

This article was downloaded by: [Cadena, Edwin A.]

On: 24 March 2010

Access details: Access Details: [subscription number 920292640]

Publisher Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t917000010>

New Podocnemidid Turtle (Testudines: Pleurodira) from the Middle-Upper Paleocene of South America

Edwin A. Cadena^{ab}, Jonathan I. Bloch^a, Carlos A. Jaramillo^b

^a Florida Museum of Natural History, Dickinson Hall, University of Florida, Gainesville, Florida, U.S.A.

^b Center for Tropical Paleoecology and Archeology, Smithsonian Tropical Research Institute, Balboa, Ancon, Panama

Online publication date: 24 March 2010

To cite this Article Cadena, Edwin A. , Bloch, Jonathan I. and Jaramillo, Carlos A. (2010) 'New Podocnemidid Turtle (Testudines: Pleurodira) from the Middle-Upper Paleocene of South America', Journal of Vertebrate Paleontology, 30: 2, 367 – 382

To link to this Article: DOI: 10.1080/02724631003621946

URL: <http://dx.doi.org/10.1080/02724631003621946>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

NEW PODOCNEMIDID TURTLE (TESTUDINES: PLEURODIRA) FROM THE MIDDLE–UPPER PALEOCENE OF SOUTH AMERICA

EDWIN A. CADENA,^{*,1,2} JONATHAN I. BLOCH,¹ and CARLOS A. JARAMILLO²

¹Florida Museum of Natural History, Dickinson Hall, University of Florida, Gainesville, Florida 32611-7800, U.S.A.,
ecadena@ufl.edu, jbloch@flmnh.ufl.edu;

²Center for Tropical Paleocology and Archeology, Smithsonian Tropical Research Institute, Balboa, Ancon AA 0843-03092,
Panama, JaramilloC@si.edu

ABSTRACT—A new pleurodiran turtle, *Cerrejonemys wayuunaiki*, from the middle to upper Paleocene, Cerrejón Formation of Colombia, is described on the basis of a complete skull, lower jaw, partial carapace and plastron, two cervical vertebrae, a right coracoid, and both pelvic girdles. *Cerrejonemys wayuunaiki* shares a suite of diagnostic characteristics with Podocnemididae, including a fully developed, medially extensive cavum pterygoidei that is almost completely covered by the prolonged posterolateral flanges of the pterygoid, a posterior elongation of the secondary roofing of the skull composed of the parietal and the quadratojugal covering two-thirds or more of the cavum tympani, a dentary covered laterally by the surangular, and no contact between the exoccipital and quadrate. *Cerrejonemys wayuunaiki* is unique among podocnemidids in having ridges on the ventral margin of the dentary, dentaries that form an acute angle at the fused symphysis, and a relatively thick (up to 35 mm) carapace and plastron. Results from a cladistic analysis of panpodocnemidids indicate that *C. wayuunaiki* is the sister taxon of the genus *Podocnemis*, which ranges from the Miocene to Recent, implying that stem of *Podocnemis* spp. were inhabiting tropical South America early in the Paleogene.

INTRODUCTION

Pleurodires or side-necked turtles, although currently restricted to freshwater environments of the southern hemisphere, have inhabited freshwater, brackish, and near-coastal environments of most continents since the Early Cretaceous (Gaffney et al., 2006). They are known from at least 150 extant and fossil species that can be recognized in five primary clades (Gaffney et al., 2006): Araripemydidae (Aptian–Albian of Brazil), Chelidae (Early Cretaceous to Recent of South America and Australia), Euraxemydidae (Albian of Brazil and Cenomanian of Morocco), Bothremydidae (Albian to Eocene of North America, South America, Europe, Africa, and India), Pelomedusidae (Early Cretaceous to Recent), and Podocnemididae (Late Cretaceous to Recent of South America, Europe, Caribbean, and Africa). Extant podocnemidids (sensu França and Langer, 2006) include six species of *Podocnemis* and *Peltocephalus dumerilianus* from South America, and *Erymnochelys madagascariensis* from Madagascar. According to França and Langer (2006), podocnemidids plus their stem representatives, *Portezueloemys patagonica*, *Cambaremys langertoni*, *Bauruemys elegans*, and *Roxochelys* spp., constitute the clade Podocnemoidae (podocnemoids). Podocnemoidae plus the speciose clade Bothremydidae constitute the clade Podocnemoidea (podocnemoideans). In a higher phylogenetic level, Podocnemoidea, *Euraxemys essweini* (Gaffney et al., 2006), and *Brasilemys josai* form the clade “Panpodocnemididae” (panpodocnemidids). Panpodocnemidids plus Pelomedusidae constitute the clade Pelomedusoides (pelomedusoids); and finally the clade “Panpelomedusoides” (panpelomedusoids), which includes Pelomedusoides plus *Araripemys barretoii*.

An important gap in the record of podocnemidids exists between the Late Cretaceous and the Neogene, particularly for the tropical part of South America (Table 1). Here we describe the

first known Paleogene podocnemidid from the northern neotropics (Fig. 1), which not only fills this substantial gap in the fossil record, but also provides new morphological data that allow for a direct test of competing phylogenetic and biogeographic hypotheses for extant Podocnemididae.

The relationship between extant podocnemidids can be explained by one of the following three hypotheses. The first hypothesis, based on cladistic analysis of morphological characteristics, was formulated by França and Langer (2006) and reiterated by Meylan et al. (2009); it proposed that *Peltocephalus dumerilianus* is related more closely to *Erymnochelys madagascariensis* than to the clade of *Podocnemis* spp. This hypothesis implies that they are relicts of a more widespread clade that inhabited the southern South America, Antarctica, and Madagascar previous to their separation during the Late Cretaceous; i.e., that the modern geographical distributions for *P. dumerilianus* and *E. madagascariensis* are due to vicariance. The second hypothesis, also based on cladistic analysis of morphological characteristics, suggests that *P. dumerilianus* and the clade of *Podocnemis* spp. are closely related and had an autochthonous origin and speciation in South America, and subsequently expanded their distribution northwards during the Cenozoic (Gaffney and Meylan, 1998; Lapparent de Broin, 2000; Romano and Azevedo, 2006; Lapparent de Broin et al., 2007). Finally, the third hypothesis, which is based on molecular phylogenetics, suggests that *Erymnochelys madagascariensis* and the clade of *Podocnemis* spp. are sister taxa (Noonan, 2000; Noonan and Chippindale, 2006). This hypothesis, which is supported by the work of Vargas-Ramirez et al. (2008), suggests that the split between *Podocnemis* spp. and *Erymnochelys* spp. occurred during the Late Cretaceous, as a consequence of the submergence of a land bridge between Madagascar and Antarctica–South America.

These three hypotheses share a common problem: the absence of unequivocal fossil record for *Peltocephalus dumerilianus* and its possible Late Cretaceous and Cenozoic fossil relatives; in the particular case of the molecular hypothesis, this is

*Corresponding author.

TABLE 1. Summary of extinct and extant South American podocnemoid turtles.

Taxa	Locality	Age	Material	Sources
<i>Brasilemys josai</i>	Ceará state, Brazil	Aptian–Albian limit	Almost complete skull, carapace, hyoid bones, left lower jaw, axis, and third cervical vertebra	Lapparent de Broin (2000)
<i>Portezueloemys patagonica</i>	Neuquén province, Argentina	Late Turonian– Early Coniacian	Partially preserved skull, carapace, and plastron	De la Fuente (2003)
<i>Bauremys elegans</i>	South-central Bauru Group, Brazil	Turonian– Maastrichtian	Several skulls, lower jaws, shells, partial coracoid, and cervical vertebra	Suarez (1969), Kischlat (1994), França and Langer (2006)
<i>Bauremys brasiliensis</i>			Partial plastron	Staesche (1937), Kischlat (1994)
<i>Roxochelys harrisi</i>			Fragmentary carapace and plastron	Pacheco (1913), Price (1953), Lapparent de Broin (1991)
<i>Cambaremys langertoni</i>	Minas Gerais, Brazil	Maastrichtian	Partial carapace and plastron, coracoids, scapula, pelvic girdles, and limb bones	França and Langer (2005)
aff. <i>Roxochelys vilavilensis</i>	Tiupampa Basin, Bolivia	early Paleocene	Several skulls, lower jaws, shells, coracoid, and cervical vertebra	Lapparent de Broin (1991)
<i>Cerrejonemys wayuunaiki</i>	Cerrejón Coal Mine, Colombia	middle–late Paleocene	Skull, lower jaw, partial carapace and plastron, coracoid, pelvic girdle, two cervical vertebra	This study
<i>Podocnemis pritchardi</i>	La Venta fauna, Colombia	middle Miocene	Nearly complete shell	Wood (1997)
<i>Podocnemis medemi</i>			Nearly complete plastron and partial carapace	
<i>Podocnemis cf. expansa</i>			Partial cranium	
<i>Bairdemys hartsteini</i>	Puerto Rico	middle Miocene	Nearly complete skull	Gaffney and Wood (2002)
<i>Bairdemys venezuelensis</i>	Urumaco fauna, Venezuela	late Miocene	Several skulls and shells	Wood and Diaz de Gamero (1971), Gaffney and Wood (2002), Sanchez-Villagra and Winkler, (2006), Gaffney et al. (2008)
<i>Bairdemys sanchezi</i>			Skull, lower jaws, anterior plastral fragment	Gaffney et al. (2008)
<i>Bairdemys winklerae</i>			Several skull, lower jaw	Gaffney et al. (2008)
<i>Stupendemys geographicus</i>			Shell, humerus, femur, scapula, two cervical vertebrae	Wood (1976)
<i>Stupendemys souzai</i>	Rio Acre, Peru and Brazil	late Miocene–early Pliocene	Costal bone, nuchal, humerus, xiphiplastron, pelvic girdle, and four cervical vertebrae	Lapparent de Broin et al. (1993), Gaffney et al. (1998), Bocquentin and Melo (2006).
<i>Podocnemis bassleri</i>	Contamana Group, Peru	late Miocene–early Pliocene	Complete skull	Williams (1956)
<i>Podocnemis negrii</i>	Acre state, Brazil	late Miocene–early Pliocene	Partial carapace and plastron, fragmentary pelvis girdle	Carvalho et al. (2002)
<i>Podocnemis expansa</i>	Principal fluvial and lake systems of northern South America	Recent	Complete skeleton	Wagler (1830), Bonin et al. (2006)
<i>P. erythrocephala</i>				
<i>P. lewyana</i>				
<i>P. sextuberculata</i>				
<i>P. unifilis</i>				
<i>P. vogli</i>				
<i>Peltocephalus dumerilianus</i>	Orinoco and Amazon basins, northern South America	Recent	Complete skeleton	Schweigger (1812), Bonin et al. (2006)

critical to calibrating the molecular clock. Only with the discovery and study of stem and fossil representatives for each of the three extant species of podocnemidids will it be possible to find support that allow the complete acceptance or rejection for any of these hypotheses. Towards this, we present here the description of a new taxon that appears to be closely related to the clade of *Podocnemis* spp.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; NFWFL, U.S. National Fish and Wildlife Forensics Laboratory, Ashland, Oregon; UNEFM-CIAPP, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; UF/IGM, University of Florida, Florida Museum of Natural History Vertebrate Paleontology Collections, Gainesville, Florida/Museo Geológico, at the Instituto Nacional de Investigaciones en Geo-

ciencias, Minería y Química, Bogotá, Colombia; YM, Peabody Museum of Natural History at Yale University, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788, sensu Joyce et al. (2004)
 PANPLEURODIRA Joyce, Prahm, and Gauthier, 2004
 PELOMEDUSOIDES Broin, 1988, sensu Joyce et al. (2004)
 PODOCNEMIDIDAE Cope, 1868

Included Genera—*Podocnemis* spp., *Erymnochelys madagascariensis*, *Peltocephalus dumerilianus*, *Dacquemis paleomorpha*, *Stupendemys* spp., *Bairdemys* spp., *Neochelys* spp., *Shweboemys* spp., *Stereogenys cromeri*, and *Cerrejonemys*, gen. nov.

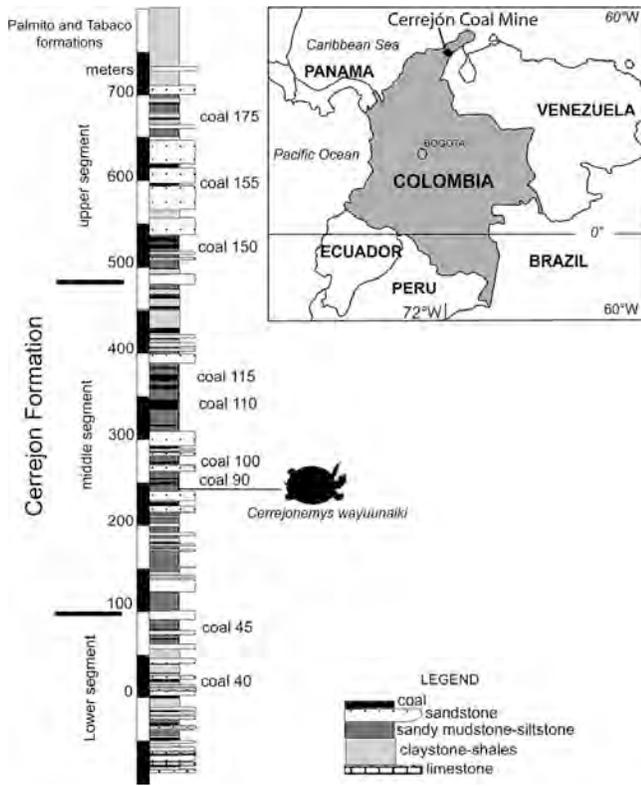


FIGURE 1. Stratigraphic column for the middle–upper Paleocene Cerrejón formation and the stratigraphic horizon from which all known fossils of *Cerrejonemys wayuunaiki* were recovered. Stratigraphic column modified from Bayona et al. (2004).

Amended Diagnosis—Differs from all other known podocnemidids in having: (1) a parietal jugal contact resulting from a relatively reduced postorbital (all others lack this contact, with both bones completely separated by the postorbital); and (2) a dorso-longitudinal ridge on the coracoid (all others have a smooth dorsal surface and lack the ridge).

Remarks—Lapparent de Broin (2000) included *Bauruemys elegans*, aff. *Roxochelys vilavilensis*, *Podocnemis* spp., *Stupendemys* spp., and *Peltocephalus dumerilianus* in the Podocnemidinae based on a single purported synapomorphic character: a cervical centra with saddle-shaped posterior condyles. We suggest that this character is shared by all podocnemidids (sensu this study), for which the cervical vertebra is known, except *Erymnochelys madagascariensis* (França and Langer, 2006).

CERREJONEMYS, gen. nov.

Etymology—From Cerrejón, the name of the type locality, and *emys*, from Greek for freshwater turtle.

Type Species—*Cerrejonemys wayuunaiki*, sp. nov.

Diagnosis—As for the type and only species.

CERREJONEMYS WAYUUNAIKI, gen. et sp. nov.
(Figs. 2, 3, 4A–J, M–O)

Etymology—Named for the language (Wayuunaiki) of the Wayuu people from the Guajira Peninsula, Colombia.

Type Locality—The La Puente Pit of the Cerrejón Coal Mine (11° 08' 30" N, 72° 33' 20" W), Guajira Peninsula, Colombia (Fig. 1).

Horizon and Age—The fossils were recovered from a layer of claystone underlying Coal Seam 90 in the middle part of the

TABLE 2. Measurements for UF/IGM 33, holotype of *Cerrejonemys wayuunaiki*, in centimeters.

Measure	UF/IGM 33
Skull	
Maximum length. Indicated as 'I' in Gaffney et al. (2006:fig. 315)	16.7
Maximum width. Indicated as 'B' in Gaffney et al. (2006:fig. 315)	10.5
Lower jaw	
Maximum length. Indicated as B in (Gaffney et al., 2006:fig. 316)	11
Maximum width measured from the most lateral margins of the articular	8.5
Sixth cervical	
Maximum length in lateral view	3.5
Maximum width in dorsal view	1.9
Maximum height in posterior view	
Seventh cervical	
Maximum length in lateral view	5.5
Maximum width in dorsal view	3.9
Maximum height in posterior view	2
Coracoid	
Maximum length in dorsal view	10.2
Maximum width in dorsal view	2.5
Carapace	
Length as preserved	40.2
Length estimated for complete carapace	100
Width as preserved	50.2
Width estimated for complete carapace	54
Thickness average of carapace measured in neurals, costals and peripherals	3
Plastron	
Length as preserved	32
Length estimated for complete plastron	80
Width as preserved	45
Width estimated for complete plastron	50
Thickness average of plastron	2.6

Estimated lengths for carapace and plastron are based on comparisons to closely related forms (e.g., *Podocnemis* spp.).

brackish-continental Cerrejón Formation (Bayona et al., 2004) (Fig. 1). The well-preserved palynoflora of the Cerrejón Formation includes *Foveotricolpites perforatus*, *Bombacacidites annae*, and the palynological assemblage, indicating a middle–late Paleocene age (palynological zone Cu-02; Jaramillo et al., 2007). Other vertebrates include the large boid snake *Titanoboa cerrejonensis* (Head et al., 2009), dyrosaurid crocodyliforms (Hastings et al., 2010), and other pleurodire turtles (Bloch et al., 2005; Cadena et al., 2008).

Holotype—UF/IGM 33: skull, lower jaw, anterior part of the carapace, middle part of the plastron, right coracoid, pelvic girdles, and the sixth and seventh cervical vertebrae. See Table 2 for measurements.

Diagnosis—*Cerrejonemys wayuunaiki* differs from all other pampelomedusoids (sensu this study) in having small ventral ridges on the medial margin of the dentary, an acute symphyseal angle between the dentaries, and a carapace and plastron both reaching a thickness of 35 mm. It further differs from *Podocnemis* spp. in the absence of an interorbital sulcus at the sutural contact between both prefrontals, a relatively longer prefrontal bone, and the absence of accessory ridges on the triturating surface of the dentary.

DESCRIPTION AND COMPARISONS

For the description of *Cerrejonemys wayuunaiki* we adopted the format used by Gaffney et al. (2006), describing first the state of preservation of each bone, its contacts, and finally comparisons focused principally on podocnemidids.

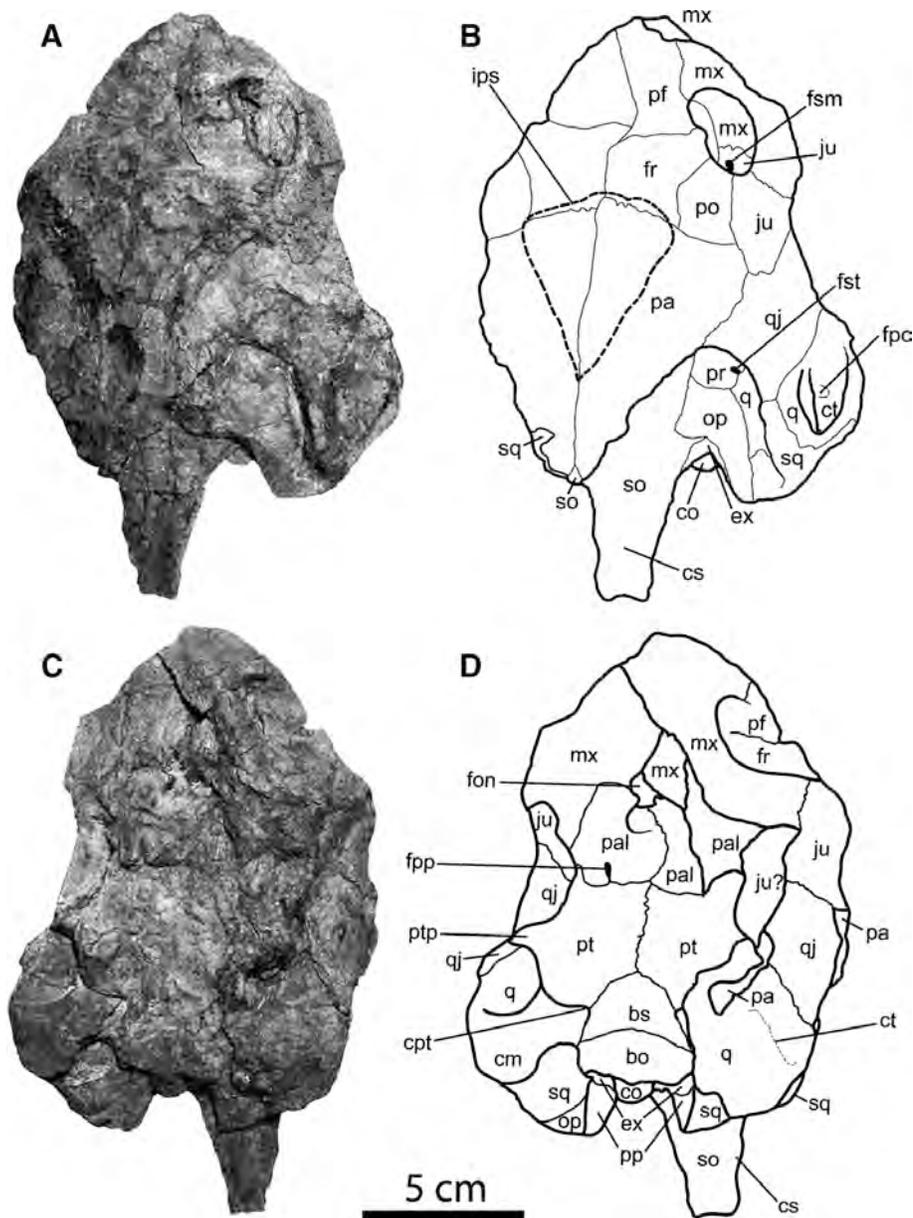


FIGURE 2. *Cerrejonemys wayuunaiki*, UF/IGM 33, holotype. Skull in **A–B**, dorsal and **C–D**, ventral views. **Abbreviations:** **bo**, basioccipital; **bs**, basisphenoid; **cm**, condylus mandibularis; **co**, condylus occipitalis; **cpt**, cavum pterygoidei; **cs**, crista supraoccipitalis; **ct**, cavum tympani; **ex**, exoccipital; **fon**, foramen orbito-nasale; **fpc**, fossa precolumelaris; **fpp**, foramen palatinum posterius; **fr**, frontal; **fsm**, foramen supramaxillare; **fst**, foramen stapedio temporale; **ips**, interparietal scale; **ju**, jugal; **mx**, maxilla; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **po**, postorbital; **pp**, processus paraoccipitalis; **pr**, prootic; **pt**, pterygoid; **ptp**, processus trochlearis pterygoidei; **q**, quadrate; **qj**, quadratojugal; **so**, supraoccipital; **sq**, squamosal.

Skull

The skull of *Cerrejonemys wayuunaiki* is known only from a single large (16.7 cm in length), relatively complete specimen (Fig. 2). The anteriormost portions of both maxillae, the posterior edges of both squamosals, and the posterior end of the crista supraoccipitalis are missing. Due to substantial crushing, the left orbit is visible in ventral view, and most of the right cavum tympani is visible in dorsal view.

Both prefrontals are preserved but are slightly broken (Fig. 2). The posterior contact with the frontal is similar to that seen in *Brasilemys josai*, *Hamadachelys escuilliei*, and all other podocnemidids except *Dacquemys paleomorpha* and *Bairdemys* spp., in which it is much wider. The anterior protrusion projects slightly over, and partially covers, the apertura narium externa, ending in an acute tip, similar to the condition in *Podocnemis* spp. and

aff. *Roxochelys vilavilensis*. *Bauruemys elegans* also has a similar condition, although in this taxon the tip is less acute. By contrast, the protrusion of the prefrontals of *D. paleomorpha*, *Stereogenys cromeri*, *Bairdemys* spp., *Shweboemys antiqua*, and especially *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis* completely covers the apertura narium externa in dorsal view, with a generally convex anterior edge. The anteromedial contact of the prefrontal in *C. wayuunaiki* lacks the interorbital sulcus seen in *Podocnemis* spp. (Lapparent de Broin, 2000). Laterally the prefrontal contacts the maxilla. The medial length of the prefrontal is as long as that of the frontal, similar to the condition in all other podocnemidids except *Podocnemis* spp., which has a very short prefrontal. In dorsal view, the prefrontal of *C. wayuunaiki* is slightly wider than those of *Podocnemis* spp. across the orbits, similar to that of aff. *Roxochelys vilavilensis* and *B. elegans*, but narrower than that of other podocnemidids, in which

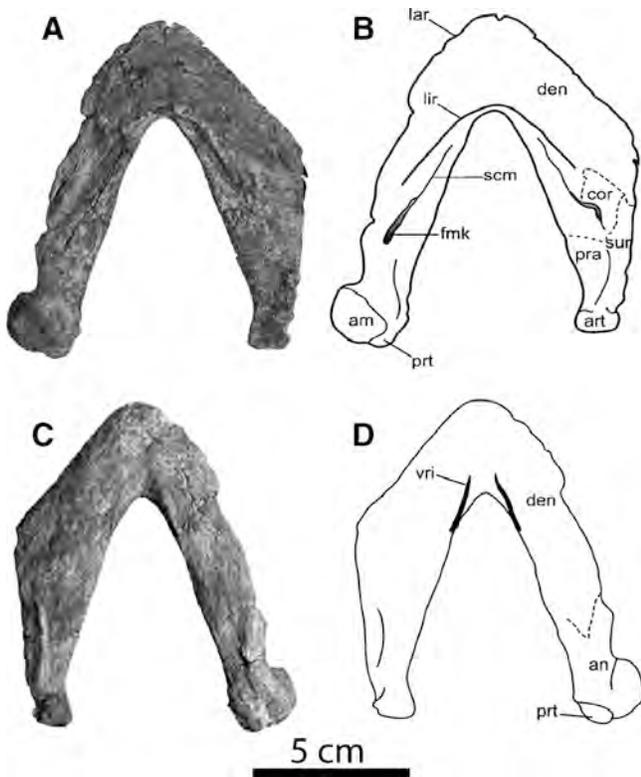


FIGURE 3. *Cerrejonemys wayuunaiki*, UF/IGM 33, holotype. Mandible in A–B, dorsal and C–D, ventral views. **Abbreviations:** am, area articularis mandibularis; an, angular; art, articular; cor, coronoid; den, dentary; fmk, fossa Meckelii; lar, labial ridge; lir, lingual ridge; pra, prearticular; prt, processus retroarticularis; scm, sulcus cartilaginis Meckelii; sur, surangular; vri, ventral ridge.

the orbits are more laterally positioned with less dorsal roofing (e.g., *D. paleomorpha*, *E. madagascariensis*, *Bairdemys* spp., and *P. dumerilianus*).

The frontals are completely preserved but slightly damaged (Fig. 2A, B). The frontal contacts the prefrontal anteriorly, the other frontal medially, forms part of the orbital margin and contacts the postorbital laterally, and the parietal posteriorly. As such, the frontal is similar to that of all other podocnemoids (sensu this study, see Fig 5, node D), for which the region is known.

Both postorbital bones are preserved in dorsal view (Fig. 2A, B). Whereas the right postorbital is complete, the left is slightly damaged laterally. As in *Podocnemis* spp., the postorbital is small and forms part of the orbital margin anteriorly, contacts the frontal medially, the jugal laterally, and the parietal posteriorly.

Whereas both parietals are preserved, they are slightly crushed. As a result, they are shifted anteriorly from their original position, resulting in total exposure of the roof of the otic chamber on the right side of the skull (Fig. 2A, B). Presumably the original condition of the parietals was more posterior, expanding the secondary roofing of the fossa temporalis (see Lapparent de Broin et al., 2007:115–116, for explanation of the evolution of this fossa) and partially covering the roof of the otic chamber in dorsal view, with posterior concave margins, as in *B. elegans*, aff. *R. vilavilensis*, *Ba. sanchezi*, and *Podocnemis* spp. In contrast, *E. madagascariensis*, *P. dumerilianus*, *S. antiqua*, *Neochelys arenarum*, *Ba. venezuelensis*, *Ba. hasrsteini*, *Ba. winklerae*, and *D. paleomorpha* exhibit secondary roofing of the fossa temporalis and possess more posteriorly expanded postero-

lateral temporal emargination of the parietals, with straight to convex posterior edges, and a parietal-squamosal contact in the case of *Dacquemys paleomorpha*. In *Brasilemys josai*, the parietals are highly concave and less advanced posteriorly, so that the roof of the otic chamber is entirely visible in dorsal aspect. This condition is also seen to a slightly more advanced degree in *H. escuilliei* and *Portezueloemys patagonica*. The parietal of *C. wayuunaiki* contacts the frontal and the postorbital anteriorly, the other parietal medially, the jugal and quadratojugal (as in *Podocnemis* spp.) laterally, and the supraoccipital posteromedially. In *Podocnemis erythrocephala*, the secondary roofing of the fossa temporalis can be more posteriorly advanced, with a slight contact between the quadrate and the parietal. Due to crushing, the contour of the cranial roof and development of a globosity (sensu Lapparent de Broin, 2000) is indeterminate for *C. wayuunaiki*.

The right jugal is preserved and completely exposed on the dorsal surface, whereas the left is poorly preserved on the ventral surface due to crushing (Fig. 2). The jugal contacts the maxilla and the orbit anteriorly, the postorbital and the parietal (as in *Podocnemis* spp.) dorsomedially, and the quadratojugal posterolaterally. The jugal plays a key role in the secondary lateral roofing of the fossa temporalis with a decrease in the amount of cheek or lateral emargination (see Lapparent de Broin, 2007:115–116, for explanation of the evolution of this character). In podocnemoids, this lateral emargination is dominated by the jugal, and in bothremyids by the quadratojugal. Unfortunately, in *C. wayuunaiki* the secondary closure of the cheek emargination is difficult to determine because of damage, but it seems to be much less advanced than in *E. madagascariensis* and *P. dumerilianus*, and similar to that seen in *Podocnemis* spp.

Both quadratojugals are fairly well preserved in dorsal aspect, although the left is poorly preserved in ventral aspect. The quadratojugal contacts the jugal anteriorly, the parietal medially, and the quadrate and the squamosal posterolaterally. The posteromedial edge of the quadratojugal forms part of the temporal emargination. In all ways, the quadratojugal is similar to that of *Podocnemis* spp.

The right squamosal is visible in dorsal aspect, whereas the left is covered by the quadrate in ventral aspect of the skull and only its posteromedial aspect is visible (Fig. 2). The squamosal of *C. wayuunaiki* contacts the quadratojugal anteriorly, the quadrate anterolaterally, and the opisthotic medially. In this way, it is similar to all other known podocnemoids, although there is an additional contact with the parietal in *D. paleomorpha*.

The right premaxilla is missing and most of the left is obscured by the right maxilla because of crushing. However, a poorly developed anteroventral hook is present, as in all other known podocnemoids, particularly in *E. madagascariensis* and *P. dumerilianus*, in which the premaxilla hook is highly developed.

Both maxillae are present, although slightly crushed, and the right is better preserved than the left (Fig. 2). The dorsal surface of the left maxilla is visible in ventral view and covers part of the right maxilla and a large portion of the right premaxilla. The maxilla contacts the prefrontal medially and the jugal posteriorly. The ventral contacts are with the palatine posteromedially and with the jugal posteriorly. *Cerrejonemys wayuunaiki* lacks accessory ridges on the ventral surface of the right maxilla. It is similar to that of all podocnemoids except *Podocnemis* spp., in which two or more accessory ridges reach the premaxilla, and *D. paleomorpha*, in which the ridges do not reach the premaxilla.

On the dorsal surface of the skull the foramen supramaxillare appears in the lower posterior aspect of the orbit (Fig. 2A, B), as is the common condition in modern *Podocnemis* spp., *P. dumerilianus*, aff. *R. vilavilensis*, *N. arenarum*, and probably other fossil podocnemoids for which this region is covered with matrix or not

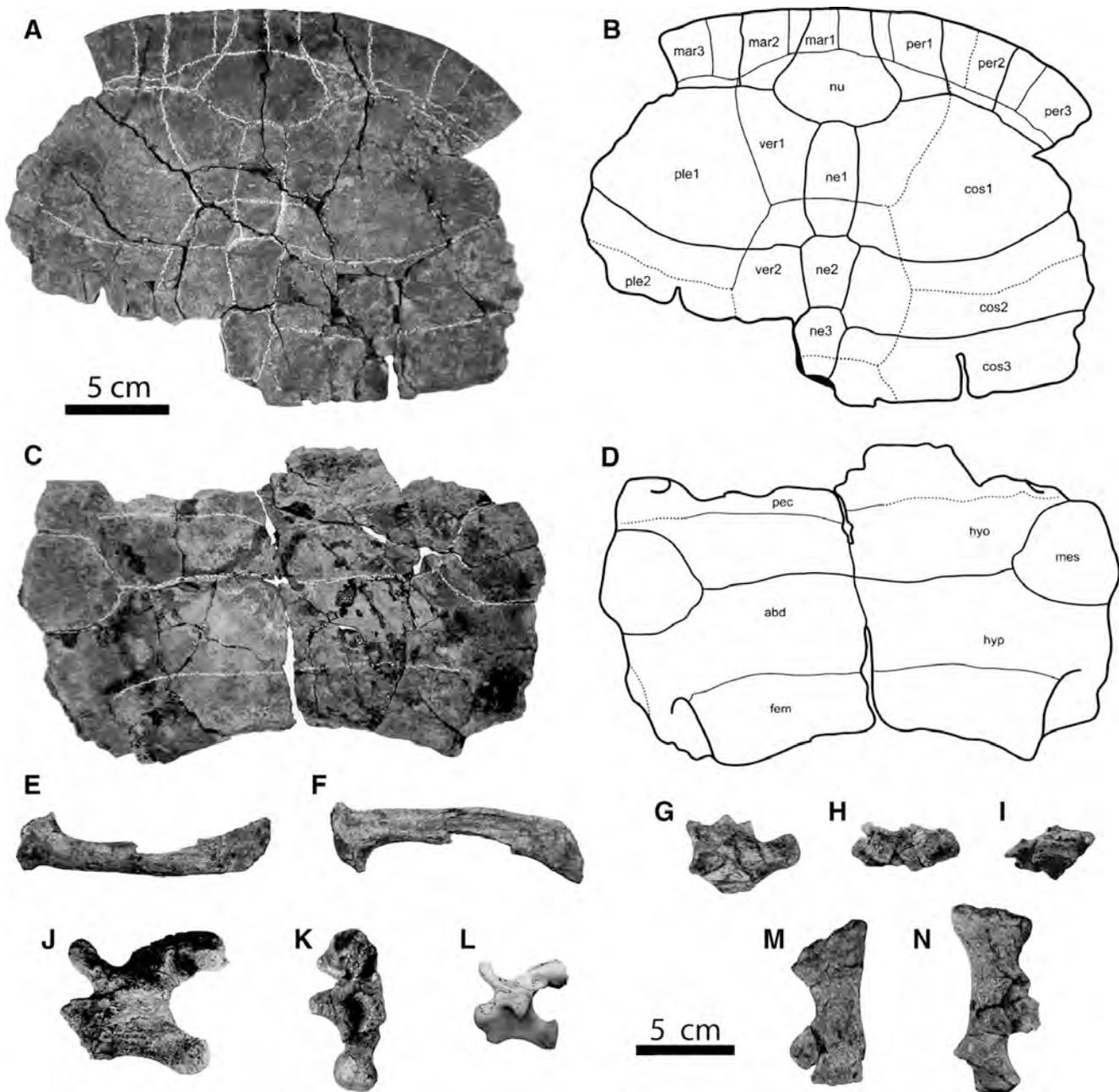


FIGURE 4. *Cerrejonemys wayuunaiki*, UF/IGM 33, holotype. **A–B**, carapace in dorsal view; **C–D**, plastron in ventral view; **E**, dorsal and **F**, ventral views of right coracoid. **G**, ventral, **H**, left lateral, and **I**, posterior views of sixth cervical vertebra. **J**, posterior and **K**, left lateral views of seventh cervical vertebra. **L**, seventh cervical vertebra of *Podocnemis expansa*, AMNH 62947, in left lateral view. **M**, left lateral and **N**, right lateral views of pelvis of UF/IGM 33. **Abbreviations:** **abd**, abdominal scale; **cos**, costal bone; **fem**, femoral scale; **hyo**, hyoplastron; **hyp**, hypoplastron; **mar**, marginal scale; **mes**, mesoplastron; **ne**, neural bone; **nu**, nuchal bone; **per**, peripheral bone; **pec**, pectoral scale; **ple**, pleural scale; **ver**, vertebral scale.

preserved. This suggests that the presence of a foramen supra-maxillare is not exclusive to *Podocnemis expansa* (Joyce, 2007).

The vomer is absent in *C. wayuunaiki*, a condition similar to that described for most podocnemids, except *B. elegans*, aff. *R. vilavilensis*, *Podocnemis bassleri*, and *Po. vogli*. In *Podocnemis unifilis*, presence of the vomer is variable.

Both palatines are preserved (Fig. 2C, D). The right one is fully exposed but slightly damaged, whereas the left one is heavily

damaged and only partly discernible in medial aspect. The palatine contacts the maxilla anterolaterally, the other palatine medially, the jugal laterally, and the pterygoid posteriorly. Anteriorly, the palatine forms the posterior margin of the apertura narium interna. The foramen palatinum posterius is very close to or intercepts the palatine pterygoid suture in *C. wayuunaiki*. A similar condition is present in *B. josai*, *Pz. patagonica*, *H. escuilliei*, and in most podocnemids, except *D. paleomorpha*, *St. cromeri*,

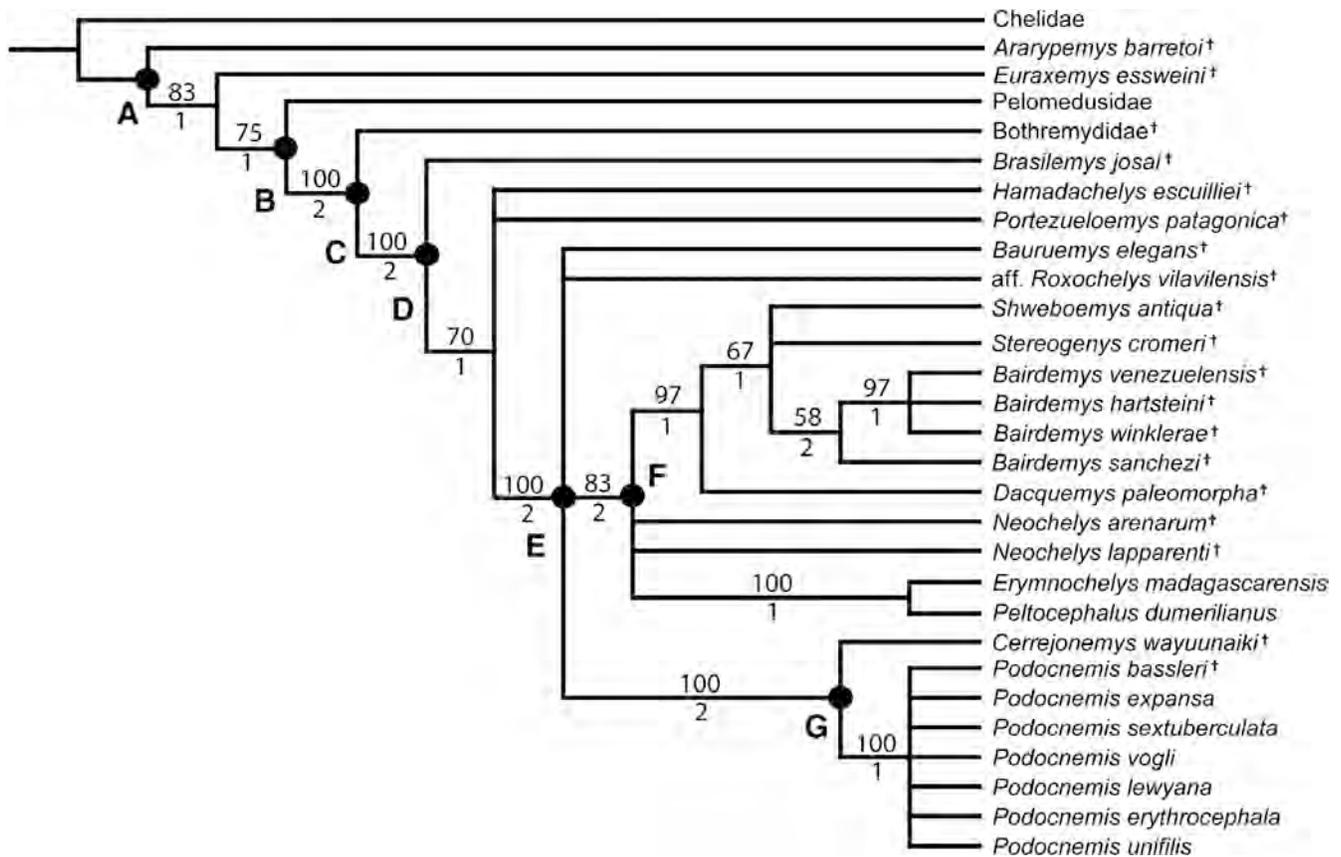


FIGURE 5. Strict consensus cladogram showing the phylogenetic relationships between panpelomedusoid turtles. **A**, Panpelomedusoides; **B**, Pelomedusoides; **C**, panpodocnemidids; **D**, Podocnemoidae; **E**, Podocnemididae; **F**, unnamed clade; **G**, *Podocnemis* spp. and *Cerrejonemys wayuunaiki*. Extinct taxa indicated with dagger superscript. Bootstrapping support values (upper numbers) from an analysis of 100 branch-and-bound replicates. Bremer decay values (lower numbers) obtained using TreeRot (Sorenson and Franzosa, 2007).

and *S. antiqua*, in which this condition is absent. In *Podocnemis* spp. and *Bairdemys* (except for *Ba. sanchezii*, which lacks the foramen), the foramen palatinum posterius is generally restricted to the palatine, well separated from the palatine pterygoid suture. In *Po. Expansa*, the foramen can be very close to the palatine pterygoid suture, or it is restricted to the palatine, as in the other species of *Podocnemis*.

Both pterygoids are preserved, although only their ventral surfaces are visible. The pterygoid contacts the palatine anteriorly, the other pterygoid medially, and the basisphenoid posteromedially.

The processus trochlearis pterygoidei projects almost directly laterally into the center of the fossa temporalis (Fig. 2C, D). This is similar to the condition of most other panpodocnemidids except *B. elegans*, aff. *R. vilavilensis*, and *P. dumerilianus*, in which the processus projects more obliquely with respect to the midline of the skull, and not as far into the fossa in the case of *P. dumerilianus*.

The pterygoid flange (França and Langer, 2006) or posterolateral wing (Lapparent de Broin, 2000) of the pterygoid, although crushed in *C. wayuunaiki*, is well developed posterolaterally and almost completely covers the cavum pterygoidei (sensu Gaffney et al., 2006; 'fossa podocnemidoid' of Lapparent de Broin, 2000) and extends to the caudal margin of the quadrate ramus. A similar condition is present in *B. elegans*, aff. *R. vilavilensis*, *Bairdemys* spp., and *Po. bassleri*. In extant podocnemidids, the pterygoid flange exhibits a similar condition, but often projects ventrally.

The basisphenoid is completely preserved in *C. wayuunaiki*, but only the ventral surface is clearly visible (Fig. 2C, D). It contacts both pterygoids anterolaterally, both quadrates posterolaterally, and the basioccipital posteriorly. In these features, it is similar to that of all other panpodocnemidids.

The basioccipital is complete in *C. wayuunaiki*. Only the ventral surface and portions of the posterodorsal surfaces are clearly visible. The basioccipital contacts the basisphenoid anteriorly, the quadrate laterally, and although the posterodorsal surface is completely crushed, appears to contact the exoccipital and participates in the structure of the condylus occipitalis. This is similar to the condition in all other podocnemoids, and many other pleurodires, except in pelomedusids and some bothremydids for which the basioccipital does not form part of the condylus occipitalis.

Both exoccipitals are preserved in *C. wayuunaiki*. Only the right exoccipital exhibits discernible contacts on the dorsal, posterior, and ventral surfaces (Fig. 2). On the dorsal surface of the skull, the exoccipital is in contact with the supraoccipital dorsally, opisthotic laterally, quadrate ventrolaterally, and the basioccipitalis ventromedially. On the posterior surface, there is evidence for the entrance of the foramen jugulare posterius, but damage makes it impossible to determine the size or its direction into the bone. The exoccipital also constitutes a major part of the condylus occipitalis, as in all other podocnemoids.

The crista supraoccipitalis of the supraoccipital is distorted and its posterior tip is damaged (Fig. 2). The entire structure has been rotated 90° from its original position, such that the dorsal edge of

the crista supraoccipitalis is now oriented laterally. The supraoccipital contacts the prootic anterolaterally, the opisthotic laterally, and the exoccipital posterolaterally. There is slight dorsomedial contact with the parietal. The crista supraoccipitalis is long, flat, and maintains a uniform width along its ventral base from anterior to the posterior aspect, similar to the condition in most extant and fossil podocnemidids. *Bairdemys* spp. differs from *C. wayuunaiki* and all other podocnemidids in having a short crista supraoccipitalis that is wider posteroventrally than anteroventrally, and that ends in a bulbous shape in dorsal view.

Both opisthotics are preserved, but only the right one is completely exposed on the dorsal aspect (Fig. 2A, B). The opisthotic contacts the quadrate anterolaterally, the squamosal posterolaterally, the exoccipital posteromedially, the supraoccipital anteromedially, and the prootic anteriorly. These contacts are similar to the condition found in all podocnemoids except in *Brasilemys josai*, in which there is no contact between the opisthotic and the prootic because these bones are separated by the supraoccipital. The processus paroccipitalis in *C. wayuunaiki* is medially narrow, elongate, and projects beyond the squamosal, ending in a tip that is broken on both sides. A similarly shaped processus paroccipitalis is seen in most all podocnemoids, except *Br. josai*, *S. antiqua*, and *Bairdemys*, which have a small, flat processus paroccipitalis that does not project beyond the squamosal.

The right prootic is exposed in dorsal aspect, although its anterior end is obscured by the quadratojugal. It contacts the opisthotic posteriorly, the quadrate laterally, and the supraoccipital parietal medially. The foramen stapediotemporale is clearly visible in the contact between the prootic and the quadrate, as in all other pleurodires.

Both quadrates are preserved, but only the right exhibits discernible contacts (Fig. 2). Dorsally the quadrate contacts the prootic anteromedially, the opisthotic posteromedially, the squamosal posterodorsally, and the quadratojugal anterodorsally. Ventrally the contacts are with the pterygoid anteromedially, the basisphenoid medially, the opisthotic posteromedially, and squamosal posteriorly. The medial contact with the prootic is not visible.

The quadrate is closed ventrolaterally around the cavum tympani, and is directed ventrally, as in all podocnemoids except *Br. josai* (Lapparent de Broin et al., 2007), although it is even more downwardly elongate in *S. antiqua*, *St. cromeri*, and in *Bairdemys*. The right quadrate preserves the cavum tympani. Due to crushing, the shape and position of the incisura, the columella auris, and eustachian tube are not discernible. In right posterior aspect of the cavum tympani, there is a shallow cavity that, although crushed and distorted to appear somewhat smaller than that of other podocnemidids, is likely the fossa precolumeralis. A small antrum postoticum, similar in size to that of other known podocnemidids, is present on the posterior part of the right quadrate.

The right condylus mandibularis is crushed and deformed. The left is completely covered by the quadrate.

Lower Jaw

Although the lower jaw of UF/IGM 33 is considerably crushed dorsoventrally, it is still fairly complete, with only the most lateral portion of the left ramus at the processus coronoideus of the dentary and the area mandibularis of the right ramus missing (Fig. 3).

The dentary contacts are indeterminate in the right ramus due to the slightly eroded bone surface, but are apparent in the left ramus. The dentary contacts the coronoid posterodorsally, the angular posteroventrally, and the surangular posterolaterally.

Both dentaries are fused at the mandibular symphysis, as in all other podocnemoids. This is also very probably the condition in *Br. josai*, for which only the left ramus is preserved (Lapparent

de Broin, 2000). Both *C. wayuunaiki* and a recently described indeterminate podocnemidid from the Miocene of Venezuela (UNEFM-CIAPP 1399; Gaffney et al., 2008) have a very acute (less than 40°) internal angle between rami in ventral view. In contrast, all other podocnemoids have a less acute angle (over 40°), with the exception of *Bairdemys*, in which this angle is greater than 90°.

In *C. wayuunaiki* the triturating surface on the dorsal surface of the dentary (Fig. 3A, B) is consistently wide from the symphysis to the coronoid region, as in all other podocnemoids except *Erymnochelys*, aff. *R. vilavilensis*, and *N. arenarum*, in which the symphysis is slightly narrower, and in *Bairdemys* spp., which has a much wider triturating surface at the symphysis than at the coronoid region. In addition, the triturating surface of *C. wayuunaiki* lacks accessory ridges, as in most of podocnemoids apart from *Podocnemis* spp.

The triturating surface is bound by lingual and labial ridges. As in other podocnemidids, the lingual ridge in *C. wayuunaiki* is higher than the labial posteriorly. In contrast, aff. *R. vilavilensis* and *P. dumerilianus* have lingual and labial ridges that are equally high posteriorly. The lingual ridge of *C. wayuunaiki* is nearly straight rather than the sigmoidal condition common to bothremiidids (Gaffney and Foster, 2003). The sulcus cartilaginis Meckelii is strongly marked on the medial surface of both dentaries in *C. wayuunaiki*, and it is considerably elongated anteriorly, as in other podocnemidids.

A narrow elongated ridge on the ventral surface is preserved on both dentaries of *C. wayuunaiki* (Fig. 3C, D). The ridge projects anteriorly from the medial margin of the ramus toward the symphysis area, at which point it disappears completely. These ridges are exclusive to *C. wayuunaiki* within the podocnemoids.

The anteroventral contact with the dentary is visible on the right angular. Otherwise, both angulars are severely crushed and all other sutural contacts are unrecognizable (Fig. 3). Only the anteromedial part of the right angular is preserved, and participates in the lateral wall of the fossa Meckelii. Its respective anterodorsal and anterolateral contacts with the coronoid and the dentary are the only recognizable contacts for this bone.

The right coronoid, although slightly crushed, is completely preserved, and is similar in height to those of *Podocnemis* spp. and other podocnemidids. It contacts the dentary anterolaterally, the surangular posterolaterally, and the prearticular ventromedially. A very small dorsomedial portion of the left coronoid is preserved, but without any recognizable contacts.

Both prearticulars are preserved, although slightly crushed, and their contacts with the angular and the articular are indeterminate. The anterodorsal process that covers the fossa Meckelii and connects the prearticular with the coronoid is broken on both sides, exposing the fossa Meckelii and the foramen intermandibularis.

The left articular is fairly complete, whereas only the anterior end of the right is preserved (Fig. 3). The contacts with the surangular and the prearticular are indeterminate. The processus retroarticularis, although poorly preserved, seems to project posteroventrally, as in *Podocnemis* and aff. *R. vilavilensis*. This is in contrast to all other podocnemidids plus *Br. josai* and *H. escuiliei*, in which the process extends more posteriorly, with variation in length among the different taxa. For example, in *P. dumerilianus* the process is slightly shorter than in *E. madagascariensis*.

The dorsal surface of the articular, which articulates with the condylus mandibularis at the posteroventral region of the skull, is slightly wider at its midpoint than at its lateral and medial margins, with a convex posterior edge. This could indicate that the condylus mandibularis of the quadrate was kidney-shaped, although more complete material is necessary to assess this interpretation more confidently. A kidney-shaped condylus mandibularis is exclusive to *Podocnemis* spp. within the podocnemoids,

and its presence in *C. wayuunaiki* might indicate a close relationship with that taxon.

Cervical Vertebrae

Fairly complete sixth and seventh cervical vertebrae constitute what is known of the axial skeleton of *C. wayuunaiki* (Fig. 4G–K).

The ventral portion of the sixth cervical, including the posterior condyle, and part of both transverse processes are preserved, albeit considerably crushed. A notable feature of this vertebra is the saddle-shaped posterior condyle, which is higher than wide, dimensions that are characteristic of cervical vertebrae of *P. dumerilianus*, *B. elegans*, aff. *R. vilavilensis*, *Podocnemis* spp., and *Stupendemys souzai* (Williams, 1950; Lapparent de Broin, 2000; Boquentin and Melo, 2006). Although Lapparent de Broin (2000) described less pronounced saddle-shaped condyles for the second through sixth vertebra for *P. dumerilianus*, this is also the condition for *C. wayuunaiki* and *Po. expansa* (Hoffstetter and Gasc, 1969:fig 12). This indicates that the saddle-shaped condyle for the seventh cervical in podocnemidids is variably present.

The left lateral part of the seventh cervical is nearly complete, except for the corner of the anterior articular surface of the centrum and the lateralmost margin of the transverse apophyses (Fig. 4J, K). However, only the medial aspect of the neural arch and the condylar region are preserved on the right side. The centrum of *C. wayuunaiki* is similar to those of *Podocnemis* spp. in being elongate, procoelous, and in lacking a ventral keel. The ventral keel is present in almost all other podocnemidids for which cervical vertebrae are known. A ventral keel has also been described for the bothremydid *Acleistochelys maliensis* (Gaffney et al., 2007). Similar to the condition in *Podocnemis expansa* (Hoffstetter and Gasc, 1969:fig 12), *P. dumerilianus*, and variable for *E. madagascariensis*, the posterior condyle of the seventh cervical is spherical and slightly taller than wide with the dorsal edge slightly concave in *C. wayuunaiki*.

The prezygapophyses of the seventh cervical of *C. wayuunaiki* are long and project almost vertically toward the vertebral centrum, as in *Podocnemis* spp., *E. madagascariensis*, and *Su. souzai*, but in contrast to the slightly shorter prezygapophyses in *Peltocephalus dumerilianus*. The transverse processes are located at the midline of the centrum, as in all podocnemidids, and the postzygapophyses are low and project posterodorsally, as in *Podocnemis* spp. This differs from that of *P. dumerilianus*, *Su. souzai*, and *E. madagascariensis*, which have more vertically oriented postzygapophyses. Additionally, both postzygapophyses of *C. wayuunaiki* are fused at the top of the pedicel, indicating the likely presence of collarette-shape postzygapophyses, as is common for podocnemidids (Lapparent de Broin et al., 2007). On the lateral surface of the pedicel, a deep concavity marks the juncture point of the prezygapophyses with the eighth cervical.

Carapace

The anterior region of the carapace is preserved in *C. wayuunaiki* (Fig. 4A, B) and includes the nuchal, right and left peripherals 1 and 2, right peripheral 3, neurals 1–3, right and left costals 1 and 2, and right costal 3. Whereas a small portion of the lateral margin of left costal 1 is crushed, the original curvature of all other elements is preserved. The carapace is slightly oval in shape and forms a low dome, as in most podocnemidids.

In *C. wayuunaiki* the dorsal surface of the carapace is smooth, and thus is similar to that in all other podocnemidids except *Roxochelys harrisi*, which exhibits marked reticulation in the form of small polygons or dichotomous sulci (Lapparent de Broin, 1991) on the dorsal surface. *Cerrejonemys wayuunaiki* has the thickest shell of all known podocnemidids, approaching an average thickness of 35 mm along the midline of the carapace and plastron.

The nuchal bone is pentagonal in shape and wider than long, with a straight anterior edge and a slightly curved posterior margin. This is similar to the condition seen in all podocnemidids except *Cambaremys lagentoni*, which has a longer than wide nuchal bone (França and Langer, 2005). Neural 1 is subrectangular in shape, almost twice as long as wide, slightly convex on its lateral and anterior edges, and with lateral contact restricted to costal 1 on both sides. This lateral contact is found in all podocnemidids except *B. elegans* and the podocnemid *Br. josai*, for which neural 1 laterally contacts right and left costals 1 and 2, and neural 2 is small and square-shaped. In the case of *Br. Josai*, the neural series is more irregular in shape, a condition seen in basal pleurodires such as *Platychelys oberndorferi* and *Notomys* spp. (Cadena and Gaffney, 2005). A particular case is seen in the podocnemid *Pz. patagonica* (De la Fuente, 2003), which has neural 1 with a restricted lateral contact with costal 1 on its right lateral margin, as in most of podocnemidids, whereas on its left margin, neural 1 contacts costals 1 and 2 as in *Br. josai* and *B. elegans*. Whether or not this dual condition for the lateral contacts of neural 1 is a pathologic effect particular to that specimen of *Pz. Patagonica*, or if it is actually evidence for an intermediate stage in the evolution of the condition seen in podocnemidids, will only be known with discovery of additional fossils of *Pz. patagonica*. Neural 3 of *C. wayuunaiki* is hexagonal in shape and contacts costal 2 anterolaterally and would have contacted neural 4 posteriorly (although it is missing in this specimen).

In *C. wayuunaiki*, costal 1 has convex anterior and posterior margins that meet laterally. The length of costal 1 is slightly more than twice the length of costal 2, a dimension that is similar to that of some species of *Podocnemis* spp. Peripheral 1 is subrectangular in shape, with the anterior margin wider than the posterior, and a curved medial contact with the nuchal. Peripheral 2 is trapezoidal in shape and peripheral 3 is rectangular.

The carapace of *C. wayuunaiki* lacks the cervical scale, as do all pelomedusoids, but this is not exclusive to this group (Lapparent de Broin, 2000). Vertebral scale 1 is wider anteriorly, almost pentagonal in shape, with convex anterior and lateral edges. It covers most of the anteromedial corner of costal 1, the posterior area of peripheral 1, and the medial to posterior area of the nuchal. Vertebral scale 2 is hexagonal in shape. It medially covers the posterior area of neural 1, neural 2, and most of neural 3. It laterally covers the posteromedial corner of the costal 1, the medial portion of costal 2, and the anteromedial corner of costal 3. In all these respects, vertebral scale 2 is similar to that of all known podocnemidids.

The marginal scales are confined to the peripherals. Marginal 1 is rectangular, wider than long, and covers the anteromedial part of the nuchal and a small portion of the anteromedial part of peripheral 1. Marginal 2 is larger than marginal 1, almost completely covering peripheral 1 and the anteromedial part of peripheral 2. The lateral contact between right marginal 3 and 4 occurs on peripheral 3. The sulcus between the pleural scales 1 and 2 is poorly marked on both right and left costal 2, although it is clearer on the left costal.

On the ventral surface, the axillary buttress scar is deeply marked and located at the midline of costal 1, as in most of podocnemidids. In *R. harrisi*, aff. *R. vilavilensis*, and *E. madagascariensis*, the axillary scar is located slightly closer to the contact between costals 1 and 2. *Peltocephalus dumerilianus* has an axillary buttress scar situated more laterally on costal 1 than in the other podocnemidids. A particular case is present in *Ba. venezuelensis*, in which the neural bones are completely absent, so that the axillary buttress scar is situated more medially on costal 1.

In *C. wayuunaiki*, the projection of the axillary scar onto the peripherals reaches the anterior margin of peripheral 3, as in *Podocnemis lewyana*, *Po. negrii*, and *E. madagascariensis*. In all other podocnemidids, the axillary scar projection enters onto the

center or at the posterior margin of peripheral 3 or on peripheral 4, as is the most common condition for *P. dumerilianus*.

Plastron

Plastral bones recovered include the left and right hypoplastra, mesoplastra, and hyoplastra, with the last slightly broken anteriorly (Fig. 4C, D). As is the case in the carapace, the plastral elements are nearly 35 mm thick.

The mesoplastra are hexagonal in shape, with the posteromedial edge slightly curved, which is typical of that in other podocnemidids. In *C. wayuunaiki* and most podocnemidids, the pectoroabdominal sulcus does not cross the mesoplastron; occasionally a slight contact with the anterior edge of the mesoplastron is seen in *Po. erythrocephala* and *Po. unifilis*, but it never crosses onto the mesoplastron. An exception to the podocnemidid condition is found in *Neochelys lapparenti*, in which the sulcus crosses the anteromedial margin of mesoplastron, and *P. dumerilianus*, in which both conditions are variably expressed.

Coracoid

The only element of the pectoral girdle preserved in *C. wayuunaiki* is the right coracoid (Fig. 4E, F). Small portions of its medial margin along the middle part of the bone and its posterolateral corner are missing.

The coracoid of *C. wayuunaiki* is a long bone with a proximal articulation and a lateral body. It is cylindrical proximally and extends longitudinally toward the distal end where it is flatter and slightly divergent. The dorsal surface exhibits a marked longitudinal ridge, previously reported as being exclusive of *Podocnemis* spp. by França and Langer (2006). However, we have seen that the some specimens of *Po. vogli* lack this ridge.

The ventral surface of the coracoid of *C. wayuunaiki*, *Podocnemis* spp., and occasionally in *E. madagascariensis* is concave, relatively deep laterally and flat distally. In contrast, the ventral surface of the coracoid of *P. dumerilianus*, *Cambaremys largentoni*, *B. elegans*, and aff. *R. vilavilensis* is nearly flat, without a marked concavity.

Pelvic Girdle

The left side of the pelvis is fairly complete, but the anterior- and posterior-most portions of the right side of the pelvis are missing (Fig. 4M, N). The left side preserves a complete ilium and a pubis that is slightly broken on its distal margin. The epipubis and the most proximal area of the ischium are recognizable in the acetabulum capsule. The suture between the ilium and the pubis is visible on both lateral and medial surfaces. On the right side, the ilium and a considerably damaged part of the acetabulum capsule, consisting of the most proximal portions of the pubis and ischium, are the only elements preserved. In the comparable aspects for which the morphology is preserved, the pelvis of *C. wayuunaiki* is similar to that of all podocnemidids and other pleurodires.

PHYLOGENETIC ANALYSIS

To examine the phylogenetic relationships of *Cerrejonemys wayuunaiki*, we included it in a cladistic analysis with other known podocnemoids that are adequately known from skull, shell, or postcranial elements. *Cambaremys largentoni*, *Shweboemys gaffneyi*, *Shweboemys pilgrimi*, *Shweboemys pisidurensis*, *Podocnemis pritchardi*, *Podocnemis medemi*, *Podocnemis negrii*, *Neochelys capellini*, *Roxochelys harrisi*, and *Stupendemys* spp. were excluded from this analysis due to missing data. A fragmentary skull of *Podocnemis* cf. *P. expansa*, which lacks a detailed published description and has been lost since its original publication (Wood, 1997), was also excluded for lack of data. However, most of the excluded taxa are considered in the comparisons.

We assembled a matrix of 26 ingroup taxa (podocnemoids) and 3 outgroup taxa (Chelidae, Pelomedusidae, and *Araripemys barretoii*; rooted to Chelidae) that were scored for the 53 morphological characters listed in Appendix 1 and coded in Appendix 2. Most of the characters were modified from previously published character matrices and detailed systematic studies including Meylan (1996), Lapparent de Broin (2000), Gaffney et al. (2002), Gaffney and Forster (2003), De la Fuente (2003), França and Langer (2006), Gaffney et al. (2006), Lapparent de Broin et al. (2007), and Gaffney et al. (2008). A few of these characters are new to this study and were defined based on direct examination of fossil and modern specimens listed in Supplementary Data 1 (www.vertpaleo.org/jvp/JVPcontents.html).

The character matrix was constructed using Mesquite 2.5 (Maddison and Maddison, 2008) and analyzed using the parsimony algorithm of PAUP 4.0b10 (Swofford, 2002). The matrix is available as a Nexus file in Supplementary Data 2 (www.vertpaleo.org/jvp/JVPcontents.html). All characters were equally weighted and unordered. Multistate characters were treated as polymorphic. We performed a branch-and-bound search in PAUP. Decay indices were computed in TreeRot 3 (Sorenson and Franzosa, 2007) and bootstrap percentages were computed in PAUP (100 branch-and-bound replicates).

Results

The cladistic analysis resulted in 1296 most parsimonious trees (length = 117 steps, consistency index = 0.83, retention index = 0.90, homoplasy index = 0.19). The strict consensus (Fig. 5) shows that *Cerrejonemys wayuunaiki* is the sister taxon of a monophyletic, but unresolved clade that includes all species of *Podocnemis*.

DISCUSSION

Our phylogenetic results suggest that the presence of the cavum pterygoidei is a synapomorphy for “Panpodocnemididae” (Bothremydidae plus Podocnemoidae; Fig. 5, node C), previously referred to as Podocnemoidea by Lapparent de Broin (2000), Gaffney et al. (2006), and “Panpodocnemididae” by França and Langer (2006), excluding *Euraxemys essweini*. Within the clade Podocnemoidea (Fig. 5, node D), *Brasilemys josai*, *Hamadachelys escuillei*, and *Portezueloemys patagonica* are basally positioned, as suggested in previous studies (Lapparent de Broin, 2000; De la Fuente, 2003; Romano and Azevedo, 2006; Gaffney et al., 2006), but in contrast to the work of França and Langer (2006), who excluded *Br. josai* from this clade. In this particular aspect, we disagree with the observations made by França and Langer (2006) on *Br. josai*, and we point out that: (1) a large antrum postoticum is also present in some bothremydids such as *Galianemys whitei* and this character is generally widely variable within Pelomedusoides (Gaffney et al., 2006); and (2) lack of a contribution of the palatine to the triturating surface is also present in some bothremydids such as *Labrostocheilus galkini* and *Taphrosphys ippolitoi* (Gaffney et al., 2006), and in *Podocnemis erythrocephala*. The high variability in these two characters among podocnemoids makes them of dubious utility for the exclusion of *Br. josai* from this clade. In addition, the pterygoid flange in *Br. josai* is much less developed than is suggested by França and Langer (2006), a condition also shared by *H. escuillei* and which, together with the presence of a shallow cavum pterygoidei that is hidden anteromedially by the underlapping basisphenoid medially and the pterygoid laterally, makes them indisputable members of Podocnemoidea.

Brasilemys josai, *H. escuillei*, and *Pz. patagonica* are excluded from Podocnemididae (Fig. 5, node E) because they lack a deep cavum pterygoid that is partially to totally covered by the pterygoid flange.

Our results agree with those from previous analyses that exclude *Bauruemys elegans* from *Podocnemis* spp. (França and Langer, 2006; Romano and Azevedo, 2006). In contrast, Lapparent de Broin (2000) considered *B. elegans* to be a member of the clade of *Podocnemis* spp. (Podocnemidinae, sensu Lapparent de Broin, 2000), based on the presence of a cervical vertebra with a saddle-shaped condyle, a condition also shared by aff. *Roxochelys vilavilensis*, *C. wayuunaiki*, *Su. souzai*, *Podocnemis* spp., and *P. dumerilianus*, making this character a potential synapomorphy for Podocnemididae, with the exception of *E. madagascariensis*, which exhibits the reversed condition (França and Langer, 2006). We note that many podocnemidid taxa are still unknown for this character and that only further fossil discoveries will help to test the validity of this character as a synapomorphy for the clade Podocnemididae.

Results from our analysis suggest that *B. elegans* and aff. *R. vilavilensis* form an unresolved polytomy within Podocnemididae. They differ from the rest of podocnemidids by: (1) a coracoid bone that is slightly curved longitudinally and much wider distally; and (2) a secondary roofing of the fossa temporalis that is medially advanced with concave margins, partially covering the otic chamber in dorsal view, a condition slightly more advanced in *C. wayuunaiki* and *Podocnemis* spp. Also, among podocnemidids two clades are well differentiated, corresponding to node F and node G in Figure 5.

The first, clade F, is formed by *Neochelys* spp., *E. madagascariensis*, *P. dumerilianus*, *D. paleomorpha*, *Bairdemys* spp., *Shweboemys antiqua*, and *Stereogenys cromeri*. This clade is supported by two synapomorphies: (1) a very advanced secondary roofing of the fossa temporalis, with convex to straight, tapering margins that totally cover the otic chamber roof in dorsal aspect (character 6, Appendix 1); and (2) an anterior protrusion of the prefrontal onto the apertura narium externa, totally covering the apertura, with its convex edge visible in dorsal view of the skull (character 7, Appendix 1). Although the consensus tree shows an unresolved polytomy for *Neochelys arenarum* and *N. lapparenti* within this clade, we favor the idea that *Neochelys* is more closely related to *E. madagascariensis*, as suggested by Lapparent de Broin (2000) based on the presence of a large intergular scale, covering the anterior margin of the entoplastron and separating the gulars (character 53, Appendix 1), a condition present in *Neochelys arenarum*.

Dacquemys paleomorpha, *S. antiqua*, *St. cromeri*, and *Ba. sanchezi* lack foramen palatinum posterius, which is present and interpreted as a reversal in *Bairdemys venezuelensis*, *Ba. hartsteini*, and *Ba. winklerae* (character 29, Appendix 1). *Dacquemys paleomorpha* is the most basal representative of this group, in part because it lacks a secondary palate (character 30, Appendix 1); the others have a secondary palate, with all *Bairdemys* species additionally having a secondary palate with ventral convexities. Additionally, all species of *Bairdemys* have a uniquely long downward projection of the quadrate that strongly separates the condylus mandibularis from the cavum tympani region (character 18, Appendix 1). It has been suggested that the evolution of a secondary palate may have happened more than once in this group, possibly as an adaptation to facilitate the crushing of mollusks (Wood, 1984). If that were the case, then the support for an affinity of *Bairdemys* with the other members of this group would be weak. However, the recently described *Ba. sanchezi* (Gaffney et al., 2008) retains the plesiomorphic condition of the absence of a foramen palatinum posterius, as seen in *D. paleomorpha*, *S. antiqua*, and *St. cromeri*, and thus seems to represent a morphological and phylogenetic intermediate between primitive members of the group and the more derived species of *Bairdemys*, in which the foramen has re-evolved.

The clade composed of *E. madagascariensis* and *P. dumerilianus* is supported by one clear synapomorphy: a very advanced secondary roofing of the cheek emargination by the descending

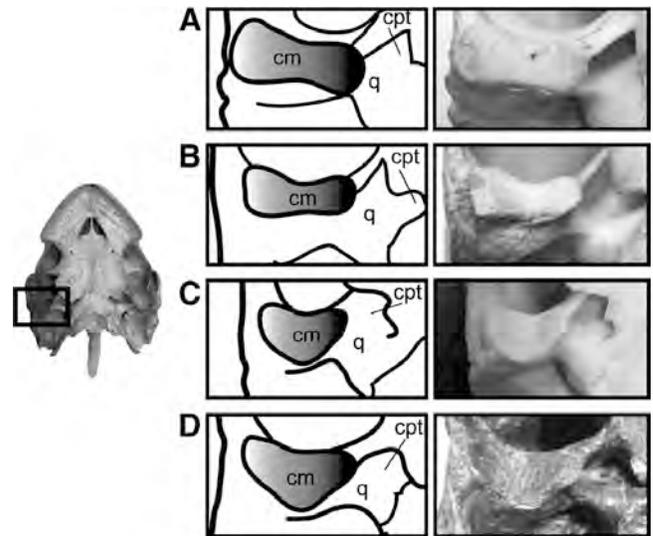


FIGURE 6. Left condylus mandibularis of quadrate in ventral view for **A**, *Erymnochelys madagascariensis*, YM 15398. **B**, *Peltocephalus dumerilianus*, NFWFL 336. **C**, *Podocnemis unifilis*, AMNH 58195. **D**, *Podocnemis bassleri*, AMNH 1622. Skull of *Podocnemis expansa* (AMNH 97124) on the left for reference. **Abbreviations:** cm, condylus mandibularis; cpt, cavum pterygoidei; q, quadrate.

jugal-quadratojugal. This condition results in a contact between the quadrate and the jugal (character 20, Appendix 1). In lateral view, the edge of the secondary roofing is almost parallel to the maxillary edge in most specimens, but occasionally a small notch is present at the posterolateral margin of the jugal with slightly less advanced secondary roofing. Another possible synapomorphy for the clade of *E. madagascariensis* and *P. dumerilianus* has been discussed in the literature (i.e., França and Langer, 2006; Lapparent de Broin, 2000): the anteriorly unrestricted roofing of an enlarged carotid canal, although the condition is less emphasized in *P. dumerilianus* than in *E. madagascariensis*. We note that the state of this character is unknown for most fossil podocnemidids, and for that reason we have excluded it from our phylogenetic analysis.

The second well-differentiated clade within podocnemidids (Fig. 5, node G) is composed of the six extant species of *Podocnemis* and the extinct *Po. bassleri* and *C. wayuunaiki*, and is supported by the following synapomorphies: (1) a parietal-jugal contact related to a reduction of the postorbital (character 11, Appendix 1); and (2) a dorsal longitudinal ridge on the coracoid (character 44, Appendix 1). Among podocnemidids, one of the unique characteristics of *Podocnemis* spp. is the presence of a slightly wider than long, kidney-shaped condylus mandibularis, with a straight to concave anterior edge and convex posterior edge (Fig. 6). However, because the region has not been recovered in *Cerrejonemys wayuunaiki*, it is not yet possible to determine whether it represents an additional synapomorphy for *Podocnemis* spp. and *C. wayuunaiki*.

The morphological evidence presented here suggests that *P. dumerilianus* and *E. madagascariensis* are more closely related to each other than either is to *Podocnemis* spp. However, it is only with new fossil discoveries, including elements such as cervical vertebrae, the coracoid, and skulls, will further resolution of podocnemidid phylogeny be possible. This is particularly the case for *Shweboemys* spp., *St. cromeri*, *Neochelys* spp., and the newly described *C. wayuunaiki*.

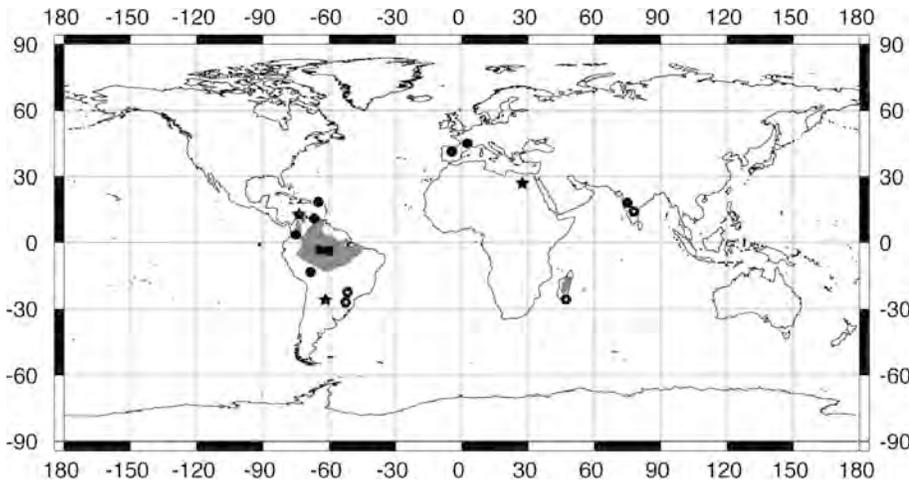


FIGURE 7. Map showing the distribution (grey shading) of modern and extinct podocnemidids. Open hexagons, stars, and closed circles for Late Cretaceous, Paleogene, and Neogene records, respectively. Template obtained and subsequently modified from Weinelt (1998).

Paleobiogeographical Scenario

During the middle–late Paleocene, the Cerrejón Formation was deposited as part of the Maracaibo crustal block, which at that time was in its southwestern-most position, 5–6° further south than today (approximately 11°) (Montes et al., 2005:fig. 16). As such, the paleolatitude of the Cerrejón flora and fauna is firmly within the tropics.

The oldest known podocnemidid is from the Upper Cretaceous of Brazil (França and Langer, 2006). Furthermore, based on the Late Cretaceous occurrence of the oldest *Erymnochelys* sp. from Madagascar (Gaffney and Forster, 2003), the split between the clade of *Podocnemis* spp. and *Cerrejonemys wayuunaiki* and the clade of *Erymnochelys* spp., *Peltocephalus dumerilianus*, *Shweboemys* spp., *Dacquemis paleomorpha*, and *Bairdemys* spp. must have occurred before then (Romano and Azevedo, 2006). However, prior to this study the oldest *Podocnemis* spp. was from the Miocene of La Venta (Wood, 1997). Occurrence of *C. wayuunaiki*, the sister taxon of a clade that includes modern *Podocnemis*, during the middle–late Paleocene reduces significantly the gap in the fossil record of this clade and provides strong support for the proposed vicariance scenario for the origin of these clades associated with the separation of South America and India/Madagascar at the end of the Cretaceous (Romano and Azevedo, 2006). As part of this model, it has also been suggested that the clade of *Podocnemis* spp. and *C. wayuunaiki* would have originated in the southern part of South America, based on the southern occurrence of the oldest known podocnemidid (Romano and Azevedo, 2006). Assuming this is true, and based on the occurrence of *C. wayuunaiki* in the paleotropics, it is clear that podocnemidids must have moved north prior to the middle–late Paleocene. What is less clear is the timing of dispersal for closely related fossil taxa, including *Shweboemys* spp., *Dacquemis paleomorpha*, *Stereogenys cromeri*, *Bairdemys* spp., and *Neochelys* spp., which were widely distributed during the Cenozoic.

Despite the paucity of relevant data to test hypotheses about the timing and routes in which podocnemidids arrived and colonized the northern-most corner of tropical South America, we consider two possible routes. The first could have been from the southeastern part of the continent, moving northward along the eastern coastal margin of South America, finally reaching the northeastern corner of the continent, in a similar way that other pelomedusoids such as bothremydids and *Hamadachelys escuiliei* dispersed from the southeastern part of South America, towards the northwestern part of Africa and Western of Europe

(Romano and Azevedo, 2006). The second possible dispersal route could have been from southcentral South America, moving northward using foreland basins developed in the Altiplano plateau during the Paleogene (Horton et al., 2001). The latter hypothesis may be supported by the occurrence of the podocnemidid aff. *Roxochelys vilavilensis* from the early Paleocene, Tiupampa Basin, Bolivia (Lapparent de Broin, 1991). However, this scenario is complicated by the lack of evidence for a complete fluvial or seaway connection between the northern and southcentral basins of South America during the Late Cretaceous–Paleocene, which would have been required for the dispersal of aquatic faunas from Tiupampa northward.

Following the Paleocene, the most important documented events in the geological history of the tropical part of South America occurred during the Neogene. These events had a strong influence over the distribution, diversification, and extinction of aquatic vertebrates (e.g., Albert et al., 2006). The first of these events, corresponding to the uplift of the Eastern Cordillera (~12 Ma), would have isolated podocnemidids and chelids, such as *Podocnemis pritchardi*, *Po. medemi*, and *Chelus colombiana*, inhabiting the Magdalena Basin from the podocnemidids and chelids inhabiting the proto-Orinoco river (*Bairdemys* spp. and *Chelus lewisi*). The second event (Albert et al., 2006) is the hydrological capture of the Amazon River by the eastern Amazon Basin from the western Amazon Basin, with the formation of the east-flowing modern Amazon River (~9 Ma). This event, which may have resulted in a larger area and more diverse habitats, could have influenced the diversification of *Podocnemis* spp. The third event, the rise of the western portion of the Merida Andes (~8 Ma), isolated the modern Maracaibo and Orinoco basins. The fourth event was the rise of the Isthmus of Panama (~3 Ma). The latter two events could have caused the geographic restriction of some species and also local extinctions due to an increase in ecological competition with other freshwater turtles such as cryptodires arriving from North and Central America.

ACKNOWLEDGMENTS

Funding for this project came from the Smithsonian Paleobiology Endowment Fund, the Florida Museum of Natural History, the National Science Foundation grant DEB-0733725, the Florida Museum of Natural History Miss Lucy Dickinson Fellowship, the Fondo para la Investigación de Ciencia y Tecnología Banco de la República de Colombia, the Unrestricted Endowments Smithsonian Institution Grants, and Carbones del Cerrejón LLC. Thanks go to C. Montes and the Cerrejón geology

team for help with logistical support during fieldwork. For access to collections, we thank J. Arenas (Ingeominas, Bogotá, Colombia); Dr. F. de Lapparent de Broin (Muséum national d'histoire naturelle, Paris, France); Dr. O. Castaño and Dr. J. Lynch (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia); Dr. E. Gaffney and C. Mehling (Fossil Amphibians, Reptiles, and Birds Collections, Division of Paleontology, American Museum of Natural History, New York, U.S.A.). For comments and improvement to the manuscript, we thank J. Bourque, editor S. Modesto, and reviewers W. Joyce and G. Oliveira. Special thanks go to F. Herrera, A. Hastings, A. Rincon, S. Moron, L. Meza, I. Gutierrez, G. Bayona, C. Sanchez, T. Gaona, S. Wing, D. Dilcher, and all other paleontologists and geologists working in the Cerrejón project at the Colombian Petroleum Institute, including H. Garcia who discovered the first vertebrate fossils from the mine in 1994, Smithsonian Tropical Research Institute, and the Florida Museum of Natural History. Thanks to R. Rueda and M. Gonzalez for their continued support and source of inspiration.

LITERATURE CITED

- Albert, J. S., N. R. Lovejoy, and W. G. R. Crampton. 2006. Miocene tectonism and the separation of cis- and trans-Andean river basins: evidence from Neotropical fishes. *Journal of South American Earth Sciences* 21:14–27.
- Batsch, A. C. 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena, 528 pp.
- Bayona, G., C. Jaramillo, M. Rueda, A. Pardo, A. Christie, and G. Hernandez. 2004. Important paleotectonic and paleogeographic considerations of the late Paleocene in the Northernmost Andes as constrained by Paleogene rocks in the Cerrejón Coal Mine, Guajira, Colombia. III Convención Técnica ACGGP. La inversión en el conocimiento geológico, P4, CD-ROM, ACGGP, Bogotá.
- Bloch, J., E. Cadena, F. Herrera, S. Wing, and C. Jaramillo. 2005. Paleocene vertebrates from the Cerrejón Formation, Guajira Peninsula, northeastern Colombia. *Journal of Vertebrate Paleontology* 25(3, Supplement):37A–38A.
- Bocquentin, J., and J. Melo. 2006. *Stupendemys souzai* sp. nov. (Pleurodira, Podocnemididae) from the Miocene-Pliocene of the Solimões Formation, Brazil. *Revista Brasileira de Paleontologia* 9:187–192.
- Bonin, F., B. Devaux, and A. Dupré. 2006. Toutes les tortues du monde. Delachaux et Niestlé, Paris, 415 pp.
- Broin, F. de. 1988. Les tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondwana et la dispersion géographique des tortues pleurodires à partir du Crétacé. *Studia Palaeocheloniologica* 2:103–142.
- Cadena, E., and E. Gaffney. 2005. *Notoemys zapatoensis*, a new side-necked turtle (Pleurodira: Platycheilyidae) from the Early Cretaceous of Colombia. *American Museum Novitates* 3470:1–19.
- Cadena, E., J. Bloch, and C. Jaramillo. 2008. Paleocene turtles from Colombia: phylogenetics, paleobiogeographic and paleoclimatic implications; pp. 56–57 in Abstracts, III Congreso Latinoamericano de Paleontología de Vertebrados. Neuquen, Patagonia, Argentina. The Argentine Paleontological Association.
- Carvalho, P., J. Bocquentin, and F. Lapparent de Broin. 2002. A new species of *Podocnemis* (Pleurodira, Podocnemididae) from the Neogene of the Solimões Formation, Acre, Brazil. *Geobios* 35:677–686.
- Cope, E. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20:242–300.
- De la Fuente, M. 2003. Two new pleurodiran turtles from the Portezuelo Formation (Upper Cretaceous) of northern Patagonia, Argentina. *Journal of Paleontology* 77:559–575.
- França, M., and M. Langer. 2005. A new freshwater turtle (Reptilia, Pleurodira, Podocnemididae) from the Upper Cretaceous (Maastrichtian) of Minas Gerais, Brazil. *Geodiversitas* 27:391–411.
- França, M., and M. Langer. 2006. Phylogenetic relationships of the Bauru Group turtles (Late Cretaceous of south central Brazil). *Revista Brasileira de Paleontologia* 9:365–373.
- Gaffney, E., and P. Meylan. 1988. A phylogeny of turtles; pp. 157–219 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds. Systematics Association Special Volume 35A*.
- Gaffney, E., and R. Wood. 2002. *Bairdemys*, a new side-necked turtle (Pelomedusoides: Podocnemididae) from the Miocene of the Caribbean. *American Museum Novitates* 3359:1–28.
- Gaffney, E., K. Campbell, and R. Wood. 1998. Pelomedusoid side-necked turtles from Late Miocene Sediments in southwestern Amazonia. *American Museum Novitates* 3245:1–12.
- Gaffney, E., H. Tong, and P. Meylan. 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History* 300:1–698.
- Gaffney, E., D. DeBlieux, E. Simons, M. Sánchez Villagra, and P. Meylan. 2002. Redescription of the skull of *Dacquemys* Williams, 1954, a podocnemidid side-necked turtle from the Late Eocene of Egypt. *American Museum Novitates* 3372:1–16.
- Gaffney, E., T. Scheyer, K. Johnson, J. Bocquentin, and O. Aguilera. 2008. Two new species of the side-necked turtle genus, *Bairdemys* (Pleurodira, Podocnemididae), from the Miocene of Venezuela. *Paläontologische Zeitschrift* 82:209–229.
- Gaffney, E., E. Roberts, F. Sissoko, M. Bouaré, L. Tapanila, and M. O'Leary. 2007. *Acleistochelys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Paleocene of Mali. *American Museum Novitates* 3549:1–24.
- Hastings, A., J. Bloch, E. Cadena, and C. Jaramillo. 2010. A new small short-snouted dyrosaurid (Crocodylomorpha, Mesoeucrocodylia) from the Paleocene of Northeastern. *Journal of Vertebrate Paleontology* 30:139–162.
- Head, J., J. Bloch, A. Hastings, J. Bourque, E. Cadena, F. Herrera, D. Polly, and C. Jaramillo. 2009. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* 457:715–718.
- Hoffstetter, R., and J. Gasc. 1969. Vertebrae and ribs of modern reptiles. *Biology of the Reptilia* 1:201–301.
- Horton, B. K., B. Hampton, and G. Waanders. 2001. Paleogene synorogenic sedimentation in the Altiplano plateau and implications for initial mountain building in the central Andes. *GSA Bulletin* 113:1387–1400.
- Jaramillo, C., G. Bayona, A. Pardo, M. Rueda, G. Harrington, and G. Mora. 2007. Palynology of the Upper Paleocene Cerrejón Formation, Northern Colombia. *Palynology* 31:153–189.
- Joyce, W. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of Peabody Museum of Natural History* 48:1–100.
- Kischlat, E. 1994. Observações sobre *Podocnemis elegans* Suarez (Chelonii, Pleurodira, Podocnemididae) do Neocretáceo do Brasil. *Acta Geológica Leopoldensia* 17:345–351.
- Lapparent de Broin, F. de. 1991. Fossil turtles from Bolivia; pp. 509–527 in R. Suarez Soruco (ed.), *Fósiles y Facies de Bolivia, Vertebrados, Volume 12(3–4)*. Revista Técnica de los Yacimientos Petrolíferos Fiscales Bolivianos. Sociedad Geología Boliviana.
- Lapparent de Broin, F. de. 2000. The oldest pre-podocnemidid turtle (Chelonii, Pleurodira), from the Early Cretaceous, Ceará state, Brasil, and its environment. *Threeballs del Museu de Geologia de Barcelona* 9:43–95.
- Lapparent de Broin, F. de, J. Bocquentin, and F. Negri. 1993. Gigantic turtles (Pleurodira, Podocnemididae) from the Late Miocene–Early Pliocene of southwestern Amazon. *Bulletin de L'Institut français d'Etudes andines* 23:657–670.
- Lapparent de Broin, F. de, M. de la Fuente, and M. Fernandez. 2007. *Notoemys laticentralis* (Chelonii, Pleurodira), Late Jurassic of Argentina: new examination of the anatomical structures and comparisons. *Revue de Paléobiologie* 26:99–136.
- Maddison, W., and D. Maddison. 2008. Mesquite: a modular system for evolutionary analysis. Version 2.5. Available at <http://mesquiteproject.org>. Accessed January 29, 2009.
- Meylan, P. 1996. Skeletal morphology and relationships of the Early Cretaceous side-necked turtle, *Araripemys barretoii* (Testudines: Pelomedusoides: Araripemydidae), from the Santana Formation of Brazil. *Journal of Vertebrate Paleontology* 16:20–33.
- Meylan, P., E. Gaffney, and D. de Almeida Campos. 2009. *Caninemys*, a new side-necked turtle (Pelomedusoides: Podocnemididae) from the Miocene of Brazil. *American Museum Novitates* 2639:1–26.
- Montes, C., R. Hatcher, and P. Restrepo. 2005. Tectonic reconstruction of the northern Andean blocks: oblique convergence and rotations

- derived from the kinematics of the Piedras-Girardot area, Colombia. *Tectonophysics* 399:221–250.
- Noonan, B. 2000. Does the phylogeny of pelomedusoid turtles reflect vicariance due to continental drift? *Journal of Biogeography* 27:1245–1249.
- Noonan, B., and P. Chippindale. 2006. Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic landbridge. *American Naturalist* 168:731–741.
- Pacheco, J. 1913. Notas sobre la geología do Vale do Rio Grande, a partir da foz do Rio Pardo até a sua confluência com o Rio Paranyha; pp 33–38 in J. Dourados (ed.), *Exploração do Rio Grande e de Seus Afluentes*. Comissão de Geografia e Geologia, Rio de Janeiro, Brazil.
- Price, L. 1953. Os quelônios da Formação Bauru, Cretáceo terrestre do Brasil Meridional. Departamento Nacional da Produção Mineral, Divisão de Geologia e Mineralogia, Boletim 147. Rio de Janeiro, Brazil, 34 pp.
- Romano, P. S., and S. A. Azevedo. 2006. Are podocnemid turtles relicts of a spread Cretaceous ancestor? *South American Journal of Herpetology* 1:175–184.
- Sánchez-Villagra, M., and J. Winkler. 2006. Cranial variation in *Bairdemys* turtles (Podocnemididae: Miocene of the Caribbean Region) and description of a new material from Urumaco, Venezuela. *Journal of Systematic Paleontology* 4:241–253.
- Schweigger, A. F. 1812. *Monographie Cheloniorum*. *Archiv für Naturwissenschaften und Mathematik* 1:271–368, 406–462.
- Sorenson, M., and E. Franzosa, 2007. TreeRot. Version 3. Available at <http://people.bu.edu/msoren/TreeRot.html>. Accessed May 10, 2009.
- Staesche, K. 1937. *Podocnemis brasiliensis* n.sp. aus der oberen Kreide Brasiliens. *Neues Jahrbuch Mineralogie, Geologie und Paläontologie B* 77:291–309.
- Suarez J. 1969. Um quelônio da Formação Bauru; pp. 168–176 in *Congresso Brasileiro de Geologia 23, Anais*, Salvador.
- Swofford, D. L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- Vargas-Ramirez, M., O. V. Castaño-Mora, and U. Fritz. 2008. Molecular and divergence times of ancient South America and Malagasy river turtles (Testudines: Pleurodira: Podocnemididae). *Organisms, Diversity & Evolution* 8:388–398.
- Wagler, J. 1830. *Natürliches System der Amphibien, mit Vorangehender Classification der Säugethiere und Vögel*. J. C. Cotta'schen München, Stuttgart, Tübingen, 354 pp.
- Weinelt, M. 1998. Ocean Drilling Stratigraphy Network, Plate Tectonic Reconstruction Service. Available at www.odsn.de/odsn/services/paleomap/paleomap.html#Form. Accessed January 29, 2009.
- Williams, E. 1950. Variation and selection in the cervical central articulations of living turtles. *Bulletin of the American Museum of Natural History* 94:505–562.
- Williams, E. 1956. *Podocnemis bassleri*, a new species of pelomedusid turtle from the Late Tertiary of Peru. *American Museum Novitates* 1782:1–10.
- Wood, R. 1976. *Stupendemys geographicus*, the world's largest turtle. *Breviora* 436:1–31.
- Wood, R. 1984. Evolution of pelomedusid turtles; pp. 120–135 in F. Lapparent de Broin, F. Jimenez, and E. Fuentes (eds.), *Studia Palaeocheloniologica I*. Ediciones Universidad de Salamanca, Salamanca, Spain.
- Wood, R. 1997. Turtles; pp. 155–170 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C.
- Wood, R., and M. Diaz de Gamero. 1971. *Podocnemis venezuelensis*, a new fossil pelomedusid (Testudines, Pleurodira) from the Pliocene of Venezuela and a review of the history of *Podocnemis* in South America. *Breviora* 376:1–23.

Submitted February 15, 2009; accepted July 7, 2009.

APPENDIX 1. Description of characters used in phylogenetic analysis. Characters were polarized with respect to Chelidae, *Araripemys barretoi*, and Pelomedusidae. Characters are from Gaffney et al. (2006) unless indicated otherwise.

Skull

- (1) Nasals: present (0); absent (1).
- (2) Prefrontals meet on midline: absent (0); present (1).
- (3) Quadratojugal: absent (0); present (1).
- (4) Squamosal parietal contact: present (0); absent (1).
- (5) Quadratojugal parietal contact: absent (0); present (1).
- (6) Temporal emargination, secondary roofing of the fossa temporalis in dorsal view, not advanced and highly concave allowing the complete exposure of the otic chamber roof (0); medially advanced with posteriorly expanded posterolateral temporal emargination of the parietals and quadratojugal with concave margins, covering partially or almost totally the otic chamber roof (1); very advanced with convex to straight tapering margins completely covering the roof of the otic chamber (2). Character modified from Lapparent de Broin (2000).
- (7) Prefrontal, anterior overhang onto apertura narium externa: shaped by the nasals (0); by the prefrontals, covering a small portion of the posterior part of the apertura, ending in acute medial tip (1); by the prefrontals, completely covering the apertura, ending in a straight to convex edge (2). Character modified from Gaffney et al. (2002).
- (8) Prefrontal, interorbital sulcus at the sutural area between both prefrontals: absent (0); present (1). Character from Lapparent de Broin (2000).
- (9) Apparent at the interorbital space: wide (0); narrow (1). Character modified from Gaffney et al. (2006).
- (10) Frontal, orientation of the orbits: orbits facing more laterally (0); orbits facing more dorsally (1).
- (11) Parietal-jugal contact: absent (0); present (1). Character from De la Fuente (2003).
- (12) Supraoccipital, crista supraoccipitalis: very short to absent (0); long, ventrally wider with uniform width from the anterior to the posterior aspect, ending in an acute tip in dorsal view (1); short, wider posteroventrally than anteroventrally, ending in a bulbous shape in dorsal view (2). In *Dacquemys paleomorpha* the crista supraoccipitalis is long, but is hidden dorsally by the large exposure of the supraoccipital at the posterior roof of the skull, coded as 1. Character modified from Gaffney et al. (2006).
- (13) Interparietal scale, anterior margin: anterior to the frontal parietal suture (0); posterior to the frontal parietal suture (1). New character.
- (14) Condylus occipitalis: formed by exoccipitals and the basioccipital (0); formed only by exoccipitals (1).
- (15) Quadrate basioccipital contact: absent (0); present (1).
- (16) Quadrate, cavum tympani, incisura columella auris: open without posterior bony restrictions (0); enclosed or with a narrow fissure separating the eustachian tube and stapes (1); enclosed together with both stapes and eustachian tube in the same oval dilated opening (2). Character modified from Gaffney et al. (2006) and Lapparent de Broin et al. (2007). For the basal bothremyidae *Cearachelys placidoi*, the incisura is open and dilated including the eustachian tube, but without the complete posterior closure of the quadrate, as in Podocnemididae (Lapparent de Broin et al., 2007) plus *Hamadachelys escuilliei*.
- (17) Quadrate, cavum tympani, fossa precolumellaris: deep (0); shallow (1); absent (2). Character modified from Gaffney et al. (2006).
- (18) Quadrate, ventral projection: very short, condylus mandibularis very close to the cavum tympani region (0); short, condylus mandibularis slightly separated from the cavum tympani region (1); long, condylus mandibularis considerably separated from the cavum tympani region (2). New character.

- (19) Quadrate, eustachian tube separated by bone from the fenestra postotica: absent (0); present (1). Character from Gaffney and Wood (2002).
- (20) Cheek emargination, secondary lateral roofing of the fossa temporalis: fossa temporalis laterally exposed without secondary roofing (0); secondary roofing slightly advanced (1); secondary roofing moderately developed by quadratojugal only (2); secondary roofing moderately developed by both jugal and quadratojugal (3); fossa temporalis completely roofed by the the jugal, resulting in a contact between the quadrate and the jugal; occasionally with a small notch at the posterolateral margin of the jugal (4). Character modified from Gaffney et al. (2006).
- (21) One or two accessory ridges on the ventral surface of the premaxilla: absent (0); present (1). One accessory ridge on the ventral surface of the premaxilla is only seen outside of the podocnemidids in the recently described bothremydids *Acleistochelys maliensis* (Gaffney et al., 2007). Within Podocnemididae, only *Dacquemys paleomorpha* exhibits similar accessory ridges, curved anteriorly to join each other, but they are restricted to the maxilla (Gaffney et al., 2002). New character.
- (22) Vomer: present (0); absent (1).
- (23) Basisoccipital: long (0); short (1).
- (24) Opisthotic, processus paroccipitalis: small and flat, does not project beyond the squamosal (0); narrow medially and elongated, projects beyond the squamosal ending in a prominent tip (1). Character modified from Gaffney et al. (2006) and Lapparent de Broin et al. (2007).
- (25) Basisphenoid quadrate contact: absent (0); present (1). Character modified from Gaffney et al. (2006).
- (26) Basisoccipital opisthotic contact: present (0); absent (1).
- (27) Pterygoid, cavum pterygoidei (= 'fossa podocnemidoid' of Lapparent de Broin, 2000): absent (0); shallow and slightly hidden anteromedially by the underlying basisphenoid medially and the pterygoid laterally (1); deep and partially to totally covered by the pterygoid flange (posterolateral wings of the pterygoid) (2). Character modified from Gaffney et al. (2006).
- (28) Pterygoid, pterygoid flange (= 'pterygoid wings' of Lapparent de Broin, 2000): absent to very short (0); moderately developed (1); well developed reaching the caudal margin of the quadrate ramus of the bone and projected ventrally (2). Character modified from França and Langer (2006) and Lapparent de Broin (2000).
- (29) Palatine, foramen palatinum posterius: present (0); absent (1). Character modified from Gaffney et al. (2006).
- (30) Palatine, second palate: absent (0); present (1).
- (31) Quadrate, condylus mandibularis shape: much wider than long, with anterior and posterior edges straight to concave making it shorter at midline (0); slightly wider than long, kidney shaped, with anterior edge straight to concave and posterior edge convex (1). New character.
- (32) Exoccipital-quadrate contact: absent (0); extensive (1); narrow (2). Character modified from Gaffney et al. (2006).
- (33) Prootic-quadrate contact: present (0); absent (1).

Lower Jaw

- (34) Dentary, fused symphysis: absent (0); present (1).
- (35) Dentary, internal angle between rami: acute, between 40° and 90° (0); obtuse, over 90° (1); very acute, less than 40° (2). Internal angle between rami less than 40° is also seen in UNEFM-CIAPP 1399, an indeterminate podocnemidid (Gaffney et al., 2008), excluded from this analysis due to poor preservation. New character.
- (36) Articular, processus retroarticularis: very short (0); short, projected posteriorly (1); short, projected ventrally (2);

- long, projected posteriorly (3). Character modified from Gaffney and Forster (2003) and Gaffney et al. (2006).
- (37) Surangular, well-extended anteriorly: absent (0); present (1).
- (38) Coronoid, wide lateral exposure: absent (0); present (1).
- (39) Dentary, accessory ridges: absent (0); present (1). Character from Gaffney and Forster (2003).
- (40) Dentary, narrow and elongated ridge, located in the medial margin on the ventral surface: absent (0); present (1). New character.

Cervical Vertebrae

- (41) Ventral keel at the posterior condyle: protuberant (0); reduced almost absent (1). Character from Lapparent de Broin (2000). The condition for bothremydids is based on the recently described *Acleistochelys maliensis* (Gaffney et al., 2007).
- (42) Posterior condyle of the sixth or previous cervical vertebrae saddle shaped, higher than wide: absent (0); present (1). Character modified from Lapparent de Broin (2000).

Coracoid

- (43) Coracoid shape: slightly curved longitudinally and much wider distally (0); narrow, almost straight longitudinally and slightly wider distally (1). Character modified from Gaffney et al. (2006).
- (44) Coracoid, dorsal longitudinal ridge: absent (0); present (1). Character from França and Langer (2006).

Carapace

- (45) Cervical scale: present (0); absent (1).
- (46) Nuchal bone: wider than long (0); longer than wide (1). Character from De la Fuente (2003)
- (47) Neural series composed of: eight or more bones (0); one to seven bones (1); neurals completely absent (2). Character modified from De la Fuente (2003)
- (48) Neural 2: present but not contacting costal 1 (0); present and contacting costal 1 (1); absent (2). Character modified from França and Langer (2006).
- (49) Lateral thickness of the shell: ≤ 20 mm (0); > 20 mm (1). Character modified from França and Langer (2006).

Plastron

- (50) Plastral bridge: short (0); elongated (1). Character from De la Fuente (2003).
- (51) Pectoral scale contact with the epiplastron: absent (0); present (1). Character from De la Fuente (2003).
- (52) Pectoral scale, contact with the entoplastron: absent (0); present (1). Character from De la Fuente (2003).
- (53) Intergular scale: large, covering the anterior margin of entoplastron, separating the gulars (0); small, restricted between the gulars, lacking contact with entoplastron (1). Character modified from Gaffney et al. (2006).

APPENDIX 2. Character matrix (29 taxa and 53 characters) used for phylogenetic analysis (Nexus file as Supplementary Data 2, www.vertpaleo.org/jvp/JVPcontents.html). Polymorphic conditions abbreviated as follows: A = 0 and 1, B = 0 and 2, C = 1 and 2.

Chelidae

```
00000000AA 00000B0000 0000000000 000A000000
0000000000 0A0
```

Ararypemys barretoii
 1111001011 00?0000001 0?00010000 0000000100
 00??100100 000
Pelomedusidae
 1111001011 00010B0003 0100A00000 0001000000
 0000111001 000
Euraxemys essweini
 111A101011 00?0001003 000A010000 0200000000
 00??110001 000
Bothremyidae
 111AAAC0AA 000A112002 0010110000 0111A3A0A0
 00001AAAA0 AA0
Brasilemys josai
 1111001000 00?0100001 0?11101000 001??11000
 ???11010? ???
Hamadachelys escuillie
 ?111101011 0?00100003 0011101000 0011011000
 ???1????? ???
Portezueloemys patagonica
 ?11110???? ???1????? 0?11101?0? ??????????
 ???111A01 010
Bauruemys elegans
 1111101011 0100120003 0011102200 0011011000
 0100111101 110
 aff. *Roxochelys vilavilensis*
 1111101011 0100120003 0011102200 0011021000
 0100111001 110
Shweboemys antiqua
 1111112000 0?00120103 0011102111 001????????
 ?????????? ???
Stereogenys cromeri
 11????2?00 ??001201?3 0011102111 001????????
 ?????????? ???
Dacquemys paleomorpha
 1110112000 0110120003 0011102110 001????????
 ?????????? ???
Cerrejonemys wayuunaiki
 111110101? 110012?0?3 ??11102200 ?011221001
 111111?01? ?1?
Neochelys arenarum
 1111112000 0100120003 0011102100 0011011000
 ???1110?1 11A

Neochelys lapparenti
 1111112000 0000120??3 0?11102?00 001????????
 ?????????? ???
Podocnemis bassleri
 1111101111 1100120003 1011102200 101????????
 ?????????? ???
Bairdemys venezuelensis
 1111112000 0200120213 0010102201 00111????0
 ???112201 110
Bairdemys hartsteini
 1111112000 0200120213 0010102201 001????????
 ?????????? ???
Bairdemys sanchezi
 11111?2000 ???0120213 0010102111 0?1112100?
 ?????????? ???
Bairdemys winklerae
 1111112000 ?2??120213 0010102201 001111100?
 ?????????? ???
Erymnochelys madagascariensis
 1111112000 0100120004 0011102200 1011011000
 0010111001 111
Peltocephalus dumerilianus
 1111112000 0100120004 0011102200 1011011000
 0110111001 010
Podocnemis expansa
 1111101111 110012B003 1011102200 1011021010
 1111111001 110
Podocnemis sextuberculata
 1111101111 1100120003 1011102200 1011021010
 1111111001 110
Podocnemis vogli
 1111101111 1100120003 1A11102200 1011021010
 1111111001 110
Podocnemis lewyana
 1111101111 1100120003 1011102200 1011021010
 1111111001 110
Podocnemis erythrocephala
 1111101111 1100120003 1011102200 1011021010
 1111111001 110
Podocnemis unifilis
 1111101111 1100120003 1011102200 1011021010
 1111111001 110