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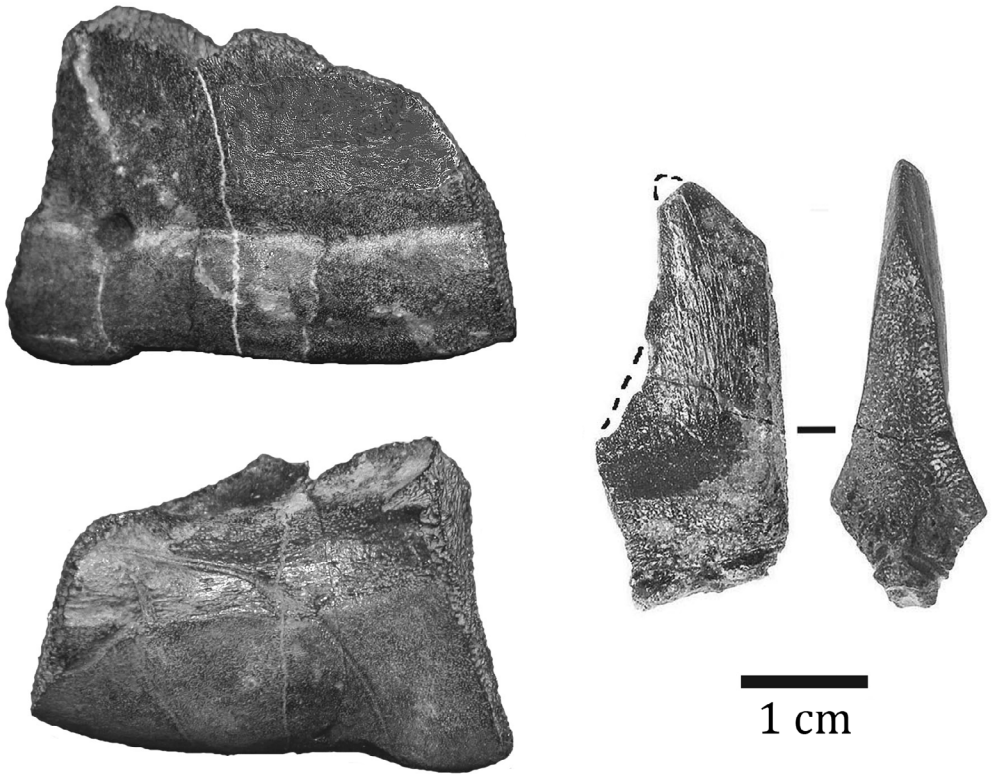

J. Howard HUTCHISON and James W. WESTGATE (2024). Reptiles from the late Eocene Jackson Group of Arkansas

Cover: Fossils of the kinosternid turtle *Xenochelys* sp. (left, UCMP 258194, left P2-P3, external view above, visceral view below,) and carettochelyid turtle *Anosteira* n. sp. (right, UCMP 258185, neural 4, holotype, right lateral and anterior views) from the Crow Creek local fauna.

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Reptiles from the late Eocene Jackson Group of Arkansas

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New reptilian fossils from the latest middle Eocene to late Eocene Crow Creek local fauna from the Jackson Group of St. Francis County, Arkansas, add four turtles and two crocodilians to the fauna. These include a new species of the carettochelyid *Anosteira*, the kinosternid *Xenochelys*, the dermatemydid *Baptemys*, an unidentified cheloniid, and crocodilians cf. *Borealosuchus* and an alligatorid. The giant snake, *Pterosphenus schucherti*, was also a member of the reptilian fauna. Several of these are the most easterly records for these taxa.

Keywords: Eocene, Reptiles, Arkansas, Jackson Group

INTRODUCTION

As noted by Westgate (2001) and Parmley et al. (2006), non-marine vertebrate faunas are extremely rare in the Paleogene of the southeastern United States. This is especially true for the reptiles. North American Eocene reptilian faunas are predominantly known from the rich and diverse faunas of the Rocky Mountain Cordillera and Texas. As such, the local fauna from Crow Creek Quarry and several nearby quarries in central Arkansas fills a biogeographic and temporal gap in that knowledge. Westgate and Ward (1981) and Westgate (1984, 2001) recognized and summarized the lower vertebrate fauna of the Arkansas Crow Creek local fauna, reporting a variety of freshwater and marine fishes and three reptiles, only one of which was turtle (*Trionyx* sp.). In the earliest paper, Westgate and Ward (1981) listed an emydid but this was dropped in later papers (Westgate 1984, 2001). Here we update and document additional reptile specimens and taxa from the main Crow Creek Quarry and additional nearby sites.

The localities occur within an approximately nine-meter-thick section in the Moodys Branch Formation, lower Jackson Group (Dockery 1977; Westgate 2012), on the western outskirts of Madison, St. Francis County, Arkansas. Based on the planktonic stratigraphy of Moodys Branch Formation sediments in Mississippi, the age of the Crow Creek fauna has been interpreted as latest middle Eocene (late Bartonian), approximately 39-37 Ma in age (Speijer et al. 2020) and corresponding to the Duchesnean North American Land Mammal Age. Dockery (1977) stated that the Crow Creek beds in Arkansas were deposited in the same northern destructional shelf facies as the Moodys Branch Formation in Mississippi and deposited under warm hyposaline conditions adjacent to marine waters (Westgate 1984).

LOCALITIES

UCMP locality V84268, Crow Creek Quarry (CC-1) is from about 0.5 m above the creek bed along a 50 m stretch about 80 m south of the U. S. Highway 70 bridge

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on the east bank of Crow Creek, 2 km east of Forrest City and 0.7 km west of Madison, T.5N., R.3E, SE1/4, SE1/4, NE1/4, SW1/4, SEC. 25; N35°01', W90°44'. Elevation 61m (see additional information in Westgate, 1984). The original collections are at USNM.

UCMP locality V84269, Honey Hole Quarry (CC-2), 91cm above creek bed, 305 m upstream of US Highway 70 bridge, on the west bank of Crow Creek, in NW1/4, SW ¼, Sec. 25, T.5E, R.3E; N35°01'30", W90°44', elevation about 64 m.

UCMP locality V84270, Crow Creek Concretion locality, 61 cm above stream bed on the east bank just above a concretion zone on the east bank of Crow Creek, 805 m south of US Highway I-40, in NE1/4, NE1/4, SW1/4, NE1/4, Sec. 23, T.5E, R.3E; N35°02', W90°45', elevation about 67 m.

UCMP locality V84271, LCC locality, Little Crow Creek, 91 cm above stream and 402 m downstream of the railroad bridge, in SE1/4, SW1/4, SW1/4, NE1/4, Sec. 36, T.5E, R.3E;N35°00', W90°44', elevation about 61 m.

MATERIALS AND METHODS

Measurements are metric. The term "peripheral length" refers to the straight line dimension of the peripheral bone between its cephalic and caudal sutures at the perimeter of the shell as seen in dorsal view. The terminology of turtle bones and scales follows Zangerl (1969). Element abbreviations: C = costal bone (e.g., C1 is the first costal bone); P = peripheral bone; N = neural bone; M = marginal scale (e.g., M1). Visceral refers to the planar view of the carapace element from the visceral cavity and external to the planar view from the external side of the carapace. NALMA = North American Land Mammal Age.a

Institutional abbreviations

AMNH = American Museum of Natural History, New York City, New York, USA; **UCMP**= University of California Museum of Paleontology, Berkeley, California, USA; **UMNH** = Utah Museum of Natural History, Salt Lake City, Utah, USA; **USNM** = National Museum of Natural History, Washington, D.C., USA.

SYSTEMATIC PALEONTOLOGY

ORDER: TESTUDINES Linnaeus, 1758

FAMILY: DERMATEMYDIDAE Gray, 1870

GENUS: *BAPTEMYS* Leidy, 1870

Baptemys sp.

Fig. 1

Referred specimens—UCMP locality V84268: UCMP 258188, right epiplastron fragment; UCMP 258189, N5?, UCMP 258190, 258191, anterior parts of two neurals; UCMP 258192, medial fragment of the left C1, UCMP 258193, posterior peripheral fragment.

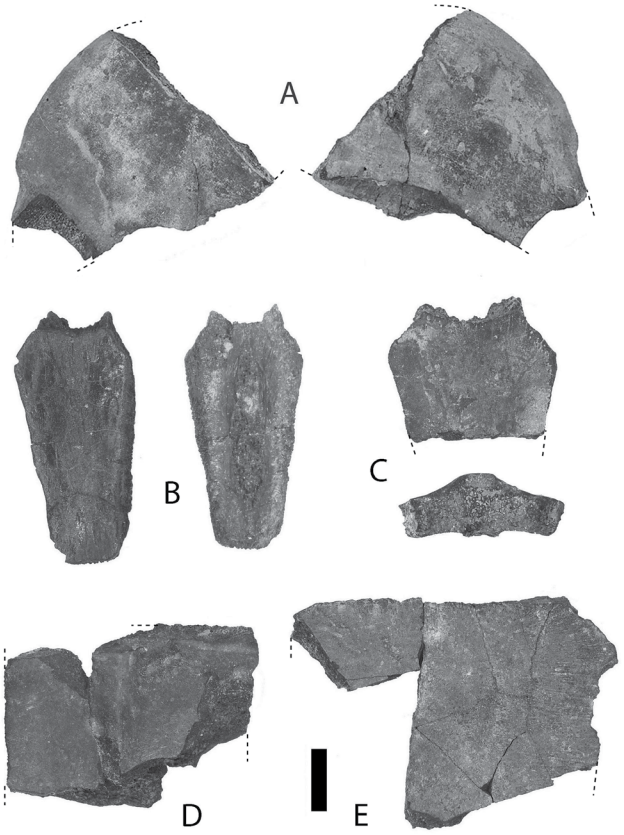

Figure 1. *Baptemys* sp., scale bar = 1 cm. **A**. UCMP 258188, right epiplastron fragment, ventral and dorsal views. **B**. UCMP 258189, neural, external and visceral views. **C.** UCMP 258190, neural, anterior fragment, external and cross section views. **D**. UCMP 258193, peripheral fragment, external view. **E**. UCMP 258192, left C1, proximal fragment, external view.

Description—The epiplastron fragment (UCMP 258188, Fig. 1A), as preserved, falls within the morphological range of *Baptemys* and in the size range of the early middle Eocene (Bridgerian NALMA) *Baptemys wyomingensis* Leidy, 1870. One complete neural (UCMP 258189, Fig. 1B, probably N5) exhibits a finely incised sulcus across the posterior part as in *Dermatemys* Gray, 1847 and *Baptemys*. The dorsal surface is slightly convex. It is 39 mm long at the midline and has a maximum width of 21 mm. The anterior moiety of another larger neural (UCMP 258190, Fig. 1C) clearly shows a longitudinal raised area that contributes to a flat-topped dorsal carina. The external surface of the C1 fragment (UCMP

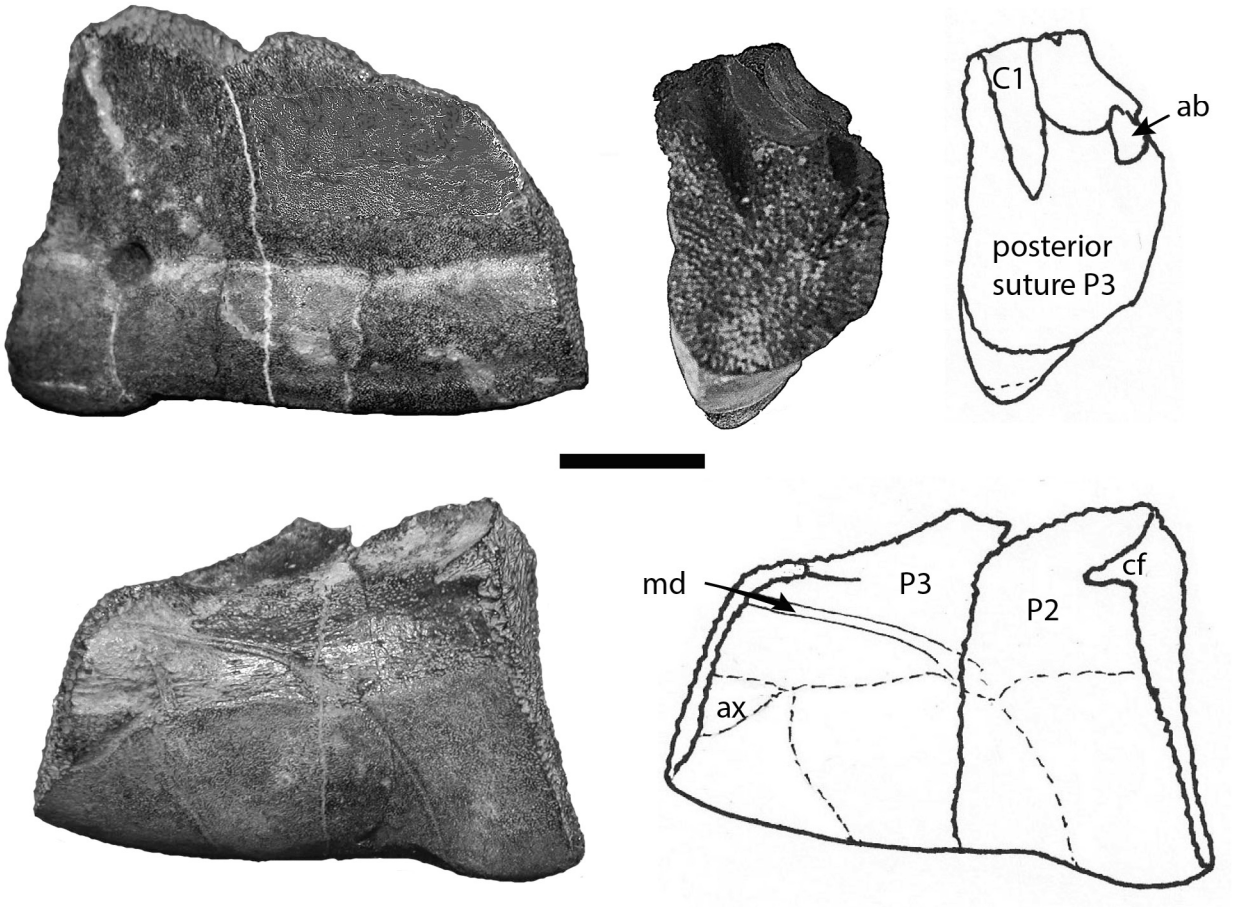

Figure 2. *Xenochelys sp.,* scale bar = 1 cm. A. UCMP 258194, left P2-P3, external, visceral, posterior views and diagrams of P2-P3in visceral view and posterior view of P3. B. P3 posterior sutural views and diagram. ab = pit for hyoplastral buttress; ab = pit for anterior buttress; ax = axillary scale; C1= grove for insertion of tip of C1 rb; cf= notch for tip of costiform presses of nuchal; md = musk duct groove.

258192, Fig. 1E) is flat with a long suture for N1 and short angled suture for N2. The fragment of a posterior peripheral (UCMP 258193, Fig. 1D) has slightly concave external surface.

Remarks—The specimens are not diagnostic to species, but they lack the well-defined costal and neural carinae of the early Eocene (Wasatchian NALMA) species. The parts preserved are indistinguishable from those of *Baptemys wyomingensis* from the early middle Eocene (Bridgerian NALMA). The low dorsal flat-topped carina on the posterior neurals resemble those of *B. wyomingensis* and an undescribed species from the Duchesnean of Utah (Eaton et al. 1999).

FAMILY: KINOSTERNIDAE Agassiz, 1857
GENUS: *XENOCHELYS* Hay, 1906
Xenochelys sp.
Fig. 2

Referred specimen—UCMP locality V84268: UCMP 258194, articulated left peripherals 2-3.

Description—Articulated peripherals 2-3 (Fig. 2) are well preserved and clearly show a musk duct groove that crosses the visceral surface of the P3. The groove extends from just ventromedial to the pit for the hyoplastral buttress and extends anterior and ventrally to the P2-P3 suture where it opens out and terminates just above the anterior edge of the marginal scale M3. A small part of the axillary scale lies dorsal to M4 and on the medial side of P3. A small V-shaped and fluted depression on the visceral side of P2 above the scale margin marks the termination of the costiform process of the nuchal. The pleural surfaces are essentially smooth. The peripherals are large with P2 shorter in perimeter length (19.8 mm) than the P3 (23.1 mm). A groove for the first costal rib crosses the posterodorsal part of P3. The dorsal suture of the P3 indicates that the costal 1-2 suture contacted

the P4. A small pit is visible on the external surface of P2 where the marginals meet the pleurals; this pathology is a Type II pit as described by Hutchison and Frye (2001).

Remarks—The posterior position of the first costal rib insertion, short musk duct groove, and posterior position of the costal 1-2 suture are diagnostic features of *Xenochelys* (Hutchison, 1991). The large size is within the range of late Eocene (Chadronian NALMA) *X. formosa* Hay 1906 as described by Hutchison (1991), but the diagnostic features of the species of *Xenochelys* lie on the plastron. On the peripherals, it differs from *X. formosa* in having the musk duct terminus at the P2-3 suture and not more anteriorly, longer hyoplastral buttress, and the axillary scale extending onto P3.

FAMILY: CARETTOCHELYIDAE Boulenger, 1889
SUBFAMILY: ANOSTEIRINAE Lydekker, 1889
GENUS: *ANOSTEIRA* Leidy, 1871
Anosteira crowcreekensis n. sp.
Figs. 3B-D

Diagnosis—Anosteirine turtle that differs from all other species in having a very high, posteriorly concave and vertical spike on neural four, vertebral sulcus crosses base of the spike as in *Kizylkumemys*; peripheral 7 lacks an intermarginal sulcus; estimated carapace size of 170 mm or more.

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Holotype—UCMP 258185, neural 4.

Paratypes—UCMP 258186, left peripheral 7; UCMP 258187, proximal costal.

Type Locality—UCMP locality V84268, Crow Creek Quarry, St. Francis County, Arkansas.

Description—The holotype is a neural (UCMP 258185, Fig. 3B) that has an extraordinarily high and laterally compressed spine on the midline that in height (maximum height 32.5 mm from ventral surface damaged tip of spike) exceeds the neural length (15.1 mm long on midline). It has a maximum width of 11.6 mm. The tip and the posterior margin of the spine are chipped. The outline of the posterior margin of the spike would have been broadly concave above the base and the anterior margin slopes anteroventrally and extends onto N 3 as in *A. pulchra* (Clark, 1932) (Fig. 3A). Very faint indications of a vertebral sulcus extend along the side of the spike and continue medially over the posterior base of the spike as in the P4 of *Kizylkumemys* Nessov, 1976. The position of this sulcus resembles that of an additional vertebral discussed by Danilov et al. (2017). *Anosteira pulcra* also has this sulcus but it extends laterally onto the costal 4 rather than being confined to the neural. *Anosteira ornata* Leidy, 1871 lacks this sulcus (Hay, 1908, text-fig. 352). The surface texture is relatively smooth except for a pattern of fine vertical striations. Estimated carapace length is about 170 mm or more.

The peripheral 7 (UCMP 258186, Fig. 3C) has a fine pattern of raised pustules on the dorsal and ventral surfaces. The medial surface supports a small sutural facet for contact with the hypoplastral process. There are no indications of sulci. The perimeter length is 23.5 mm.

The external surface of the proximal costal fragment (UCMP 258187, Fig. 3D) is smooth and shallowly parasagittally concave. The base of the rib head is long and narrow. The neural suture is deep, finely dentate and acutely angled with regard to the external surface. No sulci are evident on the fragment.

Remarks—Two species of North American *Anosteira* were recognized in the most recent summaries (Joyce 2014; Adrian et al. 2020, the genotypic species *A. ornata* from the early middle Eocene (Bridgerian NALMA) of Wyoming and *A. pulchra* from the late middle Eocene (Uintan NALMA) of Utah (Clark, 1932; Adrian et al. 2020) and Wyoming (Joyce et al. 2018). The three specimens described here are hypothesized to represent a single taxon based on size and local occurrence. The N4 spine of other *Anosteira* species, where known, is relatively low (Cheng 1961, Chow 1956, Zangerl 1947; Adrian et al. 2020) and subequal or shorter in height relative to its length (e.g., Fig. 4A). The N4 of *A. ornata* is only known from the contacts with adjoining bones (Hay 1908). The three Arkansas specimens collectively offer a mélange of features that differ from other *Anosteira*. The presence of a scale sulcus around the posterior base of the spike resembles that of Asian Cretaceous *Kizylkumemys* and *A. pulchra* but this sulcus is absent in *A. ornata,* based on the adjoining costals, and Eocene Asian species where known (Zangerl 1947). The high neural spike is better developed than in any known *Anosteira* and the posterior margin of the spike is concave rather than distinctly angled (Fig. 3B). While the absence of intermarginal sulci is usually considered a character of the Carettochelyinae (Joyce 2014:25), these may also be obscure to absent in some *Anosteira* on the posterior peripherals (e.g., UCMP 281907). The combination of characters indicates a new, distinct taxon.

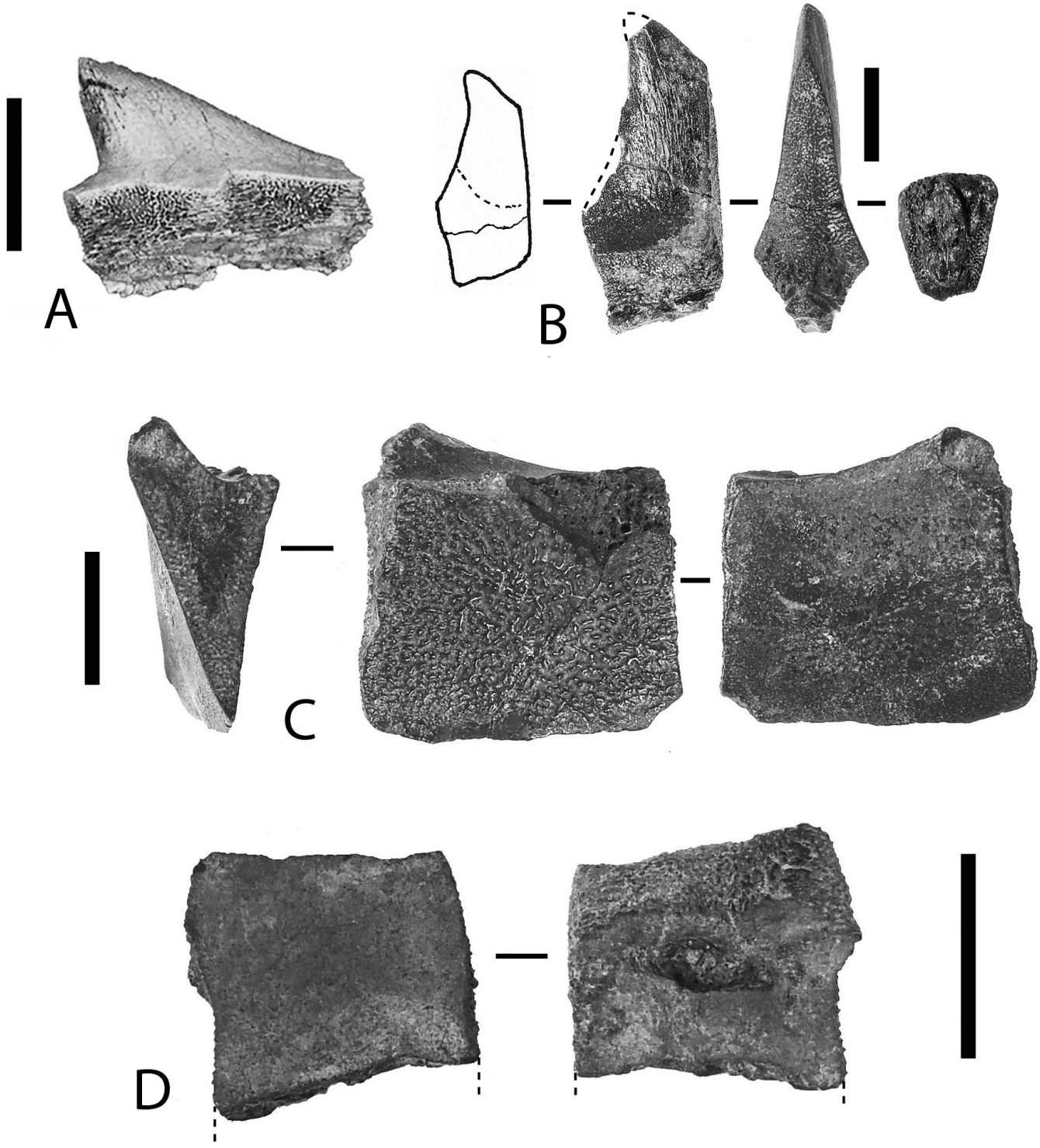

Figure 3A. *Anosteira pulchra,* UMNH field no. 15H8-8-16,N3-4, right lateral view (image reversed) from the Uinta Formation, Utah, scale bar = 1 cm. **B-C**. *Anosteira crowcreekensis*, n. sp. **B.** UCMP 258185, neural 4, holotype, right lateral, anterior and ventral views, arrowhead in diagram indicates the position of a sulcus. **C**. UCMP 258186, left P7, anterior sutural, external dorso-lateral and ventral views. **D**. UCMP 258187, proximal costal fragment, external and visceral views.

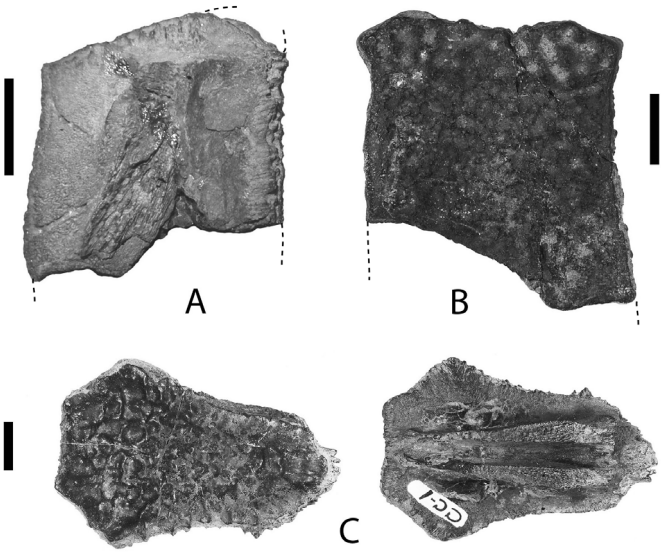

Figure 4. Trionychinae indet. , scale bar = 1 cm. **A**. UCMP 258198, proximal fragment of right C1, visceral view. **B**. UCMP 258199, C6?, external view. **C**. UCMP 258195, N6?, dorsal and ventral views.

FAMILY: TRIONYCHIDAE Gray, 1825
SUBFAMILY: TRIONYCHINAE Gray, 1825
Trionychinae indet.
Fig. 4

Trionyx sp.: Westgate 1984:540, Fig. 4A.
Trionyx sp.: Westgate 2001:287, Table 3.

Referred specimens—UCMP locality V84268: USNM 336115, costal lacking proximal end; UCMP 258195, neural (N7?); UCMP 258196, neural fragment; UCMP 258197, carapace fragment; UCMP 258198, proximal fragment of C1; UCMP 258199, proximal costal (C6?); UCMP 258200, costal fragments; UCMP 258201, scapula fragment. UCMP locality V84270: UCMP 258212, UCMP 258220, costal fragments.

Description—The distal part of a large costal (USNM 336115) was described and figured by Westgate, (1984, fig. 4A). The proximal costal fragment of right C1 (UCMP 258198, Fig. 4A) has a non-dentate anterior suture indicating a subadult with an undeveloped nuchal suture. Another proximal costal fragment (UCMP 258199, Fig. 4B) preserves three neural sutures and is probably adjacent to N5 or N6. Its proximal length is 38 mm.

The neural (UCMP 258195, fig. 4C) is large (midline length = 60.7 mm), distinctly pitted and roughly pentagonal with raised margins. The anterior end is broadest with well formed straight sutures with the costals and neural. The converging posterior margins indicate that this is the last neural, probably N6 or N7. The estimated carapace length for this specimen is over 600 mm.

Remarks—Since Meylan's (1987) revision of the extant Trionychidae to restrict *Trionyx* Geoffrey Saint-Hillaire, 1809 to Old World species, fragmentary North American trionychid material are better referred only to family or subfamily unless sufficient evidence shows otherwise. The size of the costal with an open sculpture, and unsculptured and tapered free margin appear to exclude the Plastomeninae and agree with the Trionychinae. Aside from differences in size there is no evidence of more than one taxon, and all the fragments are referred to the Trionychinae.

FAMILY: CHELONIIDAE Oppel, 1811
Cheloniidae genus indet.
Figs. 5–8

Referred specimens—UCMP locality V89268: UCMP 258202, right prefrontal; UCMP 258203, left

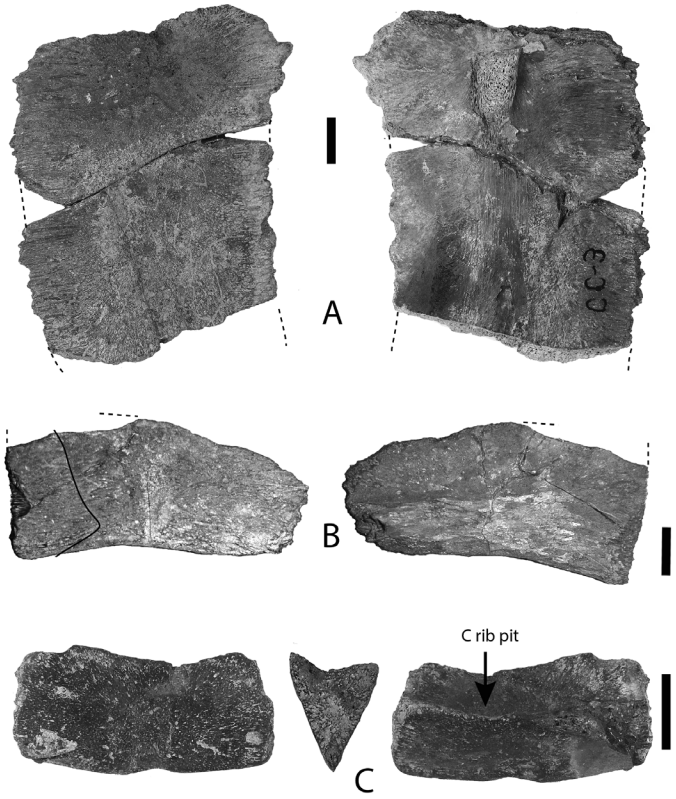

Figure 5. Cheloniidae indet. , scale bar = 1 cm. **A**. UCMP 258210, left C3 or C5, external and visceral views. **B**. UCMP 258203, left P2, lateral and visceral views. **C**. UCMP 258212, bridge P, visceral, anterior sutural and dorsal views, arrow indicates costal rib.

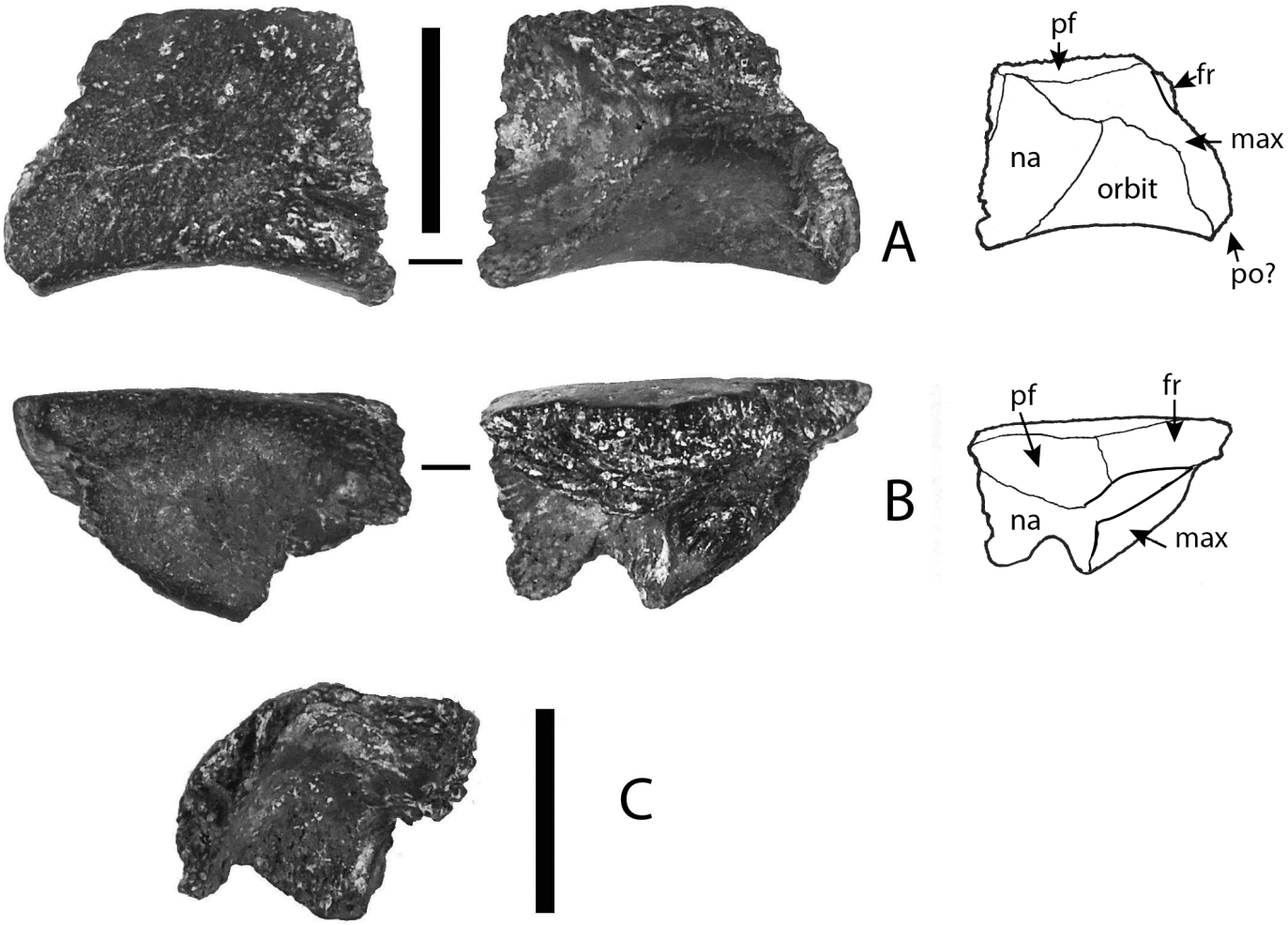

Figure 6. Cheloniidae indet., UCMP 258203, right prefrontal, scale bar = 1 cm. **A**. Dorsal, ventral and ventral diagram views. **B**. Lateral, medial and medial diagram views. [not svale bar needed as it is the same as in figure A and just rotated] **C**. Anterior view. fr = frontal suture; max = maxilla suture; na = nasal aperture; pf = prefrontal suture; po? = postorbital suture?

anterior peripheral 2; UCMP 258204, partial cervical vertebra 8; UCMP 258205, anterior caudal vertebra; UCMP 258206, dorsal vertebral centrum; UCMP 258207, peripheral fragment; UCMP 258208, shell fragments. UCMP locality V89269: UCMP 258210, proximal costal. UCMP locality V84270: UCMP 258211, nuchal? fragment. UCMP locality V84271: UCMP 258212, bridge peripheral.

Description—The prefrontal (UCMP 258202, Fig. 6) is short with a thick triangular medial suture. The nasal aperture is large with its anterior margin at about the level of the dorsal orbital rim and only narrowly separated from the orbit as in *Caretta* Rafinesque, 1814 and *Chelonia* Brongniart, 1800. The maxilla contacts the prefrontal via a slanting vertically aligned suture along the anterior surface of the maxillary process. The orbit appears to have been large. The posterior suture is angled laterally and turns transversely just over the orbit suggesting that the postorbital may have contacted the prefrontal and excluded the frontal from the orbital rim as in *Caretta*.

The proximal part of a left costal (UCMP 258210, Fig, 5A) lacks an interpleural sulcus and is either C3 or C5. The vertebral sulci indicate that the vertebrals were longer than wide as in *Chelonia* versus *Eretmochelys* Fitzinger, 1826. The proximal length is 64 mm with the maximum thickness at the neural suture of 7.4 mm. The broken base of the capitulum is slightly posterior to the center and about 4 mm lateral to the neural suture.

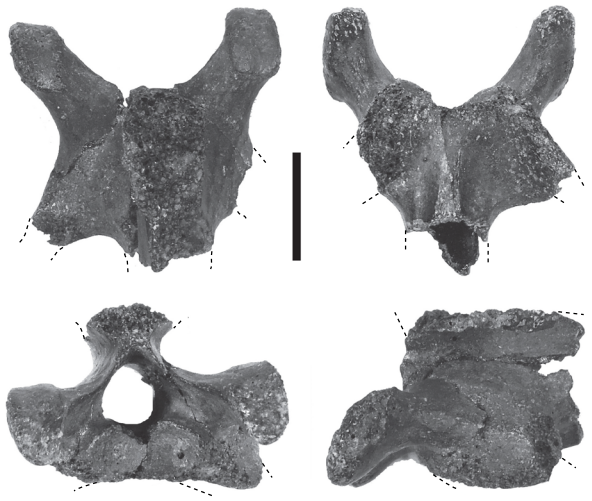

Figure 7. Cheloniidae indet., UCMP 258204, partial eighth cervical vertebra, clockwise from upper left, dorsal, ventral, left lateral posterior, and anterior views, scale bar = 1 cm.

An elongate left P2 (UCMP 258203, Fig. 5B) has a broadly concave, obtuse, but not greatly thickened free margin. The costal suture is broken anteriorly and the posterior part is knife-edged and may not have contacted C1. Viscerally, the posteroventral surface thickens toward the P2 suture. The shallow and broad intermarginal sulcus lies about one-fourth the way back from the P1 suture. It has a perimeter length of 58 mm and a maximum depth of 30 mm.

A bridge peripheral (UCMP 258212, Fig. 5C) from a smaller individual has a perimeter length of 14.2 mm. The free margin is acute. The intermarginal sulcus is obscure. The rib pit is cone-shaped and lies in the anterior moiety. The plastral and costal sutures are acute-edged and not dentate.

A partial cervical vertebra 8 (UCMP 258204, Fig. 7) lacks the posterior part and top of neural spine. The centrum is procoelous with the cotyle about twice as wide as high. The prezygapophyseal facets are elongate, oval, and convex dorsally.

The nearly complete anterior caudal vertebra (UCMP 258205, Fig. 8) is procoelous. The centrum is 21.5 mm long. There is only a flattened area for the neural spine indicating close proximity to the carapace roof. Distinct transverse processes slant posterolaterally from the middle of the centrum. A pair of low knobs at the base of the condyle indicates the presence of a chevron bone.

Remarks—Multiple named cheloniids are present in the Eocene of North America (e.g., Weems 2014; Weems and Sanders 2014; Weems and Brown 2017). However, like other Gulf Coast or Atlantic Coastal Plain Paleogene faunas (e.g., Hutchison and Weems 1998; Holroyd et al. 2005; Parmley et al. 2006) the elements in the Crow Creek fauna are either undiagnostic or unknown in several of the named taxa.

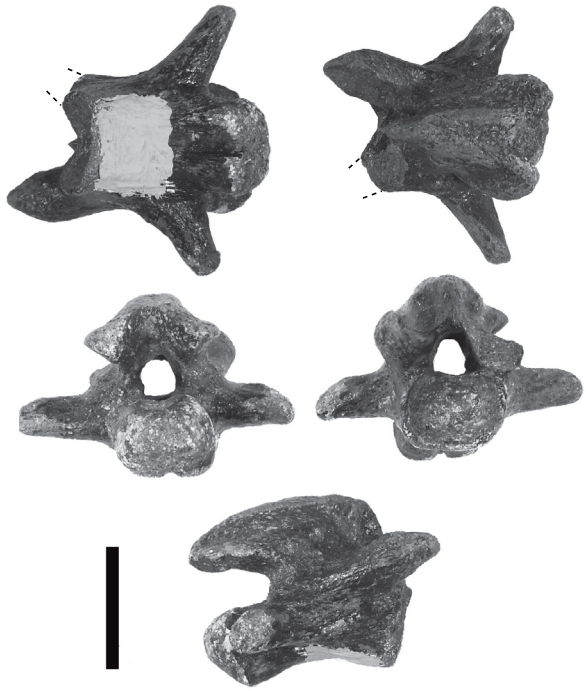

Figure 8. Cheloniidae indet., UCMP 258205, caudal vertebra, clockwise from upper left, ventral, dorsal, posterior, right lateral and anterior views, scale bar = 1 cm.

ORDER: SQUAMATA Oppel, 1811
FAMILY: PALAEOPHIIDAE Lydekker, 1888
GENUS: *PTEROPHENUS* Lucas, 1898
Pterosphenus schucherti Lucas, 1898

Pterosphenus schucherti Lucas: Westgate 1984, fig. 4E, F; 2001, fig. 11C, D

Remarks—Westgate and Ward (1981) and Westgate (1984) previously reported on the presence of this large sea snake. In addition to the Crow Creek occurrence, they noted that this snake is known from New Jersey, Georgia, Mississippi, and Alabama. A later record from Florida was published by Hutchison (1985) and Westgate (2001) extended the geographic range of *Pterosphenus* to the Texas/Mexico border. *Pterosphenus* has a Tethyan

distribution and occurs east through the Mediterranean and into India (Rage et al. 2008), Uzbekistan (Averianov 1997), and possibly southeast Asia (Head et al., 2005).

ORDER: CROCODYLIA Gmelin,1789
GENUS: *Borealosuchus* Brochu, 1997
cf. *Borealosuchus* sp.

Crocodylus Laurenti 1768: Westgate 1984:540. figs. 4B-D.

Referred specimens—UCMP loc. V84268, USNM 336116, dentary fragment (Westgate 1984, fig. 4B); USNM 336117, dorsal vertebra (Westgate 1984, fig. 4C); UCMP 258209, ventral osteoderm fragments.

Description—The only new element (UCMP 258209, Fig. 9A) we add is the right part of the anterior component of the ventral bipartite osteoderm. There are sutures on the posterior and right lateral sides and there is a wide anterior overlap zone (19.2 mm) followed by a well-defined double row of deep pits. It is 27.6 mm long and 5.5 mm thick. The width is indeterminate due to breakage but it was clearly wider than long.

Remarks—Caimans and some other alligatoroids and crocodylians outside of the alligatoroids (e.g., *Borealosuchus*) have a double ossification in place of the single ventral osteoderms present in most crocodilians. In most caimans, the anterior osteoderm is longer or nearly as long as wide, while in non-caimans such as Eocene *Borealosuchus* (Fig. 9B) and the Eurasian alligatoroid *Diplocynodon* Pomel 1847 the anterior component is distinctly wider than long, and both types support the smooth overlap zone for the preceding osteoderm row and have sutural articulations both laterally (aside from the row ends) and posteriorly. The large partial lower mandible fragment and dorsal vertebra described and figured by Westgate (1984 fig. 4B, C) may also belong with this osteoderm judging from size

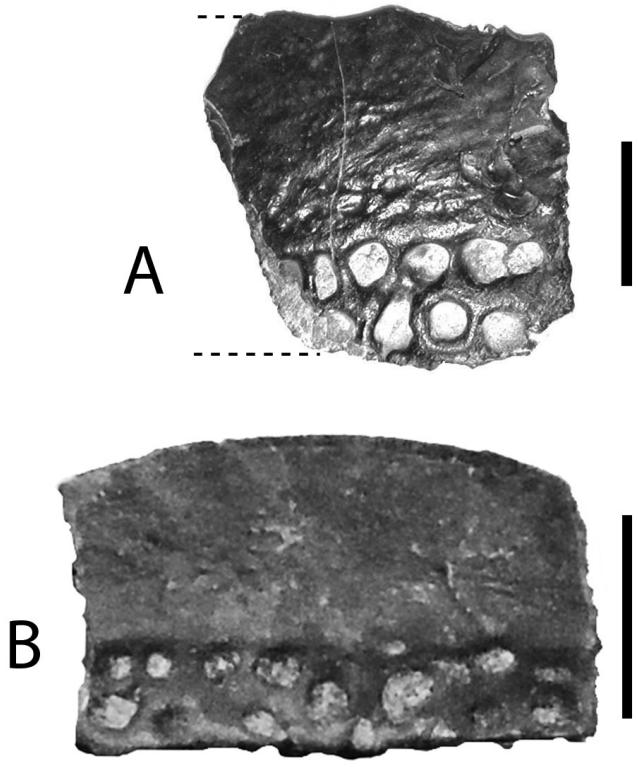

Figure 9. **A**. cf. *Borealosuchus* sp., UCMP 258209, ventral osteoderm fragment, ventral view, scale bar = 1 cm. **B**. UCMP 153205, *Borealosuchus wilsoni* (Mook 1959) from the early Eocene Wasatch Formation, southwestern Wyoming, ventral osteoderm, ventral view. Scale bar = 1 cm.

FAMILY: Alligatoridae Cuvier, 1807

Referred specimens—UCMP loc. V89269, USNM 336110, dorsal osteoderm (Westgate, 1984 fig. 4D).

Remarks—The dorsal osteoderm figured by Westgate (1984 fig. 4D) has a distinct but apparently low keel with a narrow but distinct anterior overlap zone and lateral sutures. As noted by Westgate, it is subrectangular and is longer than wide although the measurements (27.5 mm length; 33.6 mm width) were reversed. This type of dorsal osteroderm is typical of alligatorids and the dorsal osteoderms of crocodylids are usually more rounded, have very prominent keels and are typically free floating and or only loosely or not articulated laterally with adjacent osteoderms and don't imbricate with the preceding row.

CONCLUSIONS

The Crow Creek fauna, although meager, expands the known Eocene range of the Kinosternidae and Dermatemydidae, and *Anosteira* eastward. The kinosternid *Xenochelys* was previously only reported from Casa Blanca in west Texas (Westgate 1984). Dermatemydids were previously only reported from late middle Eocene rocks in west Texas (Westgate 1984) and east Texas (Holroyd, 2002) The crocodilians are more diverse than previously reported and this may be the latest record of a crocodilian with this type of bipartite belly armor, cf. *Borealosuchus*. The fauna is notably lacking in testudinoids. The only Tethyan element is the sea snake *Pterosphenus*.

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