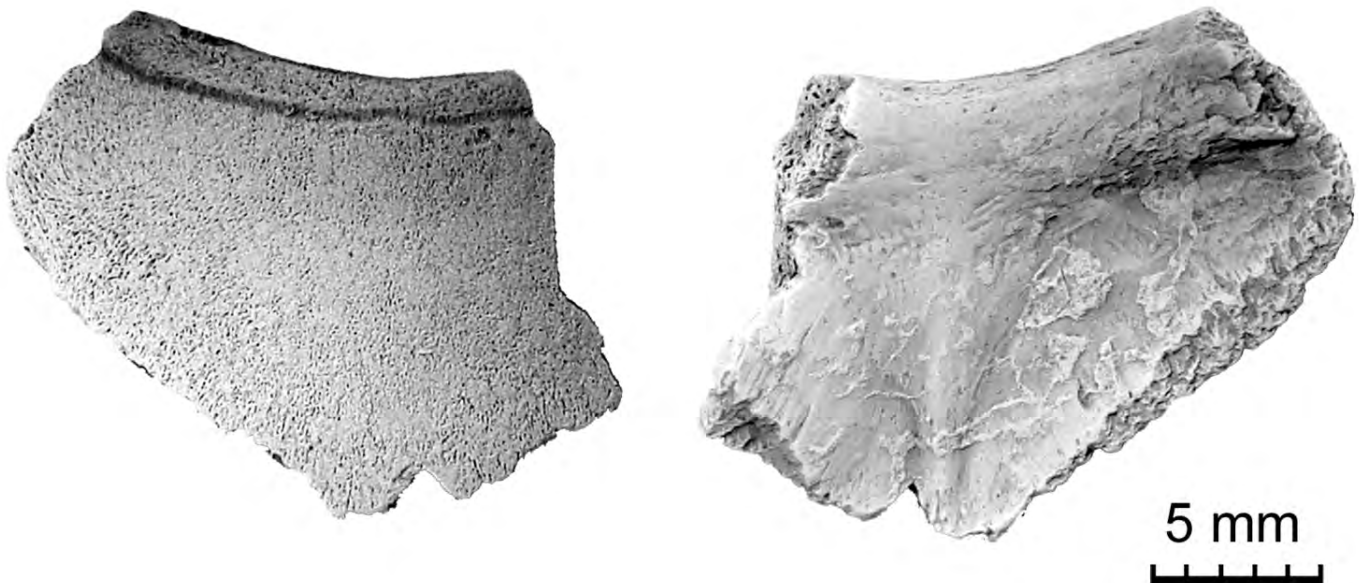
peripheral 8; CPC 372, peripheral 10; CPC 375, C1 (Figs. 4A, 7); CPC 379, costal 2 (Fig. 4B); CPC 380, costal 3; CPC 381, costal 3; CPC 383, costal 4 (Fig. 4D); CPC 384, costal 4; CPC 385, costal 4; CPC 386, costal 4; CPC 387, costal 4; CPC 391, costal; CPC 392, costal; CPC 393, costal; CPC 394, costal; CPC 395, pygal; CPC 399, hyoplastron CPC 400, hyoplastron; CPC 401, hyoplastron; CPC 409, costal 3 (Fig. 4C); CPC 410, costal 3.

Ejido of La Parrita, upper non-marine beds in the Cerro del Pueblo Formation, exact locality uncertain: CPC 283, costal 5 (Fig. 7).

Las Aguilas locality, Ejido of Porvenir de Jalpa (exact coordinates on file at the Coordinación de Paleontología, Secretaría de Educación Pública de Coahuila): CPC 897, nuchal (Figs. 2A-B, 7).

El Pelillal locality, Cañon del Tule Formation (exact coordinates on file at the Coordinación de Paleontología, Secretaría de Educación Pública de Coahuila): CPC 360, peripheral 2; CPC 355, peripheral 3; CPC 362, peripheral 4; CPC 363, peripheral 4; CPC 364, peripheral 4; CPC 341, peripheral 5 (Figs. 5E, 7); CPC 340, peripheral 6 (Figs. 5F, 7); CPC 366, peripheral 6; CPC 371, peripheral 9 (Figs. 5I, 7); CPC 413, peripheral 10; CPC 378, costal 2; CPC 382, costal 2; CPC 281, costal 2 (Fig. 7); CPC 403, costal 3; CPC 404, costal 3; CPC 405, costal 3; CPC 406, costal 3; CPC 407-408, costal 3; CPC 397, hyoplastron; CPC 398, hyoplastron.

**Etymology**—Generic name from “yelmo”, meaning helmet in Spanish, and “chelys”, meaning turtle, in reference to



**Figure 2.** Nuchal of *Yelmochelys rosarioae* gen. et sp. nov. Dorsal (left) and ventral view (right). Specimen CPC 897.

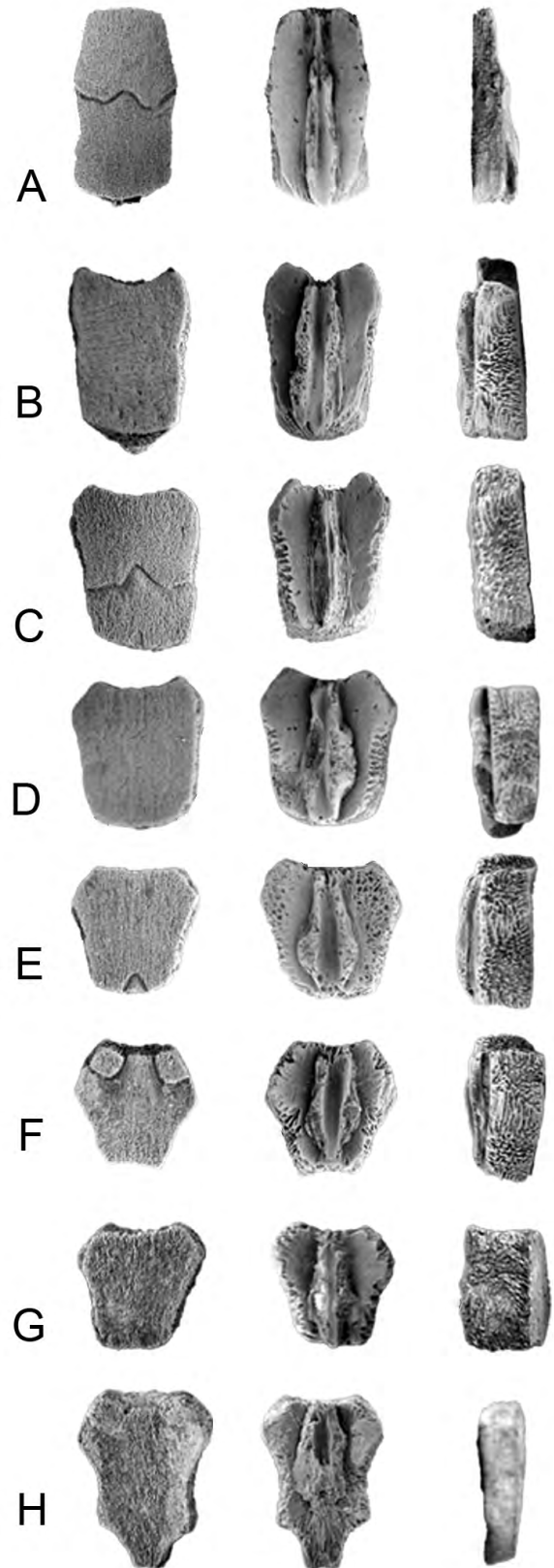
the helmet-like shape of this turtle. Specific names honors Rosario Gómez-Núñez, whose work as director of the Paleontological Commission of Coahuila has led to a great increase in awareness and understanding of the paleontological resources of Coahuila.

### Description

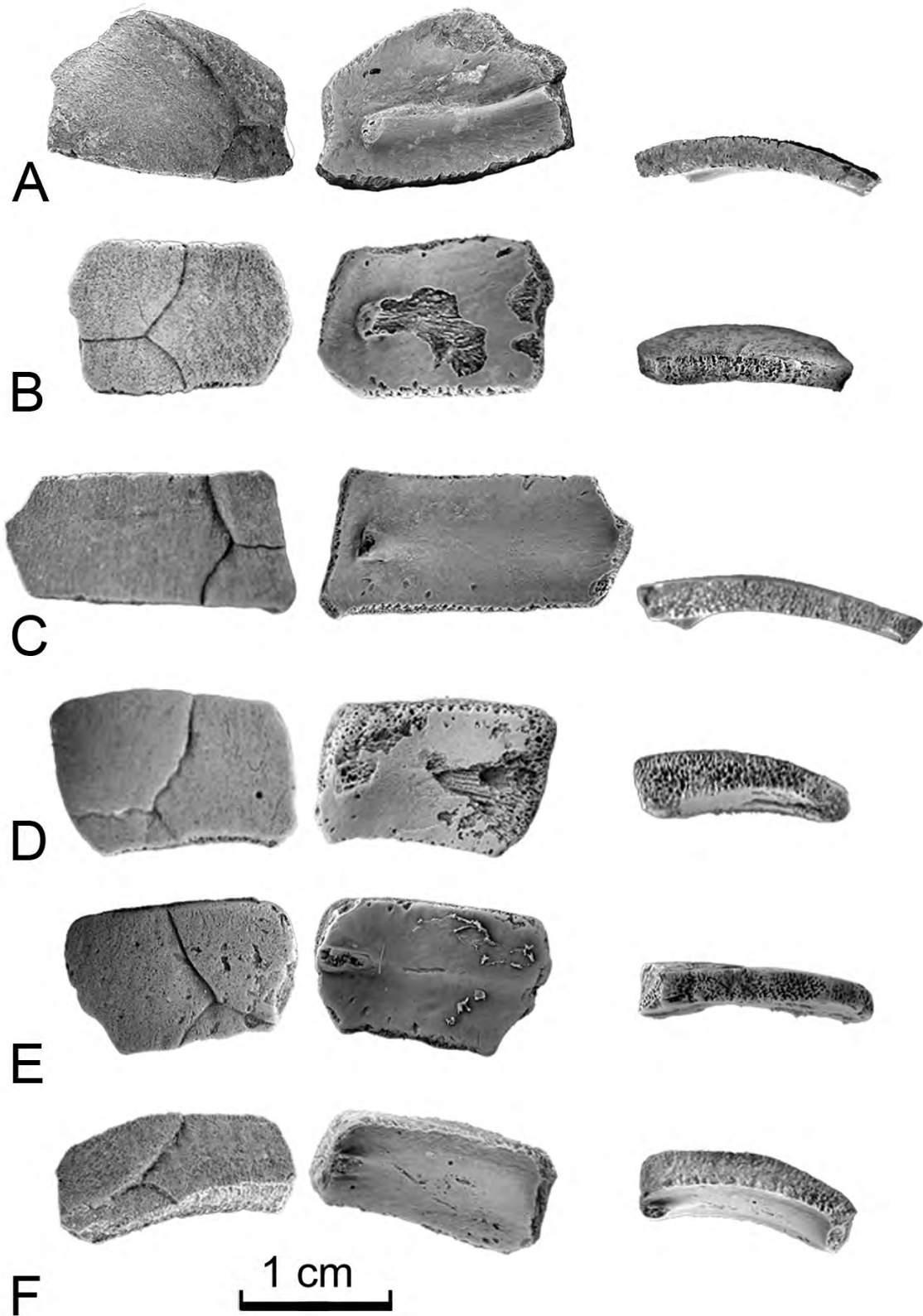
Except for the seventh and eighth costals, and the suprapygal(s), all the bones forming the carapace could be identified and most are represented by multiple specimens. With the exception of faint plications extending posteriorly from the sulci between the vertebral scales, all the shell elements are smooth.

**Nuchal**—The nuchal is a broad, triangular element with a shallow nuchal emargination (Figs. 2, 7). The cervical scale is very thin and extends along the full width of the nuchal, forming a rim along the anterior edge of the bone. The sulcus between the cervical scale and the first marginal scale was likely located on, or just adjacent to, the suture between the nuchal and first peripheral.

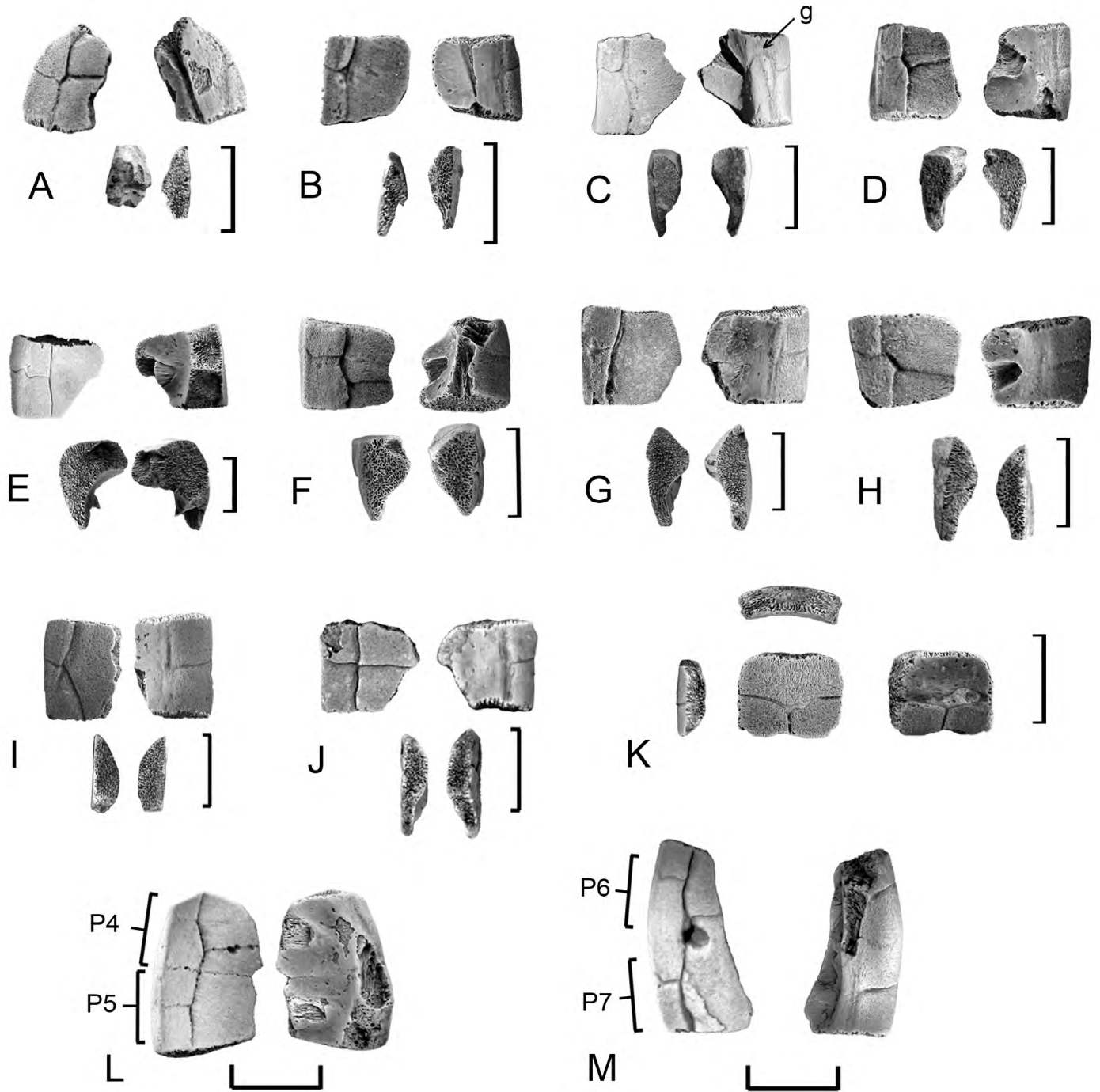
**Neurals**—Eight neurals are present (Figs. 3, 7). They differ from one another primarily in their relative length and the position of inter-vertebral sulci. The first neural is a long narrow rectangular element and in lateral view is thin compared to the more posterior neurals. The sulcus separating vertebral scales one and two, which crosses the middle of the bone, has a short anterior projection at the midline. Neural two is a relatively elongate and weakly hexagonal neural with very short antero-lateral edges. Neurals three to seven are all strongly hexagonal and all have short antero-lateral edges. The neurals decrease in length posteriorly. The sulcus between the second and third vertebral scales crosses neural three just posterior to the middle of this neural. As with the sulcus crossing neural one, the sulcus crossing neural three has a short anterior projection at the midline. The fourth neural is similar to the second in that it is not crossed by a sulcus but differs in being relatively shorter and having a more distinctly hexagonal shape. The sulcus between vertebral scales three and four, usually located on the fifth neural in other turtles, has shifted posteriorly and is located primarily on neural six. A strong anterior projection extends from neural six onto neural five. Neural seven is a short hexagonal element, about as long as it is wide. The only neural eight (Fig. 3H) is represented by a subtriangular bone (CPC 291), which is fused to neural seven.



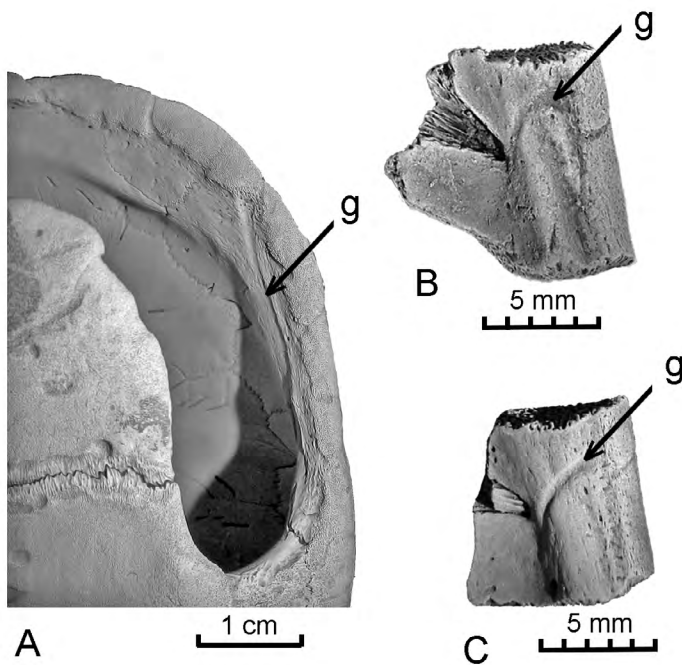
**Figure 3.** Neurals of *Yelmochelys rosarioae* gen. et sp. nov. in dorsal, ventral, and left lateral views. **A.** Neural 1, CPC 900. **B.** Neural 2, CPC 321. **C.** Neural 3, CPC322. **D.** Neural 4, CPC 336. **E.** Neural 5, CPC 327. **F.** Neural 6, CPC 328. **G.** Neural 7, CPC 332. **H.** Fused neurals 7 and 8, CPC 291. All to same scale.



**Figure 4.** Costals of *Yelmochelys rosarioae* gen. et sp. nov. in dorsal, ventral, and left lateral views. **A.** Costal 1, CPC 375. **B.** Costal 2, CPC 379. **C.** Costal 3, CPC 409. **D.** Costal 4, CPC 383. **E.** Costal 5, CPC 283. **F.** Costal 6, CPC 288. All to same scale.



**Figure 5.** Peripheral and pygal elements of *Yelmochelys rosarioae* gen. et sp. nov. in dorsal, ventral, anterior, and posterior views (clockwise in A-J). **A.** P1, CPC 337. **B.** P2, CPC 338. **C.** P3, CPC 899. **D.** P4, CPC 342, El Pelillal. **E.** P5, CPC 341. **F.** P6 CPC 340. **G.** P7, CPC 358. **H.** P8, CPC 346. **I.** P9, CPC 371 El Pelillal. **J.** P10, CPC 348. **K.** Pygal, CPC 292. **L.** P4-5 preserved in articulation, CPC 344. **M.** P6-7 preserved in articulation, CPC 898. Abbreviations: **g**, groove for musk duct; **P4**, peripheral 4; **P5**, peripheral 5; **P6**, peripheral 6; **P7**, peripheral 7. Scale bars are one cm.



**Figure 6.** Groove for the anterior musk duct of the extant kinosternid *Sternotheus* compared with the groove on the ventral surface of the third peripheral of *Yelmochelys rosarioae* gen. et sp. nov. **A.** Antero-lateral corner of the shell of *Sternotheus* in ventral view, specimen TMP 90.7.147. **B, C.** Third peripherals of *Yelmochelys rosarioae* showing variation in the development of the groove on the ventral surface of the peripheral. **B:** CPC 898(a), **C:** CPC 898(b). **g**=groove.

**Costals**—The costal series is represented by costals one to six (Figs. 4, 7). Complete costals are rare. Most specimens consist of their greatly thickened proximal ends. The costals are strongly curved when seen in edge view, indicating that the carapace was highly vaulted.

The first costal is relatively broad, triangular in shape, and bears a short articular surface for the first thoracic rib. Costals two, four, and six all bear interpleural sulci but differ in the relative position of the vertebral and pleural sulci. The vertebral scales become progressively wider posteriorly, so the sulcus marking the lateral edge of the second vertebral scale is located close to the proximal end of the second costal, while the sulcus marking the lateral edge of the fourth vertebral scale is strongly tapered and extends far laterally on the sixth costal. The third vertebral scale extends to an intermediate position on the fourth costal. Also, the position of the interpleural sulcus becomes located progressively more posteriorly on the costals. This sulcus is located just posterior to the middle of the second costal, while the sulcus is located near the posterior edge of the sixth costal. On the fourth costal the sulcus is in an intermediate position. The

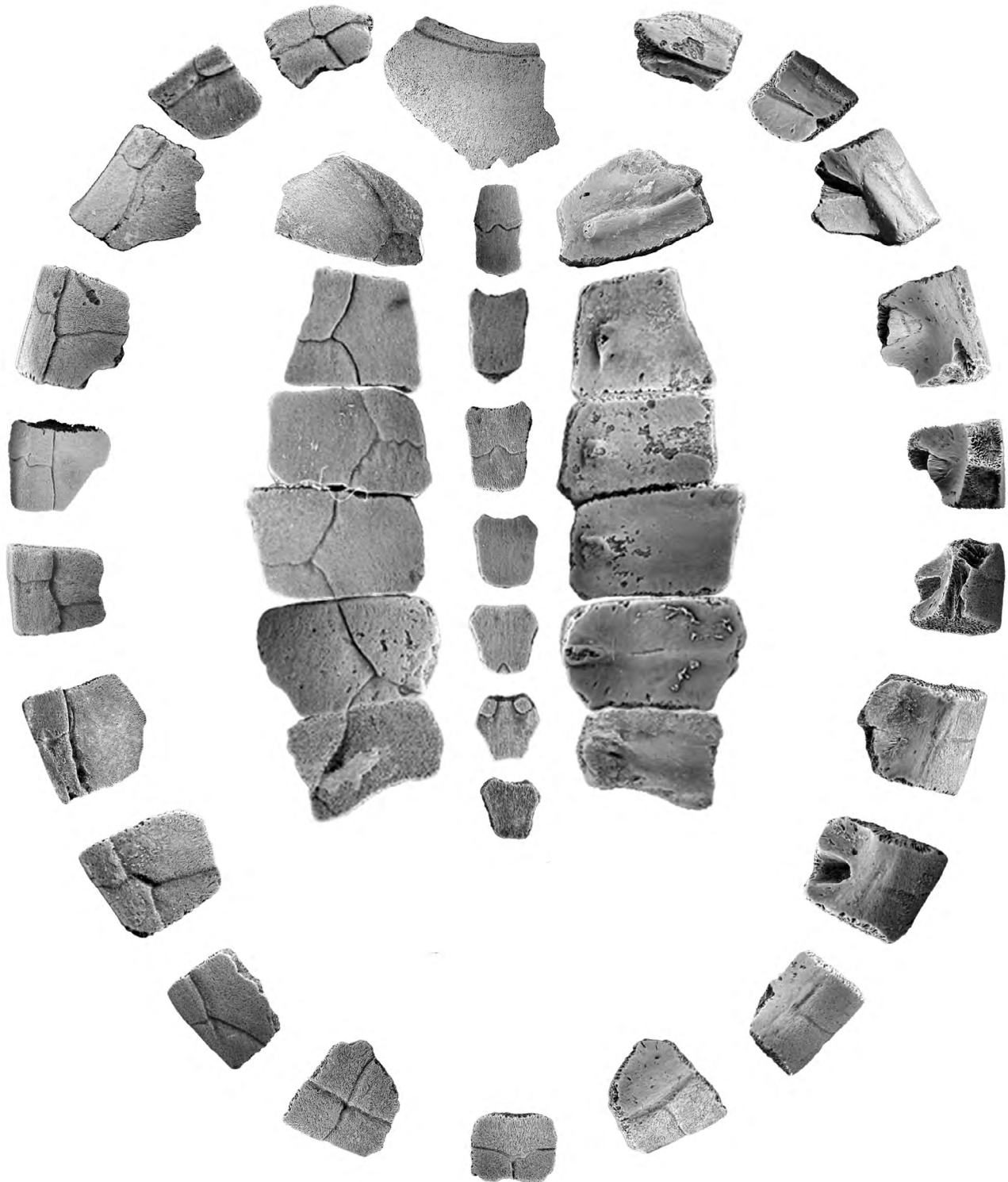
shape of the costals as seen in dorsal view varies in that the second costal is nearly straight and the sixth costal is strongly curved. Also, the position of the head of the rib of the sixth costal is reduced and located near its antero-medial corner while the head of the rib of the more anterior costals is located in a more central position.

The third and fifth costals are both crossed by the intervertebral sulci but can be differentiated by the position of the intervertebral sulcus. In the third costal, this is located mid-way along its medial end, while in the fifth, the sulcus between the third and fourth vertebral scales slopes to the posteromedial tip of the bone so that it extends onto the sixth neural, rather than the fifth as is usually the case. As a result, the fourth vertebral covers only a small triangular area along the posterior edge of the fifth costal.

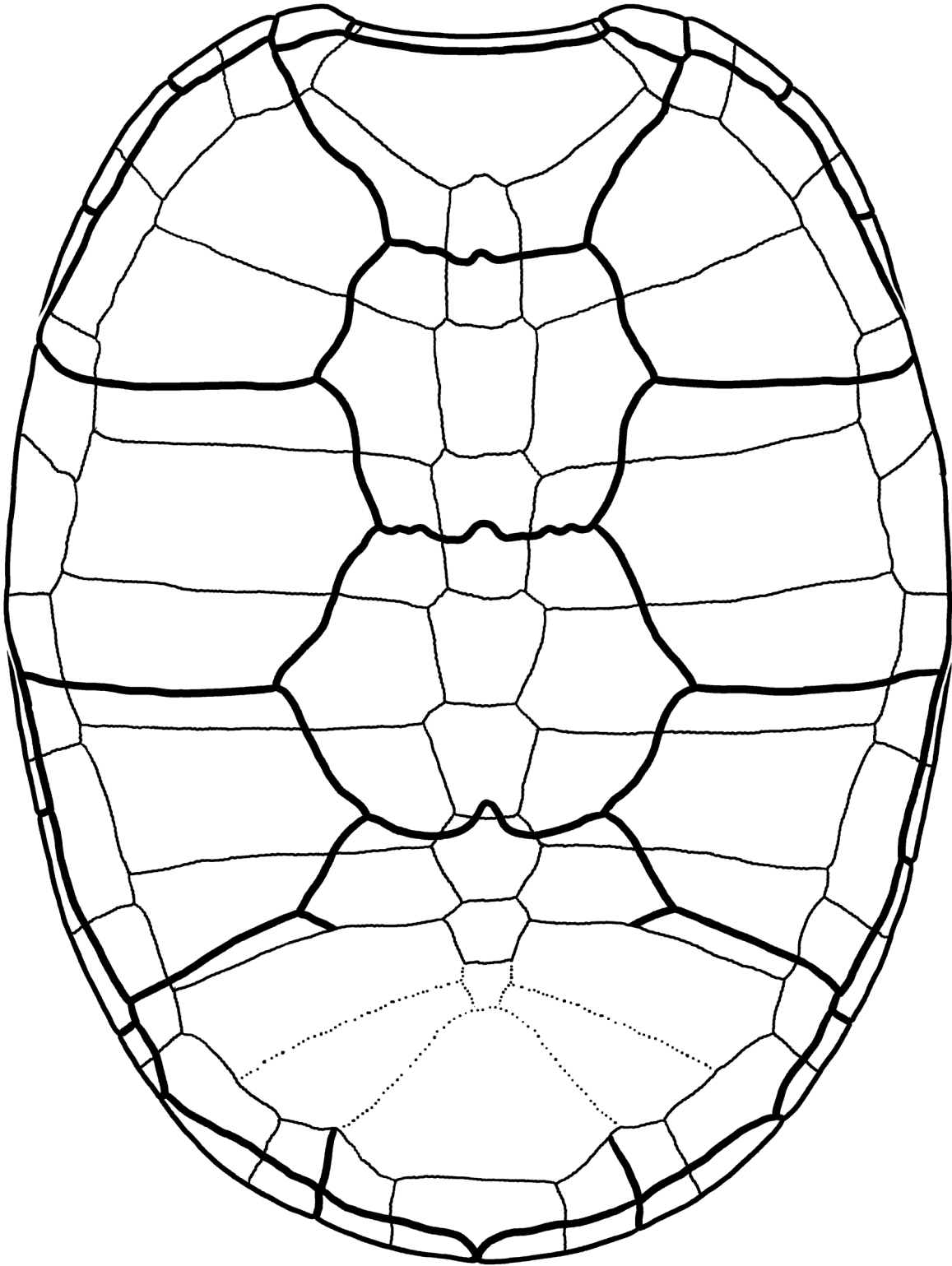
**Peripherals**—Ten peripherals are present in *Yelmochelys rosarioae* (Figs. 5-7). These could be oriented by the position of the inter-marginal sulcus, which slants anterolaterally or turns anteriorly at the free margin. The relative length of the marginal scales on the peripherals is also useful in orienting the peripherals since the anterior lapping marginal is typically shorter than the posterior one. As in the extant genus *Kinosternon*, the peripherals of *Y. rosarioae* would have been nearly vertical in orientation in the articulated shell, contributing to a highly vaulted shape. Peripherals one and two bear a groove for the costiform process of the nuchal. This groove crosses P1 and extends to, or nearly to, the posterior edge of P2. Although the costiform process nearly reaches the P2/P3 suture in more than half of the P2 specimens that were observed, this groove did not extend onto any of the P3 specimens.

Peripheral three is without inter-pleural sulci and has a posterior end that is thickened relative to the anterior end. The costal rib insertion on this peripheral forms a high angle with the medio-lateral axis of the bone, extending from the anterior corner to the middle of the element. A shallow groove on the ventral edge of P3 just posterior to the inter-marginal sulcus is interpreted as a groove for the anterior musk duct (Figs. 5C, 6). The width and depth of the groove is similar to that seen in extant kinosternids, such as *Sternotheus* (Fig. 6A), but the position of it differs. In the extant kinosternids, the groove extends forward along the ventral surface of P4 from the anterior tip of the hyoplastron to the second or first peripheral, whereas in *Yelmochelys* the groove extends laterally from its origin and crosses the ventral surface of peripheral three (Fig. 6B, C).

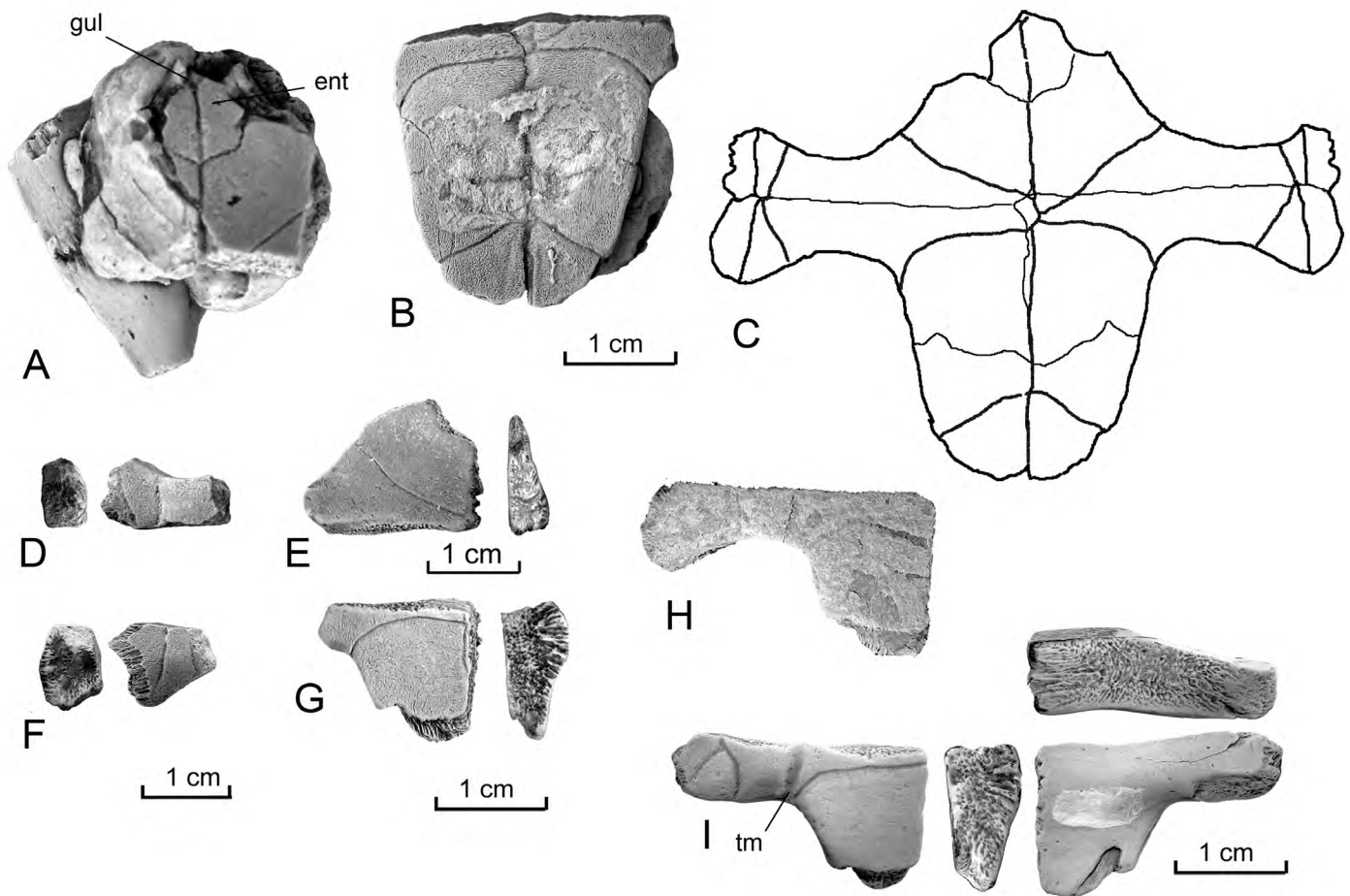
Peripherals four, five, and six are very robust elements that bear the sutural surface for the plastral bridge. The hyo- and hypoplastron both articulate with P5. The sutural surface for the hyo and hypoplastron are separated by a sharp crest.



**Figure 7.** Composite reconstruction of carapace of *Yelmochelys rosarioae* gen. et sp. nov. in exploded view (ie. peripherals and the neurals on the left and right sides are the same specimens only flipped). Specimens in this reconstruction are: nuchal, CPC 897; **P1**, CPC 337; **P2**, CPC 338; **P3**, CPC 899; **P4**, CPC 342, El Pelillal; **P5**, CPC 341; **P6**, CPC 340; **P7**, CPC 358; **P8**, CPC 346; **P9**, CPC 371; **P10**, CPC 348; pygal, CPC 292; costals; **C1**, CPC 375; **C2**, CPC 281; **C3**, CPC 282; **C4**, CPC 282; **C5**, CPC 283; **C6**, costal CPC 284; neurals; **N1**, CPC 900; **N2**, CPC 321; **N3**, CPC 322; **N4**, CPC 336; **N5**, CPC 327; **N6**, CPC 328; **N7**, CPC 332. Not to scale.



**Figure 8.** Composite reconstruction of carapace of *Yelmochelys rosarioae* gen. et sp. nov. in dorsal view based on a three-dimensional composite reconstruction of the carapace using isolated elements.



**Figure 9.** Plastron elements of *Yelmochelys rosarioae* gen. et sp. nov. Holotype, CPC 278. **A.** Partial hyoplastron and entoplastron in articulation. **B.** Right and left hypoplastra and xiphipetra in articulation. **C.** Reconstruction of plastron. **D.** Lateral end of hyoplastron in ventral and lateral articular views, CPC 352. **E.** Medial portion of hyoplastron, in ventral and medial articular views, CPC 351. **F.** Lateral end of hyoplastron in ventral and lateral articular views, CPP 399. **G.** Medial portion of hypoplastron, in ventral and medial articular views, CPC 398. **H.** Complete hypoplastron, in ventral view, CPC 353. **I.** Complete hypoplastron, with tooth marks, in ventral, dorsal, anterior articular, and medial articular views, CPC 901 from Turtle Heaven Locality, La Parrita. **ent**=entoplastron, **gul**=gular scale, **tm**=tooth mark.

The hyoplastral articular surface extends anteriorly onto P4 (Figs. 5D, 7), and the hypoplastron articular surface extends posteriorly onto P6 (Figs. 5F, 7). The sutural surface on P6 is divided into two areas, a short broad area that is a continuation of the surface on P5 that receives the hyoplastron, and a long narrow groove antero-medial to this that receives a process from the hypoplastron. This groove reaches the anterior end of P7 but, as demonstrated by a P6 and P7 preserved in articulation (Fig. 5M) and numerous isolated P7 elements, does not extend onto P7.

Peripheral seven, like P3, is without an interpleural sulcus and has one end thicker than the other but, unlike P3, the anterior end is thickest in P7. Peripherals eight-ten taper to a relatively sharp edge and show a progressive thinning of

the lateral edge of the element. Peripherals eight and nine are medio-laterally elongate elements. Peripheral 8 bears an interpleural sulcus. The fourth pleural scale has a short but distinct contact with the eighth marginal. Peripheral nine is without an interpleural sulcus. The marginal scales on this bone have a distinctive curved medial edge, with the tenth marginal scale being slightly larger than the eighth. Peripheral ten bears the sulcus separating pleural scale four from vertebral scale five. The postero-ventral corner of pleural scale four just touches the anterolateral corner of the eleventh marginal, so the pleural and marginal sulci form a cross on the external surface of this peripheral. Seen in lateral view, the tenth peripheral has a curved postero-medial edge indicating that it articulated with the suprapygal elements.

*Pygal*—The pygal is a rectangular element, slightly wider than high (Figs. 5, 7). The height of the pygal matches the height of the corresponding surface on the tenth peripheral, which, together with the evidence that the tenth peripheral contacts the suprapygal, indicates that the eleventh peripheral is absent. The vertebral-marginal sulcus is located near the posterior edge of the element.

*Carapace*—Together these elements allow for a composite reconstruction of the carapace (Figs. 7, 8). As reconstructed, the carapace is oval in shape and highly vaulted. The doming and outline of the carapace give the shell of *Y. rosarioae* a helmet-like shape similar to that of the extant *Kinosternon*. The estimated maximum length would not have exceeded 10 cm, and a length of 9 cm as in the composite reconstruction is likely more typical. A distinct but shallow nuchal emargination is present.

In general, the pattern of scales on the carapace conforms to that of extant kinosternids. The shape of the vertebral scales in *Y. rosarioae* is clearly indicated by the sulci on the costals. The first vertebral scale is wider than that of extant kinosternids with its lateral borders located on the first costal rather than the nuchal. The second to fourth vertebral scales are like those of extant kinosternids in having strongly angled lateral edges. The second vertebral scale is hexagonal in shape. The more posterior vertebral scales become wider and more distinctly diamond-shaped. The second, third, and fourth vertebral scales each have a small anterior projection at the midline. Anterior projections of the vertebral scales at the midline is also present in *Hoplochelys*, but *Yelmochelys* is unique in that the third vertebral scale extends onto the sixth neural element, rather than the fifth as is usually the case, with only the anterior projection of the fourth vertebral scale extending from the sixth onto the fifth neural bone.

All the pleural scales extend onto the peripherals. The first pleural scale has a short area of contact with the first marginal. The more posterior pleural scales have a relatively longer contact with their anterior-most marginal scales.

Eleven marginals are present. These are reduced to a narrow rim around the edge of the carapace. The contact between marginal scale 1 and the cervical scale is located at the suture between the nuchal and first peripheral, so the first marginal would have been located entirely on peripheral one. The remaining marginal scales span the peripheral elements and the sulci between adjacent marginals are generally located slightly anterior to the middle of the peripheral. Marginal ten has a distinctive curved antero-medial edge, similar in shape to the strongly curved anterior margin of this scale in *Kinosternon*, although the marginal is not as enlarged as in that genus.

*Plastron*—The plastron has a broad ventral surface and narrow bridge region (Fig. 9). The outline of the anterior lobe of the plastron is not known since no epiplastra could be identified. The posterior lobe is completely preserved in the type specimen (Fig. 9B) and is broad and has a rounded outline that shows no development of an anal notch.

The entoplastron, preserved in articulation with the hyoplastron in the type specimen (Fig. 9A), is shield-shaped with its widest point located near its posterior edge.

The hyo- and hypoplastra form most of the ventral surface of the plastron and contribute equally to the formation of the bridge. The bridge is long and round in cross section, forming a single rod-like buttress that extends from a thickened region in the center of the plastron to the peripherals. The thickest portion of this buttress is located on the hypoplastron just posterior to the hyo- hypoplastron suture.

The xiphiplastron forms the posterior half of the posterior lobe of the plastron. The suture with the hypoplastron is transversely oriented, with a short anterior projection near its lateral edge.

Sulci on the plastron are distinct. The gular scale just touches the anterior end of the entoplastron. A strong midline sulcus extends posterior to this to cross the entoplastron. Four pairs of scales cover the ventral surface of the plastron posterior to the gular scale. The most anterior of these occupies the space usually occupied by the humeral and pectoral scales. Hutchison and Bramble (1981) argued that this scale likely formed by reduction of the pectoral scale and is homologous to the humeral scale of more basal turtles. The posterior edge of the humeral scale extends from the axillary notch to the midline just posterior to the hyo-hypoplastron suture. Thus the posterior tip of this scale extends onto the hypoplastron. Posterior to the humeral scale, the normal complement of abdominal, femoral and anal scales are present. The abdominal scale has a narrow area of contact at the midline. This differs from *Hoplochelys*, where the abdominal scale has withdrawn from the midline. The posterior border of the abdominal scale extends transversely across the plastron and then curves posteriorly to end on the inguinal notch. The femoral scale covers the hypoplastron-xiphiplastron suture so the anal scale is located entirely on the xiphiplastra. The femoral/anal sulcus is V-shaped pointing anteriorly.

Two inframarginals are present, the inguinal and axillary scales. These contact one another to form a band around the lateral end of the plastral bridge.

As reconstructed, the plastron is much smaller than the carapace. The anterior lobe would have reached nearly to the anterior end of the carapace, but the posterior lobe would have extended only to the posterior third of the shell.

### Phylogenetic Analysis

The phylogenetic analysis recovered six most parsimonious trees (TL = 106; CI = 0.6604; HI = 0.3396; RI = 0.7647). The strict consensus tree has a fully resolved Kinosternidae with *Yelmochelys* retrieved as a stem kinosternid, and sister taxon to all other kinosternids (Fig. 10). This is supported by five characters: 1) presence of a groove for the anterior musk duct; 2) peripheral eleven and marginal twelve absent (character 17); 3) hexagonal or diamond-shaped vertebral scales (character 18); 4) presence of only two inframarginals (character 26); and 5) reduced extent of the plastron-carapace articulation (character 23). All relevant clades show strong support (>70% bootstrap values).

### DISCUSSION

The shell of *Yelmochelys rosarioae* is generally similar to that of extant kinosternids in being small and helmet shaped, and in that the marginals form a narrow band around the edge of the shell.

The presence of a groove for the anterior musk duct has been recognized as a feature that is restricted to kinosternids and its presence in *Yelmochelys* offers strong support for inclusion of the taxon in Kinosternidae (Hutchison 1991). A difference is present in the length of this groove in *Yelmochelys* compared to that in extant members of the group: in extant kinosternids, the groove extends forward along the ventral surface of P4 from the anterior tip of the hyoplastron to the second or first peripheral before crossing the ventral edge of the peripherals (Fig. 6A), whereas in *Yelmochelys*, the groove extends laterally from the lateral tip of the rib of the first costal so crosses the ventral surface of the third peripheral (Fig. 6B, C). Despite these differences, the groove on the third peripheral of *Yelmochelys* is identified as homologous to the groove for the musk duct of extant kinosternids because it originates from a similar position relative to the anterior lobe of the plastron, it is similar in width and depth, and crosses the ventral edge of the shell in a similar manner.

Loss of the eleventh peripheral has long been regarded to be a diagnostic feature of Kinosternidae. *Hoplochelys*, which Hutchison (1991) considered the closest relative of the Kinosternidae, has eleven peripherals, as do all other crown turtles except Carettochelyidae and Trionychidae. Although *Yelmochelys* is represented by disarticulated elements, the shape of the tenth peripheral indicates that it articulated with the suprapygal and pygal and an eleventh peripheral was absent. Hutchison (1991) suggested loss of the eleventh peripheral in kinosternids strengthened the carapace by reducing the number of bone to bone contacts present. This is consistent with other features that would have strengthened the shell, including the greatly thickened bones of the

carapace, particularly the neurals and proximal end of the costals, the helmet-like shape of the carapace, and the thick plastral bones that form a buttress extending from the sides of the carapace to the midline.

The presence of hexagonal or diamond-shaped vertebral scales was considered to be a diagnostic feature of the Kinosternidae by Hutchison (1991) because in *Hoplochelys*, and primitive turtles generally, the vertebral scales are rectangular or have only weakly angled lateral edges.

Hutchison (1991) concluded that the presence of two inframarginals was a derived feature of the Kinosternidae because *Hoplochelys* retains three inframarginals. Thus the presence of this feature supports placement of *Yelmochelys* within the family. Hutchison (1991) considered this feature as less robust in indicating relationships than the loss of the eleventh peripheral and shape of the neurals because it is also thought to be present in *Agomphus* Cope, 1871. However, a specimen of *Agomphus* Cope, 1871 in the collections of the Academy of Natural Sciences, Philadelphia (specimen ANSP 15359) suggests that more than two inframarginals are present in that genus (Joyce, pers. Comm.). However, because this could not be confirmed by direct observation, the coding of *Agomphus* used by Hutchison (1991) is retained for this analysis.

The length of the articulation between the plastron and carapace is a variable feature in extant kinosternids, but Hutchison (1991) concluded that kinosternids were derived relative to other kinosternoids in that the articulation between the plastron and carapace is reduced so extends only from P4 to P6. The condition seen in *Hoplochelys*, in which the articulation extends from P3 to P7, was interpreted as plesiomorphic for the Kinosternoidea. Thus the presence of a reduced articulation between the plastron and carapace, with the articulation being restricted to the fourth to sixth peripherals, in *Yelmochelys* supports its placement within the Kinosternidae.

A basal position of *Yelmochelys* within the Kinosternidae is indicated by the absence of three derived character-states that unite crown Kinosternidae. These are:

1. The presence of distinct abdominal scale that contact at the midline (character 30). All later members of the Kinosternidae lack a distinct abdominal scale. Thus, the presence of distinct abdominal scales in *Yelmochelys* is a primitive character-state that places it outside the crown-group. Hutchison and Bramble (1981) hypothesized that the absence of abdominal scales in kinosternids was a result of expansion of the humeral scale to occupy areas normally covered by the abdominal scale. In part, this interpretation was supported by the condition in *Hoplochelys* in which the abdominal scales are withdrawn



from the midline. If correct, the abdominal scales of *Yelmochelys* are plesiomorphic relative to both later kinosternids and *Hoplochelys* in that they contact one another at the midline. Thus, according to the results of this analysis, withdrawal of the abdominal scales from the midline must have occurred at least twice within the Kinosternoidea. An alternative interpretation is that a midline contact re-evolved twice, once in the *Dermatemys* stem lineage and once in *Yelmochelys*. However, this is considered here to be less likely because the presence of this primitive character state in the most basal and earliest member of the clade is more likely a result of retention rather than a reversal.

2. The presence of long costiform processes on the nuchal (character 4). The length of the costiform process of *Yelmochelys* agrees with that of other kinosternoids in that it does not extend into the third peripheral (character 4, state 1). However, in *Yelmochelys* the costiform process consistently extends past the middle of the second costal, generally reaching, or nearly reaching, the posterior edge of the second peripheral. In *Baltemys*, *Xenochelys*, and extant kinosternids the costiform process is also relatively shorter. As described by Hutchison (1991) in *Xenochelys lostcabinensis* Hutchison, 1991 the costiform process extends about 20% of the length of the second peripheral, while in *Baltemys* it extends about 12% of the length of the second peripheral into that bone. In extant kinosternids, the costiform process also relatively short; the length of the costiform process in *Staurotypus* is about equal to that of *Xenochelys*, while in *Kinosternon* the process barely touches the second peripheral (Hutchison, 1991). Knauss et al. (2011) considered the presence of a long costiform process to be the primitive condition for the clade including kinosternoids and chelydroids. Thus, the presence of a relatively long costiform process in *Yelmochelys* can be interpreted as a plesiomorphic condition within the Kinosternidae. According to this interpretation, *Hoplochelys* would have independently acquired the derived character-state of a short costiform process.
3. The rib of the first costal terminates within peripheral 3 (character 8). In *Baltemys* and *Xenochelys* the rib of the first costal enters the posterior half of P3 and extends through P3 to the suture with P4 or into that bone. Among recent kinosternids, both conditions are present: in *Staurotypus* the rib of the first costal extends into P4, but in *Kinosternon* it terminates within P3. *Hoplochelys* also shows the derived condition of the rib of the first costal terminating within P3. Thus, in this feature, *Hoplochelys* shows parallel development of the derived condition.

In other respects, the results of the PAUP analysis presented here match those of Knauss et al. (2011). Knauss had argued that the sister-group relationship of *Hoplochelys*, which first occurs in the late Campanian, with the Dermatemydidae indicates that the Dermatemydidae and Kinosternidae had diverged by the late Campanian. Subsequent turtle molecular divergence studies (Joyce et al. 2013, Warnock et al. 2015) agreed with these conclusions. The inclusion of *Yelmochelys* in Kinosternidae as a stem member of the group provides further supports for this.

The small size and helmet-like shape of *Yelmochelys* suggests that this body form is a basal morphotype for the Kinosternidae. However, it differs from crown-group members in that the elements of the carapace and plastron are greatly thickened. Given that moderately large durophagous crocodiles are present in the assemblage, it is reasonable to interpret the great thickness of the bones of the carapace and plastron and the helmet-like shape of the carapace of *Yelmochelys* as adaptations to prevent crushing by these predators. That *Yelmochelys* was subject to predation is documented by a tooth mark on a hypoplastron (Fig. 9I). The reduced thickness of the elements of the carapace and plastron in later kinosternids, including the Eocene genera *Baltemys* and *Xenochelys* may be associated with further elaboration of the musk duct/gland system for a defensive function. The development of this chemical defense mechanism would have allowed them to retain a small body size while living in close proximity to predators that could easily have crushed their shell.

The abundance of the small, smooth-shelled kinosternids in the Late Cretaceous of Mexico is striking. Although it is widespread in the Western Interior, it is typically rare. For example, in an inventory of 436 elements from the Fruitland/Kirkland formations, Sullivan et al. (2013) noted that only six specimens of the small, smooth-shelled kinosternid are present in museum collections. This pattern of distribution, together with the latitudinally restricted distribution of kinosternids in the Late Cretaceous of North America, agrees with the hypothesis that the group originated in the southern-most portion of the continent.

#### ACKNOWLEDGMENTS

The authors thank Rosario Gómez-Núñez (Coordinación de Paleontología, Secretaría de Educación Pública de Coahuila) and her family for unqualified support, tireless efforts, and kind hospitality throughout all phases of this project. We also thank José López-Espinoza for his assistance in the field. José Flores Ventura donated specimens he had collected for this study, including the nearly complete nuchal and the co-joined third and fourth peripherals figured in this

paper. José Ignacio Vallelo González assisted in producing a three dimensional composite reconstruction of *Yelmochelys rosarioae*, which helped visualize the relationship of the isolated elements. Xiao-chun Wu assisted with the initial phylogenetic analysis. Thanks also to Walter Joyce, Tyler Lyson, and Jason Bourque for reviewing the manuscript and making comments and suggestions. As well as providing a thorough review of the paper, Walter Joyce shared unpublished observations on *Agomphus* which help with the phylogenetic interpretations and redrafted figure 8 which greatly improved the effectiveness of that figure. The initial phases of this work were undertaken with financial support from the National Geographic Society through grant #7171-01 provided to Scott Sampson. Additional funding was provided by the Cooperating Society of the Royal Tyrrell Museum. The phylogenetic software TNT was made available by the Willi Hennig Society.

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### Appendix 1

Characters used for the PAUP analysis presented here. Unmodified from Knauss et al. (2011). Characters with an asterisk are run ordered.

1. Presence and development of projecting costal keel or tenting in adults (modified from [Hutchison and Bramble 1981](#), 11; [Hutchison 1991](#), 13): 0 = absent; 1 = present, spans majority of shell as “tenting”; 2 = present, spans majority of shell as a low, rounded, but projecting keel; 3 = present, spans majority of shell as sharp, distinct, projecting keel.
2. Presence and extent of median keel: 0 = absent; 1 = present, only developed along the posterior half of shell; 2 = present, developed along majority of shell, even if faint on the anterior half of the shell.
3. Development of median keel: 0 = consisting of multiple posteriorly fading subkeels that abut at intervertebral sulcus; 1 = consisting of a single, more or less uninterrupted keel.
- \*4. Costiform processes (modified from [Hutchison and Bramble 1981](#), 12; [Joyce 2007](#), 63): 0 = costiform processes rib-like, span two peripherals to insert in peripheral III; 1 = costiform processes tapered, span peripheral I to insert into peripheral II; 2 = costiform processes short, but tapered, inserts into peripheral I; 3 = costiform processes absent.
5. Relative position of costal I/II suture relative to peripheral series (modified from [Hutchison 1991](#), 17): 0 = contacts peripheral III; 1 = contacts peripheral IV.
6. Relative position of costal II/III suture relative to peripheral series (modified from [Hutchison and Bramble 1981](#), 14; [Hutchison 1991](#), 34): 0 = contacts peripheral IV; 1 = contacts peripheral V.
7. Relative position of costal III/IV suture relative to peripheral series (modified from [Hutchison and Bramble 1981](#), 34; [Hutchison 1991](#), 35): 0 = contacts peripheral VI; 1 = contacts peripheral V.
8. Termination of costal I rib (modified from [Hutchison 1991](#), 32): 0 = costal rib I terminates within peripheral III; 1 = costal rib I may enter peripheral III, but terminates within peripheral IV.
9. Costal rib VIII (reworded from [Hutchison 1991](#), 7): 0 = medially contacts vertebral column; 1 = medial portion of rib not developed.
- \*10. Reduction of neural column ([Hutchison and Bramble 1981](#), 9, 25, 48; [Hutchison 1991](#), 3): 0 = eight neurals present; 1 = seven neurals present; 2 = six neurals present.
11. Number of suprapyrgals ([Hutchison and Bramble 1981](#), 44; [Hutchison 1991](#), 12): 0 = two present; 1 = one present.
12. Anterior contacts of neural II (reworded from [Hutchison 1991](#), 14): 0 = costal I and II; 1 = costal II only.
13. Anterior contacts of neural III (reworded from [Hutchison 1991](#), 9): 0 = costal III only; 1 = costal II and III.
14. Anterior contacts of neural IV (reworded from [Hutchison 1991](#), 25): 0 = costal III and IV; 1 = costal IV only.
15. Anterior contacts of neural V (reworded from [Hutchison 1991](#), 28): 0 = costal V only; 1 = costal IV and V.
16. Presence and development of musk duct groove (modified from [Hutchison and Bramble 1981](#), 26, 45, 49; [Hutchison 1991](#), 11, 18): 0 = musk duct groove absent; 1 = musk duct groove present and terminates on peripheral II; 2 = groove present and terminates on peripheral I.
17. Number of peripherals ([Hutchison and Bramble 1981](#), 27; [Hutchison 1991](#), 1): 0 = 11 pairs of peripherals present; 1 = 10 pairs of peripherals present.
18. Shape of vertebrae II–IV in adult specimens (modified from [Hutchison and Bramble 1981](#), 29; [Hutchison 1991](#), 5): 0 = more or less square; 1 = more or less rectangular, at least one and a half times longer than wide; 2 = distinctly hexagonal.
19. Elevation of marginal X relative to marginal IX (modified from [Hutchison 1991](#), 6): 0 = even or only slightly elevated; 1 = distinctly elevated.
20. Posterior plastral lobe shape (modified from [Hutchison and Bramble 1981](#), 20; [Hutchison 1991](#), 20): 0 = posterior lobe tapers to a distinct point; 1 = posterior lobe rounded, anal notch absent; 2 = posterior lobe rounded, distinct anal notch present.
21. Hyoplastral buttress (modified from [Hutchison and Bramble 1981](#), 15): 0 = elongate hyoplastral buttress absent; 1 = hyoplastron forms long buttress that runs along the visceral surface of peripherals and terminates on peripherals; 2 = hyoplastron forms buttress that runs along the visceral side of the peripherals and terminates on costals.
22. Anterior extent of surficial ossified hyoplastral bridge (modified from [Hutchison and Bramble 1981](#), 13, 37; [Hutchison 1991](#), 29): 0 = hyoplastron contacts peripheral IV on the shell surface; 1 = hyoplastron contacts peripheral V on the shell surface.
- \*23. Hypoplastral buttress (modified from [Hutchison and Bramble 1981](#), 13, 37; [Hutchison 1991](#), 8): 0 = elongate hypoplastral buttress absent; 1 = hypoplastron forms buttress that runs along the visceral surface of peripherals and terminates on peripheral VII; 2 = hypoplastron forms long buttress that runs along the visceral surface of peripherals and terminates on peripheral VIII; 3 =

- hypoplastron forms long buttress that runs along the visceral surface of peripherals and terminates on peripheral IX.
24. Posterior extent of surficial ossified hypoplastral bridge (modified from [Hutchison and Bramble 1981](#), 13, 37; [Hutchison 1991](#), 8): 0 = hypoplastron contacts peripheral VI on the surface; 1 = hypoplastron contacts peripheral VII on the surface; 2 = hypoplastron contacts peripheral VIII on the surface.
  25. Entoplastron ([Hutchison and Bramble 1981](#), 52 in part; [Hutchison 1991](#), 31): 0 = present; 1 = absent.
  26. Number of inframarginals (modified from [Hutchison and Bramble 1981](#), 5, 10, 19; [Hutchison 1991](#), 4): 0 = four or more; 1 = three; 2 = two.
  27. Overlap of hyo/hypoplastral suture by inframarginal series (modified from [Hutchison and Bramble 1981](#), 6): 0 = axillary overlaps hyo/hypoplastral suture; 1 = inframarginal II or III overlap hyo/hypoplastral suture; 2 = inguinal overlaps hyo/hypoplastral suture.
  28. Intergular ([Hutchison and Bramble 1981](#), 22; [Hutchison 1991](#), 19): 0 = absent; 1 = large intergular present.
  29. Pectorals ([Hutchison and Bramble 1981](#), 2): 0 = present; 1 = absent.
  - \*30. Abdominals ([Hutchison and Bramble 1981](#), 23, 28; [Hutchison 1991](#), 2): 0 = absent; 1 = present, but medial contact absent; 2 = present, partial medial contact present; 3 = present, medial contact along almost the entire anteroposterior length (i.e., the abdominal medial length is nearly equal to or possibly greater than its lateral length).
  31. Contribution of the abdominal to the axillary notch: 0 = present, pectorals or humerals do not contact inframarginals; 1 = absent, pectorals or humerals contacts inframarginals.
  32. Anal scales ([Hutchison and Bramble 1981](#), 33): 0 = paired; 1 = fused.
  33. Orientation of epi/hypoplastral suture (modified from [Hutchison and Bramble 1981](#), 35, 40, 50; [Hutchison 1991](#), 21): 0 = oriented sloping backwards; 1 = oriented transverse or rising towards the front.
  34. Direct overlap of gular/humeral sulcus with epiento/hypoplastral suture (modified from [Hutchison 1991](#), 33): 0 = absent; 1 = present.
  - \*35. Placement of humeral/femoral sulcus (modified from [Hutchison and Bramble 1981](#), 32, 53; [Hutchison 1991](#), 26, 36): 0 = placed over hyo/hypoplastral suture; 1 = placed over hypoplastron; 2 = placed over hypo/xiphoplastral suture.
  36. Frontal contribution to orbit ([Hutchison 1991](#), 38; [Meylan and Gaffney 1989](#), 16): 0 = absent; 1 = present.
  37. Maxilla/quadratojugal contact ([Hutchison 1991](#), 39; [Meylan and Gaffney 1989](#), 17): 0 = absent; 1 = present.
  38. Lingual ridges (i.e., maxillary tooth of [Meylan and Gaffney 1989](#)) on the palate ([Hutchison and Bramble 1981](#), 16; [Hutchison 1991](#), 40; [Meylan and Gaffney 1989](#), 5): 0 = absent; 1 = present.
  39. Enlarged nose scale ([Hutchison 1991](#), 41): 0 = absent; 1 = present.
  40. Parietal contribution to processus trochlearis oticum (taken from [Hutchison 1991](#), 42; [Meylan and Gaffney 1989](#), 44): 0 = absent, or very slightly present; 1 = significant contribution present.
  - \*41. Foramen stapedio-temporale ([Hutchison and Bramble 1981](#), 4; [Meylan and Gaffney 1989](#), 1): 0 = large foramen for thick blood vessel present; 1 = stapedia foramen reduced to the size of a cranial nerve foramen; 2 = absent.
  42. Foramen posterius canalis carotici interni (modified from [Gaffney and Meylan 1988](#), 3; [Hutchison 1991](#), 43): 0 = not fully formed by bone; 1 = fully surrounded by pterygoid; 2 = fully surrounded by the pterygoid ventrally and the opisthotic dorsally.
  43. Ventral process of cervical vertebra VIII ([Hutchison and Bramble 1981](#), 31; [Hutchison 1991](#), 44; [Meylan and Gaffney 1989](#), 26): 0 = single; 1 = double, split lengthwise.
  44. Size of pectineal process (modified from [Hutchison 1991](#), 47): 0 = short; 1 = long.
  45. Orientation of pectineal process (modified from [Hutchison 1991](#), 47): 0 = anteriorly oriented; 1 = laterally oriented.
  - \*46. Thelial process (modified from [Meylan and Gaffney 1989](#), 37; see [Joyce 2007](#) for comment regarding primary homology): 0 = absent; 1 = low process developed; 2 = clear process developed.
  - \*47. Iliac notch (modified from [Meylan and Gaffney 1989](#), 36): 0 = absent; 1 = slight notch developed; 2 = deep notch developed.
  48. Medial pectoral processes and ridges: 0 = absent; 1 = present.

## Appendix 2

Character matrix. Extant and fossil turtles included in the PAUP analysis presented here and their characters. *Xenochelys bridgerensis* is not included in this analysis because it codes close to *X. lostcabinensis*. *Baltemys velogastos* from the Eocene of the Huerfano Formation of Colorado, recently described by Lichtig and Lucas (2015) was also not included because it closely resembles *B. staurogastos*. Coding of taxa presented in Knauss et al. (2011) unaltered except for *Claudius*, where in the published matrix two characters represented by dashes (characters 26 and 27) were incorrectly electronically modified by being replaced by a single m-dash. Symbols used in this matrix: a, 0/1; b, ½; ?, missing data; -, not applicable.

### *Chelydra serpentina*

00-00000000000a000000-1-0100010000-0000000000000

### *Macrochelys temminckii*

00-000000001110000000-1-01?0010000-0000001100200

### *Agomphus pectoralis*

00-30001?a?0101?010000?10 b20121000-??????????????

### *Dermatemys mawii*

00-2000002a010100102203200111310a0-a010020011111

### *Notomorpha garmanii*

221?0a00?00010100100?02101201210a0-??????????????

### *Baltemys wyomingensis*

011200a000001010010120320ab0121000-1010021010221

### *Staurotypus triporcatus*

321100111110001212000001022010-1011010101010221

### *Claudius angustatus*

00-100001110aaa2121001000--010-101-01010101010221

### *Baltemys staurogastos*

10-111011211001212000001022010-0001??????????????

### *Xenochelys lostcabinensis*

10-111011211001112120001022110-0101??????????????

### *Xenochelys formosa*

00-11101?211010112120001022110-0101??????????????

### *Kinosternon flavescens*

00-b010012110a1112ab0001122110-01020101112101221

### *Sternotherus carinatus*

00-20100121a010112120001122010-01010101112101221

### *Hoplochelys crassa* (combined)

221101a?000a1a1?0100102101201100000??????????????

### *Hoplochelys clark*

2201aaa1?0?1101?0100102101201100001??????????????

### *Yelmochelys rosarioae*

0001???0?0?010111201000002011200?0-??????????????