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UM NOVO PODOCNEMÍDEO FÓSSIL DE GRANDE PORTE DA FORMAÇÃO SOLIMÕES (MIOCENO-PLIOCENO), ACRE, BRASIL E AS RELAÇÕES FILOGENÉTICAS ENTRE OS PODOCNEMIDAE

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ÍNDICE

1. Resumo

A família Podocnemidae é representada hoje por oito espécies viventes distribuídas na América do Sul e em Madagascar. A família também possui um rico registro fóssil, encontrado em quase todo o hemisfério sul, com uma grande variedade de formas e tamanhos, assim como uma história paleobiogeográfica complexa. Aqui nós descrevemos uma nova espécie de Podocnemidae fóssil do Mioceno-Plioceno da Formação Solimões do Brasil, *Podocnemis manchineri* sp. nov., baseada em um casco quase completo, uma carapaça e plastrão fragmentários e uma carapaça fragmentária, compreendendo três diferentes indivíduos. Nós analisamos esse novo táxon e outros cinco táxons conhecidos apenas por material pós-craniano em uma análise de parcimônia usando uma matriz de caracteres extraída da literatura, além de novos caracteres criados nesse estudo baseados na observação da carapaça e plastrão de vários podocnemídeos viventes e extintos. Os resultados indicam que *P. manchineri* está aninhada dentro do gênero *Podocnemis*. Nossa análise também valida a posição de outros táxons baseados em carapaças como membros do gênero *Podocnemis* (e. g. *P. negrii*¸ *P. medemi* e *P. pritchardi*), que têm sido referidos como *incertae sedis* dentro de Podocnemidae em outros estudos. Além disso, essa análise resolveu o táxon *Stupendemys geographicus* como mais relacionado ao clado que inclui *Bairdemys* que o clado que inclui *Peltocephalus*, dentro de *Erymnochelyinae*. Adicionalmente, pela primeira vez táxons fósseis foram recuperados (*Kenyemys*, apenas conhecido por cascos, e *Turkanemys*) entre a associação comum de *Erymnochelys* e *Peltocephalus*, constante em análises filogenéticas com base em dados morfológicos. Comparações morfológicas de material fragmentário da Formação Solimões sugerem que pelo menos um terceiro táxon de Podoncmidae fóssil poderia estar presente na Amazônia Sul-ocidental. Os resultados do presente trabalho foram submetidos ao *Journal of Systematic Paleontology*, apresentamos aqui o trabalho na forma em que foi submetido ao periódico.

2. Introdução

A Formação Solimões (Mioceno-Plioceno) têm revelado muitos fósseis de vertebrados ao longo dos anos, representando uma grande variedade de peixes, crocodilianos, tartarugas e mamíferos (Barbosa-Rodrigues 1892; Price 1964; Sill 1970; Campos 1977; Campos & Broin 1981; Gasparini 1985; Bocquentin & Rancy 1987; Bocquentin & Santos 1989; Bocquentin & Souza-Filho 1989, 1990; Souza-Filho & Bocquentin 1989, 1991; Broin *et al*. 1993; Souza-Filho *et al*. 1993; Latrubesse *et al*. 1997; Bocquentin-Villanueva *et al*. 1997; Gaffney *et al*. 1998; Souza-Filho 1998; Bocquentin & Guilherme 1999; Negri & Ferigolo 1999; Bocquentin *et al*. 2001; Carvalho *et al*. 2002; Bocquentin & Melo 2006; Kay & Cozzuol 2006; Hsiou *et al*. 2007; Meylan *et al*. 2009; Hsiou 2010; Riff *et al*. 2010).

Os Testudines encontrados na Formação Solimões, em sua maioria, pertencem ao grupo Pleurodira, típico do hemisfério sul, facilmente diferenciados do subgrupo Cryptodira pelo modo de retração da cabeça. Em Pleurodira a retração é lateral e em Cryptodira ela ocorre para trás, com a cabeça se encaixando entre os ombros (Figura 9). Os Pleurodira são atualmente representados por três famílias: Podocnemidae, da América do Sul e Madagascar, com 8 espécies de água doce, de tamanho pequeno até o maior Pleurodira atual, Podocnemis expansa, que alcança 90cm de comprimento; Pelomedusidae, da África, Madagascar e Ilhas Seychelles, pequenos, com cerca de 18 espécies de água doce; e Chelidae, de porte pequeno a grande, com cerca de 40 espécies de água doce, presentes na América do Sul, Austrália e Nova Guiné (Rueda-Almonacid *et al*. 2007; Pough et al., 2008). Embora hoje apenas ocorram em ambiente dulcícola nos continentes do Hemisfério Sul, os Pleurodira ocuparam também ambientes de água salobra e ambientes próximos à costa da maioria dos continentes desde o Eocretáceo, sendo bem mais diversificado no registro fóssil (Gaffney et al., 2006).

Até agora, os Podocnemidae conhecidos da Formação Solimões incluem *Caninemys tridentata* (Meylan *et al*. 2009), *"Stupendemys" souzai* (Bocquentin & Melo 2006), e *Podocnemis negrii* (Carvalho *et al*. 2002), sendo *C. tridentata* o único táxon bem aceito. A atribuição de *S. souzai* ao gênero referido é criticada e *S. souzai* pode não representar um único táxon (Meylan *et al*. 2009; Gaffney *et al*. 2011) e *P. negrii* é considerada *incertae sedis* dentro de Podocnemidae (Meylan *et al*. 2009; Gaffney *et al*. 2011). Apenas *C. tridentata* foi incluída em uma análise filogenética até hoje. Essa ausência em estudos cladísticos provavelmente ocorre devido ao comportamento ambíguo que espécies conhecidas apenas por carapaças e plastrões apresentam nesse tipo de análise. A maior parte dos caracteres usados na filogenia de podocnemídeos são retirados do crânio e mandíbula, enquanto os caracteres pós cranianos são escassos (e. g. Meylan *et al*. 2009; Cadena *et al*. 2010, 2012; Gaffney *et al*., 2011). Interessantemente, devido à complexidade do casco dos Testudines, onde tanto o plastrão quanto a carapaça sendo compostos por uma associação de ossos superpostos por escudos dérmicos, pode se esperar que vários caracteres possam ser retirados dessa associação. Ao invés disso, os caracteres de carapaça geralmente representam menos de 25% dos caracteres usados em estudos cladísticos referentes a Podocnemidae fósseis (Tabela 6). Isso contrasta fortemente com o grande número de espécies de cágados fósseis conhecidos apenas pela carapaça. Aqui nós descrevemos uma nova espécie de podocnemídeo, proveniente da Formação Solimões, Acre, Brasil (Fig. 2), e a comparamos a outras espécies relacionadas, fósseis e atuais.

Adicionalmente, nós executamos uma análise cladística, incluindo espécies fósseis e viventes de podocnemídeos, usando uma compilação de caracteres da literatura e novos caracteres do casco. Que forneceram uma hipótese filogenética que inclui alguns táxons baseados apenas em cascos, comumente deixados de fora desse tipo de estudo (e. g. *Stupendemys geographicus*, *Podocnemis negrii*, *Podocnemis medemi*, *Podocnemis pritchardi*, and *Kenyemys williamsi*). A Sistemática Filogenética tenta descobrir o grau de relação de parentesco entre os diferentes táxons em determinado grupo de organismos, com base em caracteres derivados compartilhados (sinapomorfias). Podendo ser representado por um cladograma (Hennig, 1965). Assim, dadas três espécies A, B e C: a espécie A pode ser mais aparentada a B do que a C; a espécie A pode ser mais aparentada a C do que a B; ou as espécies B e C podem ser mais aparentadas entre si do que qualquer uma delas com A (Figura 10). A escola desenvolvida por Hennig defende que o grau de relação filogenética não pode ser inferido com base apenas em semelhanças morfológicas. As relações devem ser evidenciadas através da observação de características derivadas compartilhadas, isto é, por sinapomorfias. Isso ocorre porque caracteres podem manter-se inalterados por muito tempo durante a evolução. Assim sendo, a relação de parentesco entre espécies pode ser demonstrada apenas pela posse, em comum, de sinapomorfias (Hennig, 1965) ou, em outras palavras, a presença de sinapomorfias é a única evidência de uma origem evolutiva comum entre dois ou mais táxons.

Desta forma, o presente estudo teve como objetivos; 1 - descrever o material fóssil inédito (UFAC-1000), que consiste de carapaça quase completa, plastrão incompleto e cintura pélvica. Provavelmente relacionado ao gênero *Podocnemis* (Rancy & Bocquentin, 1987). Além de rever a classificação de outros espécimes. O que poderá aumentar de maneira significativa a resolução das relações dentro do gênero Podocnemis. 2 - avaliar mais acuradamente as relações filogenéticas dos Podocnemidae da Formação Solimões, ainda não incluídos nesse tipo de trabalhos sobre o grupo (UFAC-1000, *P. negrii*). Comparando-os com táxons em outras coleções e, se possível, incluir novos caracteres para análise, na tentativa de aumentar a resolução dos cladogramas.

3. Artigo

A new large podocnemid turtle from the upper Miocene Solimões Formation, Acre, Brazil and the phylogenetic relationships within Podocnemidae

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Abstract

The family Podocnemidae is represented today by eight moderate-sized extant species distributed in South America and Madagascar. They also have a rich fossil record, which is found over almost all the southern hemisphere, with a wide variety of forms and sizes, as well as a complex palaeobiogeographical history. Here we describe a new species of fossil Podocnemidae from the Miocene-Pliocene Solimões Formation of Brazil, *Podocnemis manchineri* sp. nov., based on an almost complete large shell, a fragmentary carapace and plastron, and a fragmentary carapace, comprising three different individuals. We analysed this new taxon and other five fossil taxa known only by shell material in a parsimony analysis using a morphological character matrix with characters extracted from the literature, as well as new characters created in this study based on observation of the carapace and plastron of several extinct and extant podocnemid taxa. The results indicate that *P. manchineri* is nested within the genus *Podocnemis*. Our analysis also validated the position of several shell taxa to the genus *Podocnemis* (e. g. *P. negrii*, *P. medemi*, and *P. pritchardi*), which have been referred as *incertae sedis* within Podocnemidae in previous studies. Furthermore, this analysis resolved *Stupendemys geographicus* as more closed related to the clade that includes *Bairdemys* than to the clade that includes *Peltocephalus* within Erymnochelyinae. Additionally, for the first time it is recovered the presence of fossil taxa (namely *Kenyemys* (also shell based) and *Turkanemys*) between the common association of *Erymnochelys* and *Peltocephalus*, commonly recovered in morphological phylogenetic approaches. Morphological comparisons of fragmentary material from the Solimões Formation also suggest that at least a third taxon of a large sized fossil podocnemid could have been present in South-western Amazonia.

Key-words: Podocnemidae, Acre, Solimões Formation, *Podocnemis*, Phylogenetic Analysis.

Introduction

The Brazilian Solimões Formation (Miocene-Pliocene) has yielded many vertebrate fossils over the years, representing a great variety of fishes, crocodilians, turtles, and mammals (Barbosa-Rodrigues 1892; Price 1964; Sill 1970; Campos 1977; Campos & Broin 1981; Gasparini 1985; Bocquentin & Rancy 1987; Bocquentin & Santos 1989; Bocquentin & Souza-Filho 1989, 1990; Souza-Filho & Bocquentin 1989, 1991; Broin *et al*. 1993; Souza-Filho *et al*. 1993; Latrubesse *et al*. 1997; Bocquentin-Villanueva *et al*. 1997; Gaffney *et al*. 1998; Souza-Filho 1998; Bocquentin & Guilherme 1999; Negri & Ferigolo 1999; Bocquentin *et al*. 2001; Carvalho *et al*. 2002; Bocquentin & Melo 2006; Kay & Cozzuol 2006; Hsiou *et al*. 2007; Meylan *et al*. 2009; Hsiou 2010; Riff *et al*. 2010). Concerning turtles, so far, the known record of Podocnemidae from the Solimões Formation includes *Caninemys tridentata* (Meylan *et al*. 2009), *"Stupendemys" souzai* (Bocquentin & Melo 2006), and *Podocnemis negrii* (Carvalho *et al*. 2002), with the only well accepted taxon being *C. tridentata*. *S. souzai* is criticized and may not represent a single taxon (Meylan *et al*. 2009; Gaffney *et al*. 2011) and *P. negrii* is considered to be *incertae sedis* within the Podocnemidae (Meylan *et al*. 2009; Gaffney *et al*. 2011). Also, only *C. tridentata* has been included in a phylogenetic analysis to date. This absence in cladistics approaches is likely due to the ambiguous behaviour that species known only by shell material show in this type of analysis. Most characters used in podocnemid phylogeny are taken from the skull and jaws, while the postcranial characters are scarce (e. g. Meylan *et al*. 2009; Cadena *et al*. 2010, 2012; Gaffney *et al*., 2011). Interestingly, due to the complexity of the turtle shell, with both carapace and plastron being composed by an association of bones superposed by an association of scales, it might be expected that several characters could be extracted from this association. Instead, shell characters generally represent less than 25% of the characters used in cladistic studies regarding fossil turtles. This strongly contrasts with the large number of fossil turtle species only based in shell materials. Here we describe a large new podocnemidid turtle uncovered from the Solimões Formation deposits, Acre, Brazil (Fig. 1), and compare it to other close related fossil and extant species. Additionally, we performed a cladistics analysis including both extant and fossil podocnemid species by using a compilation of characters in the literature and new shell characters which furnished a phylogenetic hypothesis that also includes few shell based taxa commonly not present in this kind of work (e. g.

Stupendemys geographicus, *Podocnemis negrii*, *Podocnemis medemi*, *Podocnemis pritchardi*, and *Kenyemys williamsi*).

Abbreviations

LACM – Natural History Museum of Los Angeles County; **UFAC** – Universidade Federal do Acre, Laboratório de Pesquisas Paleontológicas; **UCMP** – University of California, Museum of Paleontology, Berkeley, California.

Geological setting

The Solimões Formation, located in north-western South America, consists of claystones, sandstones and siltstones intercalated with a few lignite and limestone layers (Radambrasil 1977; Hoorn 1993). The Solimões Formation has lateral continuity on neighbour basins, receiving different names. In Pastaza, Marañón and Madre de Dios basins from Peru the Solimões Formation is known as Pebas, Ipururo, and Nauta formations. In Colombia, on Amazonas and Putumayo basins, it receives the denominations of Amazonic Tertiary and La Tagua layers (Hoorn 1993, 1994a; Campbell *et al*. 2001; Roddaz *et al*. 2005; Rebata *et al*. 2006).

Palynological data suggest an age range from Miocene to Pliocene for the Solimões Formation in the Amazonas State of Brazil (Cruz 1984). Many biostratigraphic works based on palynomorphs were carried out in central and north-western Amazonia (Hoorn 1993, 1994a, b, 1995). However, most vertebrate fossils from the Solimões Formation come from the south-western of Amazonia and no relation between the north and south sediments has been established yet (Campbell *et al*. 2000, 2001, 2006).

Other biostratigraphic propositions have been made, using mainly fossil mammals. To the south-western Brazilian Amazonia a Huayquerian, possibly reaching Montehermosian age has been suggested (upper Miocene to Pliocene) (Campbell *et al*. 1985; Frailey 1986; Latrubesse 1992; Latrubesse *et al*. 1997, 2007).

There are different palaeoenvironmental interpretations for the Solimões Formation as well, it could have been either a shallow lake, or lake system (Campbell & Frailey 1984; Frailey *et al*. 1988; Vonhof *et al*. 1998; Wesselingh *et al*. 2002); a great fluvial megafan complex (Latrubesse *et al*. 1997, 2007); a marginal marine influence area (Hoorn 1993, 1994a, b, 1995); or an internal sea (Räsänen *et al*. 1995; Hovikoski *et al*. 2005).

Fossil reptiles are abundant, with a great variety of extinct crocodilians, being represented by Crocodylidae (*Charactosuchus*), Alligatoridae (*Caiman*, *Purussaurus*, *Mourasuchus*), and Gavialidae (*Brasilosuchus*, *Gryposuchus*, and *Hesperogavialis*) (Barbosa-Rodrigues 1892; Price 1964; Sill 1970; Gasparini 1985; Bocquentin & Souza-Filho 1989, 1990; Souza-Filho 1998; Souza-Filho & Bocquentin 1989, 1991; Souza-Filho *et al*. 1993; Riff *et al*. 2010). The chelonians are represented by the Podocnemidae (*Podocnemis* and *Stupendemys*), Chelidae (*Chelus*), and Testudinidae (*Chelonoidis*) (Barbosa-Rodrigues 1892; Campos 1977; Campos & Broin 1981; Broin *et al*. 1993; Bocquentin & Rancy 1987; Bocquentin & Santos 1989; Gaffney *et al*. 1998; Bocquentin *et al*. 2001; Carvalho *et al*. 2002; Bocquentin & Melo 2006; Riff *et al*. 2010). There are also records of Squamata, represented by snakes (Aniliidae, Boidae and Colubridae) and lizards (Teiidae) (Hsiou *et al*. 2007; Hsiou 2010). All these findings tend to support a continental water body palaeoenvironmental interpretation.

Historical background

In past years various phylogenetic analyses, with both molecular and morphological data, have been contributing to the understanding of the Podocnemidae inter-relationships (Georges *et al*. 1998; França & Langer 2006; Gaffney *et al*. 2006; Noonan & Chippindale 2006; Vargas-Ramírez *et al*. 2008; Meylan *et al*. 2009; Cadena *et al*. 2010, 2012; Gaffney *et al*. 2011). However, there are still many problems to be solved in order to understand podocnemid phylogeny.

The morphological data results conflict with the molecular ones. The relationships among the living genera *Podocnemis*, *Peltocephalus*, and *Erymnochelys* are different when the two datasets are considered. For instance, the molecular data suggests a closer relation between *Podocnemis* and *Erymnochelys* (Georges *et al*. 1998; Noonan & Chippindale 2006; Vargas-Ramírez *et al*. 2008), while the morphological data suggests that *Erymnochelys* and *Peltocephalus* are sister-taxa (França & Langer 2006; Meylan *et al*. 2009; Cadena *et al*. 2010, 2012; Gaffney *et al*. 2011). In any case, those results may be of great palaeobiogeographic importance, since *Erymnochelys* is from Madagascar while the other two genera are from South America.

The Podocnemidae shell is known as very conservative, with many shell based taxa being first referred initially as *Podocnemis* and later, with skull discoveries, revised and reassigned to other genera (Gaffney *et al*. 2006, 2011). This led to a major focus on bringing new cranial characters for phylogenetic analyses, while new postcranial characters have been much rarer. Usually more than 75% of the characters in a phylogenetic analysis are from the skull and jaws (Meylan *et al*. 2009; Cadena *et al*. 2010, 2012; Gaffney *et al*. 2011). Consequently, shell based taxa, such as *Stupendemys* and *Kenyemys*, hardly produce well resolved cladograms in this context.

So far, the only Solimões Formation podocnemid included in a phylogenetic analysis is the skull based taxon *Caninemys tridentate*, whereas the shell based taxa from the Solimões Formation (*"Stupendemys" souzai* and *Podocnemis negrii*) have never been included in a cladistics study. Both shell taxa are controversial. *"Stupendemys" souzai* assignment to the genus *Stupendemys* has been criticized and the referred material may not represent a single taxon (Meylan *et al*. 2009; Gaffney *et al*. 2011). *Podocnemis negrii* has been considered as *incertae sedis* within the Podocnemidae, due to the lack of synapomorphies to support its suggested relationship as a sister-taxon to the extant *P. sextuberculata* (Carvalho *et al*. 2002; Gaffney *et al*. 2011).

There are many other indeterminate Podocnemidae fossil remains from the Solimões Formation in the UFAC collection. Among them, there is UFAC-1000 and UFAC-1001, considered until now to be an indeterminate podocnemid (Rancy & Bocquentin-Villanueva, 1987). Here we review these specimens, in addition to a third non described specimen (UFAC-1559) in order to clarify their status within the Podocnemidae.

Systematic palaeontology

Testudines Linnaeus, 1758

Pleurodira Cope,1864

Pelomedusoides Cope, 1868

Podocnemidinura Cope, 1868

Podocnemidae Cope, 1868

Podocnemis Wagler, 1830

Type species: *Emys expansa* Schweigger, 1812.

Included species: *Podocnemis expansa*, *P. vogli*, *P. unifilis*, *P. erythrocephala*, *P. lewyana*, *P. sextuberculata*, and *P. bassleri.*

Diagnosis: As in Gaffney *et al*. (2011).

Podocnemis manchineri sp. nov.

(Figs. 2 and 3)

Etymology: Named after the indigenous Manchineri tribe, living near the collection site of the holotype.

Holotype: UFAC-1000, a nearly complete carapace and plastron.

Referred materials: UFAC-1001, incomplete carapace and plastron; UFAC-1559, a fragmentary carapace.

Locality and horizon: UFAC-1000, Acre River, Seringal Bélgica, Assis Brasil, Acre State, Brazil; UFAC-1001, Juruá River, Cruzeiro do Sul, Acre State, Brazil; UFAC-1559, Upper Purus River, Purus 6 UFAC locality, AM (Fig. 1). Solimões Formation, upper Miocene (Huayqueriense) (Campbell *et al*. 1985; Frailey 1986; Latrubesse 1992; Latrubesse *et al*. 1997, 2007). All materials are deposited in the UFAC fossil vertebrate collection.

Diagnosis: A very large sized podocnemid turtle (more than a meter long shell) with the following combination of characters: vase-like shaped vertebral scutes, especially vertebral two; vertebral one significantly larger than other vertebral scutes; rounded cranial margin of the shell, without any kind of embayment; gular scales reaching the entoplastra.

Description

UFAC-1000 Carapace

The UFAC-1000 (Figs. 2A and 3A, C, and D) specimen is represented by an almost complete carapace and plastron. The carapace of the UFAC-1000 is uniformly arched, without any irregularities, ornamentations, keels or depressions. The carapace bones are regularly articulated, not presenting significant alterations due to diagenetic processes. This indicates that the dorsoventral flattening of the shell represents a feature present in the living animal, more easily seen in frontal view. The plastral bridge goes outwards, almost parallel to the dorsoventral axis. The scars left by the dermic scutes are easily seen and identifiable. The shell interior is still filled with the matrix and, therefore, not accessible. The presence or absence of ducts, such as axillary musk duct is uncertain, due to the poor preservation state of the regions where they may have been placed, such as the joining region between the plastral bridge and the peripheral bones.

Nuchal bone. It is slightly wider than long. Its widest portion is the region where it meets the first costal and the first peripherals, reaching the minimum width at the end of the first cranial quarter of the bone. The lateral edges are sinuous, while the cranial edge is curved without any embayment or notch. This gives the bone a general bulbous shape from a dorsal view.

Neural series. The carapace has seven neural bones. The first neural is oval and elongated, connected only to costals one, neural two, and the nuchal bone. All other neurals connect to two pairs of costals, the ones with the same number of the neural and the proceeding ones. The neurals two to five have six sides, with an elongated hexagonal shape, resembling a coffin. The neural six is shorter, showing a more regular hexagonal shape, and the neural seven has five sides, resembling a gem.

Suprapygal. It is wider than long and is skirt shaped. It is caudally formed by three arches, where it articulates to the pygal and the peripherals eleven. The suprapygal do not contact the neural bones.

Pygal. The caudal edge is broken, but the bone is trapezoidal in shape and wider caudally.

Costals. There are eight pairs of costals. Only the seventh and eighth pairs connect each other medially, in a slight asymmetrical way. All the others are medially connected to a neural bone. The first one is longer than the others, with a rounded anterior edge, connected to the nuchal and the peripheral bones one to four. The costals two and three are slightly arched caudally. The costal four is almost straight, and the remaining ones are sequentially more arched cranially than the anterior costal bone.

Peripherals. From the eleven pairs of peripheral bones, only the second, third and fourth are completely preserved on the right side of the shell. The others show different degrees of preservation. However, it is possible to infer the probable shell outline by the combination of the information on both sides of the shell. It would have been oval in shape, with the maximum width at the seventh or eighth peripheral. The peripherals strongly vary in shape with the peripheral one being larger than the others. The size of peripherals decreases progressively until the peripheral six, which is the smallest. From the peripheral seven onward the size gradually increases until the last bone of the series.

Vertebral scutes. The first vertebral scute is clearly wider than the others, with a different and more rounded shape. The second and third scutes are very similar, showing a vase-like shape. All the six edges are curved, arched towards the center, with the cranial edge being larger than the caudal one. The maximum width is reached where the cranial and caudal lateral edges meet. The fourth scute is similar to vertebrals two and three, being only thinner than these elements and with the caudal end arched slightly caudally, while in vertebrals two and three it is arched cranially. The fifth and last vertebral scute is wider than the others, being roughly triangular in shape, resembling a fish tail.

Pleural and marginal scutes. There are four pairs of pleural scutes and twelve pairs of marginal scutes. None of the marginal scutes reach any of the costal bones. The first marginal pair is proportionally small and roughly rectangular in shape.

Plastron

The plastron of UFAC-1000 (Fig. 3B) is almost complete. The cranial and caudal extremities are broken. The epiplastra is also broken, almost not preserved.

Entoplastra. The maximum width is reached about in the middle of the bone, despite the broken cranial edge, the different shortening of the cranial and caudal portions of the bone suggest a shorter caudal and a longer cranial portion.

Hioplastra and hipoplastra are well preserved. A small lateral mesoplastra is present. The xifiplastra caudal edge is not preserved. The caudal lobe of the plastron has an almost straight edge.

Scales. The region that would be covered by the gular and intergular scales is not preserved. The humeral scales contact each other in the midline, covering the entoplastra, what is left from the epiplastra almost completely, and a small portion of the hioplastra. The pectoral scales covers a big portion of the hioplastra, cranially it reaches the epiplastra and the entoplastra. The abdominal scales cover portions of the hioplastra, the hipoplastra, and the mesoplastra almost completely, which is also covered only by marginal scutes.

Pelvic girdle

Only the right pelvic girdle is accessible for study (Figs. 2D and 3E). It is not completely preserved, with the pubic and ischiatic processes broken. Furthermore, the ilium is broken, so that the pelvic girdle can be detached from the carapace, where the other half of the ilium is still attached to the shell. However, the pelvic girdle bones are still articulated to each other. They have a slender structure, being considerably flat. The ilium is slightly more robust than the other bones, but flattens anterocaudally, forming a small crest in its lateral portion. The acetabulum has the shape of a slightly arched drop, with the tip placed in the pubis.

UFAC-1001

The UFAC-1001 specimen (Fig. 2B) preserves the cranial right portion of the carapace, articulated to the plastron, which keeps its cranial lobe at right side. The scute scars are easily seen. Additionally, as in UFAC-1000, the region where the axillary musk ducts may have existed is not well preserved.

In the carapace of the UFAC-1001 the nuchal and costals one to three are partially preserved. Peripherals one to four are completely preserved and the fifth is almost completely preserved. The nuchal has a bulbous contour where it meets the peripheral one. The axillary buttress is preserved in the visceral portion of the costal one reaching the peripheral three. The costal two is also present but only partially.

The plastron of UFAC-1001 is represented only by its cranial portion.

Epiplastra. Only the right epiplastra is completely preserved, the left is partially preserved. They arch smoothly, delimitating the cranial edge of the plastron.

Entoplastra. It has the same shape seen in UFAC-1000 entoplastra. Such as in UFAC-1000, the caudal part of the bone is shortened abruptly, resulting in a caudal portion smaller than the cranial one. Both right hioplastra and mesoplastra are partially preserved.

Scales. The intergular scale completely separates the gulars, covering the cranial margin of the entoplastra. The gulars reach the entoplastra.

The humeral scales meet each other in the midline, covering the entoplastra almost completely, a large portion of the epiplastra, and a small portion of the hioplastra. The pectoral scales cover a large portion of what is preserved from the hioplastra, and reaches the epiplastra, and the entoplastra. The abdominal scale covers the rest of the preserved portion of the hioplastra and mesoplastra.

UFAC-1559

UFAC-1559 (Fig.2 C) consists of a carapace fragment. None of the bones is completely preserved, however it is possible to identify and delimitate them. The neural one is broken, but its caudal portion has an elongated oval shape. The neurals two to five are coffin-shaped. The axillary buttress is partially preserved in costal one. The costals two and three are partially preserved. The second vertebral scute is easily identifiable and has a vase-like shape as in UFAC-1000. It is only slightly more arched medially on the contact with pleural one than in the vertebral two of the UFAC-1000. This slight difference is the only feature that is not identical when comparing the overlapping parts of UFAC-1000, UFAC-1001, and UFAC-1559.

Comparison

Here we highlight the main differences seen in the *P. manchineri* when compared to other closely related fossil taxa. *Podocnemis manchineri* differs from *P. pritchardi* by having seven rather than six neurals, as well as by having a less extreme dorsoventral shell flattening and by not possessing an almost rectangular mesoplastra. It differs from *P. medemi* in the shape of the entoplastra, which is proportionally shorter caudally and by the shape of the plastron lobes which are shorter and more rounded in *P. medemi*. Also, the gular scales do not touch the entoplastra in *P. medemi* and only half of the entoplastra is covered by the humeral scales while in the *P. manchineri* the entoplastra is almost completely covered by humeral scales. *Stupendemys geographicus* has no connection between the last pairs of vertebrals. It is also much larger in size than *P. manchineri*, the shell has a nuchal notch, and is medially depressed. Because these differences, we rule out the possibility that the materials described here and *S. geographicus* belong to the same taxon. *P. manchineri* can also be compared to *Cerrejonemys wayuunaiki*, from the Palaeocene of Colombia, the shell of *C. wayuunaiki* is thicker, despite the preserved bones having a similar length and width when compared to *P. manchineri* shells. Considering that, and also their different ages, it does not seem reasonable to consider both as the same taxa (Table 1).

According to Meylan *et al*. (2009), using skull-shell ratios of recent podocnemid species, it is hypothesized that the shell *of Caninemys tridentata* would be less than 1.2-1.5 meters, compatible with the *P. manchineri* shell size (1.2 meters). The skull of *P. bassleri* is slightly shorter (15.7 cm) than that of *C. tridentata* (16.5 – 17.0 cm) (Meylan *et al*. 2009) and the *Carbonemys cofrinii* holotype skull is even larger (21 cm) than *C. tridentata* (Cadena *et al*. 2012). Therefore all these taxa could also be compatible in size with the shell of *P. manchineri*.

The extant species of *Podocnemis* are much smaller than *P. manchineri*. The larger extant member of the genus *P. expansa* can reach a maximum total length of about 90 cm (Rueda-Almonacid *et al*. 2007), while the shell of *P. manchineri* is much larger (1.2 meters). Due to the massive difference in size, as well as some morphological differences, such as the axillary buttress reaching peripheral 3 in *P. manchineri*, instead of peripheral 2 in all other *Podocnemis* extant species except in *P. vogli*, we discard the idea of *P. manchineri* belonging to any extant species (Table 2).

Phylogenetic analysis

To examine the phylogenetic relationships of *P. manchineri*, , we included several podocnemid taxa for which the skull is known, as well as some shell based taxa, commonly excluded from the analyses due to missing data, such as *Stupendemys geographicus*, *P. medemi*, *P. negrii*, *P. pritchardi*, and *Kenyemys williamsi*.

We analyzed a data matrix with 45 taxa and 122 morphological characters. 109 characters were extracted or modified from published works (Lapparent de Broin 2000; De la Fuente 2003; Gaffney & Forster 2003; França & Langer 2006; Gaffney *et al*.

2006, 2011; Meylan *et al*. 2009; Cadena *et al*. 2010; Aquentin 2012), and 13 are new. These new characters regard carapace and plastron and where based on first-hand observation of some taxa, as well as from literature review of fossil and recent podocnemid species.

All taxa were coded on species level except by the outgroups Chelidae (*Chelus fimbriatus*, *Phrynops geoffroanus*), Pelomedusidae (*Pelomedusa*, *Pelusios*), Bothremydidae (*Kurmademys*, *Cearachelys*, *Foxemys*) and the podocnemids *Neochelys* (*N. fajumensis* and *N. zamorensis*), and *Stereogenys* (*S. cromeri* and *S. libyca*). The coding was based on direct observation and on photographs of fossil and recent species of podocnemids, as well as from literature (Wood & Díaz de Gamero 1971; Wood 1976, 1983, 1997, 2003; Lapparent de Broin 2000; De la Fuente 2003; Gaffney & Forster 2003; França & Langer 2006; Meylan 2006; Gaffney *et al*. 2006, 2011; Meylan *et al*. 2009; Cadena *et al*. 2010, 2012). The outgroups were chosen based on Gaffney *et al*. (2006).

The character matrix was constructed using NEXUS Data Editor and analyzed using PAUP 4.0 beta 10 (Swofford 2000). The following protocol was used in the analyses: random addition sequence with 100,000 replicates as addition sequence method, Three Bisection and Reconnection (TBR) as swapping algorithm. The branches were also collapsed if the minimum branch length is zero, and synapomorphies for the nodes follow ACCTRAN character optimization. No topological constrains were used.

A second analysis without *P. bassleri* was conducted, since this taxon has been constantly referred as problematic or a wildcard in phylogenetic analyses, being commonly excluded (e. g. Meylan *et al*. 2009; Gaffney *et al*. 2011; Cadena *et al*. 2012). Additionally, it is the only taxa assigned to the genus *Podocnemis* known only by skull material. We also conducted a test by coding the postcranial characters of *P. manchineri* in two skull only taxa, *P. bassleri* and *Caninemys tridentata*, to compare changes in the first cladogram and look for possible relations.

Results

From the 122 characters (Appendix 1), 11 were parsimony uninformative (characters 1, 2, 14, 50, 61, 78, 81, 83, 85, 88 and 97), and character 47 was constant

(Appendix 2). None of the new characters were uninformative or constant. The analysis of 45 taxa yielded 134 most parsimonious trees of 331 steps (CI excluding uninformative characters = 0.5266; RI = 0.7615; RC = 0.4141). The analysis without *P. bassleri* (44 taxa) resulted in 12 most parsimonious trees of 331 steps (CI excluding uninformative characters = 0.5266; RI = 0.7588; RC = 0.4126). The strict consensus in both cases is very similar (Figs. 4 and 5). The only difference is within the *Podocnemis* genus, which is less resolved when *P. bassleri* is included in the analysis (Fig. 4). The results using only the holotype of *P. manchineri* or the information available from all referred specimens were the same. The combination of *P. manchineri* and *P. bassleri* data does not change the position of any other taxa in the analysis, and this combination of taxa takes the position of *P. manchineri* in the cladogram without *P. bassleri*. On the other hand, the combination of *P. manchineri* and *C. tridentata* resulted in a large polytomy within the subfamily Erymnochelyinae.

Our analysis yielded trees with similar topologies to the trees from other works, which are also based on morphology (e. g. Meylan *et al*. 2009; Cadena *et al*. 2010, 2012; Gaffney *et al*. 2011). Among these previous works, the tree found in our study is more similar to that of Gaffney *et al*. (2011). The topology for the taxa outside Podocnemidae is the same (Chelidae (Pelomedusidae + *Araripemys*) (Euraxemydidae (Bothremydidae (*Brasilemys* (*Hamadachelys* + *Portezueloemys* + Podocnemidae)))))), as well as the topology of the clade that includes Cretaceous taxa, such as: (*Bauruemys* (*Peiropemys* (*Pricemys* + *Lapparentemys*))). The position of *Cerrejonemys* is the same as in Cadena *et al*. (2010, 2012), being the sister-taxa of the genus *Podocnemis*.

Discussion

Taxonomy and phylogenetic relationships of *P. manchineri*

None of the extant podocnemid taxa compares with the proportions of the *P. manchineri* shell. From the extinct taxa, the ones that could be as large as the *P. manchineri* are *Podocnemis pritchardi* and *Podocnemis medemi*, from the middle Miocene of Colombia, *Cerrejonemys wayuunaiki* and *Carbonemys cofrinii*, from the middle-upper Palaeocene of Colombia, *Stupendemys* and *Caninemys tridentata*, from the late Miocene of Amazonia, and *Podocnemis bassleri*, from the Mio-Pliocene of Peru. All comparable taxa are different from the *P. manchineri*.

In any case, our analysis support a *Podocnemis* monophyly that includes all the recent species (*Podocnemis expansa, P. vogli, P. unifilis, P. erythrocephala, P. lewyana*, and *P. sextuberculata*) plus the fossil species, both skull (*P. bassleri*) and shell based (*P. manchineri, P. negrii, P. pritchardi* ,and *P. medemi*), which is supported by the following unambiguous synapomorphies: prefrontal with an interorbital sulcus at the sutural area between both prefrontals (character 7) and dentary with accessory ridges (character 77) (Fig. 4).

Phylogenetic analysis

Here we resolved the position of three fossil Podocnemidae previously regarded as *incertae sedis* (*P. negrii, P. medemi*, and *P. pritchardi*) (Fig. 4). Since the most basal taxon within the genus *Podocnemis* in our analysis (excluding *P. bassleri*) is the recent *P. erythrocephala*, we assume that the *incertae sedis* taxa analysed here actually belong to the genus *Podocnemis* (Fig. 5). From those, *P. negrii* is the sister-taxon of *P. sextuberculata*, as has been already suggested by Carvalho *et al*. 2002. This close relationship is supported by the following unambiguous synapomorphies: carapace with keeled neurals, 92 (0→1) and carapace with the second vertebral scute hexagonal in shape, 103 (2→1). *P. pritchardi* and *P. medemi* relations are less cleared, but both belong to the *Podocnemis* clade (Fig. 4).

In the subfamily Erymnochelyinae our topology for *Caninemys*, *Dacquemys* and the unnamed taxon UCMP-42008 is the same as in Gaffney *et al*. (2011). An interesting new result is the relationships of *Peltocephalus*, *Turkanemys*, *Kenyemys*, and *Erymnochelys*, which comprise a monophyletic clade, (*Peltocephalus* (*Kenyemys* (*Turkanemys* + *Erymnochelys*))). In all morphological cladistic analyses *Peltocephalus* and *Erymnochelys* are depicted as sister-taxa (e. g. França & Langer 2006; Meylan *et al*. 2009; Cadena *et al*. 2010, 2012; Gaffney *et al*. 2011), this more common topology would represent a huge gap in the known fossil record, since both species are living representatives and considering that *Peltocephalus* is from South America and *Erymnochelys* from Madagascar. In this case we would have two possibilities to explain their relationship: first, somehow they, or their ancestral, managed to overcome huge biogeographical barriers: second, they have a vicariant origin dating prior to the broke up of the Gondwana, with fossil specimens yet to be found, either on continental Africa or Antarctica. Anyhow, both explanations would need more evidence to be adequately supported (like saltwater tolerance in recent species, or new fossil findings). In our analysis, however, the presence of African species between *Peltocephalus* and *Erymnochelys* furnishes new information to subsequent studies on biogeographical history of these two extant taxa (Fig. 4).

Although we had a polytomy comprising *Stupendemys*, all the *Bairdemys* species, *Cordichelys, Latentemys, Mogharemys, Papoulemys, Neochelys* and *Brontochelys* (*Lemurchelys* (*Shweboemys* (*Stereogenys*))), we provide for the first time a phylogenetic proposition to *Stupendemys*. However, the relationships among those taxa are not well established. In any case, our topology within the genus *Bairdemys*, and the topology of the clade comprising *Brontochelys, Lemurchelys*, *Shweboemys*, and *Stereogenys* agree with that of Gaffney *et al.* (2011).

In our study we observed a clear division within Podocnemidae with one clade leading to the genus *Podocnemis* and the other one leading to the clade that includes the other extant Podonemidae and *Bairdemys.* These two clades have been previously regarded as the subfamilies Podocneminae and Erymnochelyinae. Here we propose the phylogenetic definitions for the two clades as follows: Erymnochelyinae would be the stem-based clade defined as all Podocnemidae more related to *Erymnochelys madagascariensis* than to *Podocnemis expansa*. However, due to the conflict between morphological and molecular datasets we propose a new name to the Erymnochelyinae subfamily, Peltocephalinae. The morphological data yield a clear division within Podocnemidae, where *Erymnochelys madagascariensis* is more related to *Peltocephalus dumeriliana* than to *Podocnemis expansa*. However, the molecular data shows a closer relationship between *E. madagascariensis* and *P. expansa*. That would leave *P. dumeriliana* in a third subfamily, not supported by morphological data. Therefore, we prefer to use *P. dumeriliana* as the type species for the subfemily, Peltocephalinae. Being the stem-based clade defined as all Podocnemidae more related to *Peltocephalus dumerilianus* than to *Podocnemis expansa* and Podocneminae is the stem-based clade defined as all Podocnemidae more related to *Podocnemis expansa* than to *Peltocephalus dumerilianus.*

This arrangement sustains the division of the Podocnemidae in two subgroups, observed in morphological dataset cladograms, without the use of *E. madagascariensis* which is depicted as more related to *Podocnemis expansa* than to *Peltocephalus dumerilianus* in molecular dataset cladograms, that would leave *Peltocephalus dumerilianus* in a third subfamily, not well recognizable in morphological analyses, if *E. madagascariensis* is used to define a clade. So, this division works well with both current molecular and morphological datasets.

Large podocnemid fossil taxa in western Amazonia

This new species confirms that there is at least two very large podocnemids in the late Miocene of Amazonia (Lapparent de Broin *et al*. 1993; Gaffney *et al*. 1998; Meylan *et al*. 2009). Since *Stupendemys* is a shell-based taxon, it could not be compared to the skull based taxa like *Caninemys* and *P. bassleri*. Our analysis suggests that *P. manchineri* and *Stupendemys* are two distinct large podocnemid shell based taxa from the late Miocene of Acre mainly based on the differences observed in overall shell morphology.

Additionally, we consider the possibility that there are more than two species of large Podocnemidae in the late Miocene of Amazonia. There are some odd bones such as UFAC-901, UFAC-637, and UFAC-933, as well as the possibility that the fossils assigned to *"Stupendemys" souzai* may actually belong to more than one taxa (Meylan *et al*. 2009).

Due to the fragmentary nature of some bones from the Miocene of Acre, they are hard to classify. However, there is a large, upwardly curved, broken nuchal bone numbered UFAC-901 that would likely be a podocnemid, or a testudinid, due to the occurrence of those families in the region (Barbosa-Rodrigues 1892; Campos 1977; Campos & Broin 1981; Broin *et al*. 1993; Gaffney *et al*. 1998; Carvalho *et al*. 2002; Bocquentin & Melo 2006; Riff *et al*. 2010) and the absence of a cervical scute. It is clearly different from the nuchals of *P. manchineri* and the LACM-131946 material, assigned to *"Stupendemys" souzai*, which is strongly upturned (Gaffney *et al*. 1998; Bocquentin & Melo 2006). There is also a coffin shaped, flat neural bone (UFAC-637), which is almost identical in shape, length and width to some of the neurals in UFAC-1000 specimen. The neural UFAC-637 and the nuchal UFAC-901 share a similar feature, both are very thick (up to 31 and 25mm, respectively). Their thickness is neither compatible with *Stupendemys* nor *P. manchineri* shells, either when compared to bones similar in length and width, or with the overall shell thickness. Those are also incompatible with the testudinids already known from the Solimões Formation. Because of that, they could represent another large taxon of either a testudinid or a podocnemid with a thicker shell, like *Cerrejonemys* (Fig. 6, 7 and Tables 4, 5).

There are some comparable fossil cervical vertebrae showing again that there may have been more than two large podocnemids in the Miocene of south-western Amazonia. Unfortunately, one of them is missing from the collection of University of Acre. Only a cast from the UFAC-1542 has left. However, it still can provide some valuable information. The vertebra is typically podocnemid in shape, with a saddle shaped centra. It strongly resembles the cervical vertebrae of the living *Podocnemis* species, except for its greater size. This vertebra is clearly different from the other large sized vertebrae assigned to *"Stupendemys" souzai* (e. g. UFAC-1163, UFAC-1553, UFAC-1554, and UFAC-5275), being smaller and more elongated. They likely represent the same taxon as the LACM-131949, also from the late Miocene of Amazonia (Gaffney *et al*. 1998). All the vertebrae assigned to *S. souzai* are considered to be from the caudal part of the cervical series, each one being probably the eighth or seventh vertebra of the series (Negri & Bocquentin 1998; Bocquentin & Melo 2006). From these, we highlight UFAC-5275 where the ventral surface is much more arched and the neural channel is considerably smaller than all the other vertebrae. Also, the UFAC-5275 has a more robust constitution. These different features indicate that the UFAC-5275 might represent a third taxon, different from *S. souzai* and UFAC-1542 (Fig. 8).

Conclusions

A new podocnemid, *Podocnemis manchineri*, from the Solimões Formation from Brazil is described. It is distinguished from other *Podocnemis* by the following association of characteristics: vase-like shaped vertebral scutes, especially vertebral two; vertebral one significantly larger than other vertebral scutes; rounded cranial margin of the shell, without any kind of embayment; and gular scales reaching the entoplastra.

Here we could differentiate it from all other species with overlapping parts, as well as include *P. manchineri* and several shell based taxa in a phylogenetic analysis. Moreover, it is very likely that a third large sized podocnemid lived in the Miocene-Pliocene of South-western Amazonia.

We also conclude that the presence of fossil species between the common association of *Peltocephalus* and *Erymnochelys* showed here could help to explain the relationship and biogeographic history of those extant taxa.

We also provide phylogenetic definitions for the subfamilies Erymnochelyinae and Podocneminae. Erymnochelyinae is the stem-based clade defined as all Podocnemidae more related to *Peltocephalus dumerilianus* than to *Podocnemis expansa* and Podocneminae is the stem-based clade defined as all Podocnemidae more related to *Podocnemis expansa* than to *Peltocephalus dumerilianus.*

After the inclusion of new characters regarding carapace and plastron in the data matrix and according to our analysis, we conclude that although the podocnemid shell morphology is generally referred as conservative it can provide important phylogenetic information. Our phylogenetic analysis supports the assignment of *P. negrii*, *P. medemi*, and *P. pritchardi* to the genus *Podocnemis*. The analysis also depicted a better idea of the phylogenetic position of *Stupendemys geographicus*, regarded as a member of Erymnochelyinae. Also, one of the main problematic taxa in several phylogenetic analyses, *P. bassleri*, known only from skull material is recovered as a *Podocnemis* as well. Interestingly, in contrast with other phylogenetic analyses based on morphological data, the resolution of the analysis within *Podocnemis* decreased with the inclusion of *P. bassleri*, while the analysis with shell based fossil taxa resulted in a more resolved topology. Since we included new shell character in the analysis, it may suggest that they can be as important as skull characters in cladistics studies concerning chelonians.

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Appendix 1: Character list

1. Nasals: (0) present; (1) absent. (Gaffney *et al*., 2006).

2. Prefrontals meet on midline: (0) absent; (1) present. (Gaffney *et al*., 2006).

3. Prefrontal, anterior overhang onto apertura narium externa: (0) shaped by the nasals ; (1) by the prefrontals, covering a small portion of the posterior part of the apertura, ending in acute medial tip; (2) by the prefrontals, completely covering the apertura, ending in a straight to convex edge. (Cadena *et al*., 2010).

4. Frontal, orbital position: (0) Facing laterally/anterolaterally; (1) dorsolaterally; (2) dorsally. (Cadena *et al*., 2010).

5. Frontal, interorbital groove: (0) absent; (1) present. (Gaffney *et al*., 2011).

6. Prefrontal/frontal: (0) flat or slight convex; (1) strongly convex dorsally. (Gaffney *et al*., 2011).

7. Prefrontal, interorbital sulcus at the sutural area between both prefrontals: (0) absent; (1) present. (Broin, 2000).

8. Prefrontal at the interorbital space: (0) wide; (1) narrow. (Cadena *et al*., 2010).

9. Parietal, quadratojugal-parietal contact: (0) absent; (1) short contact; (2) long contact. (Gaffney *et al*., 2011).

10. Parietal, parietal-pterygoid contact in septum orbitotemporale: (0) absent; (1) present and wider; (2) present and narrower. (Gaffney *et al*., 2011).

11. Parietal, temporal emargination (Gaffney *et al*, 2011): (0) moderate to absent; (1) extreme, as in Pelusios; (2) shallow, cheek emargination extensive; (3) emargination absent due to expanded parietal/supraoccipital. (Gaffney *et al*., 2011).

12. Temporal emargination, secondary roofing of the fossa temporalis in dorsal view: (0) not advanced and highly concave allowing the complete exposure of the otic chamber roof; (1) 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; (2) very advanced with convex to straight tapering margins completely covering the roof of the otic chamber. (Broin, 2000).

13. Parietal, interparietal scale: (0) absent; (1) equilateral triangle; (2) elongate triangle; (3) parallel sided; (4) broad posteriorly. (Gaffney *et al*., 2011).

14. Parietal, interparietal scale, anterior margin: (0) anterior to the frontal parietal suture; (1) posterior to the frontal parietal suture. (Cadena *et al*., 2010).

15. Jugal-parietal contact: (0) absent; (1) present. (De la Fuente, 2003).

16. Jugal-quadrate contact: (0) absent; (1) present. (Gaffney *et al*., 2011).

17. Jugal, cheek emargination: (0) slight; (1) reaches level of orbit; (2) reaches above level of orbit; (3) reaches above quadrate. (Gaffney *et al*., 2011).

18. Squamosal, ventral vertical flangea: (0) absent; (1) present. (Gaffney *et al*., 2011).

19. Squamosal-parietal contact: (0) present; (1) absent. (Gaffney *et al*., 2006).

20. Postorbital, size: (0) equal to orbit; (1) smaller than orbit. (Gaffney *et al*., 2011).

21. Premaxillae, reach apertura narium interna: (0) no; (1) yes. (Gaffney *et al*., 2011).

22. Premaxillae, pinched snout: (0) absent; (1) concave outline near premaxilla-maxilla contact, snout not elongated; (2) concave outline posterior to premaxilla-maxilla contact, snout elongated. (Gaffney *et al*., 2011).

23. Premaxillae, one or two accessory ridges on the ventral surface of the premaxilla: (0) absent; (1) present. (Cadena *et al*., 2010).

24. Premaxillae, foramen prepalatinum in suture with maxilla (Meylan *et al*, 2009): (0) in premaxilla only; (1) in premaxillamaxillary suture; (2) absent. (Meylan *et al*., 2009).

25. Premaxillae, foramen prepalatinum relative to triturating ridge: (0) on flat surface; (1) under triturating ridge; (2) absent. (Meylan *et al*., 2009).

26. Maxilla, medial expansion of triturating surface (Gaffney *et al*, 2011): (0) absent; (1) present, forming median maxillary ridge; (2) secondary palate with midline cleft. (Gaffney *et al*., 2011).

27. Maxilla, secondary palate long: (0) no; (1) yes. (Gaffney *et al*., 2011).

28. Maxilla, triturating surface convexity: (0) absent or shallow; (1) deep. (Gaffney *et al*., 2011).

29. Maxilla, labial ridge: (0) high and narrow; (1) low and thick. (Gaffney *et al*., 2011).

30. Maxilla, accessory ridges: (0) absent; (1) one or two. (Gaffney *et al*., 2011).

31. Maxilla, meet broadly on midline: (0) no; (1) yes. (Gaffney *et al*., 2011).

32. Maxilla, median maxillary ridge: (0) absent; (1) present. (Meylan *et al*., 2009).

33. Vomer: (0) present; (1) absent. (Gaffney *et al*., 2006).

34. Palatine, medial edges of palatal cleft: (0) absent; (1) parallel; (2) curved. (Gaffney *et al*., 2011).

35. Palatine, palatine extent in triturating surface: (0) narrow or absent; (1) moderate, but much less than maxilla extent; (2) large, equal or slightly less than maxilla extent. (Gaffney *et al*., 2011).

36. Palatine, dorsal process of palatine contacts parietal in septum orbitotemporale: (0) no; (1) yes. (Gaffney *et al*., 2011).

37. Palatine, dorsal process reaches frontal: (0) no; (1) yes. (Gaffney *et al*., 2011).

38. Palatine, fossa orbitalis posterior pocket: (0) absent; (1) present in septum orbitotemporale. (Gaffney *et al*., 2011).

39. Palatine-basisphenoid contact separates pterygoids: (0) no; (1) yes. (Gaffney *et al*., 2011).

40. Palatine, second palate: (0) absent ; (1) present. (Gaffney *et al*., 2006).

41. Palatine, foramen palatinum posterius: (0) present; (1) absent. (Meylan *et al*., 2009).

42. Quadrate, antrum postoticum: (0) large; (1) smaller; (2) smallest and slitlike. (Gaffney *et al*., 2011).

43. Quadrate, fossa precolumellaris: (0) very small to absent; (1) present but shallow; (2) deep and well defined. (Gaffney *et al*., 2006).

44. Quadrate, eustachian tube separated from fenestrapostotica; (0) no ; (1) yes. (Gaffney & Wood, 2002).

45. Quadrate, incisura columellae auris: (0) no posterior bony restrictions; (1) eustachian tube separated from stapes by bone or narrow fissure; (2) eustachian tube and stapes enclosed or nearly enclosed by bone. (Gaffney *et al.*, 2011).

46. Quadrate, quadrate-basioccipital contact: (0) absent ; (1) present. (Gaffney *et al.*, 2006).

47. Quadrate, medial process reaches braincase: (0) absent ; (1) present. (Gaffney *et al.*, 2011).

48. Quadrate, ventral projection: (0) very short, condylus mandibularis very close to the cavum tympani region; (1) short, condylus mandibularis slightly separated from the cavum tympani region; (2) long, condylus mandibularis considerably separated from the cavum tympani region. (Cadena *et al.*, 2010).

49. Quadrate, condylus mandibularis shape: (0) much wider than long, with anterior and posterior edges straight to concave making it shorter at midline ; (1) slightly wider than long, kidney shaped, with anterior edge straight to concave and posterior edge convex. (Cadena *et al.*, 2010).

50. Quadratojugal: (0) absent; (1) present. (Gaffney *et al.*, 2006).

51. Pterygoid, cavum pterygoidei: (0) absent ; (1) partial ; (2) complete. (Gaffney *et al.*, 2011).

52. Pterygoid, anterior opening of cavum pterygoidei: (0) absent; (1) small opening; (2) moderate opening; (3) large opening with foramen cavernosum inroof. (Gaffney *et al.*, 2011).

53. Pterygoid flange around cavum pterygoidei: (0) absent or very small; (1) partial; (2) complete. (Gaffney *et al.*, 2011).

54. Pterygoid, processus trochlearis pterygoidei: (0) absent; (1) oblique; (2) right angle. (Gaffney *et al*., 2011).

55. Supraoccipital, on roof exposure: (0) absent or slight; (1) present, small; (2) present, very large. (Gaffney *et al*., 2011).

56. Supraoccipital, horizontal plate along ventral edge of cristasupraoccipitalis: (0) absent ; (1) present. (Gaffney *et al*., 2011).

57. Supraoccipital, crista supraoccipitalis: (0) very short to absent; (1) long, ventrally wider with uniform width from the anteriorto the posterior aspect, ending in an acute tip in dorsal view; (2) short, wider posteroventrally than anteroventrally, ending in a bulbous shape in dorsal view. (Cadena *et al*., 2010).

58. Exoccipital, occipital condyle: (0) basioccipitals plus exoccipitals; (1) exoccipitals only. (Gaffney *et al*., 2011).

59. Exoccipital, foramen jugulare posterius: (0) closed partially; (1) closed completely. (Gaffney *et al*., 2011).

60. Exoccipital, foramen nervi hypoglossi: (0) separated; (1) combined and recessed. (Gaffney *et al*., 2011).

61. Exoccipital-quadrate contact: (0) absent ; (1) extensive ; (2) narrow. (Cadena *et al*., 2010).

62. Basioccipital very short: (0) no ; (1) yes. (Gaffney *et al*., 2011).

63. Basiocipital tubera width: (0) closer to median; (1) farther from median. (Gaffney *et al*., 2011).

64. Basioccipital, horizontal occipital shelf: (0) absent; (1) present. (Gaffney *et al*., 2011).

65. Basioccipital-opisthotic contact: (0) present ; (1) absent. (Gaffney *et al*., 2006).

66. Prootic, ventral exposure: (0) completely exposed; (1) at least partially covered. (Gaffney *et al*., 2011).

67. Prootic, pterygoid covers prootic: (0) no ; (1) at least in part. (Gaffney *et al.*, 2011).

68. Prootic, foramen posterius canalis carotici interni: (0) in prootic ; (1) in basisphenoid within cavum pterygoidei; (2) variably in pterygoid, quadrate, basisphenoid ; (3) pterygoid and basisphenoid. (Gaffney *et al*., 2011).

69. Prootic-quadrate contact: (0) present ; (1) absent. (Gaffney *et al*., 2006).

70. Opisthotic, processus interfenestralis ventral exposure: (0) exposed ; (1) covered. (Gaffney *et al*., 2011).

71. Opisthotic, fenestra postotica: (0) open; (1) at least partially closed. (Gaffney *et al*., 2011).

72. Opisthotic, processus paroccipitalis: (0) small and flat, does not project beyond the squamosal ; (1) narrow medially and elongated, projects beyond the squamosal ending in a prominent tip. (Cadena *et al*., 2010).

73. Basisphenoid, foramen nervi abducentis: (0) small; (1) moderate to large. (Gaffney *et al*., 2011).

74. Basisphenoid-quadrate contact: (0) present; (1) absent. (Gaffney *et al*., 2011).

75. Dentary, symphyseal contact: (0) fused; (1) sutured. (Gaffney *et al*., 2011).

76. Dentary, internal angle between rami: (0) acute, between 40 and 90 degrees; (1) obtuse, over 90 degrees; (2) very acute, less than 40 degrees. (Cadena *et al*., 2010).

77. Dentary, accessory ridges: (0) absent; (1) present. (Gaffney & Forster, 2003)

78. Dentary, narrow and elongated ridge, located in the medial margin on the ventral surface: (0) absent; (1) present. (Cadena *et al*., 2010).

79. Articular, processus retroarticularis: (0) very short ; (1) short, projected posteriorly ; (2) short, projected ventrally ; (3) long, projected posteriorly. (Cadena *et al*., 2010).

80. Articular, chorda tympani enclosed in processus retroarticularis: (0) no ; (1) yes. (Gaffney *et al*., 2011).

81. Coronoid, wide lateral exposure (Gaffney *et al*, 2006): (0) absent ; (1) present. (Gaffney *et al*., 2006).

82. Surangular, well-extended anteriorly: (0) absent ; (1) present. (Gaffney *et al*., 2006).

83. Splenial: (0) present ; (1) absent. (Gaffney *et al*., 2011).

84. Vertebrae, cervical centra saddle shaped: (0) absent, procoelous; (1) completely heterocoelic as in Podocnemis; (2) wide as in Erymnochelys. (Gaffney *et al*., 2011).

85. Vertebrae, second cervical biconvex: (0) no; (1) yes. (Gaffney *et al*., 2011).

86. Vertebrae, cervical zygapophyses: (0) none fused; (1) some fused. (Gaffney *et al*., 2011).

87. Vertebrae (cervical), Ventral keel at the posterior condyle: (0) protuberant ; (1) reduced almost absent. (Broin, 2000).

88. Carapace, cervical scale: (0) present ; (1) absent. (Gaffney *et al*., 2006).

89. Carapace, nuchal bone width: (0) width 2 or more times length ; (1) width greater than length but less than 2 times; (2) width equals length; (3) width less than length; (4) nuchal retracted, not contacting peripheral bones (Araripemys condition). (Gaffney *et al*., 2011).

90. Carapace, neural series extent: (0) to suprapygal; (1) to costals 8; (2) to costals 7; (3) to costals 6; (4) neurals discontinuous or absent. (Gaffney *et al*., 2011).

91. Carapace, neural number: (0) 8 or more; (1) 7; (2) 6; (3) 5 or fewer. (Gaffney *et al*., 2011).

92. Carapace, keeled neurals: (0) none; (1) some. (Gaffney *et al*., 2011).

93. Carapace, four-sided neural: (0) first neural; (1) second neural; (2) third neural; (3) neurals absent or discontinuous; (4) four-sided neural absent, neurals. (Gaffney *et al*., 2011).

94. Carapace, costal two anterior edge thickened near buttress: (0) no; (1) yes. (Gaffney *et al*., 2011).

95. Carapace, axillary buttress: (0) reaches peripheral 3; (1) reaches peripheral 2. (Gaffney *et al*., 2011).

96. Carapace, Neural 2: (0) present but not contacting costal 1; (1) present and contacting costal 1; (2) absent. (França & Langer, 2006).

97. Carapace, Lateral thickness of the shell: (0) less or equal to 20 mm; (1) more than 20 mm. (França & Langer, 2006).

98. Carapace, medial embayment on contact between vertebrals 3 and 4: (0) cranial; (1) caudal ; (2) absent. Character modified from Aquentin (2012).

99. Carapace, shell nuchal embayment: (0) absent UFAC-1000; (1) small Podocnemis expansa; (2) large Stupendemys. (Gaffney *et al*., 2006).

100. Carapace, peripheral 6 exterior edge: (0) medially inclined towards cranial edge; (1) almost parallel to cranio-caudal axis; (2) medially inclined towards caudal edge. (New character).

101. Carapace, last neural connects to: (0) 2 pairs of costals; (1) 3 pairs of costals; (2) 1 pair of costals. (New character).

102. Carapace, first vertebral scute width: (0) about the same width as vertebral 2; (1) larger than vertebral 2; (2) smaller than vertebral 2. (New character).

103. Carapace, second vertebral scute shape.: (0) quadrangular; (1) hexagonal; (2) vase; (3) trapezoidal. (New character).

104. Carapace, first marginal scute shape: (0) trapezoidal; (1) rectangular; (2) triangular. (New character).

105. Carapace, supra-pygal - peripheral 11 contact: (0) large; (1) small. (New character).

106. Carapace, pygal shape: (0) rectangular; (1) trapezoidal. (New character).

107. Carapace, vertebral scutes 2 to 4 longer than wide: (0) no; (1) yes. (New character)

108. Plastron, axillary musk duct (1): (0) in buttress; (1) absent in buttress. (Gaffney *et al*., 2011).

109. Plastron, axillary musk duct (2): (0) not in bridge; (1) one opening in bridge; (2) three in bridge; (3) four in bridge. (Gaffney *et al*., 2011).

110. Plastron, mesoplastra: (0) absent ; (1) small and lateral. (Gaffney *et al*., 2011).

111. Plastron, pectoral scales contact mesoplastra: (0) yes ; (1) no. (Gaffney *et al*., 2011).

112. Plastron, pectoral scales contact entoplastron: (0) no; (1) yes. (Gaffney *et al*., 2011).

113. Plastron, pectoral scales contact epiplastra: (0) no ; (1) yes. (Gaffney *et al*., 2011).

114. Plastron, Plastral bridge: (0) short; (1) elongated. (De la Fuente, 2003).

115. Plastron, Intergular scale: (0) medium, covering the cranial margin of entoplastron, separating only the gulars ; (1) small, restricted between the gulars, lacking contact with entoplastron ; (2) large, separating the gulars and the humerals. Character modified from Gaffney *et al*., (2006).

116. Plastron, epiplastra exterior outline: (0) smooth curve; (1) angular; (2) straight line. (New character).

117. Plastron, entoplastra shape: (0) cranial and caudal portions about the same length. (diamond shaped); (1) caudal part smaller; (2) caudal part longer, projecting caudally; (3) pentagonal. (New character).

118. Plastron, caudal lobe lateral outline: (0) almost straight lined; (1) smoothly curved; (2) sinuous. (New character).

119. Plastron, plastral bridge height very short: (0) no; (1) yes. (New character).

120. Plastron, gular scales reach entoplastra: (0) yes; (1) no. (New character).

121. Coracoid, shape: (0) slightly curved longitudinally and much wider distally ; (1) narrow, almost straight longitudinally and slightly wider distally. (Cadena *et al*, 2010).

122. Coracoid, dorsal longitudinal ridge: (0) absent ; (1) present. (França & Langer, 2006).

Appendix 2: Data matrix

Chelidae
000(01)000(01)00 2000003000 0001000000 1000000000 0020201000 0001100010
0000000000 0000(01)00000 00000000(012)(024) (0123)0(023)0(01)00(012)01
0100000??0 ?1100012?1 00

Pelomedusidae
1111000100 1010001010 1002200000 0010(01)00000 0020201001 0001000110
0001000000 0000(01)00000 00101001(12)(12) (0123)00000001(01) ?0(12)???(01)??1
0001?????? 00

Araripemys barretoi
1111000100 100?001010 1000000000 0010000000 0020001001 00010000(01)0
0000100000 0000100000 1010110140 0030010020 2222010??0 ?000?2?0?? ??

Euraxemydidae
1111000110 000?0010(01)0 0000000000 0000000000 0010001001 0001100000
2000110301 1(01)00100001 0010110110 0000000?01 0??010???1 00010000?1 ??

Bothremydidae
11(12)(012)000(01)(01)0 0(01)000(01)00(01)0 0(01)00000000 0000(01)00(01)00
0(01)(02)0111001 000(12)000(01)00 1010110211 10010(01)(01)03(01)
0(01)101(01)01(012)(023) (123)0(014)00(01)0(02)(01)(01) (01)011(01)(01)0??1
0(01)0(01)0(01)0(01)01 00

Podocnemis negrii
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????2 11?1?101?0 0?1?111??? 111?001??1 ??

Podocnemis expansa
1111101122 0020101011 0011110001 1110100000 0110211011 2222111010
0011011111 1111001020 0111101112 1001110010 0020111111 1111001211 11

Podocnemis unifilis
1111101120 0020101010 0010110001 1110100000 0120211011 2122111010
0011011111 1111001020 0111101112 1101110010 0020011121 111100?01? 11

Podocnemis erythrocephala
1111101120 0010101011 1010110001 0110100000 0120211011 2222111010
0011011111 1111001020 0111101122 100?110211 ?011??0021 111100?11? 11

Podocnemis sextuberculata
1111101122 0020101011 1011110001 0110100000 0110211011 2222111010
0011011111 1111001020 0111101112 1101110010 ?210??1121 111100?01? 11

Podocnemis lewyana
1111101122 0020101011 0010110001 0110100000 0120211011 2122111010

0011011111 1111001020 0111101102 1001110010 ?020??1?31 111100?21? 11

Podocnemis vogli
1111101120 0010101011 0010110001 0100100000 0120211011 2122111010
0011011111 1111001020 0111101112 1001010010 ?020??1131 111100?01? 11

Portezueloemys patagonica
?1?1?0??(12)? 00?????01? ??0???00?? ??000???0? ???0?11??1 1112?????? ?00?0111?1
11?1?????? ???????1?2 204??(01)00?1 123???0??1 1101000?0? ??

Brasilemys josai
?111000000 00??0??010 ??0??00000 0??000?000 ?010011001 11110?0?00 0000010011
11?10?0011 01?0?0?121 204??0020? 1101?????? ?????????? ??

Hamadachelys escuilliei
1111000110 0020001010 ?00??00000 000000?000 0120211001 111200?000 0001011111
110100001? 011??????? ?????????? ?????????? ?????????? ??

Bauruemys elegans
1112000110 0010001010 0000100000 0000100000 0120211001 2122101000
0001011111 1101?00010 0110?00122 2011000001 1101010??1 11111010?0 00

Pricemys caiera
???1?????? 0?3??02??? ?????00000 ???010??0? ?110211??? 212211?010 ?011?111?1
1?11?????? ?????????? ?????????? ?????????? ?????????? ??

Peiropemys mezzalirai
1??100??20 0?1?0020?0 00???00000 0?0010?00? ?120211??? 212211?110 ?011?111?1
1??1?????? ?????????? ?????????? ?????????? ?????????? ??

Lapparentemys vilavilensis
1??100??20 0?1?0020?0 00???00000 0?0010?00? ?110211??? 2122?1?010 ?01??111?1
1?010???(12)0 ???1?0?112 100?01?101 1001000??1 0???1000?1 ??

Turkanemys pattersoni
1??000??2? 0?1?0000?0 10???10001 0?101??00? ?110211??? 2?220??010 ?011??11?1
???10???(12)1 ??1210?113 200?110011 0021010??1 1111(01)0(03)100 ??

Erymnochelys madagascariensis
1120000020 0120010010 1000110001 0110100000 0120211011 2322001010
0010011111 1101000011 0112100113 2001110001 00210?0001 11111001?0 10

Peltocephalus dumerilianus
1120000020 0140010010 1102210001 0110100000 0110211011 2322001(01)10
0010011111 1101000011 0111100112 1001010211 0010010001 110100(03)001 10

Neochelys
1120(01)00021 0110000010 1000110000 0010100000 0110211001 232201(01)010
0010011111 11?1000011 01????11(23) (12)00?0(01)?001 00200(01)0??1

(01)111(12)(01)0(01)?0 ??

Papoulemys laurenti
1??000??2? 0?1?0000?0 ?0???10000 0??01??00? ?110211??? 2?2201?110 ?010?111?1
1??1?????? ?????????? ?????????? ?????????? ?????????? ??

Dacquemys paleomorpha
112000002? 3111000000 0002210001 111010?000 0110211001 2?22211010
0011011111 1101?????? ?????????? ?????????? ?????????? ?????????? ??

UCMP 42008
1??000??2? 3???010??0 ?0???10001 ???010?00? ???0211??? 2?222??0?0 ?0???11??1
1??1?????? ?????????? ?????????? ?????????? ?????????? ??

Mogharemys blanckenhorni
???000???1 ?????????0 ?????100?1 ???010100? ?100211??? 2322???011 ?010?111?1
1??1?????? ?????????? ?????????? ?????????? ?????????? ??

Brontochelys gaffneyi
1??000???1 ?????????? ?????20010 0?1220?10? ?????11??? 2322????11 ?010?111?1
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Lemurchelys diasphax
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1??1?????? ?????????? ?????????? ?????????? ?????????? ??

Shweboemys pilgrimi
11200000(12)1 ?1?00??010 1100021010 0011211?11 1???11101 2?22????11
011?011?1? ?1???????? ?????????? ?????????? ?????????? ?????????? ??

Stereogenys
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11010???(12)1 ???????111 1?3??1?220 0211000??1 11112121?1 ??

Latentemys plowdeni
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1?01?????? ?????????? ?????????? ?????????? ?????????? ??

Cordichelys antiqua
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1??1?????? ???????113 200??1?222 0100010??1 111?1010?0 ??

Bairdemys hartsteini
1120010021 013000?110 100??20100 0?1220?101 ?201211201 23220?2011 0010011111
10?1?????? ???1?????? ?????????? ?????????? ?????????? ??

Bairdemys venezuelensis
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0010011111 10?101?0(12)? ????????14 3031120?00 ????01???1 1111?000?? ??

Bairdemys sanchezi
1120010021 0???001110 100??20000 0??220?101 ?201211201 2??201?010 ?0??0???1?
?0???10?2? 01???????? ?????????? ?????????? ????0????1 ??

Bairdemys winklerae
112000002? 01???01110 120??20?00 0??22???01 ??01211201 2??2??2??? 0010011?11
?0???10?1? 01???????? ?????????? ?????????? ?????????? ??

Stupendemys geographicus
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ???1???110 100??1?02? 010??11??1 1????????? ??

Kenyemys williamsi
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?????????? ???????122 210?010111 1000010??1 1111110100 ??

Cerrejonemys wayuunaiki
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?1??02012? 01?1??111? ??0?011?0? ?011??0??1 1????????? 11

Podocnemis bassleri
11111?11(12)? ?0?01???1? ??1???0??? ??0??????0 ??2021?011 2?2???10?? 0???0???1?
?1???????? ?????????? ?????????? ?????????? ?????????? ??

Podocnemis manchineri
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?????????? ???????112 100001000? 0121011??1 1111001010 ??

Caninemys tridentata
111100002? 0220000010 0000110001 0100100000 0200211001 2?22?1?010
0011011111 11?1?????? ?????????? ?????????? ?????????? ?????????? ??

Podocnemis pritchardi
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ???????113 2?0??1?000 0120011??1 1111001211 ??

Podocnemis medemi
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????

?????????? ???????11? ??0??1??0? ?121??1??1 11110001?1 ??

Tables

Table 1. Comparison among *P. manchineri* and other large sized fossil Podocnemidae.

Taxon	Neural number	Shorter caudal portion of entoplastra	Plastron lobes short and rounded	Carapace bones very thick	Vase shaped vertebral scutes	Gular scales reach entoplastra
P. manchineri	7	yes	no	no	yes	yes
P. medemi	?	no	yes	no	yes	no
P. pritchardi	6	yes	no	no	yes	no
S. geographicus	7	?	?	no	no	?
C. wayuunaiki	?	?	?	yes	no	?

Table 2. Postcranial characters of the genus *Podocnemis*, according to Gaffney *et al.* (2011), preserved in *P. manchineri*. *The paper says costal 8, but is actually costal 7 in all *Podocnemis* species.

Taxon	Nuchal bone wider than long	Seven neurals reaching costal 7*	Axillary buttress reaching peripheral 2	Pectoral scales reach mesoplastra	Pectoral scales reach entoplastra and epiplastra
P. manchineri	yes	yes	no	no	yes
P. expansa	yes	yes	yes	no	yes
P. unifilis	yes	yes	yes	no	yes
P. lewyana	yes	yes	yes	no	yes
P. erythrocephala	yes	yes	yes	no	yes
P. sextuberculata	yes	yes	yes	no	yes
P. vogli	yes	yes	no	no	yes

Table 3. Measurements of nuchal, neural bones, and vertebral scutes for UFAC-1000 and UFAC-1559 specimens. Asterisk indicates an estimated measure.

Bone/Scute	UFAC-1000		UFAC-1559	
	Length (mm)	Width (mm)	Length (mm)	Width (mm)
Nuchal	205	210	-	-
Neural 1	151	82	-	-
Neural 2	92	96	90	86
Neural 3	100	88	99	92
Neural 4	91	83	86	83*
Neural 5	89	85	-	-
Neural 6	65	77	-	-
Neural 7	56	70	-	-
Vertebral 1	224	260	199	242*
Vertebral 2	193	188	-	-
Vertebral 3	188	150	-	-
Vertebral 4	210	152	-	-
Vertebral 5	225	325	-	-

Table 4. Measurements of podocnemid fossil neural bones from the UFAC collection. Asterisk indicates an estimated measure. N2, N3, and N4 stands for neural 2, 3, and 4 respectively.

Specimen number	Midline length (mm)	Maximum width (mm)	Thickness (mm)
UFAC-1559 N2	90	86	17
UFAC-1559 N3	99	92	15
UFAC-1559 N4	86	83*	14
UFAC-637	91	70	25
UFAC-860	49	46	10
UFAC-884	71	60*	15
UFAC-915	180*	100	17
UFAC-917	72	61	17
UFAC-929	60	52	13
UFAC-933	83	76	13

Table 5. Measurements of podocnemid fossil and recent neural bones from the UFAC collection. Asterisk indicates an estimated measure. R represents recent species (*P. expansa* and *P. unifilis*).

Specimen number	Anterior width (mm)	Thickness (mm)
R-061	54	8.4
R-084	57	6.3
R-190	27	4.9
UFAC-1000	120	23
UFAC-1947	9	1.1
UFAC-1948	17	2.4
UFAC-2127	21	2.5
UFAC-2307	23	2.7
UFAC-603	77	15
UFAC-901	88	31

Figures

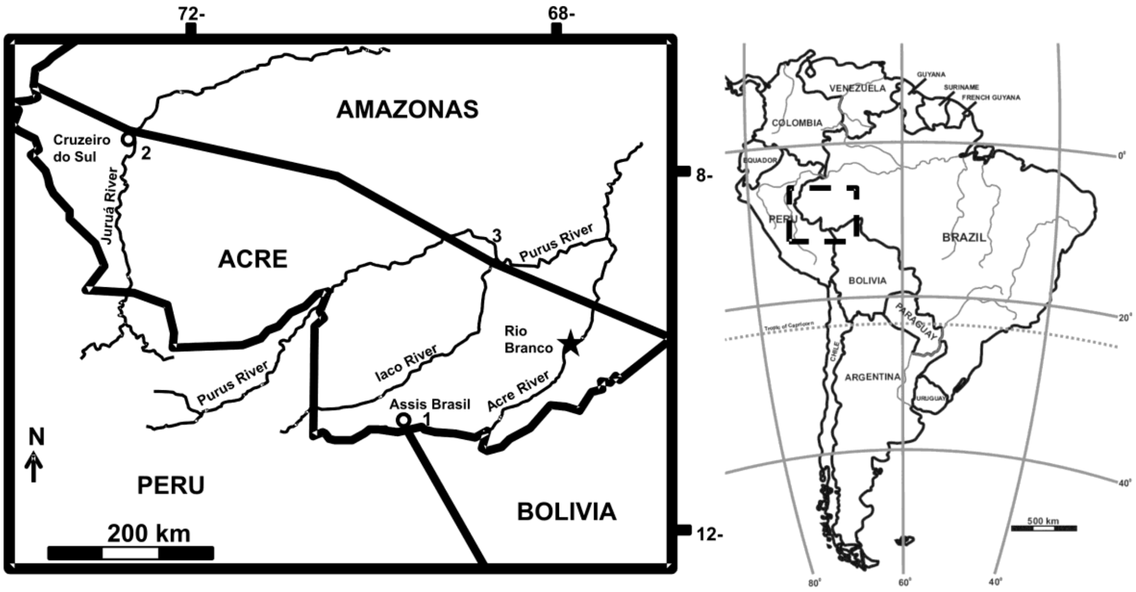

Figure 1. Location map showing *P. manchineri* findings. **1,** UFAC-1000; **2,** UFAC-1001; **3,** UFAC-1559. Modified from Hsiou (2010).

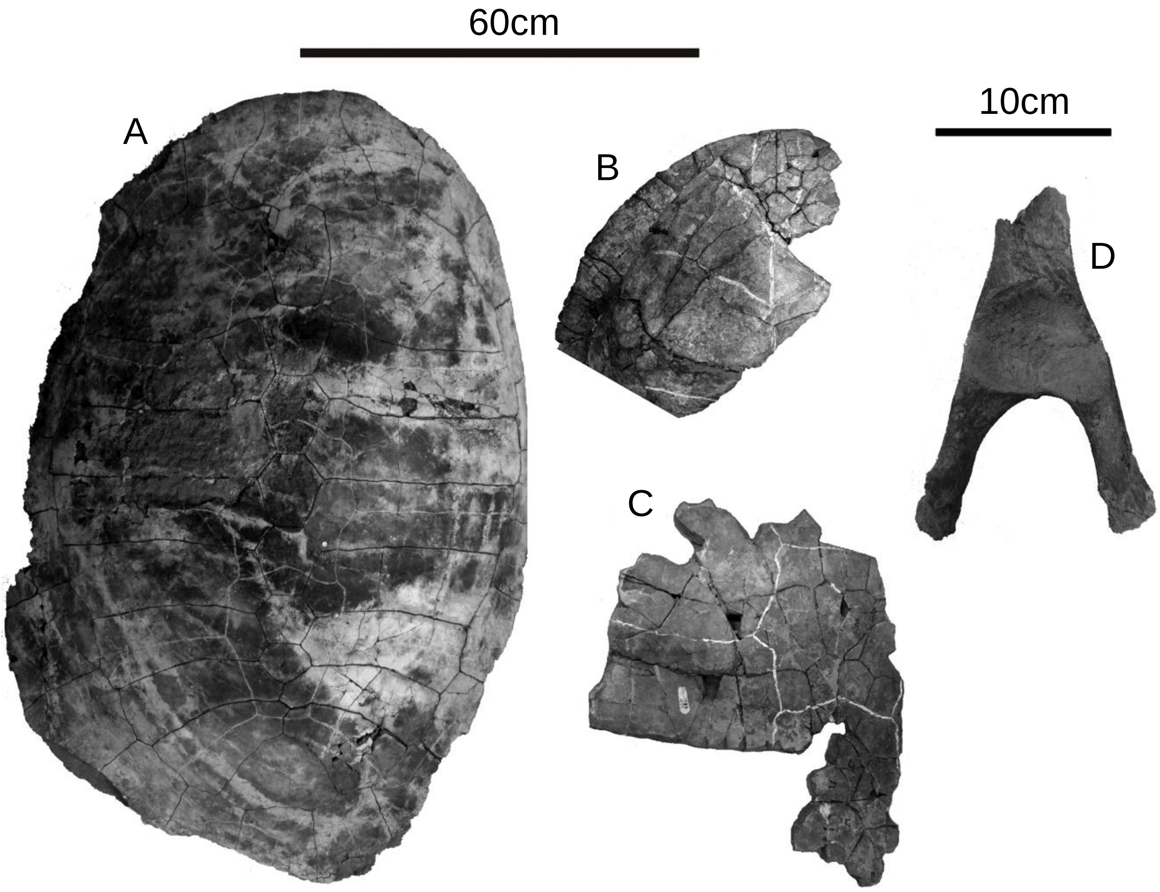

Figure 2. *Podocnemis manchineri*, holotype and referred materials. **A,** UFAC-1000 in dorsal view**; B,** UFAC-1001 in ventral view**; C,** UFAC-1559 in dorsal view**; D,** UFAC-1000 right pelvic girdle in lateral view.

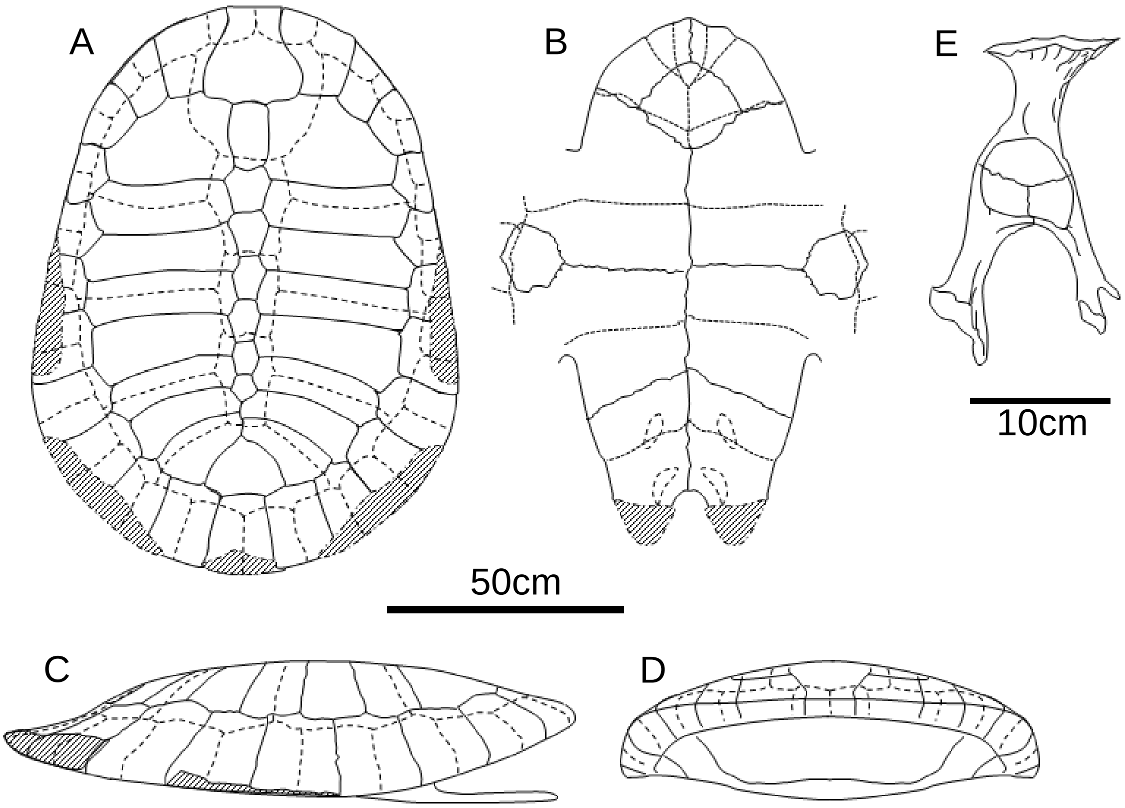

Figure 3. *Podocnemis manchineri* reconstruction. Based on UFAC-1000 and UFAC-1001. **A,** shell in dorsal view**; B,** plastron in ventral view**; C,** shell in lateral view**; D,** shell in frontal view**; E,** right pelvic girdle in lateral view. **B** and **E** modified from Rancy & Bocquentin-Villanueva (1987). Striped areas are inferred from the probable shell outline and comparison with other *Podocnemis* species.

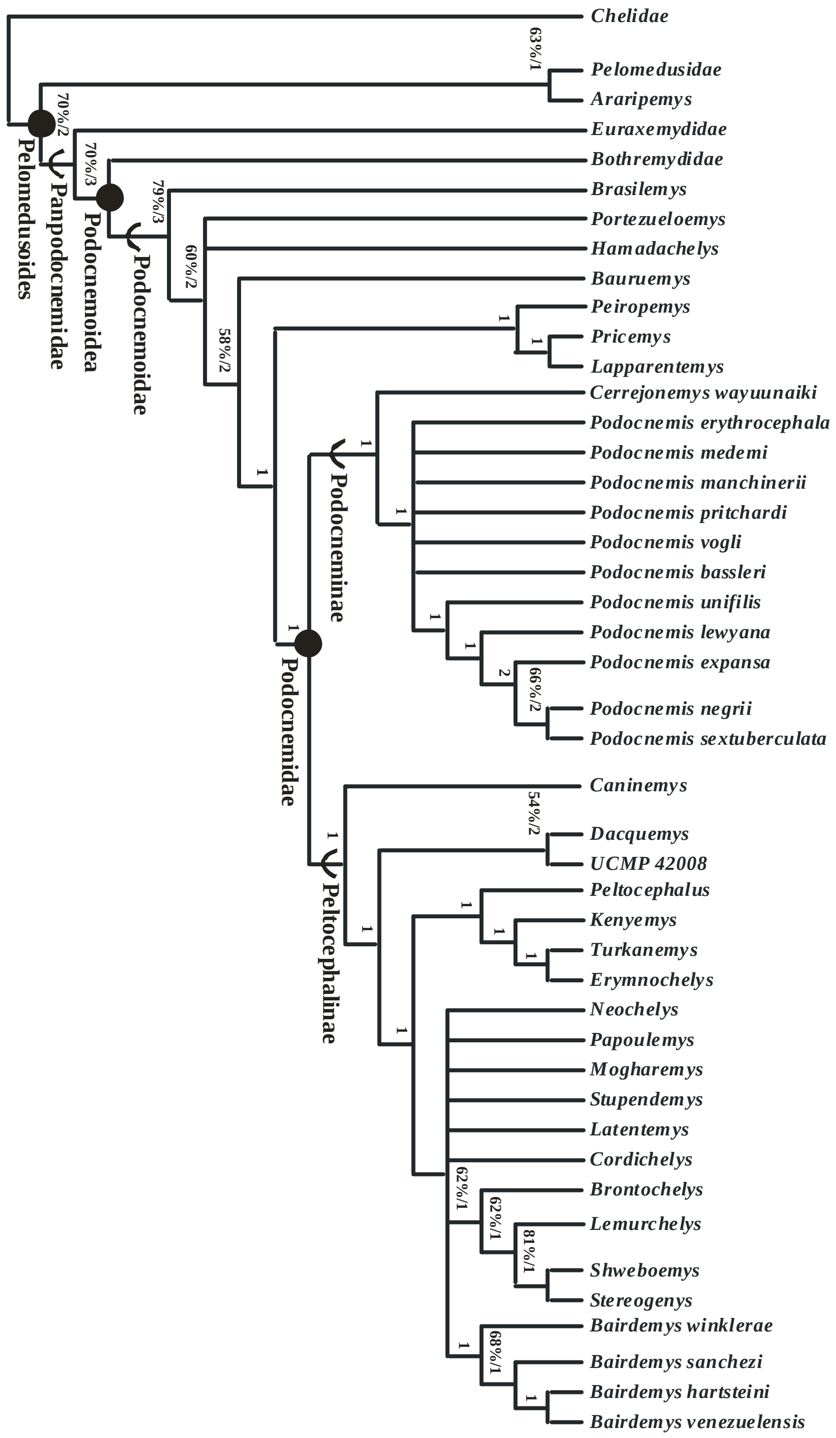

Figure 4. Strict consensus of 134 most parsimonious trees (45 taxa and 122 characters) depicting the phylogenetic position of *Podocnemis manchineri* and the phylogenetic relationships within Podocnemidae. Numbers associated to certain clades refer to bootstrap and Bremer support values.

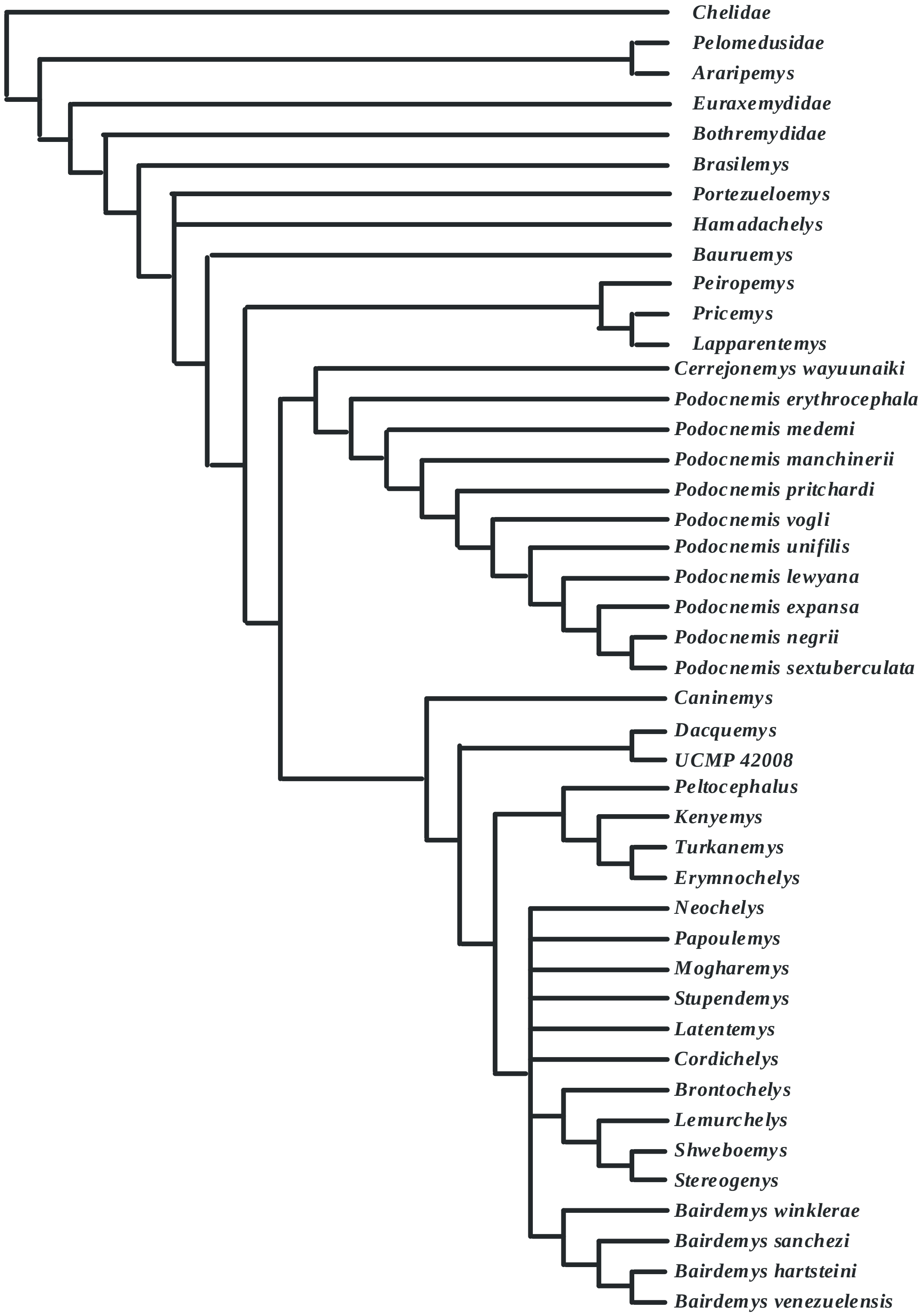

Figure 5. Strict consensus of 12 most parsimonious trees (44 taxa and 122 characters) depicting the phylogenetic position of *Podocnemis manchineri* and the phylogenetic relationships within Podocnemidae after the exclusion of the skull based taxon *Podocnemis bassleri*.

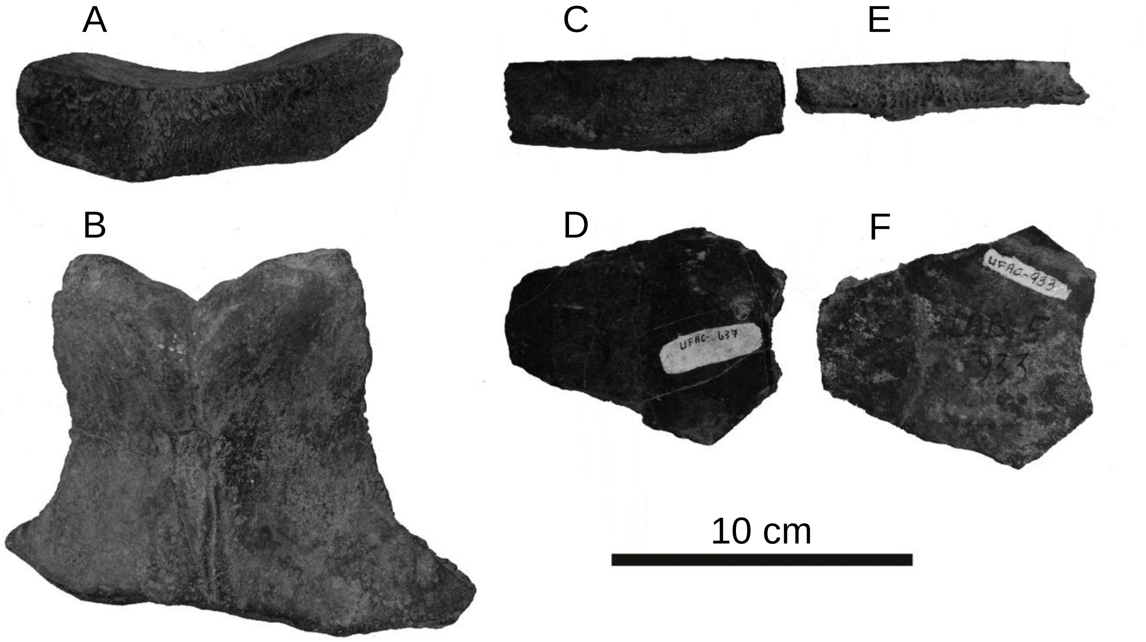

Figure 6. Possible podocnemid taxa with thick shell bones. **A, B,** UFAC-901 in lateral and dorsal views; **C, D,** UFAC-637 in lateral and dorsal views. Thinner podocnemid neural bone with comparable proportions. **E, F,** UFAC-933 in lateral and dorsal views.

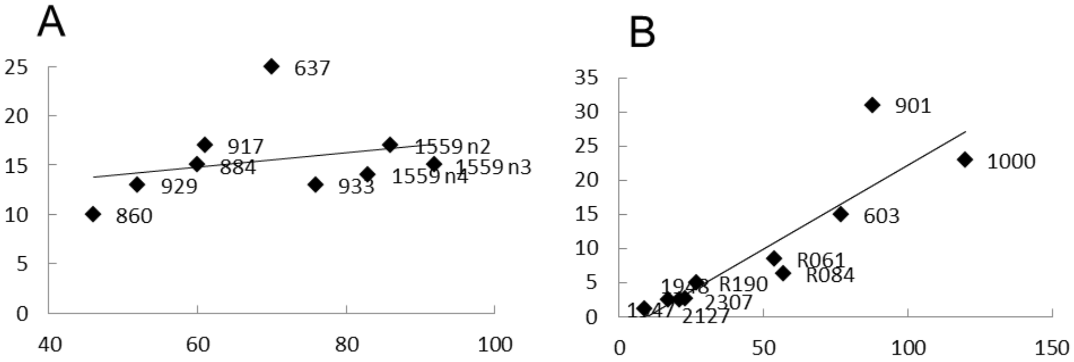

Figure 7. A, maximum width versus thickness of fossil neural bones. **B,** anterior width versus thickness of fossil and recent nuchal bones. Numbers refers to the specimen catalogue number from the UFAC collection, n2= neural 2, n3= neural 3, n4= neural 4.

R represents recent species (*P. expansa* and *P. unifilis*). All measurements in millimetres.

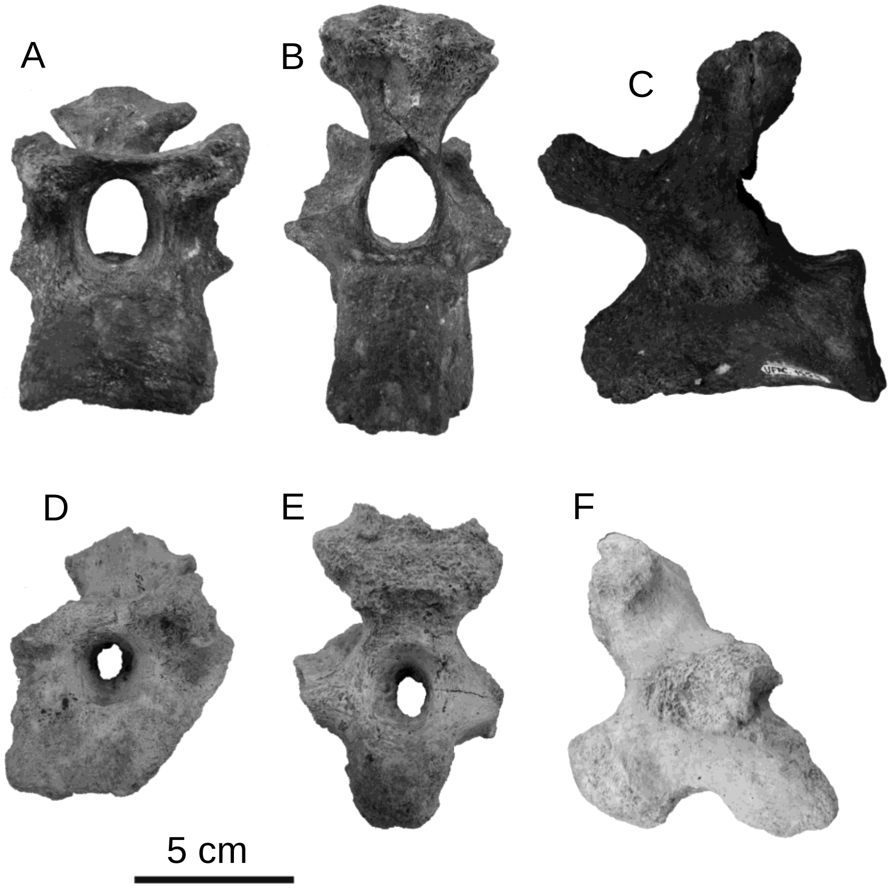

Figure 8. "*Stupendemys" souzai* vertebrae. **A-C,** UFAC-1553 in anterior, posterior, and left lateral views, respectively**; D-E,** UFAC-5275 in anterior, posterior, and right lateral views, respectively.

4. Conclusões

Um novo podocnemídeo, *Podocnemis manchineri*, da Formação Solimões é descrito. Ela se distingue de outras *Podocnemis* pela associação das características a seguir: escudos vertebrais em forma de vaso, especialmente o vertebral dois; vertebral um significantemente maior que outros escudos vertebrais; margem cranial da carapaça arredondada, sem nenhum tipo de reentrância; e escudos gulares alcançando o entoplastrão.

Aqui pudemos diferenciá-la de todas as outras espécies com partes coincidentes, assim como incluir *P. manchineri* e vários outros táxons baseados em carapaças em uma análise filogenética. Além disso, é bem provável que um terceiro táxon de podocnemídeo de grande porte tenha vivido no Mioceno-Plioceno da Amazônia Sul-ocidental.

Nós também concluímos que a presença de espécies fósseis entre a associação comum de *Peltocephalus* e *Erymnochelys* mostrada aqui poderia ajudar a explicar as relações e história biogeográfica desses táxons viventes.

Nós também provemos uma definição filogenética para as subfamílias Erymnochelyinae e Podocneminae, sendo que renomeamos Erymnochelyinae como Peltocephalinae. Devido às diferenças entre os dados morfológicos e moleculares. Os dados morfológicos provêm uma divisão clara entre a família Podocnemidae, onde o táxon *Erymnochelys madagascariensis* é mais relacionado à *Peltocephalus dumeriliana* do que a *Podocnemis expansa*. Entretanto os dados moleculares mostram uma relação mais próxima entre *E. madagascariensis* e *P. expansa*. Isso deixaria *P. dumeriliana* em uma terceira subfamília, não suportada pelos dados morfológicos. Sendo assim, preferimos aqui utilizar *P. dumeriliana* como a espécie tipo da subfamília. Desta forma, Peltocephalinae é o clado “stem-based” definido como todos os Podocnemidae mais relacionados à *Peltocephalus dumerilianus* do que à *Podocnemis expansa* e Podocneminae é o clado “stem-based” definido como todos os Podocnemidae mais relacionados à *Podocnemis expansa* do que à *Peltocephalus dumerilianus.*

Após a inclusão de novos caracteres referentes à carapaça e o plastrão na matriz de dados e de acordo com nossa análise, nós concluímos que embora a morfologia do casco dos Podocnemidae seja geralmente referida como conservativa ela pode prover informações filogenéticas importantes. Nossa análise filogenética suporta a inclusão de

P. negrii, *P. medemi*, e *P. pritchardi* ao gênero *Podocnemis*. A análise também proveu uma ideia melhor da posição de *Stupendemys geographicus*, como membro de Erymnochelyinae. Além disso, um dos principais táxons problemáticos em várias análises filogenéticas, *P. bassleri*, conhecida apenas por material do crânio é também recuperada como uma *Podocnemis*. De maneira interessante, em contraste com outras análises filogenéticas baseadas em caracteres morfológicos, a resolução da análise dentro de *Podocnemis* caiu com a inclusão de *P. bassleri*, enquanto a análise com os táxons fósseis baseados na carapaça resultaram em uma topologia mais resolvida. Já que incluímos caracteres da carapaça e plastrão na análise, isso pode sugerir que eles podem ser tão importantes quanto os caracteres cranianos em estudos cladísticos a respeito de podocnemídeos.

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6. Tabelas e figuras

Tabela 6. Comparação entre o uso de caracteres do crânio e mandíbula e pós cranianos em trabalhos recentes.

Trabalho	Caracteres		
	Crânio e mandíbula	Pós crânio	Pós crânio %
França & Langer (2006)	20	12	37,5
Meylan *et al*. (2009)	50	13	20,6
Cadena *et al*. (2010)	40	13	24,5
Gaffney *et al*. (2011)	57	17	23,0
Cadena *et al*. (2012)	36	10	21,7

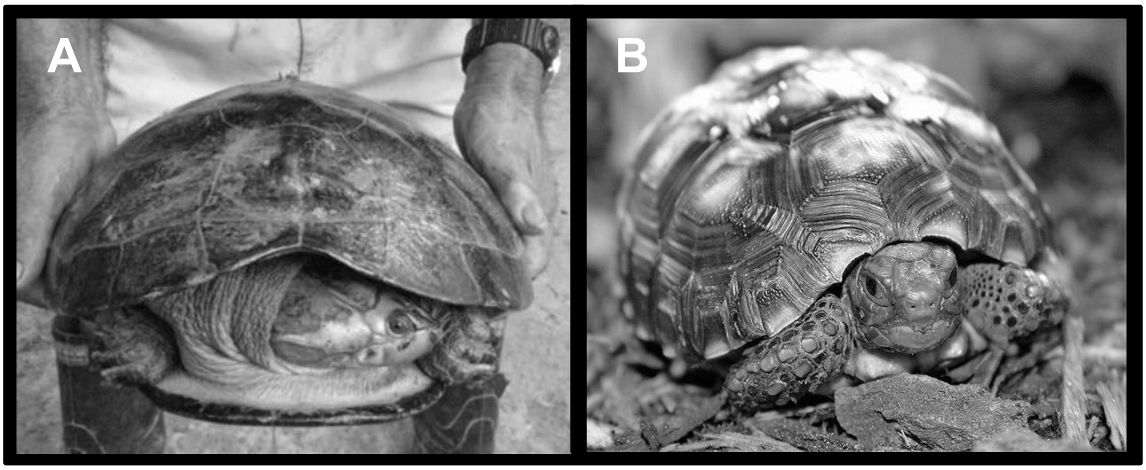

Figura 9. Modo de retração da cabeça de A – Pleurodira (*Podocnemis unifilis*), lateralmente e B – Cryptodira (*Geochelone carbonaria*), encaixe da cabeça entre os ombros. Fonte das imagens: A - http://www.fundacionbiodiversa.org B - http://paoeecologia.wordpress.com acessados em 21/01/2011.

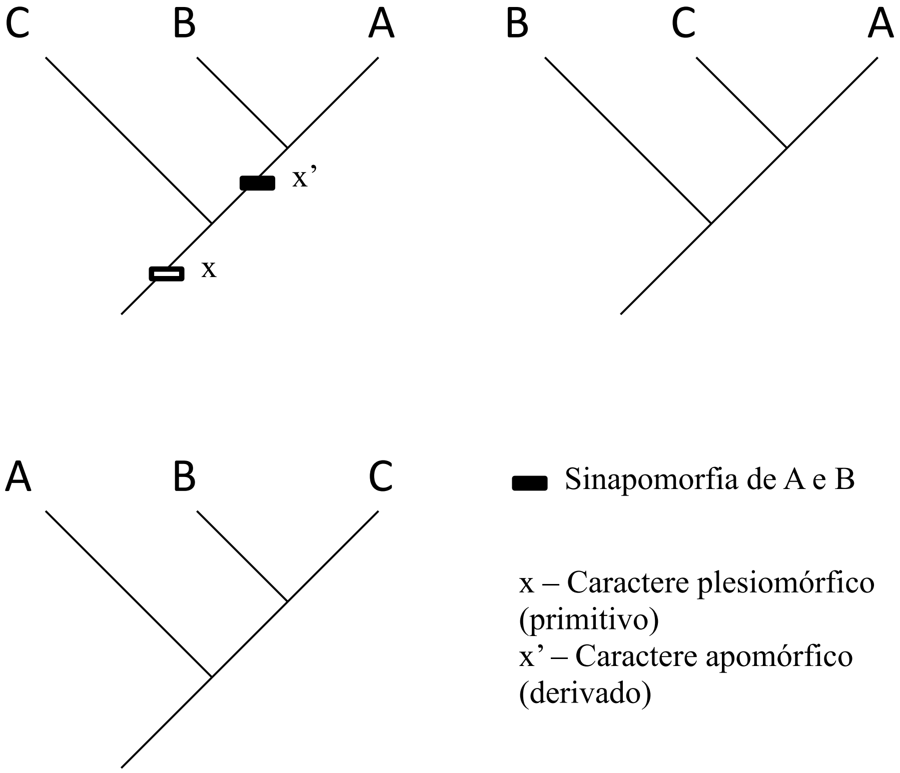

Figura 10. Possíveis relações entre os táxons A, B e C. (Baseado em Hennig, 1987)