

NEW BOTHREMYDID TURTLE (TESTUDINES, PLEURODIRA) FROM THE PALEOCENE OF NORTHEASTERN COLOMBIA

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ABSTRACT—A new turtle, *Puentemys mushaisaensis*, from the middle to late Paleocene Cerrejón Formation of Colombia, is described on the basis of a partial skull and many partial to nearly complete carapaces and plastrons representing multiple ontogenetic stages. Whereas *P. mushaisaensis* is unique in aspects of its shell morphology, it shares many diagnostic characteristics of bothremydids, including a long exoccipital-quadrato contact, a very low and rounded almost circular carapace, and a thinner internal bone cortex than that of the external cortex in both the carapace and plastron. With a maximum carapacial length of 151 cm, *P. mushaisaensis* is the largest known bothremydid turtle and represents the first occurrence of bothremydids in the Paleocene of South American tropics. Results from a cladistic analysis of bothremydids indicate that *P. mushaisaensis* shares a close relationship with *Foxemys mechinorum* from the Late Cretaceous of Europe, indicating a wide-spread geographical distribution for bothremydids during the Late Cretaceous–Paleocene.

INTRODUCTION

BOTHREMYDIDS WERE the most abundant and globally widespread pleurodires (side-necked turtles) from the Early Cretaceous (Albian) through the Paleocene. They have been recovered from sediments deposited in freshwater and brackish-coastal environments of North and South America, Europe, Africa, and India. Following the publication of an extensive overview of the morphology, evolution, and phylogeny of bothremydids (Gaffney et al., 2006), more recent studies include: descriptions of a new species, *Acleistochelys maliensis* from the Paleocene of Mali (Gaffney et al., 2007); a re-description of *Ummulisanis rutgersensis* from the Eocene of Morocco (Gaffney and Tong, 2008); a new species *Kinkonychelys rogersi* from the Late Cretaceous of Madagascar (Gaffney et al., 2009b); new material of bothremydids from the Gulf Coastal Plain of North America (Gaffney et al., 2009a); and a new species, *Chupacabrachelys complexus*, from the Cretaceous of Texas (Lehman and Wick, 2010).

The South American record of definitive bothremydids has been restricted to *Cearachelys placidoi* from the Santana Formation, Ceara, Brazil, probably Albian in age. *Cearachelys* was described from skulls and complete shells (Gaffney et al., 2001) and is the oldest bothremydid so far known. The only other possible record from South America, *Taphrosphys olssoni* Schmidt, 1931 from the Eocene of Peru, is represented by fragmentary pieces of shell and its affinities remain uncertain (Gaffney et al., 2006). Here we describe the first middle to late Paleocene South American bothremydid turtle, from the Cerrejón Formation, Cerrejón Coal Mine, Guajira Peninsula, Colombia, discuss its phylogenetic and paleobiogeographical implications and the ontogenetic variation of the shell characters.

The flora and fauna collected from the Cerrejón Coal Mine constitute the most complete Paleocene neotropical ecosystem so far known, including fossil leaves, fruits, seeds, flowers, pollen and spores, and in terms of vertebrates a predominance of reptiles: the giant snake *Titanoboa cerrejonensis* Head et al., 2009; the crocodiles *Cerrejonisuchus improcerus* Hastings et al., 2010 and *Acherontisuchus guajiraensis* Hastings et al., 2011; the turtles *Cerrejonemys wayuunaiki* Cadena et al., 2010, *Carbonemys cofrinii* Cadena et al., 2012, and the new bothremydid described here.

Institutional Abbreviations.—NCSU/P=North Carolina State University, Paleontology Lab Collections, Raleigh, North Carolina, U.S.A.; UF/IGM=University of Florida, Florida Museum of Natural History Vertebrate Paleontology Collections, Gainesville, Florida/Museo Geológico José Royo y Gómez at the Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Bogotá, Colombia; USNM=Smithsonian National Museum of Natural History, Washington, D.C., U.S.A.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788

PLEURODIRA Cope, 1874

BOTHREMYDIDAE Baur, 1891

BOTHREMYDINI Gaffney et al., 2006

PUENTEMYS new genus

Etymology.—From La Puente “The Bridge” (name of the largest pit at the Cerrejón coal mine).

Type species.—*Puentemys mushaisaensis* new species.

Diagnosis.—As for type and only known species.

Discussion.—*Puentemys mushaisaensis* n. gen. n. sp. is classified as a bothremydid based on the presence of a long exoccipital-quadrato contact (Gaffney et al., 2006); a very low and rounded almost circular shell (Lapparent de Broin, 2000); and a carapace and plastron with internal bone cortex thinner than the external cortex (Scheyer and Sanchez-Villagra, 2007). We further classify it in the Tribe Bothremydini on the basis of the presence of a supraoccipital-quadrato contact (Gaffney et al., 2006).

PUENTEMYS MUSHAISSENSIS new species

Diagnosis.—Differs from all other bothremydids in having pectoral scales shorter than humeral, abdominal, and femoral scales at midline of the plastron; small and very shallow medial notch at the anterior margin of the nuchal; vertebral 1 much wider than the others; axillary buttress scar oriented greater than 60° with respect to the posterior margin of costal 1; and short, wide, and rounded prezygapophyses on the first thoracic vertebrae.

Etymology.—From Mushaisa (name of the Cerrejón Coal Mine base town), and also word used by the local Wayuu Indians to designate ‘land of coal.’

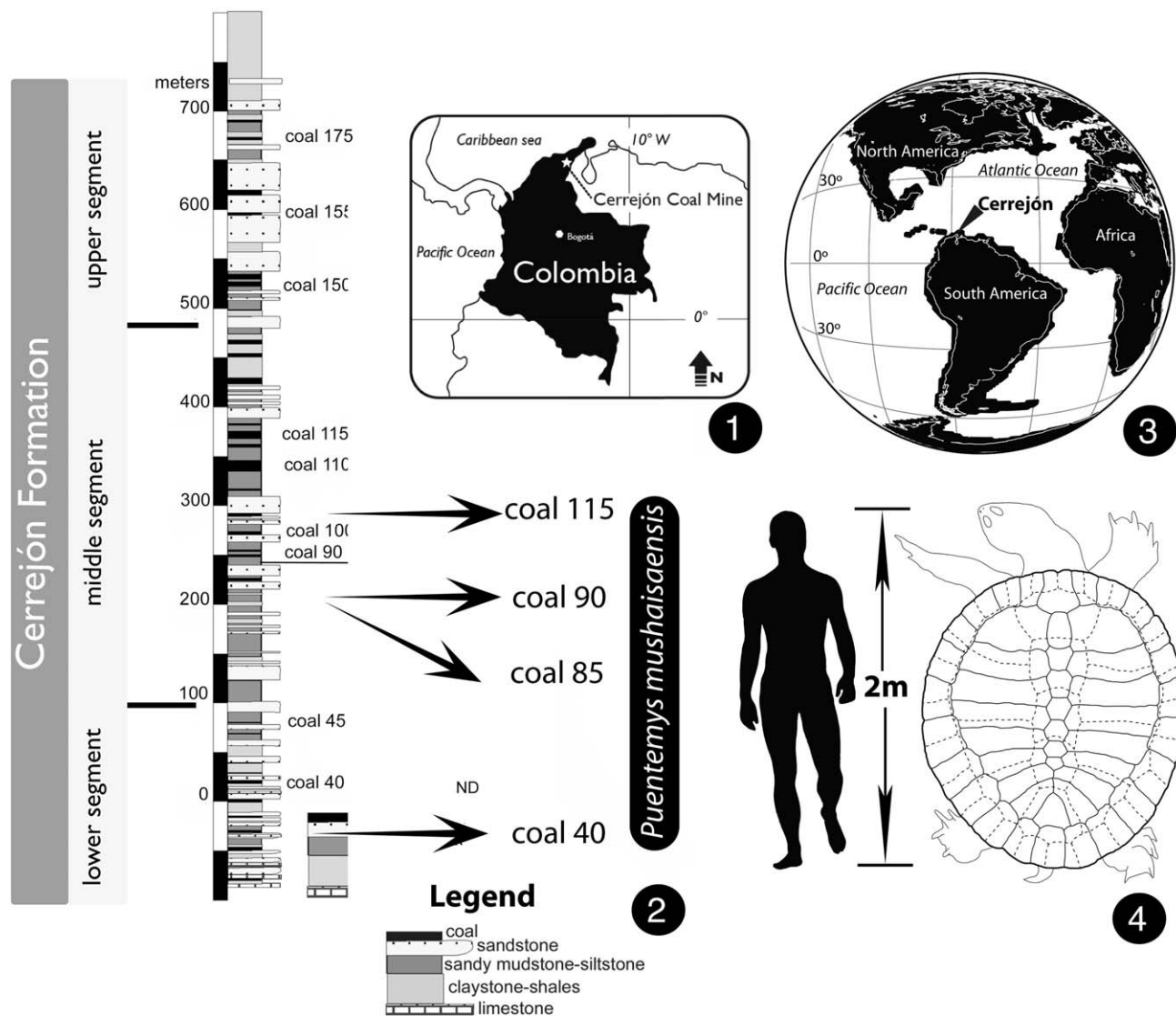


FIGURE 1—1, map of Colombia showing the Cerrejón coal mine locality; 2, stratigraphic column for the middle-late Paleocene Cerrejón Formation with arrows indicating the four horizons where *Puenteimys mushaisaensis* occurs; 3, paleo-reconstruction of continental platforms for (60 Ma) Paleocene, indicating the location of Cerrejón deltaic-coastal plain system near the seaway connecting the Atlantic with the Pacific Ocean; reconstruction downloaded from the Paleobiology Database on 10 August 2011; 4, reconstruction of *P. mushaisaensis* and comparison to scale with a 2 m human body.

Holotype.—UF/IGM 50 (Fig. 1.4 reconstruction, Fig. 2.1–2.4), complete carapace and hyoplastron. La Puente Pit, Cerrejón Coal Mine, Guajira Peninsula, Colombia (N 11°08'30", W 72°33'20") (Fig. 1.1).

Occurrence.—Claystone layer underlying Coal Seams 40, 85, 90, and 115, lower and middle segments of the Cerrejón Formation (Fig. 1.2); middle-late Paleocene (58–60 Ma) (Fig. 1.3) based on correlations using pollen and spores (Jaramillo et al., 2007).

Referred material.—UF/IGM 51 (Fig. 3.1–3.8) posterior portion of the skull. UF/IGM 52 (Fig. 4.1–4.2), a complete plastron. UF/IGM 53, left portion of the carapace and complete plastron. UF/IGM 54 (Fig. 4.3–4.6), a nearly complete carapace, with partial nuchal, left peripheral 2, and right peripherals 2–3 preserved, plus the complete plastron. UF/IGM 55, anterior portion of the carapace and right anterior plastral lobe. UF/IGM 56 (Fig. 4.7–4.9), a nearly complete carapace, preserving the nuchal and left peripherals 1, 2, 5, 6, and the anterior portion of the plastron, missing costals 4, neural 4, right costal 1, and the rest of peripherals.

UF/IGM 57, a complete plastron. UF/IGM 58, anterior portion of the carapace with nuchal and peripherals 1 preserved, plus the anterior plastral lobe. UF/IGM 59, partial carapace. UF/IGM 60, complete carapace. UF/IGM 61, complete carapace. UF/IGM 62, nearly complete carapace and the anterior plastral lobe. UF/IGM 63, complete carapace. UF/IGM 64 (Fig. 4.10, 4.11), posterior plastral lobe. See Table 1 for measurements. Ontogenetic stages were defined according to the following ranges: hatchling (≤ 15 cm), juvenile (15–50 cm), adult (≥ 50 cm).

Remarks.—*Puenteimys mushaisaensis* n. gen. n. sp. is identified as a bothremydid by 1) long exoccipital-quadrato contact (Gaffney et al., 2006); 2) very low and rounded almost circular shell (Lapparent de Broin, 2000); and 3) carapace and plastron with internal bone cortex thinner than the external cortex (Scheyer and Sanchez-Villagra, 2007). *Puenteimys mushaisaensis* belongs to Tribe Bothremydini based on the presence of a supraoccipital-quadrato contact (Gaffney et al., 2006). It resembles *Foxemys mechinorum* Tong et al., 1998 and *Polysternon provinciale* Matheron, 1896 in having a large

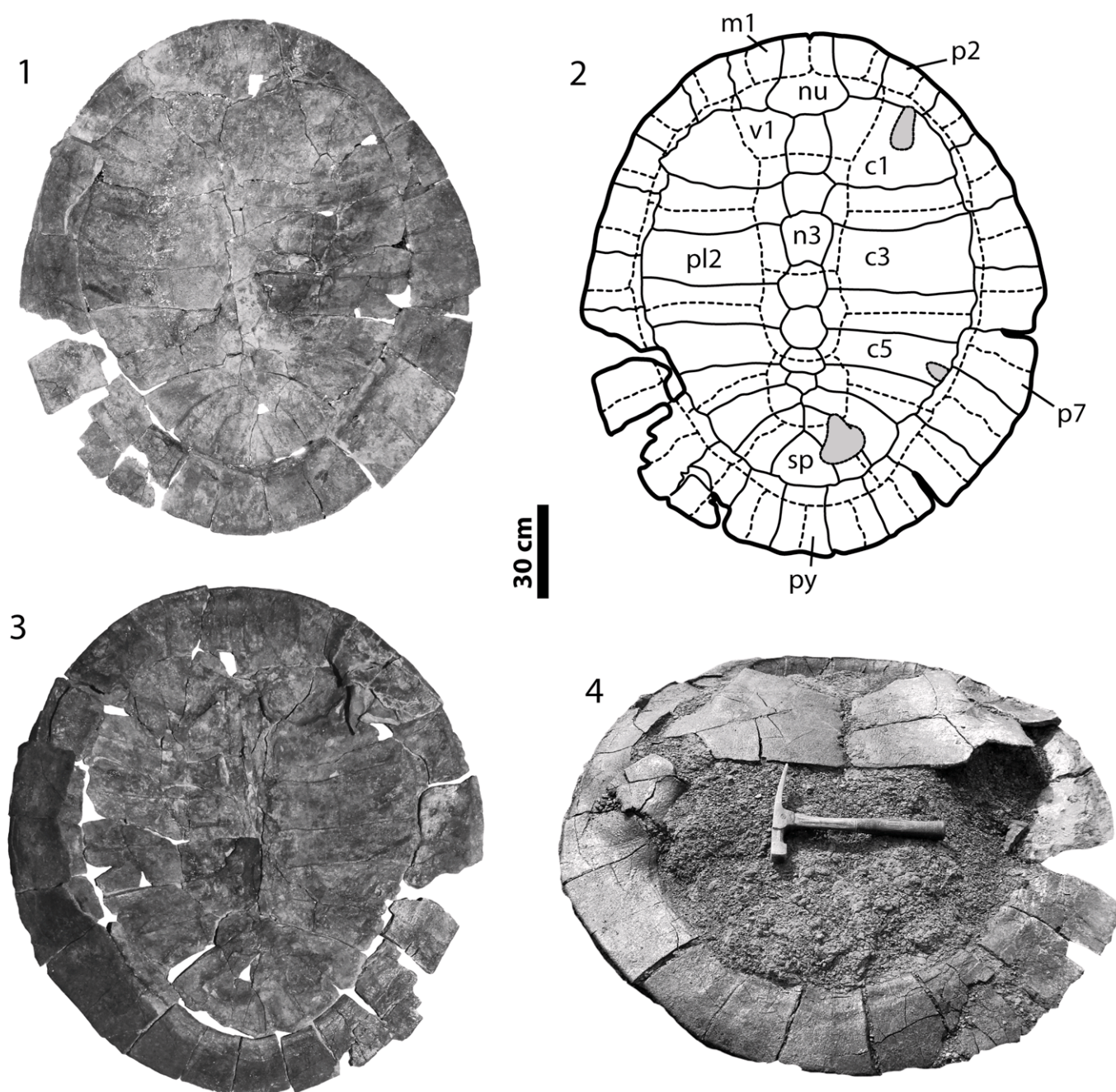


FIGURE 2—Holotype of *Puentemys mushaisaensis* (UF/IGM 50), articulated shell. 1, 2, carapace dorsal view; 3, carapace ventral view; 4, articulated carapace and hyoplastra in situ at the claystone layer underlying coal seam 90, La Puente pit, Cerrejón Formation. Abbreviations: c=costal; m=marginal; n=nuchal; p=peripheral; pl=pleural; py=pygal; sp=suprapygale; v=vertebral.

diamond-shaped entoplastron with its posterior tip reaching the level of the carapace-plastron bridge and an inguinal scar short, slightly wider laterally, shallow, and located at the posterolateral corner of costal 5. It shares with *F. mechinorum* a vertebral 1 almost pentagonal in shape, reaching the posteromedial corner of peripheral 2, a shallow axillary scar wider posteromedially than anterolaterally, located laterally at the mid-part of costal 1, and an ischiac scar triangular in shape with its posterior tip placed very anterior to the anal notch.

DESCRIPTION AND COMPARISONS

Skull.—A single fragmentary specimen has been recovered that preserves aspects of the cranial morphology including both otic chambers (crushed and poorly preserved) and the

basisphenoidal-basioccipital region (UF/IGM 51). Whereas this specimen was found about three meters away from the holotype (UF/IGM 50) in the same claystone layer, suggesting at least the possibility that they could belong to the same individual (albeit with considerable transport), they are cataloged separately to reflect uncertainty regarding this association.

The supraoccipital bone extends laterally and reaches the quadrate, as in all other bothremydids (Fig. 3.1, 3.2) except Taphrosphyini (Gaffney et al., 2006). The foramen stapediotemporale is visible on the left side, located between the quadrate and the prootic. There is an incipient paraoccipital process of the left opisthotic but it ends far anterior to the squamosal.

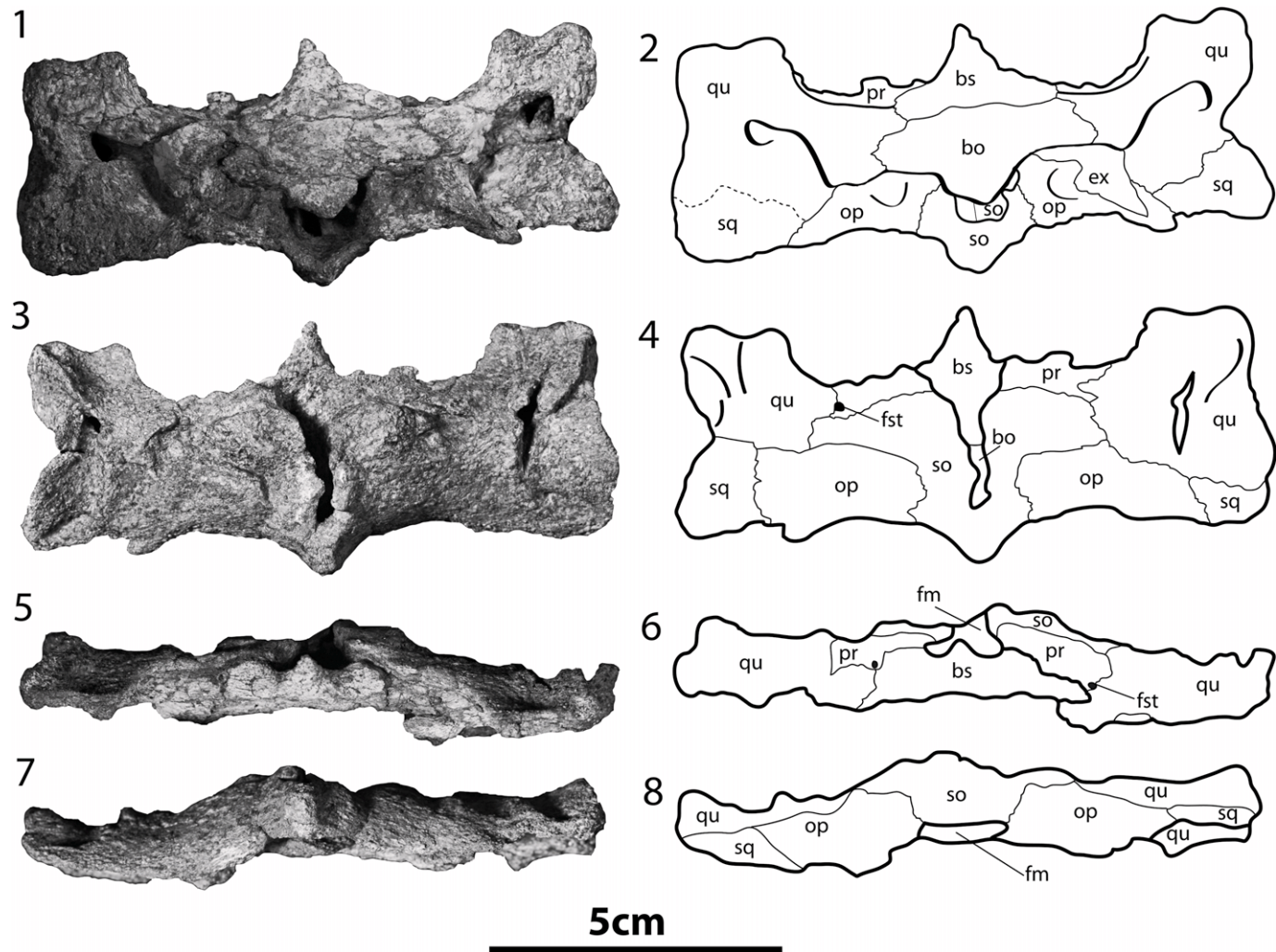


FIGURE 3—Posterior portion of the skull of *Puentemys mushaisaensis* (UF/IGM 51). 1, 2, ventral view; 3, 4, dorsal view; 5, 6, anterior view; 7, 8, posterior view. Abbreviations: bo=basioccipital; bs=basisphenoid; ex=exoccipital; fm=foramen magnum; fst=foramen stapedio temporale; op=opisthotic; pr=prootic; qu=quadrate; so=supraoccipital; sq=squamosal.

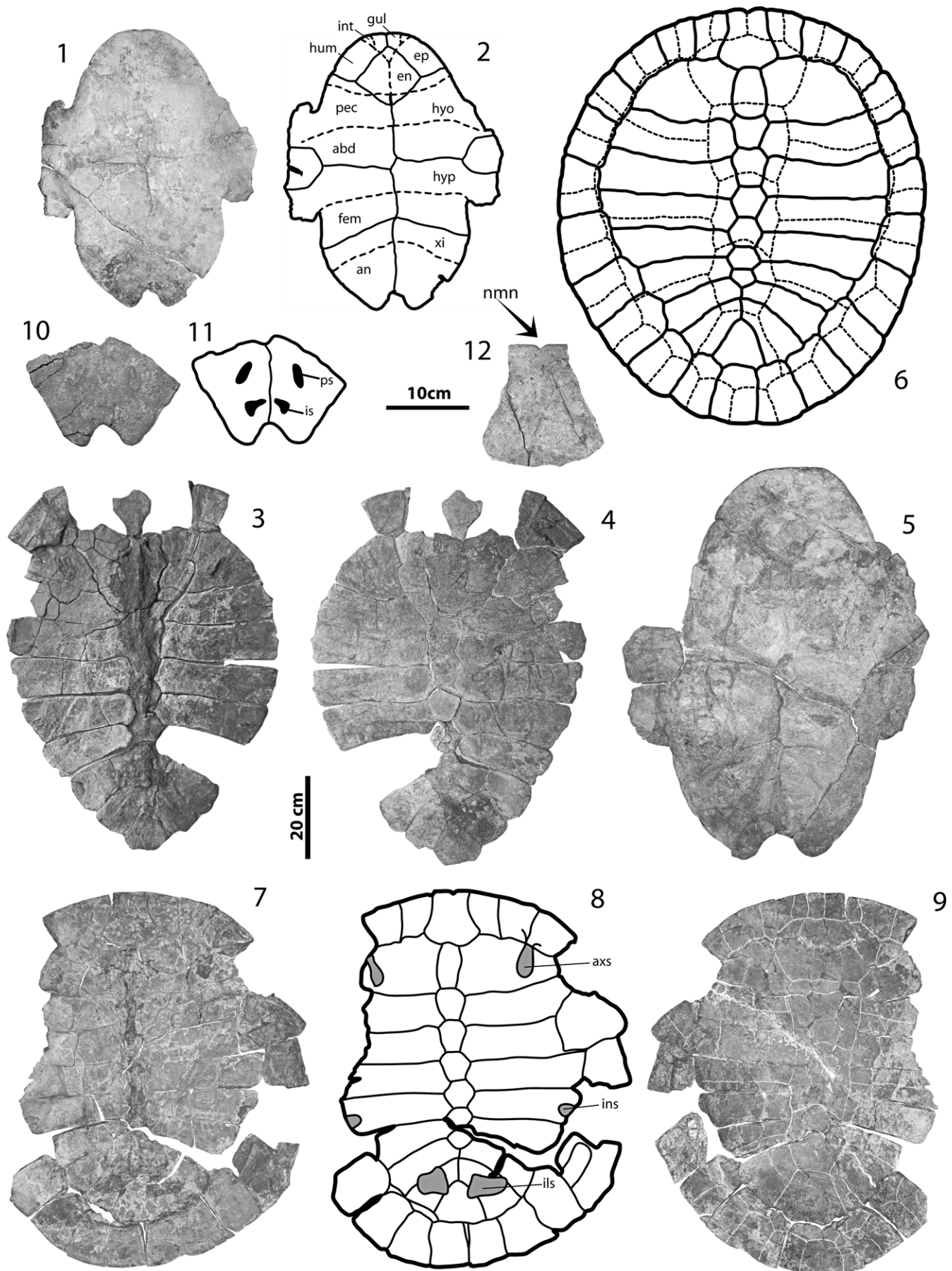
The most posterior portion of the basisphenoid is preserved, which shows its contacts with the quadrate laterally and the basioccipital posteriorly. On the right side, the exoccipital is in contact with the quadrate (Fig. 3.3, 3.4), as in all other bothremydids (Gaffney et al., 2006).

Shell.—The carapace and plastron of *Puentemys mushaisaensis* are almost identical in size, with the anterior and posterior margins of the plastron reaching the same level of the margins of the carapace, and all diagnostic characters are present in the different ontogenetic stages. The roundness of the carapace is the only character that shows ontogenetic variation, from slightly elongate in hatchlings (UF/IGM 60)

and juveniles (UF/IGM 56, UF/IGM 53) to spherical in adults (UF/IGM 50).

Carapace.—The carapace is smooth, lacking decoration on the surface in the holotype and all referred specimens of *Puentemys mushaisaensis*. The nuchal bone is pentagonal in shape, slightly longer than wide, and the anterior edge is straight as in *Foxemys mechinorum*, *Cearachelys placidoi*, and *Kurmademys kallamedensis* Gaffney, 2001. There is a particular small, V-shaped notch on the medial nuchal (Fig. 4.12), which does not imply an embayment of the nuchal area as in *Polysternon provinciale*, *Rosasia soutoi* Carrington da Costa, 1940, and *Chedighaii barberi* Schmidt, 1940. The nuchal

FIGURE 4—*Puentemys mushaisaensis* juvenile and adult specimens. 1, 2, UF/IGM 53, complete plastron of a juvenile specimen in ventral view, found in the claystone layer underlying coal seam 85; 3, UF/IGM 54, carapace from an adult specimen of *P. mushaisaensis* in ventral view, scale is 10 cm; 4, UF/IGM 54, carapace in dorsal view; 5, UF/IGM 54, plastron in ventral view, found articulated with the carapace shown in 3 and 4; 6, *Puentemys mushaisaensis* carapace reconstruction based on specimens UF/IGM 51 and UF/IGM 54; 7, 8, UF/IGM 62, carapace of an adult specimen in ventral view; 9, UF/IGM 62, carapace in dorsal view; 10, 11, UF/IGM 64, xiphiplastra of a juvenile specimen in dorsal view; 12, UF/IGM 52, isolated nuchal bone clearly showing the shallow nuchal marginal notch. Scale applies only for 3. Abbreviations: abd=abdominal; an=anal; axs=axillary buttress scar; en=entoplastron; ep=epiplastron; fem=femoral; gul=gular; hum=humeral; hyo=hyoplastron; hyp=hypoplastron; ils=ilium scar; ins=inguinal scar; int=intergular; is=ischial scar; nm=nuchal marginal notch; pec=pectoral; ps=pubic scar; xi=xiphiplastron.



medial notch is an ontogenetically conservative character in *P. mushaisaensis*, present in hatchlings (UF/IGM 60, UF/IGM 59), juveniles (UF/IGM 56, UF/IGM 53), and adults (UF/IGM 62, UF/IGM 55, UF/IGM 50, UF/IGM 54, UF/IGM 58).

The neural series includes seven bones in most of the specimens of *Puentemys mushaisaensis*, except in UF/IGM 60 and UF/IGM 59, which have six. The presence of six or seven neurals is common for bothremydids except *C. placidoi*, which has eight. Neural 1 in *P. mushaisaensis* is subrectangular, much longer than wide, and in exclusive lateral contact with costal 1, as in all other bothremydids and podocnemidids, except *C. placidoi*, which has a hexagonal neural 1, and lateral contact with costals 1 and 2. Neurals 2 through 5 or 6 in *P. mushaisaensis* are hexagonal in shape, slightly longer than wide (Figs. 2.2, 4.6). The last neural bone (6 or 7 depending of the total number of neurals) is always pentagonal in shape, as in all other bothremydids and podocnemidids.

Eight pairs of costal bones, eleven pairs of peripherals, a single suprapygal, and a single pygal constitute the rest of the carapace bones of *Puentemys mushaisaensis*. Costal 1 is longer than costal 2, and the two most posterior costal pairs contact each other medially, resembling all other bothremydids, except *C. placidoi*, which has a continuous neural series from nuchal to suprapygal, avoiding a medial contact between costals. A continuous neural series, it is also the condition present in the podocnemidid *Stupendemys geographicus* Wood, 1976 and *Pelomedusoides incertae sedis* Taxon A, (Cadena et al., 2012).

While the cervical scale is absent as in all other pelomedusoids, this condition is not exclusive to this group (Gaffney et al., 2011; Lapparent de Broin, 2000). Vertebral 1 is almost pentagonal in shape and reaches the posteromedial corner of peripheral 2 in all known carapaces of *P. mushaisaensis*, indicating that this is another ontogenetically conservative character (Figs. 2.2, 4.6). The condition of vertebral 1 reaching peripheral 2 is also present in *F. mechinorum*. In all other pelomedusoids, vertebral 1 only reaches peripheral 1, occasionally reaching the sutural contact between peripherals 1 and 2. Additionally, vertebral 1 is wider than vertebral 2 in *P. mushaisaensis*, a condition also shared by *Po. provinciale* and *Elochelys convenarum* Laurent et al., 2002 within bothremydids. In *F. mechinorum* and *K. kallamedensis* vertebral 1 is as wide as vertebral 2 and in all other bothremydids vertebral 1 is narrower than vertebral 2.

In ventral view of the carapace (Figs. 2.3, 4.3, 4.7, 4.8), the position and shape of the axillary, inguinal, and iliac scars as well as the thoracic and sacral vertebrae series are well preserved (UF/IGM 62, UF/IGM 54, UF/IGM 53, UF/IGM 56, UF/IGM 59, UF/IGM 60, UF/IGM 55).

On the ventral surface of costal 1 and ontogenetically conservative in all specimens of *Puentemys mushaisaensis*, the axillary scar is shallow, slightly elevated, positioned around one third of the total width of costal 1, its shape is oval, elongated, slightly wider posteromedially than anterolaterally, and laterally projected towards the medial part of peripheral 3, similar to *F. mechinorum*. In *Po. provinciale* the axillary scar is slightly narrower posteromedially than anterolaterally, in *K. kallamedensis* it is extremely narrow, and in *Ch. barberi*, *Taphrosphys sulcatus* Leidy, 1856, and *Chupacabrachelys complexus* it is positioned closer to the posterior margin of costal 1 and its lateral projection is onto the sutural contact between peripherals 3 and 4. *Araiochelys hirayamai* Gaffney et al., 2006 has an axillary scar more medially advanced inside costal 1, closer to its posterior margin and much wider posteromedially than anterolaterally. The shape and position

of the axillary scar in *C. placidoi*, *R. soutoi*, and *Elochelys* spp. is unknown.

The inguinal scar in *Puentemys mushaisaensis* is also ontogenetically conservative in shape and position, being low, shallow, and positioned at the posterolateral margin costal 5, and slightly projected medially as in *F. mechinorum* and *Po. provinciale*. In all other bothremydids the inguinal scar is much longer, narrower, and more anterolaterally positioned in costal 5. The inguinal scar is unknown for *C. placidoi*, *R. soutoi*, and *Elochelys* spp.

The iliac scar in *Puentemys mushaisaensis* is almost triangular in shape and positioned on the ventral surface of costal 8, almost reaching the posteromedial portion of costal 7 and a small part of the anteromedial portion of the suprapygal, as in *Po. provinciale*, *Ch. barberi*, *Chu. complexus*, and *K. kallamedensis*. The condition is unknown for the other bothremydids.

Thoracic vertebra 1, clearly seen in UF/IGM 62, is positioned under neural 1 and is strongly sutured laterally to thoracic rib 1. It has short, wide, and rounded prezygapophyses. While this condition is unknown for other bothremydids, in all extant podocnemidids the prezygapophyses of thoracic vertebra 1 are longer, thinner, and with a more acute ending tip.

Plastron.—The anterior plastral lobe of *Puentemys mushaisaensis* (Fig. 4.1, 4.2, 4.5) is short and wide at the base, with the anterior margin nearly straight as in *F. mechinorum*. In all other bothremydids the anterior plastral lobe is much shorter, except in *C. placidoi*, which has a longer anterior lobe reaching the same level as the anterior margin of the carapace. The posterior plastral lobe of *P. mushaisaensis* is shorter than the total length of the bridge, with nearly convex lateral margins as in *P. provinciale*. The anal notch of *P. mushaisaensis* is wide with an opened V-shape as in *F. mechinorum*, *Ch. barberi*, *C. placidoi*, *Chu. complexus*, and *Elochelys* spp. A much narrower anal notch is present in *Po. provinciale*, a very wide U-shaped anal notch is present in *Taphrosphys* spp., and a very deep anal notch is present in *A. hirayamai*. In *K. kallamedensis*, the anal notch has a particularly straight medial margin.

In dorsal view, the ischiac and pubic scars are clearly visible (UF/IGM 52, UF/IGM 64, UF/IGM 54) (Fig. 4.10, 4.11). The ischiac scar is elongated and triangular in shape with its anterior margin transverse and the posterior tip ending far anterior to the medial point of the anal notch, as in *F. mechinorum* and *R. soutoi*. In *Taphrosphys* spp. the ischiac scar is almost circular in shape and almost contacts the medial margins of the anal notch; in all other bothremydids the ischiac scar is positioned very close to or at the same level as the medial point of the anal notch. In *Ummulisani rutgersensis* (Gaffney et al., 2006) the ischiac scar is also circular in shape, but larger than that of *Taphrosphys* spp. and separate from the medial anal notch margins. The pubic scar of *P. mushaisaensis* is elongate, oval in shape, located very close to the medial contact between the xiphiplastra as in *F. mechinorum* and *P. provinciale*. In *A. hirayamai*, *Chu. complexus*, and *Ch. barberi* the pubic scar is narrower, more longitudinally orientated, and more laterally positioned on the xiphiplastron. A very narrow and very long pubic scar is characteristic of *Taphrosphys* spp. and *U. rutgersensis*. The ischiac scar is unknown for *C. placidoi* and *Elochelys* spp.

The scute sulci and sutures of the plastron bones are best preserved in UF/IGM 53, UF/IGM 54, UF/IGM 60, and UF/IGM 55 (Fig. 4.1, 4.2). The entoplastron is large, diamond shaped, slightly wider than long, and with its posterior corner reaching the level of the carapace-plastron bridge as in *F.*

TABLE 1—Measurements (in cm) for 12 specimens of *Puentemys mughaisaensis*. Abbreviations: 1=UF/IGM 62; 2=UF/IGM 53; 3=UF/IGM 52; 4=UF/IGM 54; 5=UF/IGM 55; 6=UF/IGM 56; 7=UF/IGM 57; 8=UF/IGM 58; 9=UF/IGM 64; 10=UF/IGM 59; 11=UF/IGM 60; 12=UF/IGM 50; L=length as preserved; Le=total estimated length; W=width as preserved; We=total estimated width; —=not measured.

Measurements	1	2	3	4	5	6	7	8	9	10	11	12
Carapace												
L	118	82	—	112	45	64	—	70	—	25	36	151
W	103	39	—	85	65	45	—	55	—	18	16	135
Le	118	82	—	120	105	80	—	120	—	30	45	141
We	108	65	—	105	95	58	—	85	—	24	35	135
Plastron												
L	—	76	58	105	—	—	64	—	—	—	—	—
W	—	48	35	75	—	—	45	—	40	—	28	126
Le	—	76	58	105	97	72	64	107	62	—	38	135
We	—	52	35	75	68	51	48	73	48	—	28	126

mechinorum and *Po. provinciale*. In *U. rutgersensis* the entoplastron is also large, but does not reach the bridge level. In all other bothremydids the entoplastron is smaller, slightly wider than long, and located anterior to the bridge level. A much longer than wide entoplastron is characteristic of *Chu. complexus*. The mesoplastron is laterally positioned, hexagonal in shape with rounded margins as in all other podocnemidoideans (podocnemidids and bothremydids) turtles.

The intergular scale is pentagonal and elongated in shape, wider anteriorly, completely separating the gulars and covering the anterior corner of the entoplastron as in *F. mechinorum*, *Po. provinciale*, *Ch. barberi*, and *R. soutoi*. In *C. placidoi* and *Elochelys* spp. the intergular reaches the central point of the entoplastron, whereas in *Taphrosphys* spp. it covers more than 50% of the entoplastron, and in *U. rutgersensis* covers the total length of the entoplastron, reaching the sutural point between entoplastron and hyoplastron. In *Taphrosphys* spp. *U. rutgersensis*, and *Elochelys* spp. the intergular completely separates the humeral scales. The intergular is unknown for *K. kallamedensis*, *Chu. complexus*, and *A. hirayamai*. The gular scales in *P. mughaisaensis* are triangular in shape, located anterior to the anterolateral margin of the entoplastron as in *F. mechinorum*, *C. placidoi*, *Po. provinciale*, *R. soutoi*, *Ch. barberi*, and *Elochelys* spp. In

Taphrosphys spp. the gulars reach the entoplastron-epiplastron suture, and cross the anterolateral margin of the entoplastron in *U. rutgersensis*. The humeropectoral sulcus in *P. mughaisaensis* crosses the entoplastron at its posterior corner and continues laterally without crossing the epiplastral-hyoplastral suture, as in *Ch. barberi*, *Taphrosphys* spp., and *U. rutgersensis*. The humeropectoral sulcus crosses the midline of the entoplastron and continues laterally over the epiplastron-hyoplastron suture or slightly anterior to this one in *F. mechinorum*, *Elochelys* spp. and *Po. provinciale*, whereas in *C. placidoi* and *R. soutoi* the sulcus slightly touches the posterior corner of the entoplastron and continues laterally parallel to the epiplastron-hyoplastron suture, but never goes over this one. The pectoroabdominal sulcus does not cross the mesoplastron and only makes a slight contact at its anterior margin in UF/IGM 60 and UF/IGM 55. A similar condition is present in *F. mechinorum*, *Po. provinciale*, *Taphrosphys* spp., and *Elochelys* spp. The sulcus is more anterior to the mesoplastron in *K. kallamedensis* and *A. hirayamai*. In *P. mughaisaensis* (UF/IGM 63), *C. placidoi*, *R. soutoi*, *Ch. barberi*, and *U. rutgersensis* the pectoroabdominal sulcus crosses the anterior margin of the mesoplastron. The pectoral scales of *P. mughaisaensis* are shorter than the humerals, abdominals, and femorals at the midline of the plastron, a

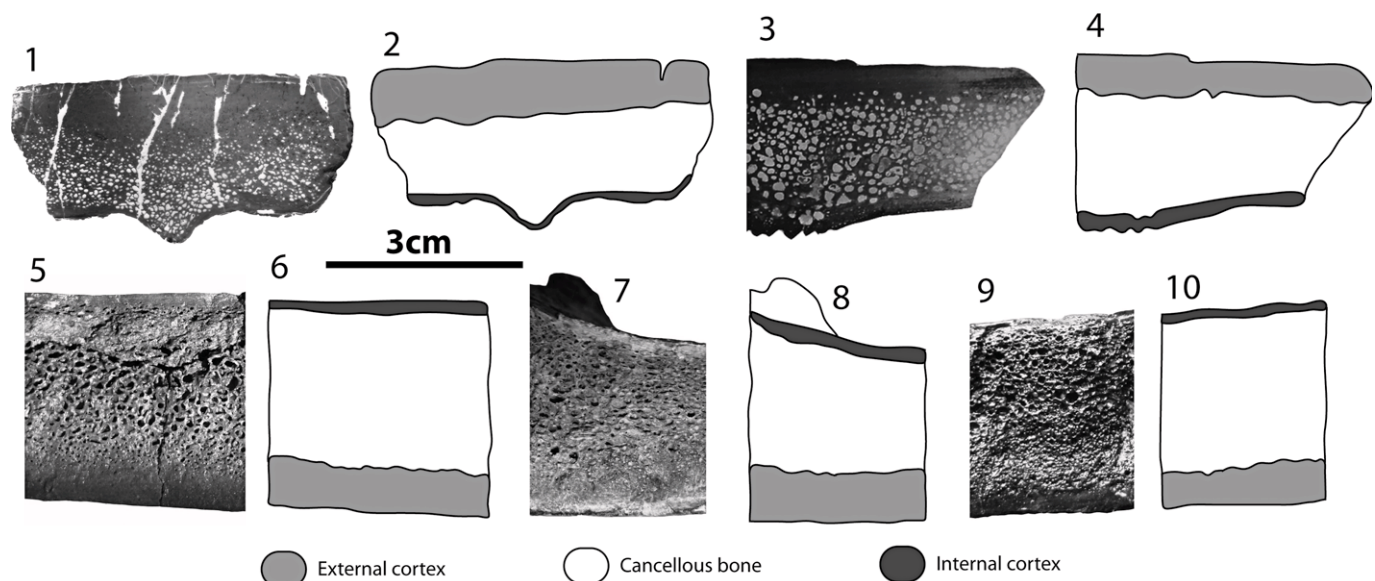
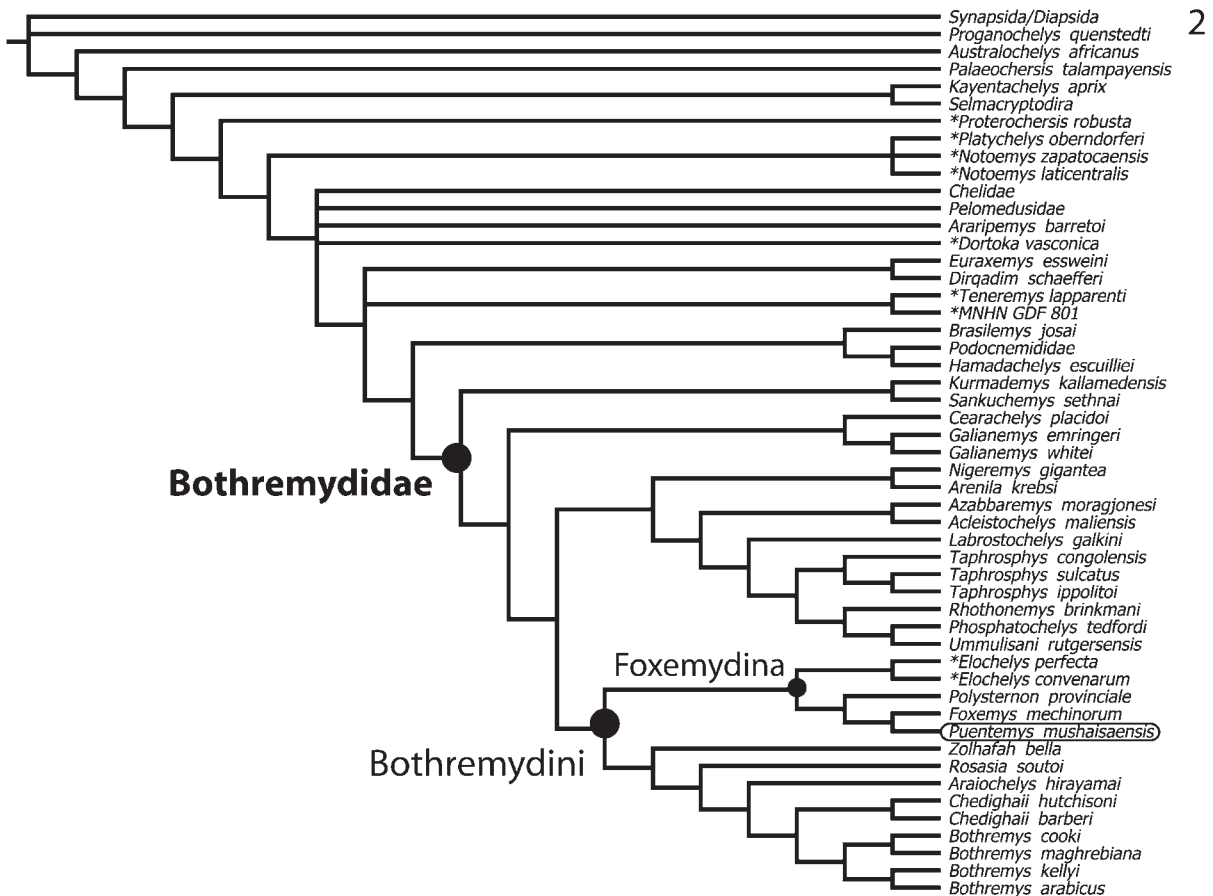
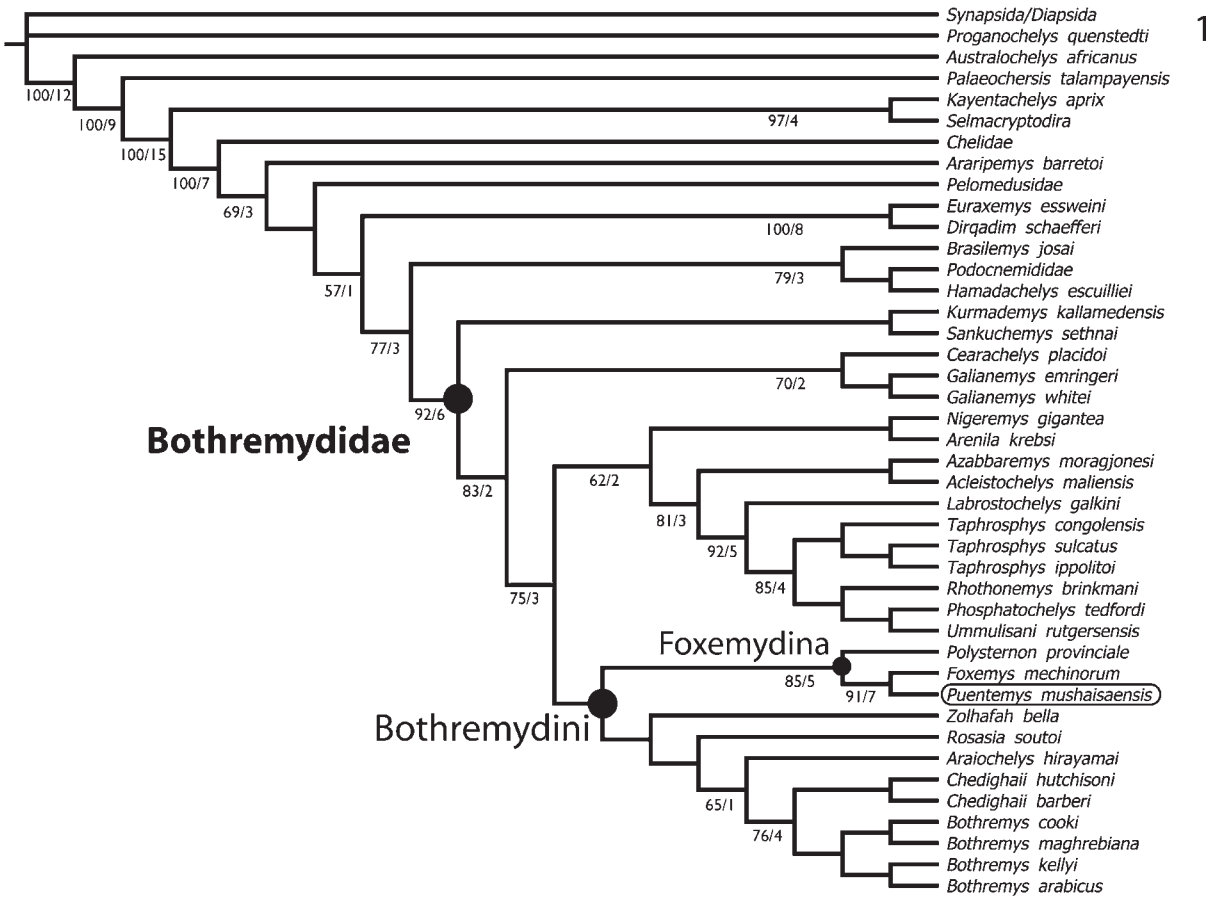


FIGURE 5—Bone histology of *Puentemys mughaisaensis* and other bothremydids. 1, 2, UF/IGM 65, bone thin section of a neural 4 from an adult specimen of *P. mughaisaensis*; 3, 4, NCSU/P 001, bone thin section of a neural 4 from a Bothremydini from the Late Cretaceous of North Carolina; 5, 6, UF/IGM 66, left hyoplastron from an adult specimen of *P. mughaisaensis* in cross section; 7, 8, USNM 357125, left hyoplastron from *Taphrosphys* sp. in cross section; 9, 10, NCSU/P 002, left hyoplastron from an adult specimen of Bothremydini from Late Cretaceous of North Carolina.



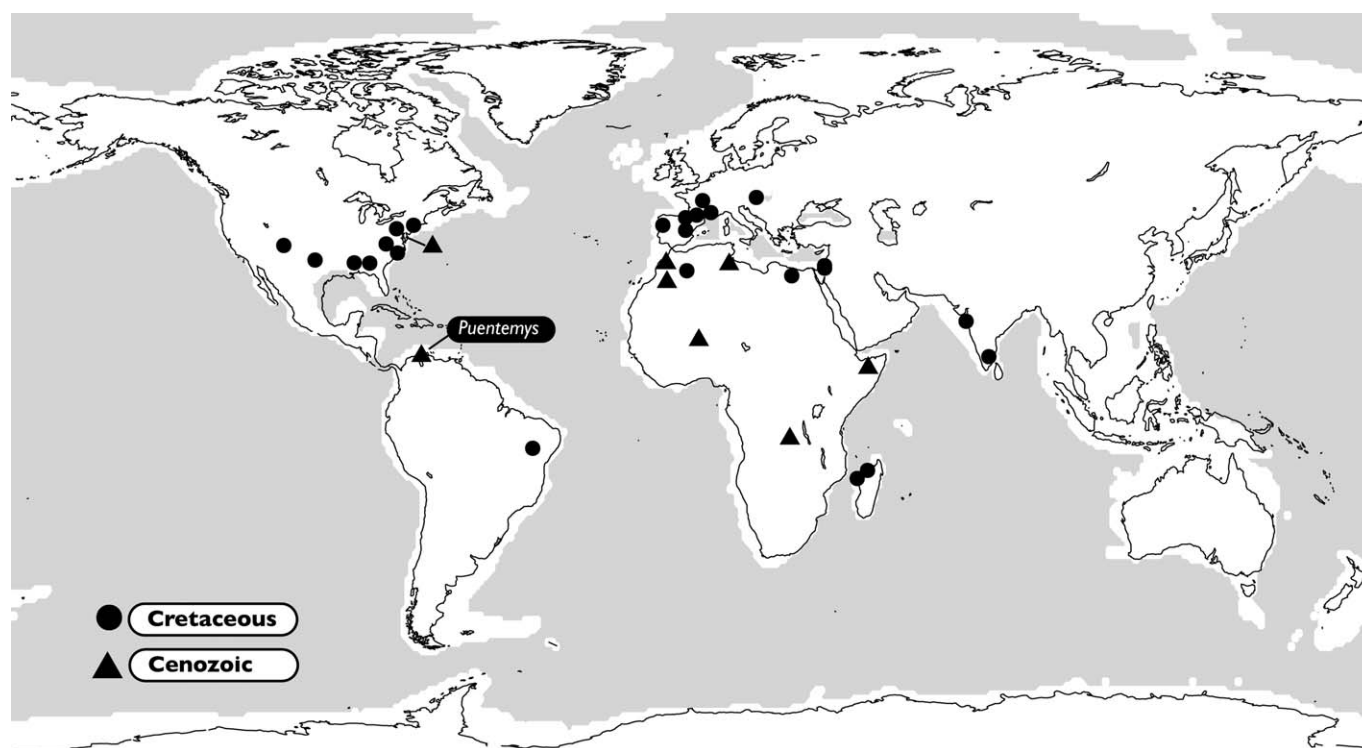


FIGURE 7—Map showing the distribution of Cretaceous (circles) and Cenozoic (triangles) bothremydids. Distributional data were downloaded from the Paleobiology Database on 10 August 2011, using the group name ‘Bothremydidae’ and the following parameters: time intervals=Cretaceous and Cenozoic together fused in a single map.

condition unique among bothremydids. In *K. kallamedensis*, *C. placidoi*, *F. mechinorum*, *Po. provinciale*, *R. soutoi*, and *Elochelys* spp. the humerals, pectorals, and abdominals have similar medial length. *A. hirayamai*, *B. barberi*, *Taphrosphys* spp., and *U. rutgersensis* have abdominal scales much shorter than the pectorals and femorals. The abdominofemoral sulcus in *P. mushaisaensis* is straight, ending laterally at the hypoplastral bridge notch. The femoroanal is slightly convex as in *F. mechinorum* and *Po. provinciale*; in other bothremydids the sulcus tends to be straight.

BONE HISTOLOGY

Two bone thin sections were created from pieces of carapace and plastron of *Puentemys mushaisaensis*: a right hyoplastron (UF/IGM 65) and a neural 4 (UF/IGM 66). An additional thin section of a neural 4 (NCSU/P 001) from a bothremydine from the Late Cretaceous of North Carolina (Gaffney et al., 2009a) was also included for comparison. Procedures follow those described by (Schweitzer et al., 2008), briefly summarized here: bone was embedded in Silmar resin (SurfSource, USA), sectioned to 1.5 mm slides, ground to a thickness of 60–80µm, polished, and examined with a Zeiss Axioskop 2 plus biological microscope and a Zeiss Axioskop 40 petrographic polarizing microscope. Images were taken using Axiovision software package (vers. 4.7).

In all three bone thin sections studied, the internal cortex is extremely reduced in thickness compared to the external cortex (Fig. 5.1–5.6); this is also the pattern observed in a hyoplastron fragment of *Taphrosphys* sp. (USNM 357125) (Fig. 5.7, 5.8), and in a left hyoplastron from an adult specimen of Bothremydini from Late Cretaceous of North Carolina, NCSU/P 002 (Fig. 5.9, 5.10). Reduced thickness of the internal cortex of the shell elements was defined by (Scheyer and Sanchez-Villagra, 2007) as a potential synapomorphy for Bothremydidae, further supporting our classification of *Puentemys mushaisaensis* as bothremydid.

PHYLOGENETIC ANALYSIS

A cladistic analysis was performed on a character-taxon matrix building on that published by Gaffney et al. (2006). We added *Puentemys mushaisaensis* and added five new characters (Appendix 1). We also added *Notoemys zapatoensis* (Cadena and Gaffney, 2005) and CNRST-SUNY 199 to modify previous codings for *Acleistochelys maliensis* (Gaffney et al., 2007). In total, the analysis included 180 morphological characters coded for 60 taxa (see Nexus file, online supplementary material). All characters were equally weighted and unordered. Multistate characters were treated as polymorphic. Bothremydidae was defined as the ingroup, including all taxa analyzed and shown in Gaffney et al. (2006; fig. 292).

←

FIGURE 6—Cladogram showing the phylogenetic relationships between *Puentemys mushaisaensis* and bothremydids. 1, single most parsimonious cladogram of the dataset in Supplementary material 01, only skull-shell taxa included, as in the cladogram of (Gaffney et al., 2006; fig. 288); *Puentemys mushaisaensis* is placed inside the Tribe Bothremydini, Subtribe Foxemydina, as sister taxon of *Foxemys mechinorum*; 2, strict consensus cladogram of six most parsimonious trees, including nine shell-only taxa indicated by asterisk (*); the place of *P. mushaisaensis* is kept as in the cladogram shown in 1. Bootstrap support values (left number before dash) and Bremer decay indices (right numbers after dash) are indicated above the branch to which they pertain.

The analysis was performed in PAUP 4.0b10 (Swofford, 2002) using heuristic search, 10,000 replicates, TBR branch-swapping option. Bootstrap values were calculated from 100 replicates using the same settings as the primary search, and Decay (Bremer) indices were obtained to estimate statistical support for nodes using the MacClade v. 4.05 (Maddison and Maddison, 2002) and in PAUP 4.0b10 (Swofford, 2002). Tree lengths for alternative phylogenetic hypotheses were explored using Mesquite v. 2.74 (Maddison and Maddison, 2010).

A first analysis was run including all 180 characters, but excluding all shell-only taxa (marked with asterisk in online supplementary material), similar to the analysis shown in Gaffney et al. (2006; fig. 288). A single most parsimonious tree was obtained (Fig. 6.1), with a tree length of 523 steps, consistency index of 0.721, retention index of 0.821, rescaled consistency index of 0.592, and homoplasy index of 0.547. The topology of this cladogram is similar to the result obtained by Gaffney et al. (2006), plus the inclusion of *Puentemys mushaisaensis*, which is placed in the Tribe Bothremydini, Subtribe Foxemydina, and as sister taxon of *Foxemys mechinorum*. A second analysis was run including all 180 characters and the addition of nine shell-only taxa, as in Gaffney et al. (2006; fig. 292). Six most parsimonious trees were obtained, with a consensus tree shown in Figure 6.2 and the following statistics: tree length 1320 steps, consistency index 0.687, retention index 0.807, rescaled consistency index 0.554, and homoplasy index 0.570. In contrast to the result obtained by Gaffney et al. (2006), Chelidae, Pelomedusidae, *Araipemys barretoii*, and *Dortoka vasconica* are placed in an unresolved polytomy at the base of Eupleurodira. *Puentemys mushaisaensis* retains the same position in the cladogram as for the first analysis, and *Elochelys perfecta* and *Elochelys convenarum* are included in the Subtribe Foxemydina.

DISCUSSION

The middle-late Paleocene occurrence of *Puentemys mushaisaensis* constitutes the first record of bothremydids in the tropics of South America (Fig. 7), supporting once again the wide-spread distribution of bothremydids during the Paleogene, particularly members of Tribe Bothremydini previously mentioned by Gaffney et al. (2006). Although, independently acquired in different clades of Testudines, a bone histology pattern of an internal cortex extremely reduced in comparison with the external cortex is a unique feature of bothremydids among Pelomedusoides. Similarities between *P. mushaisaensis* and the Paleogene European bothremydids indicate that this clade of bothremydids was able to disperse long distances through coast lines and probably marine currents through the Atlantic Ocean.

Puentemys mushaisaensis is the largest bothremydid ever found. This species and two others also from the Cerrejón Formation, *Carbonemys cofrinii* and Pelomedusoides Taxon A (Cadena et al., 2012), are the largest Paleogene turtles known. Although large body size in bothremydids and podocnemidids was phylogenetically independently acquired, it appeared contemporaneously in both groups during the Late Cretaceous–Paleogene, potentially persisting in podocnemidids until the late Miocene–Pliocene with *Stupendemys geographicus* and the large skulls of *Caninemys tridentata* (Meylan et al., 2009) and *Podocnemis bassleri* (Williams, 1956). Despite fluctuations in climate (Liu et al., 2009; Zachos et al., 2008; Zachos et al., 2001), large pelomedusoid turtles have a long history in the tropics of South America, culminating in maximum size of

90 cm total midline shell length for the largest extant podocnemidid, *Podocnemis expansa* from the Amazon and Orinoco basins.

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