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

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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 podocnemids 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 podocnemidids 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): Araripemysidae (Aptian–Albian of Brazil), Chelidae (Early Cretaceous to Recent of South America and Australia), Euraxemydidae (Albian of Brazil and Cenomanian of Morocco), Bothremydididae (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 podocnemids (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), podocnemids plus their stem representatives, Portezuelaemys patagonica, Cambaremys langertoni, Bauruemys elegans, and Roxochelys spp., constitute the clade Podocnemidae (podocnemoids). Podocnemoidae plus the speciose clade Bothremydiidae constitute the clade Podocnemoida (podocnemoidans). In a higher phylogenetic level, Podocnemoidae, Euraxemys essweini (Gaffney et al., 2006), and Brasiltemys josi (Gaffney et al., 2006), and Brasiltemys josi form the clade “Panpodocnemididae” (panpodocnemids). Panpodocnemididae plus Pelomedusidae constitute the clade Pelomedusoides (pelomedusoids); and finally the clade “Panpelomedusoides” (panpelomedusoids), which includes Pelomedusoides plus Arratipemys barroti.

An important gap in the record of podocnemids 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 podocnemid 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 podocnemids 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
### TABLE 1. Summary of extinct and extant South American podocnemoid turtles.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Locality</th>
<th>Age</th>
<th>Material</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brasilemys josai</td>
<td>Ceará state, Brazil</td>
<td>Aptian–Albian limit</td>
<td>Almost complete skull, carapace, hyoid bones, left lower jaw,</td>
<td>Lapparent de Broin (2000)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>axis, and third cervical vertebra</td>
<td>De la Fuente (2003)</td>
</tr>
<tr>
<td>Portezieloemys</td>
<td>Neuquén province, Argentina</td>
<td>Late Turonian–Early</td>
<td>Partially preserved skull, carapace, and plastron</td>
<td>De la Fuente (2003)</td>
</tr>
<tr>
<td>Bauremys elegans</td>
<td>South-central Bauru Group, Brazil</td>
<td>Turonian–Maastrichtian</td>
<td>Partial plastron, fragmentary carapace, and plastron</td>
<td>Staesche (1937), Kischlat (1994), Paecheco (1913), Price (1953), Lapparent de Broin (1991)</td>
</tr>
<tr>
<td>Bauremys brasiliensis</td>
<td>Minas Gerais, Brazil</td>
<td>Maastrichtian</td>
<td>Partial carapace and plastron, coracoids, scapula, pelvic girdles, and limb bones</td>
<td>França and Langer (2005)</td>
</tr>
<tr>
<td>Roxocheles harrisi</td>
<td>Minas Gerais, Brazil</td>
<td>Maastrichtian</td>
<td>Several skulls, lower jaws, shells, coracoid, and cervical vertebra</td>
<td>Lapparent de Broin (1991)</td>
</tr>
<tr>
<td>Cambaremys langertoni</td>
<td>Minas Gerais, Brazil</td>
<td>Maastrichtian</td>
<td>Skull, lower jaw, partial carapace and plastron, coracoid, pelvic girdle, two cervical vertebra</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Nearly complete shell</td>
<td>Wood (1997)</td>
</tr>
<tr>
<td>Podocnemis pritchardi</td>
<td>La Venta fauna, Colombia</td>
<td>middle Miocene</td>
<td>Nearly complete plastron and partial carapace</td>
<td>Gaffney and Wood (2002)</td>
</tr>
<tr>
<td>Podocnemis cf. expansa</td>
<td>Puerto Rico</td>
<td>middle Miocene</td>
<td>Nearly complete skull</td>
<td>Gaffney et al. (2008)</td>
</tr>
<tr>
<td>Bairdemys hartsteini</td>
<td>Urumaco fauna, Venezuela</td>
<td>late Miocene</td>
<td>Several skulls and shells</td>
<td>Gaffney et al. (2008)</td>
</tr>
<tr>
<td>Bairdemys venezuelensis</td>
<td></td>
<td>late Miocene</td>
<td>Skull, lower jaws, anterior plastral fragment</td>
<td>Gaffney et al. (2008)</td>
</tr>
<tr>
<td>Bairdemys sanchezii</td>
<td></td>
<td></td>
<td>Several skull, lower jaw</td>
<td>Gaffney et al. (2008)</td>
</tr>
<tr>
<td>Stupendemys winkleriae</td>
<td></td>
<td></td>
<td>Shell, humerus, femur, scapula, two cervical vertebrae</td>
<td>Wood (1976)</td>
</tr>
<tr>
<td>Stupendemys geographicus</td>
<td></td>
<td></td>
<td>Costal bone, nuchal, humerus, xiphiplastron, pelvic girdle, and four cervical vertebrae</td>
<td>Lapparent de Broin et al. (1993), Gaffney et al. (1998), Bocquentin and Melo (2006)</td>
</tr>
<tr>
<td>Stupendemys souai</td>
<td>Rio Acre, Peru and Brazil</td>
<td>late Miocene–early</td>
<td>Complete skull</td>
<td>Gaffney et al. (2008)</td>
</tr>
<tr>
<td>Podocnemis bassleri</td>
<td>Contamana Group, Peru</td>
<td>Pliocene</td>
<td>Partial carapace and plastron</td>
<td>Lapparent de Broin (1991)</td>
</tr>
<tr>
<td>Podocnemis negrii</td>
<td>Acre state, Brazil</td>
<td>late Miocene–early</td>
<td>Fragmentary pelvis girdle</td>
<td>Carvalho et al. (2002)</td>
</tr>
<tr>
<td>Podocnemis expansa</td>
<td>Principal fluvial and lake systems of northern South America</td>
<td>Recent</td>
<td>Complete skeleton</td>
<td>Wagler (1830), Bonin et al. (2006)</td>
</tr>
<tr>
<td>P. erythrocephala</td>
<td>Orinoco and Amazon basins, northern South America</td>
<td>Recent</td>
<td>Complete skeleton</td>
<td>Schweigger (1812), Bonin et al. (2006)</td>
</tr>
<tr>
<td>P. lewana</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. sextuberculata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. unifilis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. vogli</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peltocephalus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dameriulianus</td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

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 podocnemids 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; NEWFL, U.S. National Fish and Wildlife Forensics Laboratory, Ashland, Oregon; UNEFM-CIAPP, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; UFJFM, University of Florida, Florida Museum of Natural History Vertebrate Paleontology Collections, Gainesville, Florida/Museo Geológico, at the Instituto Nacional de Investigaciones en Geociencias, 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, Praham, and Gauthier, 2004

**TESTUDINES** Broin, 1988, sensu Joyce et al. (2004)

**PODOCNEMIDIDAE** Cope, 1868

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 dorsolongitudinal ridge on the coracoid (all others have a smooth dorsal surface and lack the ridge).

Remarks—Lapparent de Broin (2000) included Bauuermys elegans, aff. Roxocheles vilavilensis, Podocnemis spp., Stupende- mys 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° 35' 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 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 cerrejoniensis* (Head et al., 2009), dyosaurid crocodyliforms (Hastings et al., 2010), and other pleurodira 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 panpolumedomidids (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.

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

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

Estimated lengths for carapace and plastron are based on comparisons to closely related forms (e.g., *Podocnemis* spp.).
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 Brasillemys josai, Hamadachelys escuilliei, and all other podocnemids 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. Roxocheles 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 Peltcephalus 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 podocnemids 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. Roxocheles vilavilensis and B. elegans, but narrower than that of other podocnemids, in which
FIGURE 3. *Cerrejonemys wayuunaikii*, 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; fnk, fossa Meckelii; lar, labial ridge; lr, lingual ridge; pr, pr acicular; 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. dumeriliana*).

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. dumeriliana*, *S. antiqua*, *Neochelys arenarum*, *Ba. venezuelensis*, *Ba. harsteini*, *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. esculii* and *Portezueloemys patagonica*. The parietal of *C. wayuunaikii* contacts the frontal and the postorbital anteriorly, the other parietal medially, the jugal and quadratejugal (as in *Podocnemis* spp.) laterally, and the supraoccipital postero- medially. 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. wayuunaikii*.

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 quadrate and the squamosal 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 bothremydids by the quadratejugal. Unfortunately, in *C. wayuunaikii* 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. dumeriliana*, and similar to that seen in *Podocnemis* spp.

Both quadratejugalts are fairly well preserved in dorsal aspect, although the left is poorly preserved in ventral aspect. The quadratejugal contacts the jugal anteriorly, the parietal medially, and the quadrate and the squamosal posterolaterally. The postero- medial edge of the quadratejugal forms part of the temporal emargination. In all ways, the quadratejugal 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 postero- medial aspect is visible (Fig. 2). The squamosal of *C. wayuunaikii* contacts the quadratejugal 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. dumeriliana*, 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 postero- medially and with the jugal posteriorly. *Cerrejonemys wayuunaikii* 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. dumeri- liana*, aff. *R. vilavilensis*, *N. arenarum*, and probably other fossil podocnemoids for which this region is covered with matrix or not.
preserved. This suggests that the presence of a foramen supramaxillare 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 posterior 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 podocnemoids, except *D. paleomorpha*, *St. cromeri*. 

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FIGURE 5. Strict consensus cladogram showing the phylogenetic relationships between panpelomedusoid turtles. A, Panpelomedusoides; B, Pelomedusoides; C, panpodocnemidids; D, Podocnemididae; E, Podocnemididae; F, unnamed clade; G, Podocnemis spp. and Cerejeironemys 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 (Franc¸a 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 posteroonal surfaces are clearly visible. The basioccipital contacts the basisphenoid anteriorly, the quadrate laterally, and although the posterostral 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 basioccipital 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 supraoc-
cipital contacts the prootic anterolaterally, the opisthotic late-
erally, and the exoccipital posterolaterally. There is slight dorso-
medial contact with the parietal. The crista supraoccipitalis is long,
flat, and maintains a uniform width along its ventral base from an-
terior to the posterior aspect, similar to the condition in most
extant and fossil podocnemids. Bairdemys spp. differs from C.
wayuunaiki and all other podocnemids in having a short crista
supraoccipitalis that is wider posterovertrally than anteroven-
trally, and that ends in a bulbous shape in dorsal view.

Both opisthotics are preserved, but only the right one is com-
pletely exposed on the dorsal aspect (Fig. 2A, B). The opisthotic
contacts the quadrate anterolaterally, the squamosal posterolat-
erally, the exoccipital posteromedially, the supraoccipital ante-
medially, and the prootic anteriorly. These contacts are similar
to the condition found in all podocnemids except in Brasilemys
josai, in which there is no contact between the opisthotic and
the prootic because these bones are separated by the supraoc-
cipital. The processus paroccipitalis in C. wayuunaiki is medi-
nally narrow, elongate, and projects beyond the squamosal, end-
ing in a tip that is broken on both sides. A similarly shaped
processus paroccipitalis is seen in most all podocnemids, ex-
cept 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 quadratejugal. It contacts the
opisthotic posteriorly, the quadrate laterally, and the supraoc-
cipital parietal medially. The foramen stapedio-temporal 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 quadratejugal anterodo-
sally. Ventrally the contacts are with the pterygoid anterome-
dially, 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 tym-
pani, and is directed ventrally, as in all podocnemids 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 podocnemids, is likely the fossa precolularis. A small
antrum postoticum, similar in size to that of other known podo-
cnemids, 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
dorsosventrally, it is still fairly complete, with only the most lateral
portion of the left ramus at the processus coronoides of the den-
tary 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 ra-
um. The dentary contacts the coronoid posterodorsally, the an-
gular posterovertrally, and the surangular posterolaterally.

Both dentaries are fused at the mandibular symphysis, as in all
other podocnemids. 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 podocnemid 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 podocnemids 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 symph-
ysis to the coronoid region, as in all other podocnemids 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 coro-
noid region. In addition, the triturating surface of C. wayuunaiki
lacks accessory ridges, as in most of podocnemids apart from
Podocnemis spp.

The triturating surface is bound by lingual and labial ridges.
As in other podocnemids, the lingual ridge in C. wayuunaiki is
higher than the labial posteriorly. In contrast, aff. R. vilavil-
ensis and P. dumeriliatus 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
bothremydids (Gaffney and Foster, 2003). The sulcus cartilagin-
us Meckeli is strongly marked on the medial surface of both den-
taries in C. wayuunaiki, and it is considerably elongated anteri-
orly, as in other podocnemids.

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 to
ward the symphysis area, at which point it disappears completely.
These ridges are exclusive to C. wayuunaiki within the podoc-
cnemids.

The anterovertral contact with the dentary is visible on the
right angular. Otherwise, both angulares are severely crushed and
all other sutural contacts are unrecognizable (Fig. 3). Only the an-
teromedial part of the right angular is preserved, and participates
in the lateral wall of the fossa Meckeli. Its respective anterodor-
sal 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 podocnemids. It contacts the dentary anterolaterally,
the surangular posterolaterally, and the prearticular ventrome-
dially. 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 indeter-
minate. The anterodorsal process that covers the fossa Meckeli
and connects the prearticular with the coronoid is broken on both
sides, exposing the fossa Meckeli and the foramen intermandibu-
laris.

The left articular is fairly complete, whereas only the ante-
rior 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 pos-
terovertrally, as in Podocnemis and aff. R. vilavilensis. This is in
contrast to all other podocnemids plus Br. josai and H. escul-
liet, in which the process extends more posteriorly, with variation
in length among the different taxa. For example, in P. dumerili-
tians 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 mar-
gins, with a convex posterior edge. This could indicate that the
condylus mandibularis of the quadrate was kidney-shaped, al-
though more complete material is necessary to assess this inter-
pretation more confidently. A kidney-shaped condylus mandibu-
laris is exclusive to Podocnemis spp. within the podocnemids,
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 souzaei (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 podocnemids 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 podocnemids for which cervical vertebrae are known. A ventral keel has also been described for the bothremydid C. wayuunaiki and Po. expansa (Hoffstetter and Gasc, 1969:fig 12). This indicates that the saddle-shaped condyle for the seventh cervical in podocnemids 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 podocnemids for which cervical vertebrae are known. A ventral keel has also been described for the bothremydid C. wayuunaiki and Po. expansa (Hoffstetter and Gasc, 1969:fig 12). This indicates that the saddle-shaped condyle for the seventh cervical in podocnemids is variably present.

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 podocnemids, and the postzygapophyses are low and project posteriorly, 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 podocnemids (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 podocnemids.

In C. wayuunaiki the dorsal surface of the carapace is smooth, and thus is similar to that in all other podocnemids except 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 podocnemids. A particular case is present in B. venezuelensis, in which the neural bones are completely absent, so that the axillary buttress scar is situated more medially on costal 1.

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 podocnemids except Cambaroemyx lagenion, 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 podocnemids 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 podocnemids 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 podocnemids, 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 podocnemids, 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 podocnemids.

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 podocnemids. 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 podocnemids. A particular case is present in B. 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 lewyna, Po. negrii, and E. madagascariensis. In all other podocnemids, 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 postomedial edge slightly curved, which is typical of that in other podocnemids. In *C. wayuunaiki* and most podocnemids, thepectoroadominal 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 podocnemid 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. wayunaiki* 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. wayunaiki* 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 same specimens of *Po. vogli* lack this ridge.

The ventral surface of the coracoid of *C. wayunaiki*, *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. vitaviensis* 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. wayunaiki* is similar to that of all podocnemoids and other pleurodires.

**PHYLOGENETIC ANALYSIS**

To examine the phylogenetic relationships of *Cerrejonemys wayunaiki*, 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 pilgrimii*, *Shweboemys pisidurensis*, *Podocnemis pritchardi*, *Podocnemis medemi*, *Podocnemis negrii*, *Neochelys capellini*, *Roxocheles harrii* 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 barretoi*; rooted to *Chelidae*) that were scored for the 55 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), Laparent de Broin (2000), Gaffney et al. (2002), Gaffney and Forster (2003), De la Fuente (2003), França and Langer (2006), Gaffney et al. (2006), Laparent 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 wayunaiki* 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 Podocnemideoidea by Lapparent de Broin (2000), Gaffney et al. (2006), and “Panpodocnemididae” by França and Langer (2006), excluding *Euraxemys essweini*. Within the clade PodocnemIDEOidea (Fig. 5, node D), *Brasilemus josai*, *Hamadachelys escuilliei*, and *Portezuelomys patagonica* are basally positioned, as suggested in previous studies (Lapparent de Broin, 2000; De la Fuente, 2003; Romano and Azavedo, 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 *Galeneumys 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 *Labrostrochelys 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. escuilliei* and which, together with the presence of a shallow cavum pterygoidei that is hidden anteromedially by the underlapping basiophenoid medially and the pterygoid laterally, makes them indisputable members of Podocnemideoidea. *Brasilemus josai*, *H. escuilliei*, and *Pz. patagonica* are excluded from Podocnemidoidea (Fig. 5, node E) because they lack a deep cavum pterygoidei that is partially to totally covered by the pterygoid flange.
Our results agree with those from previous analyses that exclude *Bauernemys 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. Roxocheles 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 podocnemid 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, clade F, is form by *Neocheles* 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 aperture narium externa, totally covering the aperture, with its convex edge visible in dorsal view of the skull (character 7, Appendix 1). Although the consensus tree shows an unresolved polytomy for *Neocheles arenarum* and *N. lapparenti* within this clade, we favor the idea that *Neocheles* 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 *Neocheles arenarum*.

*Daqueymys paleomorpha*, *S. antiqua*, *St. cromeri*, and *B. sanchezii* lack foramen palatinum posterius, which is present and interpreted as a reversal in *Bairdemys venezuelensis*, *Ba. hartsteini*, and *Ba. winklerae* (character 29, Appendix 1). *Daqueymys 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. sanchezii* (Gaffney et al., 2008) retains the plesiomorphic condition of the absence of a foramen palatinum posterior, 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 jugal-quadratejugal. 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 postero-lateral 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*, *Neocheles* spp., and the newly described *C. wayuunaiki*. 

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’). As such, the paleolatitude of the Cerrejón flora and fauna is firmly within the tropics.

The youngest known podocnemid 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 wayunanaiki and the clade of Erymnochelys sp., 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. wayunanaiki, 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. wayunanaiki would have originated in the southern part of South America, based on the southern occurrence of the oldest known podocnemid (Romano and Azevedo, 2006). Assuming this is true, and based on the occurrence of C. wayunanaiki in the paleotropics, it is clear that podocnemids 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 Neocheles spp., which were widely distributed during the Cenozoic.

Despite the paucity of relevant data to test hypotheses about the timing and routes in which podocnemids 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 escuillier 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 podocnemid aff. Roxochelys vilavilensis from the early Paleocene, Tiupampa Basin, Bolivia (Laparent 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 podocnemids and chelids, such as Podocnemis pritchardi, Po. medemi, and Chelus colombiana, inhabiting the Magdalena Basin from the podocnemids and chelids inhabiting the proto-Orinoco river (Bairdemys spp. and Chelus lewisii). 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 (Museo Nacional de Historia Natural, Paris, France); Dr. O. Castaño and Dr. J. Lynch (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia); Dr. E. Gaffney and C. Mehlng (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. Dícker, and all other paleontologists and geologists working in the Cerrejón project at the Colombian Petroleum Institute, including H. García 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


APPENDIX 1. Description of characters used in phylogenetic analysis. Characters were polarized with respect to Chelidae, Araripemys barretoi, and Podocnemididae. 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 marginal, secondary roofing of the fossa temporals in dorsal view, not advanced and highly concave allowing the complete exposure of the otic chamber roof (0); medially advanced with posteriorly expanded postero-lateral temporal marginal of the parietals and quadra-
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 sutureal area between both prefrontals: absent (0); present (1). Character from Lapparent de Broin (2000).
9. Prefrontal 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. Supraoccipitalis, 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 anteroven-
13. Interparietal scale, anterior margin: anterior to the frontal parietal suture (0); posterior to the frontal parietal suture (1). New character.
15. Quadratojugal: absent (0); present (1).
16. Quadratojugal parietal contact: absent (0); present (1).
17. Quadratojugal, as in Podocnemididae (Lapparent de Broin et al., 2000).
(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 quadroarticular (2); secondary roofing moderately developed by both jugal and quadroarticular (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 podocnemids in the recently described bothremydid Aeleistocheles maliensis (Gaffney et al., 2007). Within Podocnemididae, only Ducquemys 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) Basioccipital: 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) Basioccipital 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 underlapping 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-quadratojugal contact: absent (0); extensive (1); narrow (2). Character modified from Gaffney et al. (2006).

(33) Prootic-quadrate contact: absent (0); present (1). Character modified from Lapparent de Broin (2000). The condition for bothremydids is based on the recently described Aeleistocheles maliensis (Gaffney et al., 2007).

(34) Intergular scale: large, covering the anterior margin of entoplastron (0); small, restricted between the gulars, lacking contact with entoplastron (1). Character modified from Gaffney and Forster (2003) and Gaffney et al. (2006).

(35) Neural 2: present but not contacting costal 1 (0); present and contacting costal 1 (1); absent (2). Character modified from Franc¸a and Langer (2006).

(36) 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 Aeleistocheles maliensis (Gaffney et al., 2007).

(37) Surangular, well-extended anteriorly: absent (0); present (1).

(38) Coronoid, wide lateral exposure: absent (0); present (1).

(39) Denticus, accessory ridges: absent (0); present (1). Character from Gaffney and Forster (2003).

(40) Ventral keel at the 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). New character.

Cervical Vertebrae

(41) Cervical 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 Aeleistocheles 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 Fran¸ca 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 Fran¸ca and Langer (2006).

(49) Lateral thickness of the shell: ≤ 20 mm (0); > 20 mm (1). Character modified from Fran¸ca 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.vertepaleo.org/jpv/JPVContents.html). Polymorphic conditions abbreviated as follows: A = 0 and 1, B = 0 and 2, C = 1 and 2.

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