

PHYLOGENETIC RELATIONSHIPS OF THE BAURU GROUP TURTLES (LATE CRETACEOUS OF SOUTH-CENTRAL BRAZIL)

MARCO AURÉLIO GALLO DE FRANÇA & MAX CARDOSO LANGER

Laboratório de Paleontologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes, 3900, Ribeirão Preto, 1414040-901, Brasil. marquinhobio@yahoo.com.br; mclanger@ffclrp.usp.br

ABSTRACT – No chelonian of the Bauru Group (Late Cretaceous of south-central Brazil) has so far been included in a numerical cladistic analysis with an explicit taxon-character data matrix. Out of the five taxa formally described from that stratigraphic unit, those based on more complete specimens - *Bauruemys elegans*, *Cambaremys langertoni*, and *Roxochelys wanderleyi* – were considered in a cladistic study of the pro-Podocnemidae Pelomedusoides. The resulting hypothesis of relationships places the specimen known as FR-4922 and *Brasilemys josai* among Pelomedusoides basal to Podocnemoidea. Within that clade, the Bauru Group taxa lie basal to Podocnemidae. *Roxochelys* is revealed to be a monophyletic genus, closer to Podocnemidae than the other analyzed Cretaceous forms. Among these, *Bauruemys elegans* is more derived than *Portezueloemys patagonica*, while the position of *Cambaremys langertoni* is ambiguous. Within extant Podocnemidae, a sister group relationship between *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis* is proposed.

Key Words: Podocnemidae, *Bauruemys elegans*, *Cambaremys langertoni*, *Roxochelys wanderleyi*, Bauru Group, Late Cretaceous.

RESUMO – Nenhum quelônio do Grupo Bauru (Cretáceo Superior do centro-sul do Brasil) teve, até o presente momento, sua posição filogenética determinada por meio de uma análise numérica com matriz de dados explícita. Dos cinco táxons formalmente descritos para esta unidade estratigráfica, os três mais completos - *Bauruemys elegans*, *Cambaremys langertoni* e *Roxochelys wanderleyi* - foram aqui incluídos em um estudo filogenético dos Pelomedusoides pró-Podocnemidae. A filogenia resultante apresenta a forma conhecida informalmente como FR-4922 e *Brasilemys josai* como Pelomedusoides na linhagem de Podocnemoidea, mas basais a este clado. Dentre os Podocnemoidea, os táxons do Grupo Bauru posicionaram-se na linhagem dos Podocnemoidae, porém basais a Podocnemidae. *Roxochelys* foi considerado um gênero monofilético, mais próximo aos Podocnemidae que as demais formas cretácicas analisadas. Dentre estas, *Bauruemys elegans* é mais derivada que *Portezueloemys patagonica*, enquanto o posicionamento de *Cambaremys langertoni* se apresenta bastante instável. Com relação aos Podocnemidae viventes, ficou evidenciada a maior afinidade entre os gêneros *Peltocephalus dumerilianus* e *Erymnochelys madagascariensis*.

Palavras-chave: Podocnemidae, *Bauruemys elegans*, *Cambaremys langertoni*, *Roxochelys wanderleyi*, Grupo Bauru, Cretáceo Superior.

INTRODUCCION

Various studies investigate the phylogenetic relationships of major chelonian groups (Gaffney, 1975; Gaffney & Meylan, 1988; Gaffney *et al.*, 1991; Shaffer *et al.*, 1997), but few include a broad sampling of pelomedusoid turtles, especially Podocnemidae. Broin (1988, see also Lapparent de Broin, 2000) depicts the relationship of pelomedusoids including *Schweboemys*, *Brasilemys*, *Hamadachelys*, *Erymnochelys*, and *Podocnemis* in the form of cladograms, but these were not generated by explicit analyses. Meylan (1996) produced the first explicit cladistic phylogeny of the group, but a more comprehensive analysis was provided by de la Fuente (2003). This last author

reviewed previous works and concluded that forms such as *Brasilemys josai*, *Hamadachelys escuillei*, and *Portezueloemys patagonica* represent non-Podocnemidae Podocnemoidea. In addition to these morphological studies, Seddon *et al.* (1997), Georges *et al.* (1998), and Noonan (2000) conducted molecular analyses of extant Pleurodira, and found *Podocnemis* to be more closely related to *Erymnochelys madagascariensis* than to *Peltocephalus dumerilianus*.

The palaeocheloniofauna of the Bauru Group (Late Cretaceous of the Paraná Basin) in south-central Brazil (Figure 1) was not considered in any of the above mentioned analyses. The fauna includes five formally described taxa (Kischlat *et al.*, 1994; França & Langer, 2005): “*Podocnemis*”

harrisi Pacheco, 1913, "*P.*" *brasiliensis* Staesche, 1937, *Roxochelys wanderleyi* Price, 1953, *Bauruemys elegans* (Suarez, 1969, gen. Kischlat, 1994), and *Cambaremys langertoni* França & Langer, 2005. Although some of these are based on fragmentary material, others are complete enough to be incorporated in a cladistic study. Indeed, the phylogenetic position of *Bauruemys elegans* was already discussed in abstracts by Kischlat (1996) and Romano & Azevedo (2005). It was considered to be the sister-taxon of *Portezueloemys patagonica* plus Podocnemidae by the latter authors and as a basal podocnemid by the former. The major aim of this work is to investigate the phylogenetic position of the better known turtles of the Bauru Group, including *Roxochelys wanderleyi*, *Bauruemys elegans*, and *Cambaremys langertoni* within a comprehensive cladistic study of pro-Podocnemidae Pelomedusoides.

MATERIALS AND METHODS

The analysis is based on 32 morphological characters (Appendix 1), scored for 14 terminal taxa, namely: *Araripemys barretoii*, *Bauruemys elegans*, *Brasilemys josai*, Bothremydidae (based on *Cearachelys placidoi*, *Foxemys mechinorum*, and *Rosasia soutoi*, *Galianemys whitei*), *Cambaremys langertoni*, Chelidae (based on *Prochelidella portezuelae*, *Yaminuechelys gasparinii*, *Phrynops geoffroanus*, and *Hydromedusa tectifera*), *Erymnochelys madascariensis*, FR-4922 (Gaffney & Meylan, 1991), Pelomedusidae (based on *Pelomedusa subrufa* and *Pelusios* spp.), *Peltocephalus dumerilianus*, *Podocnemis* spp., *Portezueloemys patagonica*, *Roxochelys vilavilensis*, and *R. wanderleyi*. The basal condition of the composite terminal taxa was accessed according to Langer & Benton (2006), based

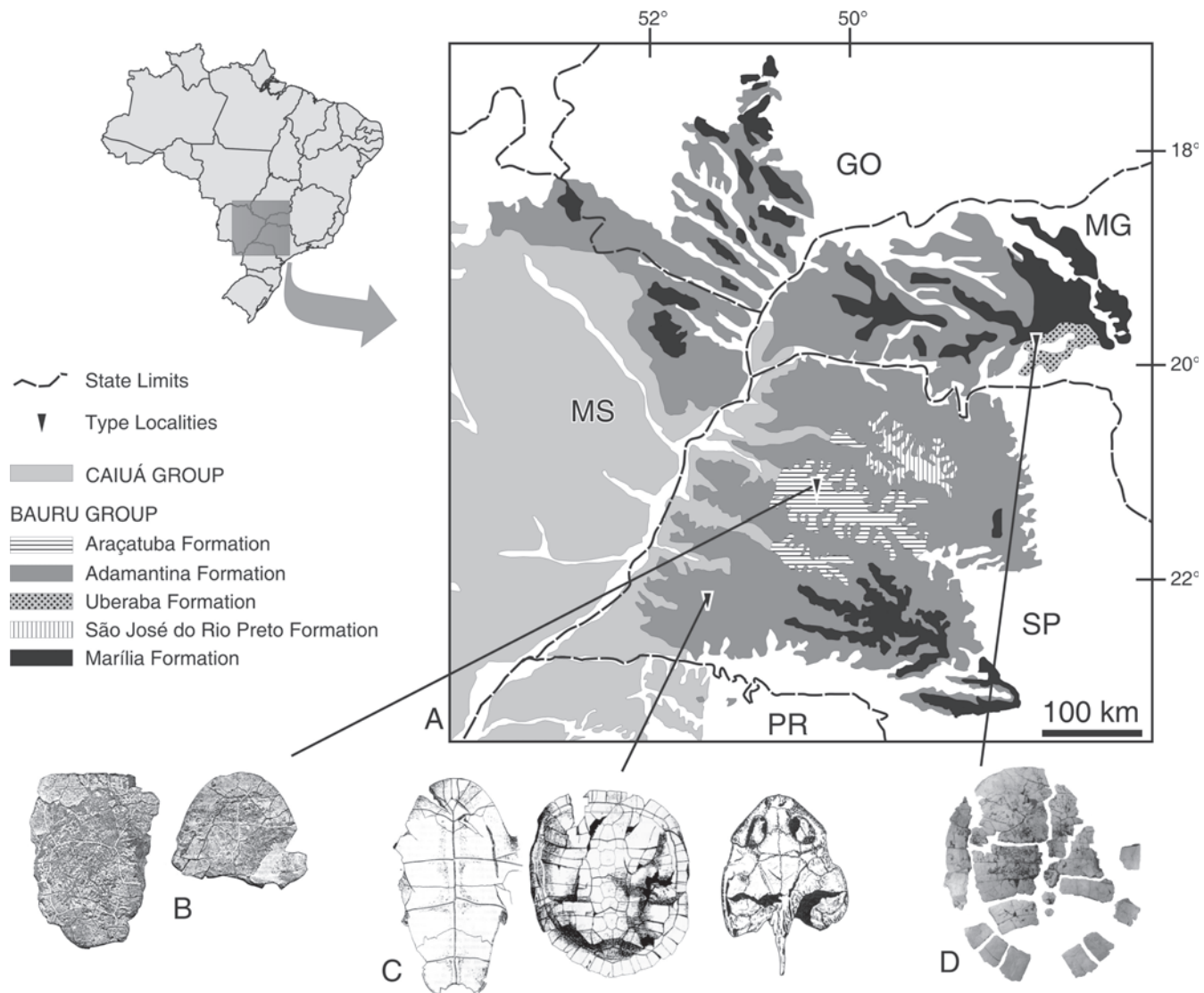


Figure 1. Fossil turtle occurrences in the Bauru Group (arrows indicate type-localities of the figured taxa): **A**, surface distribution of the Caiuá Group and stratigraphic sub-unities of the Bauru Group (after Fernandes & Coimbra, 1996) in the states of Goiás (GO), Mato Grosso do Sul (MS), Minas Gerais (MG), Paraná (PR), and São Paulo (SP); **B**, type material of *Roxochelys wanderleyi* (after Price, 1953); **C**, part of the type material of *Bauruemys elegans* (after Suarez, 1969); **D**, part of the type material of *Cambaremys langertoni* (after França & Langer, 2005).

on the phylogenetic studies of Seddon *et al.* (1997), Georges *et al.* (1998), Tong *et al.* (1998), Noonan (2000), de la Fuente *et al.* (2001), and de la Fuente (2003). Out of the five chelonian taxa formally described for the Bauru Group, “*Podocnemis*” *brasiliensis* and “*P.*” *harrisi* were not included in the study, because of their fragmentary condition. “*P.*” *brasiliensis* is represented only by a partial plastron (Price, 1953), and “*P.*” *harrisi* by lost specimens (Kischlat *et al.*, 1994).

Most characters employed in this analysis were modified from the literature (Meylan, 1996; Tong *et al.*, 1998; Lapparent de Broin & Murelaga, 1999; de la Fuente, 2003), but a few are newly proposed (Appendix 1). Their codification was based on various literature sources (Price, 1953, 1973; Williams, 1954; Suarez, 1969; Broin, 1971, 1980, 1988; Wood & Diaz de Gamero, 1971; Gaffney, 1979; Antunes & Broin, 1988; Gaffney & Meylan, 1991; Gaffney *et al.*, 1991; de la Fuente, 1993, 2003; Fernandez & de la Fuente, 1994; Kischlat, 1994; Kischlat *et al.*, 1994; Meylan, 1996; Tong *et al.*, 1998; Lapparent de Broin & Werner, 1998; Lapparent de Broin, 2000; de la Fuente *et al.*, 2001; Gaffney *et al.*, 2001, 2002; Gaffney & Wood, 2002; França & Langer, 2005), but also on the direct examination of recent and fossil specimens, namely: *Bauruemys elegans* (URC R47, R58, R59), *Cambaremys langertoni* (CPP 0252), *Chelus fimbriatus* (MZUSP 1027), *Hydromedusa tectifera* (MZUSP 2022, 4104, 305), *Peltocephalus dumerilianus* (MZUSP 3216, 3138, 3137, 3139, 2753), *Phrynops geoffroanus* (MZUSP 2633, 2638, 2637), *Podocnemis erythrocephala* (INPA 10274), *P. expansa* (LIRP unnumbered; MZUSP 2810, 2761, 2844), *P. unifilis* (MZUSP 3209, 2026, 2809; INPA 11559), and *P. sextuberculata* (INPA 8953) (Institutional abbreviations: CPP - Centro de Pesquisas Paleontológicas “Llewellyn Ivor Price”, Uberaba; INPA - Instituto Nacional de Pesquisas na Amazônia, Manaus; LIRP - Laboratório de Ictiologia de Ribeirão Preto, Ribeirão Preto; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo; URC - Museu de Paleontologia e Estratigrafia, Prof. Dr. Paulo Milton Barbosa Landim, Rio Claro).

All characters were equally weighted and those with multiple states that can be arranged into morphoclines ordered. The data matrix (Appendix 2) was analyzed with the software PAUP* (Phylogenetic Analysis using Parsimony* and other methods), version 4.0b2a (Swofford, 2001). The search was rooted in the outgroup, i.e.: Chelidae (see Broin, 1988; Meylan, 1996; Lapparent de Broin & Murelaga, 1999; Lapparent de Broin, 2000; de la Fuente, 2003), and the “Branch and Bound” search mechanism was employed.

The taxon names used here are defined in Appendix 3, following the principles of Phylogenetic Nomenclature (de Queiroz & Gauthier, 1990; Cantino & de Queiroz, 2004). Those definitions attempt to reproduce both the original meaning of the names (Cope, 1868; Baur, 1893; Broin, 1988) as well as their first use on Phylogenetic Nomenclature grounds (Joyce *et al.*, 2004).

RESULTS

The analysis revealed five most parsimonious trees (MPTs), with 70 steps (Figure 2A) and statistics given as: CI

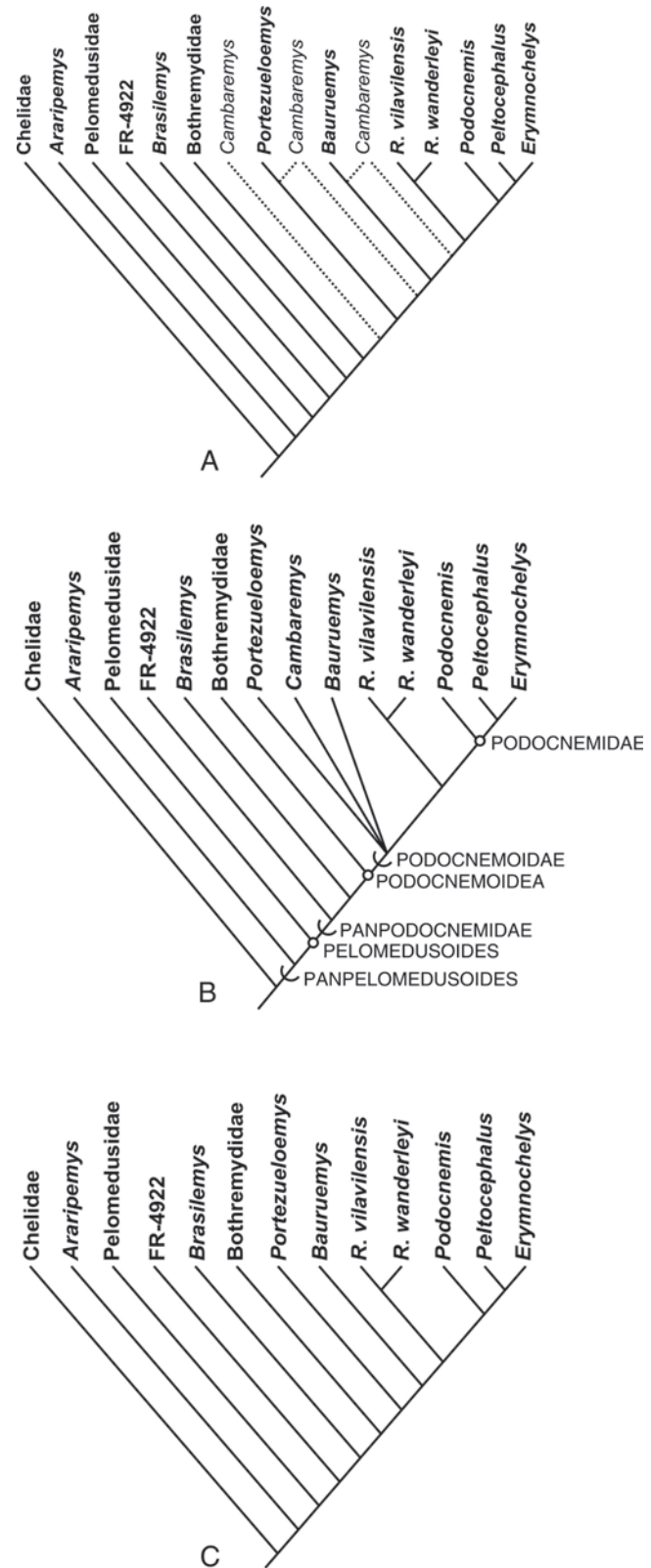


Figure 2. Cladogram depicting the phylogenetic relationships among pelomedusoid turtles, with emphasis on the Bauru Group taxa: **A**, five most parsimonious trees found in the first analysis, showing the alternative positions of *Cambaremys langertoni*; **B**, strict consensus of those five MPTs; **C**, single MPT found in the analysis without *Cambaremys langertoni*.

=0.757; RI=0.823; RC=0.623; HI=0.471. The strict consensus of these trees (Figure 2B) is formed by a pectinate part with *Araripemys*, Pelomedusidae, FR-4922 (Gaffney & Meylan, 1991), *Brasilemys*, and Bothremydidae, as successive sister taxa to a polytomy. This polytomy includes *Cambaremys*, *Bauruemys*, *Portezueloemys*, and a clade composed of *Roxochelys wanderleyi* plus ?*R. vilavilensis* at the base, followed by the extant podocnemid genera. Within that clade,

Erymnochelys and *Peltocephalus* form a monophyletic group to the exclusion of *Podocnemis*. Given that the five MPTs of the first analysis differ only in the position of *Cambaremys* (Figure 2A), a second analysis was conducted without that taxon, and a single MPT was recovered. This has the same number of steps and statistics as the MPTs of the first analysis, and is congruent to all of them. The polytomy at the base of Podocnemoidae is resolved, and *Bauruemys* is

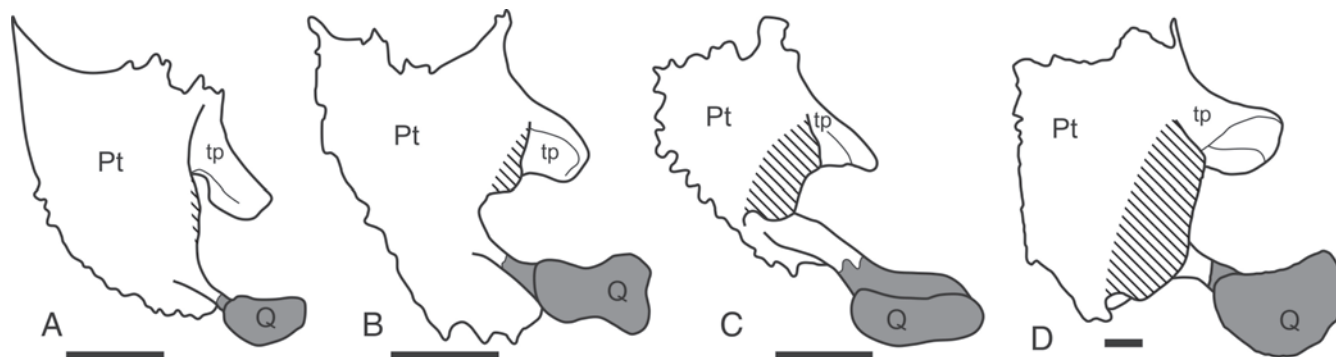


Figure 3. Palatal area of pterygoid and quadrate of Panpelomedusoides turtles in ventral view, showing the states of character 14. Quadrate highlighted in gray and pterygoid flange striped. **A**, *Araripemys barretoii*. **B**, FR-4922. **C**, *Cearachelys placidoi*. **D**, *Podocnemis expansa* (LIRP unnumbered). **Abbreviations:** Pt = pterygoid; Q = quadrate; tp = trochlear process. Scale bar = 0,50 mm. A, B and C modified, respectively, after Meylan (1996), Gaffney & Meylan (1991) and Gaffney et al. (2001).

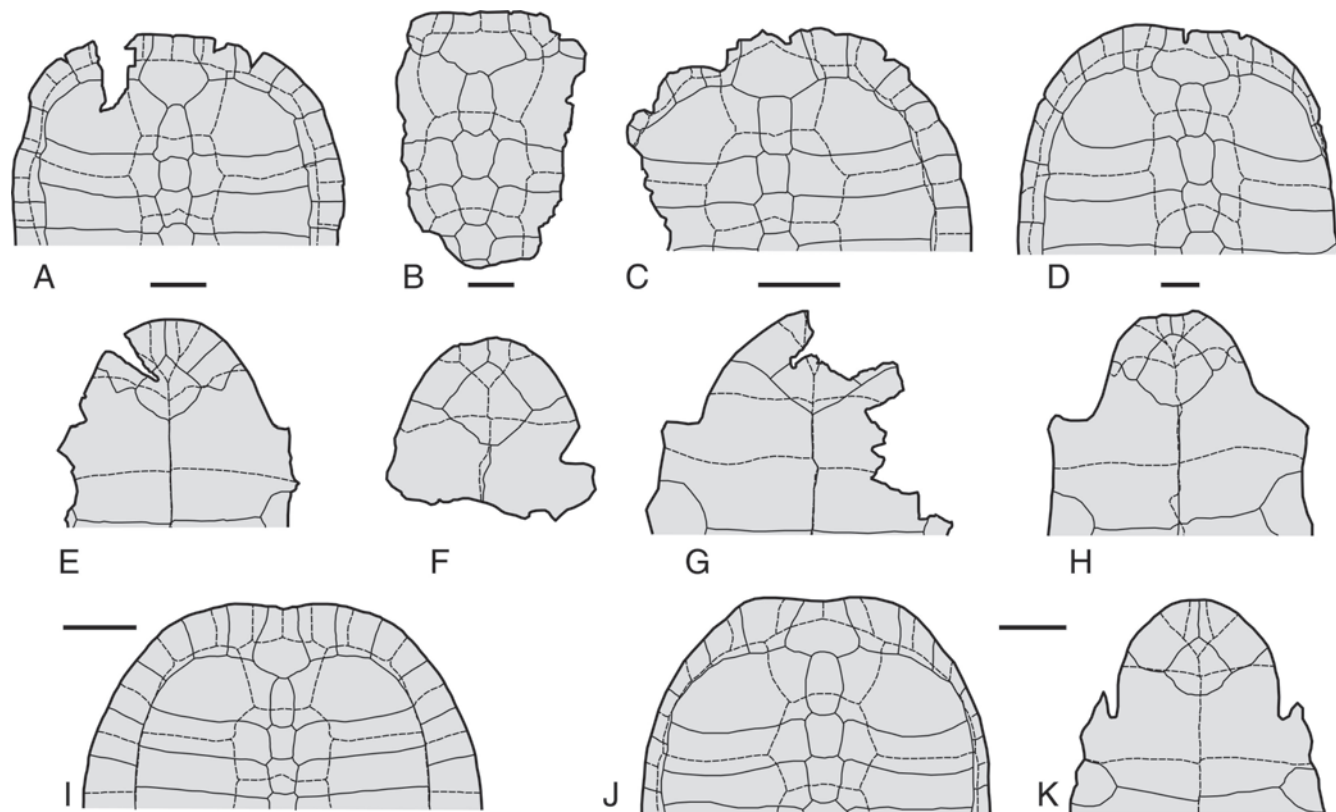


Figure 4. Shell morphology among Podocnemoidae, carapace in dorsal aspect (**A-D**, **I**, **J**) and plastron in ventral aspect (**E-H**, **K**). **A**, **E**, *Bauruemys elegans* (after Suarez, 1969); **B**, **F**, *Roxochelys wanderleyi* (after Price, 1953); **C**, **G**, *Portezueloemys patagonica* (after de la Fuente, 2003); **D**, **H**, ?*Roxochelys vilavilensis* (after Broin, 1971); **I**, *Cambaremys langertoni* (after França & Langer, 2005); **J**, **K**, *Podocnemis unifilis* (after de la Fuente, 1993). Scale bar = 40 mm.

considered more derived than *Portezueloemys*, as proposed by Romano & Azevedo (2005).

DISCUSSION

The phylogeny proposed herein greatly agrees with previous studies of Pelomedusoides relationships (Broin, 1988; Kischlat, 1996; Meylan, 1996; Lapparent de Broin, 2000; de la Fuente, 2003; Romano & Azevedo, 2005). Exceptions are the position of FR-4922 (Gaffney & Meylan, 1991) and *Brasilemys josai*, as well as the relationships among the extant podocnemid genera. FR-4922 was found to represent a basal Pelomedusoides (Figure 2), as suggested by Kischlat (1996) and Lapparent de Broin (2000), in opposition to its placement as the sister-taxon to *Araripemys*, as proposed by Meylan (1996). This is based on traits that FR-4922 shares with other Pelomedusoides, to exclusion of *Araripemys*, namely: a reduced temporal skull emargination (Appendix 1; character 2), *chorda tympani* entering the retroarticular process (character 7), well-developed pterygoid flange (character 14; Figure 3B), retroarticular process projected dorsally to the articular surface of the lower jaw (character 20), and pectoral scute not encroaching the entoplastron (character 29).

Brasilemys josai was placed basal to the Podocnemioidea clade (Figure 2), and not within Podocnemoidae as previously proposed (Lapparent de Broin, 2000; de la Fuente, 2003). Indeed, the only trait that supports the latter arrangement is the enlargement of the carotid canal (de la Fuente, 2003). This was included in the present analysis (character 11), but was not enough to enforce that hypothesis of relationship. Instead, Podocnemoidae (exclusive of *Brasilemys*) and Bothremydidae share a reduced or absent *antrum postoticum* (character 5), a substantial contribution of the palatine to the triturating surface of the upper jaw (character 13), and a pterygoid flange occupying the almost entire post-trochlear lateroventral margin of the bone (character 14; Figure 3C).

Among the extant Podocnemidae, a sister group relationship between *Peltocephalus* and *Erymnochelys* is advocated here (Figure 2). This disagrees with both molecular data (Seddon *et al.*, 1997; Georges *et al.*, 1998; Noonan, 2000), which suggest a closer relationship between *Erymnochelys* and *Podocnemis*, and more traditional taxonomic propositions (Gaffney & Meylan, 1988; Broin, 1988) that group the neotropical forms together. Indeed, according to de la Fuente (2003), the only morphological feature that supports the *Podocnemis* plus *Peltocephalus* clade is the presence of cervical centra with saddle-shaped caudal condyles. Yet, that character was also reported for some putatively basal fossil forms such as *Stupendemys* (Wood, 1976), *?Roxochelys vilavilensis* (Broin, 1971), and cf. *Roxochelys* sp. (Kischlat *et al.*, 1994). Its absence in *Erymnochelys* is, therefore, better interpreted as a reversion to a more basal condition, and not the retention of a plesiomorphy. Besides, in the context of the present study, the only character that supports the “molecular” *Podocnemis* plus *Erymnochelys* clade is the presence of the pectoral scute contacting the epiplastron (character 28).



Figure 5. Scapular morphology among Pleurodira; dorsal (A, C, E) and ventral (B, D, F) aspects. A-B, *Cambaremys langertoni* (CPP 0252). C-D, *Hydromedusa tectifera* (MZUSP 2022). E-F, *Podocnemis expansa* (MZUSP 2761).

As with the previous character, this trait is also shared by basal taxa such as *Bauruemys* and *?Roxochelys vilavilensis*, and the condition in *Peltocephalus* is better considered a reversal. The cranial restriction of the carotid canal roof might (character 12), on the other hand, represent a synapomorphy of *Peltocephalus* plus *Erymnochelys*, but this is not presently determinable for fossil forms like *Bauruemys*, *Portezueloemys*, and *?Roxochelys vilavilensis*, shading some doubts upon its significance. The *Peltocephalus* plus *Erymnochelys* clade is, however, supported by other morphological traits (Williams, 1954; Gaffney & Meylan, 1988), namely: interorbital groove absent, reduced external narial opening, pre-frontal longer than frontal, jugal-quadrate contact (but see Lapparent de Broin & Werner, 1998), and reduced lateral skull emargination.

All Bauru Group turtles lie along the Podocnemoidae lineage, which is characterized by a major reduction of temporal skull emargination (character 2) and a pectoral scute that does not contact the mesoplastron (character 30; Figures 4E-H, K). Within Podocnemoidae, *Bauruemys* is more derived than *Portezueloemys*, sharing with *Roxochelys* and extant podocnemids a pterygoid flange that overlaps the craniomedial part of the podocnemoid fossa (character 17) and a pectoral scute that encroaches the epiplastron (character 28; Figures 4E-H, K). Neither of these characters is possible to codify for *Cambaremys langertoni*, and the phylogenetic position of this taxon is highly unstable (Figure 2A).

In the context of the present analysis, the genus *Roxochelys* was found to represent the sister-taxon to the extant podocnemids. The morphological traits that support the monophyly of that genus, i.e.: the sister group relationship between *R. wanderleyi* and *?R. vilavilensis*, include thick shell bones (character 22), entoplastron wider than half the

width of the cranial plastral lobe (character 31; Figures 4E-H, K), and the reversal to a nuchal bone wider than long (character 23; Figures 4A-D, I, J). *Roxochelys* and Podocnemidae form a monophyletic group based on the sharing of a pterygoid that ventrally covers the prootic (character 15), cervical centra with saddle-shaped caudal condyles (character 21), and a closed *incisura columellae auris* (character 6; convergently acquired by Pelomedusidae and some bothremydids). Extant podocnemids, on the other hand, share a reduced to absent vomer (character 10) and a thick and narrow coracoid lamina (character 32; Figure 5). Nonetheless, a more comprehensive analysis, including Cenozoic fossils, is needed to better determine the transformations of several of these characters along the Podocnemoidae lineage.

CONCLUSION

All well-known chelonians of the Bauru Group are closely related to the extant podocnemids. However, Podocnemidae is currently node-based defined as a crown-group, with *Podocnemis*, *Peltocephalus*, and *Erymnochelys* as internal specifiers (Joyce *et al.*, 2004), and all fossil forms dealt with here are basal to that clade. Accordingly, *Bauruemys elegans*, *Cambaremys langertoni*, and *Roxochelys wanderleyi* are better considered taxa on the stem-lineage to Podocnemidae, but not Podocnemidae *sensu stricto*.

ACKNOWLEDGEMENTS

The authors are grateful to the following people and institutions for allowing the study of specimens under their care: Luiz Carlos Borges Ribeiro (Centro de Pesquisas Paleontológicas “Llewellyn Ivor Price”), Richard Carl Vogt (Instituto Nacional de Pesquisas na Amazônia), Hussam El Dine Zaher (Museu de Zoologia da Universidade de São Paulo), and Ricardo Macedo Corrêa e Castro (Laboratório de Ictiologia de Ribeirão Preto). We are much indebted to Eugene Gaffney, Walter Joyce, and the editors for comments and suggestions that improved the manuscript. Thanks are also extended to FAPESP for providing financial support for this study. This paper was a contribution to the XIX Brazilian Paleontological Congress and VI Latin American Paleontological Congress, held in August, 2005, in Aracaju (SE, Brazil).

REFERENCES

- Antunes, M.T. & Broin, F.L. 1988. Le Crétacé de Beira Litoral, Portugal: remarques stratigraphiques et écologique, étude complémentaire de *Rosasia soutoi* (Chelonii, Bothremydidae). *Ciências da Terra*, **9**:153-200.
- Baur, G. 1893. Notes on the classification of the Cryptodira. *American Naturalist*, **27**:672-675.
- Broin, F. 1971. Une espèce nouvelle de Tortue pleurodire (?*Roxochelys vilavilensis* n. sp.) dans le Crétacé supérieur de Bolivie. *Bulletin de la Société Géologique de France (7ème Série)*, **13**:445-452.
- Broin, F. 1980. Les tortues de Godoufaoua (Aptian du Niger); a peu sur la paléobiogéographie des Pelomedusidae (Pleurodira). *Mémoires de la Société Géologique de France*, **139**:39-43.
- Broin, F. 1988. Les tortues et le Gondwana. Examen des rapports entre la fractionnement du Gondwana et la dispersion géographique des tortues pleurodires a partir du Crétacé. *Studia Geologica Salmanticensia, Studia Paleocheloniologica*, **2**:103-142.
- Cantino, P.D. & de Queiroz, K. 2004. PhyloCode: A phylogenetic code of biological nomenclature, Version 2b (june 17, 2004). Available at <http://www.ohio.edu/phylocode>.
- Cope, E.D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1868**:242-300.
- de la Fuente, M.S. 1993. Un posible Podocnemididae (Pleurodira: Pelomedusoides) en el Cretácico Tardío de la Patagonia. *Ameghiniana*, **30**:423-433.
- de la Fuente, M.S. 2003. Two new pleurodiran turtles from the Portezuelo Formation (Upper Cretaceous) of northern Patagonia, Argentina. *Journal of Paleontology*, **77**:559-575.
- de la Fuente, M.S.; Lapparent de Broin, F. & Bianco, T.M. 2001. The oldest and first nearly complete skeleton of a chelid, of the Hydromedusa sub-group (Chelidae, Pleurodira), from the Upper Cretaceous of Patagonia. *Bulletin de la Société Géologique de France*, **172**:237-244.
- de Queiroz, K. & Gauthier, J. 1990. Phylogeny as a central principle on taxonomy: Phylogenetic definitions of taxons names. *Systematic Zoology*, **39**:307-322.
- Fernandes, L.A. & Coimbra, A.M. 1996. A bacia Bauru (Cretáceo Superior, Brasil). *Anais da Academia Brasileira de Ciências*, **68**(2):195-205.
- Fernandez, M.S. & de la Fuente, M.S. 1994. Redescription and phylogenetic position of *Notoemys*: The oldest Gondwanian pleurodiran turtle. *Neues Jahrbuch Geologie und Paläontologie Abhandlungen*, **193**:81-105.
- França, M.A.G. & Langer, M.C. 2005. A new freshwater turtle (Reptilia, Pleurodira, Podocnemidae) from the Upper Cretaceous (Maastrichtian) of Minas Gerais, Brazil. *Geodiversitas*, **27**(3):391-411.
- Gaffney, E.S. 1975. A phylogeny and classification of the higher categories of turtles. *Bulletin of the American Museum of Natural History*, **155**:387-436.
- Gaffney, E.S. 1979. Comparative cranial morphology of recent and fossil turtles. *Bulletin of the American Museum of Natural History*, **164**:65-376.
- Gaffney, E.S.; Campos, D.A. & Hirayama, R. 2001. *Cearachelys*, a new side-necked turtle Pelomedusoides: Bothremydidae) from the Early Cretaceous of Brazil. *American Museum Novitates*, **3319**:1-20.
- Gaffney, E.S. & Meylan, P.A. 1988. A phylogeny of turtles. In: M. J. Benton (ed.) *The phylogeny and classification of the tetrapods, vol 1, Amphibians, Reptiles, Birds*, Systematics Association, special volume 35A, Clarendon Press, p. 157-219.
- Gaffney, E.S. & Meylan, P.A. 1991. Primitive Pelomedusid turtle. In: J.G. Maisey (ed.) *Santana fossils: an illustrated atlas*, TFH Publications, p. 335-339.
- Gaffney, E.S.; Meylan, P.A. & Wyss, A.R. 1991. A computer assisted analysis of the relationships of the higher categories of turtles. *Cladistics*, **7**:313-335.
- Gaffney, E. S.; Tong, H. & Meylan, P.A. 2002. *Galianemys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the

- late Cretaceous of Morocco. *American Museum Novitates*, **3379**:1-20.
- Gaffney, E.S. & Wood, R.C. 2002. *Bairdemys*, a new side-necked turtle (Pelomedusoides: Podocnemididae) from the Miocene of the Caribbean. *American Museum Novitates*, **3359**:1-28.
- Georges, A.; Birrell, J.; Saint, K.M.; Mccord, W. & Donnellan, S.C. 1998. A phylogeny for side-necked turtles (Chelonia: Pleurodira) based on mitochondrial and nuclear gene sequence variation. *Biological Journal of the Linnean Society*, **67**:213-246.
- Joyce, W.G.; Parham, J.F. & Gauthier, J.A. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology*, **78**:989-1013.
- Kischlat E-E. 1994. Observações sobre *Podocnemis elegans* Suarez (Chelonii, Pleurodira, Podocnemididae) do Neocretáceo do Brasil. *Acta Geologica Leopoldensia*, **39**:345-351.
- Kischlat, E.-E. 1996. Preliminary phylogenetic analysis of the pleurodiran chelonians from the Cretaceous of Brazil. *Anais da Academia Brasileira de Ciências*, **68**(2):288-289.
- Kischlat, E.-E.; Barberena, M.C. & Timm, L.L. 1994. Considerações sobre a queloniofauna do Grupo Bauru, Neocretáceo do Brasil. In: SIMPÓSIO SOBRE O CRETÁCEO DO BRASIL, 3, 1994. *Resumos expandidos*, Rio Claro, UNESP, p. 105-107.
- Langer, M.C. & Benton, M.J. 2006. Early dinosaurs: a phylogenetic study. *Journal Systematic Paleontology*, **4**(4):1-50.
- Lapparent de Broin, F. 2000. The oldest pre-podocnemidid turtle (Chelonii, Pleurodira), from the Early Cretaceous, Ceará State, Brasil, and its environment. *Treballs del Museu de Geologia de Barcelona*, **9**:43-95.
- Lapparent de Broin, F. & Murelaga, X. 1999. Turtles from the Upper Cretaceous of Laño (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Alava*, **14**:135-211.
- Lapparent de Broin, F. & Werner, C. 1998. New Late Cretaceous turtles from the Western Desert, Egypt. *Annales de Paleontologie*, **84**(2):131-214
- Meylan, P.A. 1996. Morphology and relationships of the Early Cretaceous side-necked turtle, *Araripemys barretoii* (Testudines: Pelomedusoides: Araripemydidae) from the Santana Formation of Brazil. *Journal of Vertebrate Paleontology*, **16**:20-33.
- Noonan, B.P. 2000. Does the phylogeny of pelomedusoid turtles reflect vicariance due to continental drift? *Journal of Biogeography*, **27**:1245-1249.
- Pacheco, J.A. 1913. Notas sobre a geologia do Vale do Rio Grande, a partir da foz do Rio Pardo até a sua confluência com o Rio Paranaíba. In: J. Dourados (ed.) *Exploração do Rio Grande e de seus afluentes*. Comissão de Geografia e Geologia, São Paulo p. 33-38.
- Price, L.I. 1953. Os quelônios da Formação Bauru, Cretáceo terrestre do Brasil Meridional. Rio de Janeiro, Departamento Nacional da Produção Mineral, Divisão de Geologia e Mineralogia, 34 p. (Boletim 147).
- Price, L.I. 1973. Quelônio amphichelydia no Cretáceo Inferior do Nordeste do Brasil. *Revista Brasileira de Geociências*, **3**:84-96.
- Romano, P.S. & Azevedo, S.A. 2005. Phylogenetic position of *Bauruemys elegans* and the biogeography of Podocnemidid turtles (Pleurodira: Pelomedusoides). In: ANNUAL MEETING SOCIETY OF VERTEBRATE PALEONTOLOGY, 65, 2005. *Abstracts of Papers*, Mesa Southwest Museum and Phoenix Marriott Mesa, Mesa, Arizona, p. 106A.
- Seddon, J.M.; Georges, A.; Baverstock, P.R. & McCord, W. 1997. Phylogenetic relationships of chelid turtles (Pleurodira: Chelidae) based on mitochondrial 12S rRNA sequence variation. *Molecular Phylogenetic Evolution*, **7**:55-61.
- Shaffer, H.B.; Meylan, P. & McKnight, M.L. 1997. Tests of turtle phylogeny: Molecular, morphological, and paleontological approaches. *Systematic Biology*, **46**:235-268.
- Staesche K. 1937. *Podocnemis brasiliensis* n. sp. aus der Oberen Kreide Brasiliens. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie B*, **77**:291-309.
- Suarez J.M. 1969. Um quelônio da Formação Bauru. In: CONGRESSO BRASILEIRO DE GEOLOGIA, 23, 1969, *Anais*, Salvador, p. 168-176.
- Swofford, D.L. 2001. PAUP* 4.0b3: Phylogenetic Analysis Using Parsimony, version 4.0. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Tong, H.; Gaffney, E.S. & Buffetaut, E. 1998. *Foxemys*, A new side-necked turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. *American Museum Novitates*, **3251**:1-19.
- Williams, E.E. 1954. A key and description of the living species of the genus *Podocnemis* (sensu Boulenger) (Testudines, Pelomedusidae). *Bulletin of the Museum of Comparative Zoology*, **111**(8):279-295.
- Wood, R. C. 1976. *Stupendemys geographicus*, the world's largest turtle. *Breviora*, **436**:1-31.
- Wood, R.C. & Dias de Gamero, M.L. 1971. *Podocnemis venezuelensis*, a new fossil pelomedusid (Testudines, Pleurodira) from the Pliocene of Venezuela and a review of the history of *Podocnemis* in South América. *Breviora*, **376**:1-23.

Received in October, 2005; accepted in October, 2006

Appendix 1. List of characters. All character listed in previous numerical cladistic studies of Pelomedusoides (Meylan, 1996; Tong *et al.*, 1998; de la Fuente, 2003) were analyzed. Those invariable for the ingroup or autapomorphic, in the context of the present analysis, were excluded. Invariable characters: 4, 5, 14, 26, 27, 28, 29, 31, 32, 34 (Meylan, 1996); 13, 14 (Tong *et al.*, 1998); 1, 2, 4, 6, 9, 28, 31, 32, 37, 39, 44, 45, 46, 48, 49 (de la Fuente, 2003). Autapomorphic characters: 1(0), 9, 11, 16(1), 17 (2), 18 (Meylan, 1996); 1, 2, 3, 5, 7, 8(1), 9(2), 10, 17, 18, 19, 20, 21, 22, 23 (Tong *et al.*, 1998); 7(0), 14, 16, 17, 18, 19, 22(2), 23, 26, 33(0), 41, 42, 50 (de la Fuente, 2003). This exclusion left 55 informative characters: 22 from Meylan (1996), 8 from Tong *et al.* (1998), and 25 from de la Fuente (2003). When characters of different authors dealing with equivalent transformations were united in single characters the total number was reduced to 26. Six characters (2, 21, 24, 25, 30, 31) were used for the first time in the context of a phylogenetic analysis.

(1) Contact parietal-quadratojugal (0) absent or (1) present (de la Fuente, 2003, char. 5)

Regarding other characters of the temporal area, the parietal-jugal contact was considered apomorphic for *Roxochelys*, FR4922, and extant podocnemids by Meylan (1996; char. 1), and for the latter group by de la Fuente (2003; chars. 3, 7). However, this contact seems to be restricted to the genus *Podocnemis*, as discussed by Lapparent de Broin & Werner (1998; see also Broin, 1991; Gaffney & Meylan, 1991).

(2) Temporal emargination occupying about (0) 50%, (1) 35% or (2) 25 % of the axial length of the skull (based on Lapparent de Broin, 2000).

(3) Contact quadrate-basisphenoid behind the prootic (0) absent or (1) present (de la Fuente, 2003, char. 12).

(4) Contact quadrate-basioccipital (0) absent or (1) present (Meylan, 1996, char. 10; Tong *et al.*, 1998, char. 4; de la Fuente, 2003, char. 13).

(5) *Antrum postoticum* (0) large or (1) moderate to absent (Meylan, 1996, char. 17; Tong *et al.*, 1998, char. 9; de la Fuente, 2003, char. 22). Given that only some bothremydids possess a "very small to absent *antrum postoticum*", this character was not considered multistate as in previous phylogenies.

(6) *Incisura columellae auris* (0) open or (1) closed (Meylan, 1996, char. 35; Tong *et al.*, 1998, char. 16; de la Fuente, 2003, char. 24). Meylan (1996) coded this character as "0" for Chelidae, but we follow de la Fuente (2003), and accept it as polymorphic. We also consider this character polymorphic for Bothremydidae (Tong *et al.*, 1998; Gaffney *et al.*, 2001; de la Fuente, 2003; *contra* Meylan, 1996).

(7) *Chorda tympani* (0) not entering or (1) entering the retroarticular process (Meylan, 1996, char. 21; de la Fuente, 2003, char. 30).

(8) Precolumelar fossa (0) present or (1) absent (Meylan, 1996, char. 16; Tong *et al.*, 1998, char. 8). Given that only pelomesusids possess a "deep precolumelar fossa", this character was not considered multistate as in previous phylogenies. Meylan (1996) and Tong *et al.* (1998) code a moderate precolumelar fossa for *Podocnemis*, but this fossa varies from deep (*P. unifilis*) to very shallow (*P. erythrocephala*) or absent (*P. expansa*) within that genus. Hence, this character is coded as polymorphic for *Podocnemis*, as is also the case of Chelidae (see Lapparent de Broin & Werner, 1998; *contra* Meylan, 1996).

(9) Vomer (0) extends or (1) not caudal to the choana (de la Fuente, 2003; char. 9).

(10) Vomer occupying about (0) 20% or (1) 15% or (2) less than 10% of the choanal width or absent (Meylan, 1996; char. 3; de la Fuente, 2003, char. 8). Based on the narrowing trend observed in the vomer of extant *Podocnemis*, we tentatively accept the absence of that bone as a result of its lateromedial constriction. de la Fuente (2003) considered that pelomedusids have a "strongly developed" vomer, but we follow Meylan (1996; see Lapparent de Broin & Werner, 1998), accepting it as absent in those forms. Although Meylan (1996) and de la Fuente (2003) scored this character for *Araripemys*, we follow the description of Meylan (1996), and consider that codification ambiguous.

(11) Carotid canal (0) not enlarged or (1) enlarged (Meylan, 1996, char. 6; de la Fuente, 2003, char. 10).

(12) Roofing of the carotid canal (0) restricted or (1) not restricted cranially (Meylan, 1996, char. 7; de la Fuente, 2003, char. 26). de la Fuente (2003) scored that character as "0" for Podocneminae, defining it as autapomorphic for Erymnochelynae. We follow the more explicit scoring of Meylan (1996), and consider *Peltocephalus* to have the derived condition.

(13) Palatine contribution to the triturating surface (0) absent, restricted, or (1) substantial (Meylan, 1996, char. 33; Tong *et al.*, 1998, char. 15). Meylan (1996) considered that character indeterminate for Chelidae, but we follow Lapparent de Broin & Werner (1998) and code it as plesiomorphic.

(14) Pterygoid flange is (0) absent, feeble, or (1) well-developed, (2) occupying the almost entire post-trochlear lateroventral margin of the pterygoid, and (3) reaching the caudal margin of the quadrate ramus of the bone (Meylan, 1996, char. 15; de la Fuente, 2003, char. 21). Extra steps were defined for this character in order to include more detailed information regarding the caudal development of the pterygoid flange.

(15) Pterygoid (0) does not cover, or (1) covers the prootic ventrally (Meylan, 1996, char. 8; de la Fuente, 2003, char. 11).

(16) Caudal margin of the ventral portion of the pterygoid trochlear process forms an (0) oblique or (1) right angle to skull axis (de la Fuente, 2003, char. 20; Meylan, 1996, char. 12). Meylan (1996) scored that character as "0" for *Peltocephalus*, but we follow de la Fuente (2003; see Lapparent de Broin & Werner, 1998) and code it as apomorphic.

(17) Pterygoid flange (0) does not overlap or (1) overlaps ventrally the craniomedial part of podocnemoid fossa (de la Fuente, 2003, char. 25).

(18) Podocnemoid fossa (0) absent or (1) present in the prootic area (de la Fuente, 2003, char. 23).

(19) Lower jaw symphysis (0) fused or (1) sutured (Meylan, 1996, char. 19). Meylan (1996) scored that character as "0" for Chelidae, but we consider it polymorphic (Gaffney, 1979).

(20) Retroarticular process of the articular (0) does not project or (1) projects caudally to the articular face of the lower jaw in dorsal aspect (Meylan, 1996, char. 20; de la Fuente, 2003, char. 29). Given that only bothremydids possess a "large retroarticular process", this character was not considered multistate as in previous phylogenies.

(21) Cervical centra (0) lack or (1) possess saddle-shaped caudal condyles (Meylan, 1996, char. 30; de la Fuente, 2003, char. 47). Kischlat *et al.* (1994) considered ambiguous the presence of heterocelic cervical vertebrae in *Roxochelys vilavilensis*, but we follow Broin (1971) and Meylan (1996) and score this character as "1" for the taxon. On the contrary, we follow Kischlat *et al.* (1994, *contra* Lapparent de Broin, 2000), and score the plesiomorphic condition for *Bauruemys*.

(22) Shell bones (0) thin or (1) thick (based on Price, 1953, and Kischlat *et al.*, 1994).

(23) Nuchal bone (0) wider than long or (1) longer than wide (de la Fuente, 2003, char. 33).

(24) Neural series (0) complete or (1) incomplete (Meylan, 1996, char. 22; Tong *et al.*, 1998, char. 11; de la Fuente, 2003, char. 38).

(25) Neural series composed of (0) eight or more, (1) seven, or (2) six or less bones.

(26) Second neural bone (0) does not contact or (1) contact the first costal bone.

(27) Plastral bridge (0) short or (1) elongated (de la Fuente, 2003, char. 43).

(28) Pectoral scute (0) does not contact or (1) contacts the epiplastron (Meylan, 1996, char. 25; de la Fuente, 2003, char. 36). Meylan (1996) and de la Fuente (2003) scored that character as "0" for bothremydids, but *Foxemys* bears the apomorphic condition (Tong *et al.*, 1998), and we consider it polymorphic. Meylan (1996) scored the apomorphic condition for *Peltocephalus*, but direct examination of specimens reveals the contrary (see also de la Fuente, 1993).

(29) Pectoral scute (0) does not contact or (1) contacts the entoplastron (Meylan, 1996, char. 24; Tong *et al.*, 1998, char. 12; de la Fuente, 2003, char. 35). Meylan (1996) scored that character as "1" for Chelidae, but we follow de la Fuente (2003), and consider it as polymorphic. On the contrary, de la Fuente (2003) scored the plesiomorphic condition for Bothremydidae, but we code it as polymorphic (Antunes & Broin, 1988; Meylan, 1996; Tong *et al.*, 1998; Gaffney *et al.*, 2001).

(30) Pectoral scute (0) encroaching or (1) not the mesoplastron (Meylan, 1996, char. 23; de la Fuente, 2003, char. 34). Given that only *Pelusios* possess an "intervening hinge", this character was not considered multistate as in previous phylogenies. de la Fuente (2003) coded that character as variable for Chelidae, but we follow Meylan (1996), and consider it as plesiomorphic. de la Fuente (2003) considered the condition variable for Podocneminae, but the apomorphic condition was observed in all analyzed specimens of *Podocnemis* and *Peltocephalus*.

(31) Entoplastra (0) narrower (1) or broader than half the width of cranial plastral lobe (based on Broin, 1971).

(32) Coracoid lamina (0) thin and expanded or (1) narrow and deep (based on Kischlat *et al.*, 1994).

Appendix 2. Data matrix used in the present analyses (32 morphological characters and 14 pleurodiran taxa). The notation “a” represents polymorphism (0&1).

Taxa	Characters																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32		
<i>Araripemys</i>	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	?	0	0		
<i>Bauruemys</i>	1	2	?	1	?	0	?	1	1	0	1	?	1	3	0	1	1	1	?	?	0	0	1	1	2	1	1	1	1	1	0	0		
Bothremyidae	0	1	1	1	1	a	1	1	1	1	0	0	1	2	0	a	0	1	a	1	0	0	1	a	a	a	1	a	a	0	0	?		
<i>Brasilemys</i>	0	1	1	1	0	0	?	0	1	?	1	?	0	1	0	0	0	1	0	1	0	0	0	1	1	1	1	?	?	?	?	?		
<i>Cambaremys</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	1	0	1	?	?	1	?	0	
Chelidae	0	0	0	0	0	a	0	a	0	0	0	0	0	0	0	0	0	a	0	0	0	0	a	0	0	0	0	a	0	0	0	0	0	
<i>Erymnochelys</i>	1	2	1	1	1	1	1	0	?	2	1	1	1	3	1	1	1	1	0	1	0	0	1	1	1	0	1	1	1	1	1	0	1	
FR-4922	1	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	?	
Pelomedusidae	0	0	0	0	0	1	0	0	?	2	0	0	0	0	0	0	0	a	0	0	0	1	1	?	0	0	0	0	0	0	0	0	0	
<i>Peltocephalus</i>	1	2	1	1	1	1	1	0	?	2	1	1	1	3	1	1	1	1	0	1	1	0	1	1	1	0	1	1	0	1	1	0	1	
<i>Podocnemis</i>	1	2	1	1	1	1	0	a	1	2	1	0	1	3	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	
<i>Portezueloemys</i>	?	2	1	1	?	?	?	?	1	1	1	?	?	2	?	1	0	1	?	?	?	0	1	1	2	a	1	0	1	1	0	?		
<i>?R. vilavilensis</i>	1	2	?	1	1	1	?	0	1	0	1	?	1	3	1	1	1	1	0	1	1	1	0	1	1	0	1	1	1	1	1	1	0	
<i>R. wanderleyi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 3. Phylogenetic definitions employed in this study.

“Panpelomedusoides” Joyce, Parham & Gauthier, 2004
 Stem-based taxon including all turtles that share a more recent common ancestor with *Pelomedusa subrufa* and *Podocnemis expansa* than with *Chelus fimbriatus* and *Chelodina longicollis* (based on the first phylogenetic definition of the taxon by Joyce *et al.*, 2004).

Pelomedusoides (Broin, 1988 *nomen translatum ex* Pelomedusidae Cope, 1868)
 Node-based taxon including *Pelomedusa subrufa*, *Podocnemis expansa*, and all descendents of their most recent common ancestor (based on the first phylogenetic definition of the taxon by Joyce *et al.*, 2004).

“Panpodocnemidae” Joyce, Parham & Gauthier, 2004
 Stem-based taxon including all turtles that share a more recent common ancestor with *Peltocephalus dumerilianus* and *Podocnemis expansa* than with *Pelomedusa subrufa* and *Pelusios*

subniger (based on the first phylogenetic definition of the taxon by Joyce *et al.*, 2004).

Podocnemoidea Broin, 1988, *nomen translatum ex* Podocnemidae Baur, 1893
 Node-based taxon including *Podocnemis expansa*, *Bothremys cooki*, and all descendents of their most recent common ancestor (first phylogenetic definition of the taxon based on Broin, 1988).

Podocnemoidae Broin, 1988, *nomen translatum ex* Podocnemidae Baur, 1893
 Stem-based taxon including all turtles that share a more recent common ancestor with *Podocnemis expansa* than with *Bothremys cooki* (first phylogenetic definition of the taxon based on Broin, 1988).

Podocnemidae Baur, 1893 (= Podocnemididae Cope, 1868)
 Node-based taxon including *Podocnemis expansa*, *Erymnochelys madagascariensis*, *Peltocephalus dumerilianus*, and all descendents of their most recent common ancestor (based on the first phylogenetic definition of the taxon by Joyce *et al.*, 2004).