A new freshwater turtle (Reptilia, Pleurodira, Podocnemidae) from the Upper Cretaceous (Maastrichtian) of Minas Gerais, Brazil

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ABSTRACT

The fossil fauna of freshwater turtles from the Bauru Basin, south central Brazil, includes only podocnemids (Pleurodira, Pelomedusoides). A new genus and species, *Cambaremys langertoni* n. gen., n. sp., represents a taxon in the stem-lineage to the crown-Podocnemidae. This phylogenetic position is given by the joint presence of a plesiomorphically expanded coracoid and an apomorphic cranially displaced caudal margin of the pectoral scute. Its holotype and only specimen was collected from Late Cretaceous (Maastrichtian) rocks of the Serra da Galga Member (Marília Formation, Bauru Group), in the area of Uberaba, Minas Gerais. Although no autapomorphic features were recognised for *Cambaremys langertoni* n. gen., n. sp., the taxon is distinct from all other South American Cretaceous podocnemids based on an unique suite of shell features, namely: a narrow nuchal plate, seven neural plates, a second neural plate that contacts the first costal plates, a pectoro-abdominal sulcus that does not penetrate the mesoplastra, and xiphiplastra with a deep anal notch and subtriangular ischiadic sutures.

KEY WORDS
Reptilia,
Pleurodira,
Podocnemidae,
Cambaremys langertoni n. gen., n. sp.,
Late Cretaceous,
Bauru Group,
Brazil,
osteology,
new genus,
new species.

RÉSUMÉ

Une nouvelle tortue d'eau douce (Reptilia, Pleurodira, Podocnemidae) du Crétacé supérieur (Maastrichtien) de Minas Gerais, Brésil.

Les faunes fossiles de tortues d'eau douce du Bassin du Bauru (centre-sud du Brésil) n'incluent que des podocnémidés (Pleurodira, Pelomedusoides). Un nouveau taxon, *Cambaremys langertoni* n. gen., n. sp., proche des Podocnemidae, est décrit. Cette position phylogénétique est définie par la présence conjointe d'un caractère plésiomorphe (coracoïde étendu) et d'un caractère apomorphe (bord caudal de l'écaille pectorale déplacé crânialement). L'holotype et seul spécimen connu a été collecté dans les sédiments du Crétacé supérieur (Maastrichtien) du Membre Serra da Galga (Formation Marília, Groupe du Bauru) dans la région d'Uberaba, Minas Gerais. Bien qu'aucun caractère autapomorphe n'a été identifié chez *Cambaremys langertoni* n. gen., n. sp., le taxon se distingue de tous les autres podocnémidés crétacés d'Amérique du Sud par une série unique de caractères de la carapace, notamment une plaque nucale étroite, sept plaques neurales et un contact entre la première plaque costale et la deuxième plaque neurale, un sillon pecto-abdominal qui ne pénètre pas le mesoplastron et un xiphiplastron présentant une encoche anale profonde et des sutures ischiatiques subtriangulaires.

MOTS CLÉS
Reptilia,
Pleurodira,
Podocnemidae,
Cambaremys langertoni n. gen., n. sp.,
Crétacé supérieur,
Groupe du Bauru,
Brésil,
ostéologie,
nouveau genre,
nouvelle espèce.

RESUMO

Uma nova tartaruga de água-doce (Reptilia, Pleurodira, Podocnemidae) do Cretáceo superior (Maastrichtiano) de Minas Gerais, Brasil.

A paleofauna de tartarugas de água doce da Bacia Bauru, centro-sul do Brasil, inclui somente podocnemídeos (Pleurodira, Pelomedusoides). Um novo táxon, *Cambaremys langertoni* n. gen., n. sp., pertence à base da linhagem que conduz ao clado congregando todos Podocnemidae viventes. Tal posição filogenética se baseia na ocorrência conjunta de coracóide plesiomorficamente expandido e margem caudal do escudo peitoral apomorficamente deslocada na direção cranial. O tipo e único espécime conhecido foi coletado em rochas do Cretáceo Superior (Maastrichtiano) do Membro Serra da Galga (Formação Marília, Grupo Bauru) na região de Uberaba, Minas Gerais. Mesmo que nenhuma autapomórfia tenha sido reconhecida em *Cambaremys langertoni* n. gen., n. sp., o táxon se distingue dos demais podocnemídeos do Cretáceo Superior Sul-Americano por um conjunto único de características do casco. Estas incluem uma placa nucal estreita, sete placas neurais, contato entre segunda placa neural e primeiras placas costais, sulco pectoro-abdominal que não penetra no mesolastão, e xifiplastão com entalhe anal profundo e suturas isquiáticas subtriangulares.

PALAVRAS CHAVE
Reptilia,
Pleurodira,
Podocnemidae,
Cambaremys langertoni n. gen., n. sp.,
Cretáceo Superior,
Groupo Bauru,
Brasil,
osteologia,
novo gênero,
nova espécie.

INTRODUCTION

The Bauru Basin, in south central Brazil, was built during the event of isostatic compensation that followed the Early Cretaceous (137 ± 0.7-126 ± 2.0 Ma) basaltic magmatism responsible for the accumulation of the Serra Geral Formation. It was filled by a package of alluvial, fluvial, and eolian sedimentary rocks that dates from the Aptian to the Maastrichtian (Dias-Brito *et al.* 2001).

These deposits have yielded a relatively rich fossil fauna of freshwater turtles (Pacheco 1913; Staesche 1937; Price 1953; Arid & Vizotto 1966; Suárez 1969; Kischlat *et al.* 1994; Langer 1996). Yet, all specimens described so far were assigned to the Podocnemidae, which is the only major group of turtles known in the Brazilian continental Cretaceous. Four nominal taxa have been proposed, namely: *Podocnemis harrisi* Pacheco, 1913, *P. brasiliensis* Staesche, 1937, *P. elegans* Suárez, 1969, and *Roxochelys wanderleyi* Price, 1953. In the most recent review of these forms, Kischlat *et al.* (1994) considered *P. harrisi* a *nomen dubium*, allocating the remaining taxa into two genera:

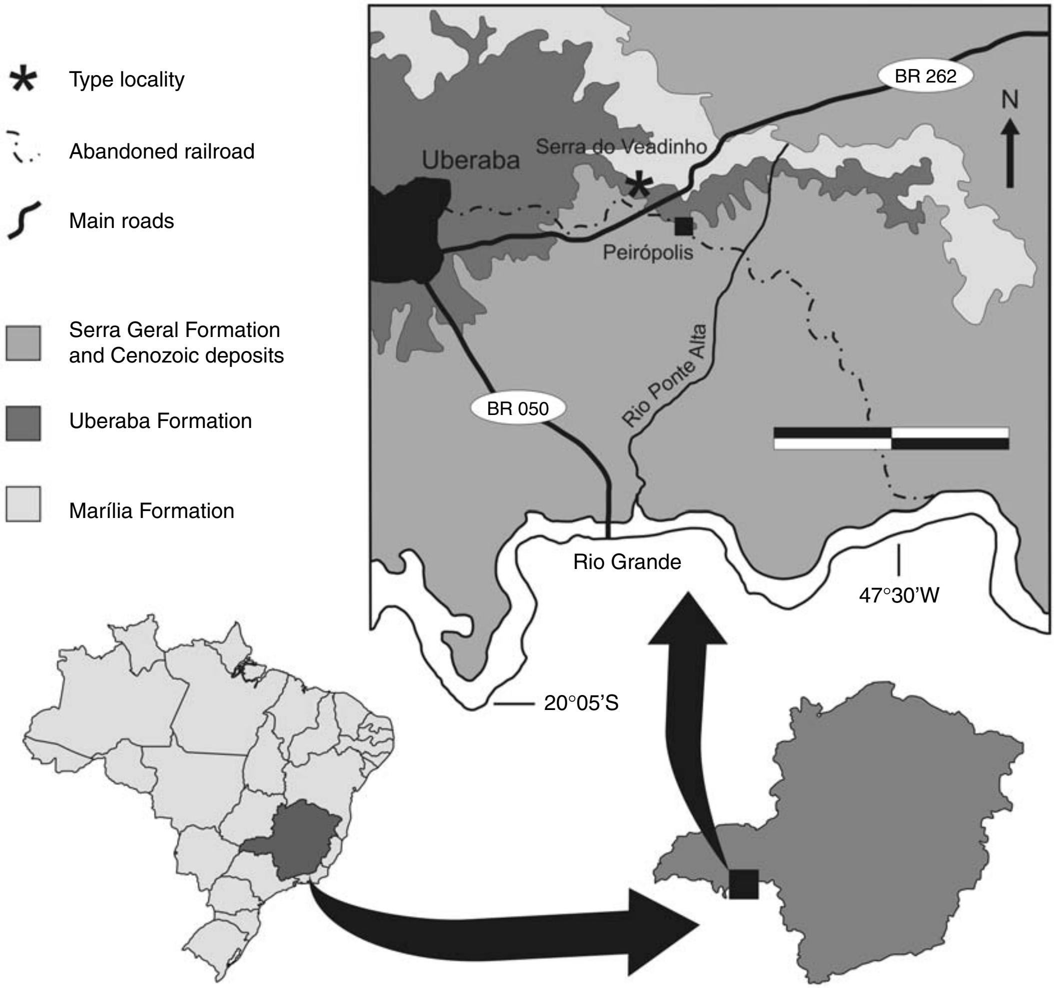

FIG. 1. — Map showing the location of the Serra do Veadinho fossil-area, East of Uberaba, Minas Gerais state, Brazil. Scale bar: 20 km.

Roxochelys Price, 1953, including *R. wanderleyi*, and *Bauruemys* Kischlat, 1994, including "*Podocnemis*" *elegans*, and possibly "*P.*" *brasiliensis*. *Bauruemys elegans* is based on various articulated skeletons, derived mainly from a very rich accumulation in the Adamantina Formation of southwestern São Paulo (Suárez 2002). Indeed, most Testudines recorded in the Bauru Basin have been collected in the state of São Paulo, from deposits assigned to the Adamantina Formation (*sensu* Fernandes & Coimbra 1996). The age of this stratigraphic unit is controversial, but it apparently belongs to the Late Cretaceous (Dias-Brito *et al.* 2001; Gobbo-Rodrigues *et al.* 2003).

In the region known as Triângulo Mineiro, at the western corner of the state of Minas Gerais (Fig. 1), the Bauru Group includes the correlated Uberaba and Adamantina formations, which are covered by the Marília Formation (Fúlfaro & Barcelos 1991; Fernandes & Coimbra 2000). This is a mainly alluvial sequence of Maastrichtian age (Dias-Brito *et al.* 2001), deposited by medial and distal alluvial fans and braided fluvial systems, with subordinate eolian dunes, in a semi-arid climate. It includes the Ponte Alta Member, which suffered post-depositional carbonatic cementation by underground water (Goldberg & Garcia 1995), and the Serra da Galga Member that is composed of non-cemented conglomeratic sandstones. From the site known as Serra do Veadinho, nearby the village of Peirópolis, the Serra da Galga Member has yielded the largest fossil vertebrate collection of the Bauru Basin, including anurans (Baez & Perí 1989), squamates (Estes & Price 1973), crocodiles (Price 1955; Carvalho *et al.* 2004), and dinosaurs (Price 1951, 1961; Kellner 1996; Campos & Kellner 1999; Santucci & Bertini 2001; Powell 2003).

In the austral spring of 1995, during the excavation of Quarry 2, in Serra do Veadinho, which is the sole example of systematic fossil prospecting carried out in Brazilian Mesozoic deposits, the crew of the Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price" collected the semi-articulated post-cranium of a freshwater turtle. This specimen was subject of preliminary studies by Langer (1996) and França & Langer (2003), and is the focus of this contribution. It represents the first relatively complete testudine specimen rescued from the Marília Formation, and is unique among Cretaceous podocnemids for the nearly complete preservation of its appendicular skeleton.

The collection of the Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price" (CPP), located at the former train station of the village of Peirópolis, includes several testudine specimens collected at Quarry 2. Most of which consist of taxonomically indeterminate shell fragments, whereas the semi-articulated post-cranium of CPP-0252 is a notable exception. It was compared to *Bauruemys elegans* based on URC-R47, R58, R59, and R60, to other fossil pleurodires based on the literature, as well as to skeletons of various recent South American chelids and podocnemids, i.e. *Chelus fimbriata* (Schneider, 1783), MZUSP-1027; *Hydromedusa tectifera* (Cope, 1969), MZUSP-2022, 4104, 305; *Phrynops geoffroanus* (Schweigger, 1812), MZUSP-2633, 2638, 2637; *Peltocephalus dumerilianus* (Schweigger, 1812), MZUSP-3216, 3138, 3137, 3139, 2753; *Podocnemis erythrocephala* (Spix, 1824), INPA-10274; *P. expansa* (Schweigger, 1812), MZUSP-2810, 2761, 2844, LIRP unnumbered; *P. sextuberculata* (Cornalia, 1849), INPA-8953; and *P. unifilis* (Troschel, 1848), MZUSP-3209, 2026, 2809, INPA-11559. The nomenclature proposed by Zangerl (1969) for the dermal scutes and bony plates of the turtle shell is employed here, while the anatomical terms and orientation of the limb bones of these animals are those of Walker (1973) and Gaffney (1990). In the Systematics section, the phylogenetic meanings of the names are as proposed by Meylan (1996). Regarding the family-group names derived from *Podocnemis* Wagler, 1830, we employ the suffixation of Baur (1893; see Joyce *et al.* 2004), i.e. Podocnemidae and coordinates. Yet, following the *International Code of Zoological Nomenclature* (ICZN 1999: Art. 36), the authorship is referred to Cope (1868), who first proposed a family-group name based on that genus.

ABBREVIATIONS

CPP	Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price", Uberaba;
INPA	Instituto Nacional de Pesquisas na Amazônia, Manaus;
LIRP	Laboratorio 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.

SYSTEMATICS

TESTUDINES Linnaeus, 1758
PLEURODIRA Cope, 1865
PELOMEDUSOIDES Cope, 1868 (Broin 1988)
PELOMEDUSOIDEA Cope, 1868 (Lindholm 1929)
PODOCNEMOIDAE Cope, 1868 (Meylan 1996)
PODOCNEMIDAE Cope, 1868

Genus *Cambaremys* n. gen.

TYPE SPECIES. — *Cambaremys langertoni* n. gen., n. sp. by present designation.

ETYMOLOGY. — In allusion to Cambará, the former name of the village of Peirópolis, Minas Gerais, near which the type locality is located (Fig. 1).

DISTRIBUTION. — Latest Cretaceous (Maastrichtian) of the Bauru Basin in the region known as "Triângulo Mineiro", Minas Gerais, Brazil.

DIAGNOSIS. — As for the type species, by monotypy.

Cambaremys langertoni n. sp.

HOLOTYPE. — CPP-0252, cervical vertebra, partial carapace, right mesoplastron, both xiphiplastra, both coracoids, right scapula, both humeri, left radius, both ulnae, both pelvic girdles, right femur, both tibiae, both fibulae, along with other disarticulated remains including carpals, tarsals, metapodials, and phalanges, including an ungual (Figs 2-8).

ETYMOLOGY. — In honor to Sr. Langerton Neves da Cunha, "field-man" of Llewellyn Ivor Price during the 1960s and early 1970s, and collector of many important fossils in the area of Peirópolis.

TYPE HORIZON. — Serra da Galga Member, Marília Formation, Bauru Basin (Fernandes & Coimbra 2000). Studies based on microfossils (Dias-Brito *et al.* 2001; Gobbo-Rodrigues *et al.* 2003) and vertebrates (Santucci & Bertini 2001) agree with a latest Cretaceous (most probably Maastrichtian) age for this stratum.

TYPE LOCALITY. — 19°43'12"S, 47°45'04"W. Quarry 2 of Price (see Campos & Kellner 1999), at 900 m high, in the Serra do Veadinho area, municipality of Uberaba, Minas Gerais, Brazil; about 2.5 km to the N-NW of the village of Peirópolis (Fig. 1).

DIAGNOSIS. — Podocnemid with a pectoral scute that does not touch the mesoplastron and an expanded coracoid. Distinct from other named South American Cretaceous members of the group for its thin shell bones, narrow nuchal plate, seven neural plates, and contact between first costal and second neural plates.

DESCRIPTION

Axial skeleton (Fig. 2; Table 1)

Of the vertebral column, only two cervicovertebral fragments were preserved, one including the centrum and the other most of the neural arch. Both encompass parts of the transverse processes, which are incomplete distally, and located at the middle of the axial length, as common among eupleurodires (Lapparent de Broin 2000). Those fragments were not found in articulation, but giving their similar size and contact, they will be treated as a single element. Considered together, these account for a vertebra slightly longer than high. The centrum is procoelous, possessing a distinct ventral keel that extends more ventrally

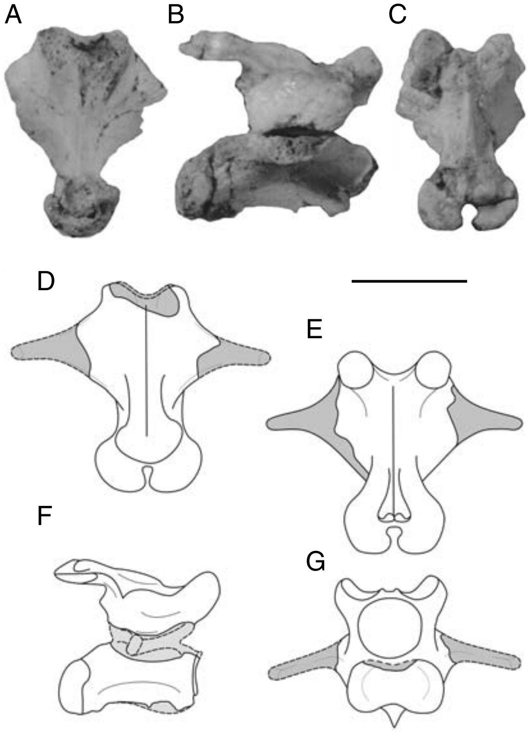

FIG. 2. — Cervicovertebral elements of *Cambaremys langertoni* n. gen., n. sp. (CPP-0252), possibly from the same vertebra; **A**, centrum, ventral aspect; **B**, centrum and neural arch, right lateral aspect; **C**, neural arch, dorsal aspect; **D**-**G**, reconstruction of cervical vertebra; **D**, ventral aspect; **E**, dorsal aspect; **F**, right lateral aspect; **G**, cranial aspect. Non-preserved parts in gray. Scale bar: 15 mm.

TABLE 1. — *Cambaremys langertoni* n. gen., n. sp. (CPP-0252), measurements of the cervicovertebral elements (mm). Abbreviations: **dv**, dorsoventral; **lm**, lateromedial.

Centrum length	13.5
Centrum cranial articulation width (dv × lm)	5.0 × 7.0
Centrum caudal articulation width (dv × lm)	4.5 × 5.0
Neurocentral articulation length	6.9
Neural arch total length	14.5
Neural arch maximum height (caudal)	7.0
Prezygapophyseal width	7.8
Postzygapophyseal width	6.9
Neural channel middle width	3.1

at its cranial part. The neural arch bears a low neural spine extending along most of its dorsal surface. The prezygapophyses project cranially as separate elements, while the postzygapophyses are supported by a common elevated process (pedicel), as also typical of eupleurodires (Lapparent de Broin 2000), that expands caudodorsally. Its dorsal surface bears a pair of rounded protuberances, caudal to which the postzygapophyses extend to form a nearly continuous rounded articulation surface. Differently from *Araripemys* (Meylan 1996), the postzygapophyses are not fused together.

The position in the neck of the recovered vertebral elements of CPP-0252 is not clear. Put together, they differ from the eighth cervical vertebra of extant podocnemids (*Peltocephalus* and *Podocnemis*) for the caudally inclined pedicel and least developed ventral keel, and from the other caudal cervical vertebrae of those Testudines for the more discernible neural spine. If the cranial position of these elements is confirmed, their procelic centrum suggests a basal phylogenetic position for CPP-0252 in relation to the crown-Podocnemidae (Joyce *et al.* 2004), the cranial cervical vertebra of which have apomorphic heterocelic caudal condyles. According to Kischlat *et al.* (1994; but see Broin 1991; Lapparent de Broin 2000), such a plesiomorphic condition is shared by *Roxochelys* and *Bauruemys*, while in other South American fossil podocnemids (Broin 1971; Wood 1976) most of the neck is composed of heterocelic vertebrae.

Carapace (Figs 3-5)

The nuchal plate, the entire neural series, and most costal and marginal elements were preserved, but not the pygal or suprapygal plates. These, as well as the plastron bones, are not particularly thick, differing from forms attributable to the genus *Roxochelys* (Price 1953; Broin 1991), and no distinctive ornamentation pattern has been observed on their external surface. The round shape (25 cm long, 20 cm wide) and relatively flat (5 cm high) carapace of *Cambaremys* n. gen. is most similar to those of small ?*Roxochelys villavilensis* (Broin 1991) and some specimens from the Bauru Group (Arid & Vizotto 1966; Suárez 1969), but distinct from the deeper, more dorsally convex, and elongated carapace of other South American Cretaceous podocnemids (Broin 1971; De la Fuente 1993, 2003; Kischlat *et al.* 1994; Lapparent de Broin 2000). Yet, the shape of the carapace is highly variable among modern members of the group, and might reflect the developmental stage of the individuals (Broin 1991), the more rounded morphotype representing the juveniles. Accordingly, the size and shape of the type carapace of *Cambaremys* n. gen. might indicate a subadult condition, but a direct relation between the size and shape of the carapaces is not seen among various observed specimens of *Bauruemys elegans* (URC-R47, R58, R59).

The nuchal embayment is shallow and restricted to the cranial margin of the nuchal plate. This is elongated, articulates with the first peripheral plates along its slightly concave lateral margins, and expands caudally to contact the first neural and costal plates along a rounded caudal margin. This condition approaches that of *Bauruemys elegans*, although the nuchal plate of this taxon has a more extensive contact with the pair of first costals. A much broader nuchal plate is, however, characteristic of other South American Cretaceous podocnemids (Price 1953; Broin 1971; Lapparent de Broin 2000; De la Fuente 2003).

There are seven preserved neural plates, which represent the entire series. As in most non-araripemydid Pelomedusoides (Meylan 1996), this series does not reach the suprapygal plate. The number of neural plates varies between six and seven within the extant Podocnemidae, while South American fossil forms with six (Suárez 1969; De la Fuente 1993, 2003) and seven (Arid & Vizotto 1966; Broin 1971; Wood 1976; Lapparent de Broin 2000; Carvalho *et al.* 2002) neural plates are also known. The first neural plate is subrectangular and more elongated if compared to the following ones. It meets the nuchal plate cranially, and its slightly convex lateral and caudal margins articulate respectively with the pair of first costals and with the second

FIG. 3. — Partial carapace of *Cambaremys langertoni* n. gen., n. sp. (CPP-0252), dorsal aspect. Scale bar: 20 mm.

neural plates. This arrangement is similar to that of most fossil podocnemids (Price 1953; Arid & Vizotto 1966; Broin 1971; Lapparent de Broin 2000; Carvalho *et al.* 2002), but differs from that of *Bauruemys* (Suárez 1969; URC-R47, R58), in which the first neural plate is much broader caudally, and the second neural plate square-shaped. This peculiar arrangement of plates allows the contact between the first neural plate and the pair of second costal plates, preventing a contact between the second neural plate and the pair of first costal plates. Yet, the difference between this and the standard podocnemid morphology must be considered carefully, given that variation seems to occur within major groups (Gaffney *et al.* 2001), extant species (E.-E. Kischlat pers. comm.

FIG. 4. — Partial carapace of *Cambaremys langertoni* n. gen., n. sp. (CPP-0252), visceral aspect. Scale bar: 20 mm.

1995), and even individuals (De la Fuente 2003; see also Lapparent de Broin 2000).

Neural plates 2-6 of *Cambaremys* n. gen. are hexagonal, their cranial and caudal margins contact the adjacent costal plates, while their lateral margins are divided in shorter laterocranial and longer laterocaudal facets, which respectively contact the anterior and the corresponding costal plates. Of these, the sixth neural plate is shorter craniocaudally, possessing a more rounded caudal margin. As with the sixth, the seventh neural plate was not preserved in articulation to the rest of the carapace and its margins are not complete. It has a subpentagonal shape, reflecting its condition as the last plate of the neural series. It has a pinched caudal

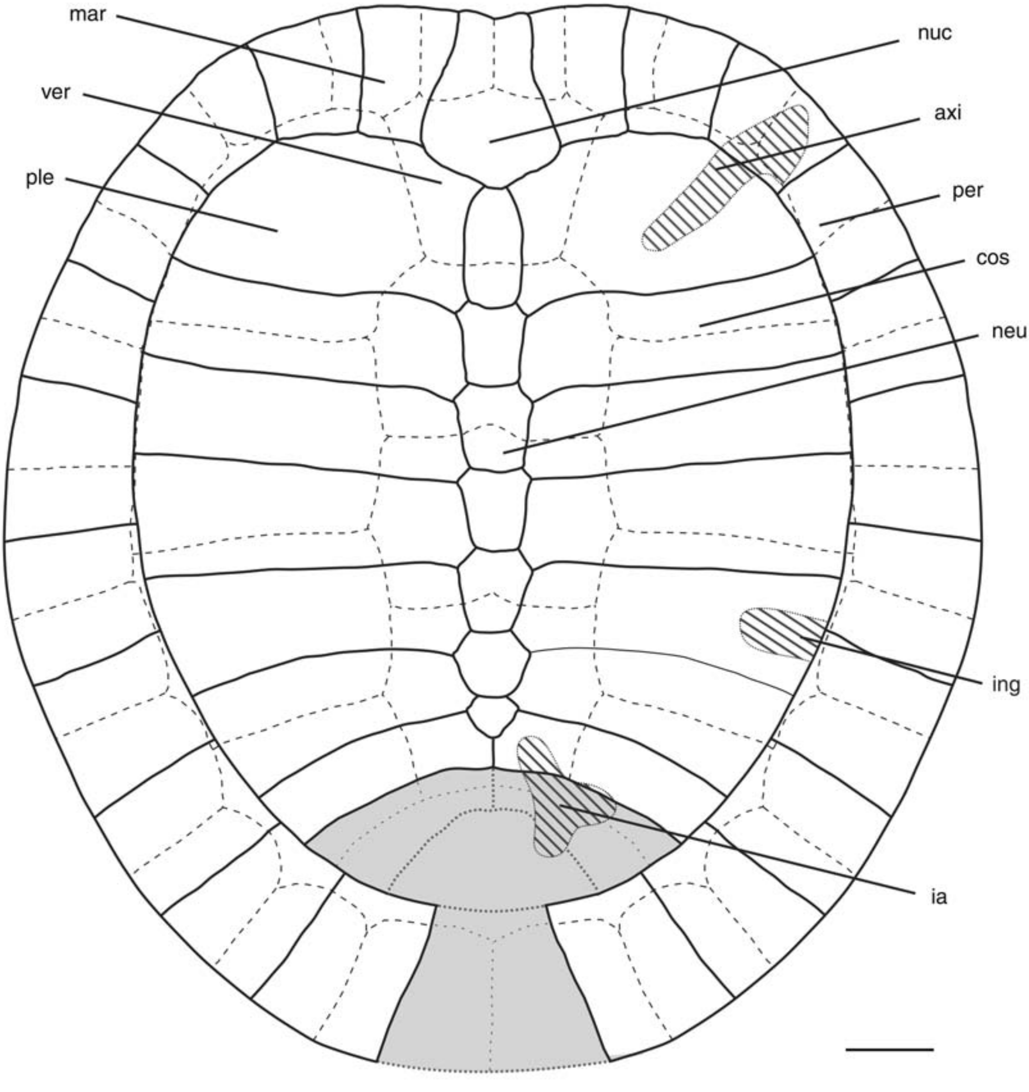

FIG. 5. — Reconstruction of the carapace of *Cambaremys langertoni* n. gen., n. sp. (CPP-0252), dorsal aspect. Abbreviations: **axi**, axillary process; **cos**, costal plate; **ia**, iliac articulation; **ing**, ingunal process; **mar**, marginal scute; **neu**, neural plate; **nuc**, nuchal plate; **per**, peripheral plate; **ple**, pleural scute; **ver**, vertebral scute. Hatched areas indicate structures on the inner side of the carapace. Non-preserved parts in gray. Scale bar: 20 mm.

margin that articulates only with the pair of seventh costal plates.

Costal plates 1-7 were preserved partially articulated on the left side of the carapace, while the eighth plate was not recovered. The first costal plates are longer craniocaudally than the rest. Their rounded cranial margins contact the nuchal plate and peripheral plates 1-4. Costal plates 2-7 are subrectangular, their lateral portion curves cranially in the more cranial plates and caudally in the more caudal ones. Laterally, they contact peripheral plates 4-10 as shown in Figure 5, and only the seventh pair contacts one another medially. Although only left peripheral plates 1-7 were found in articulation, it was possible to reconstruct the entire series (1-11) with elements from at least one of the sides of the carapace (Figs 3-5). These are subrectangular and have slightly convex distal margins, which form the carapace border. Cranial and caudal peripheral plates are elongated proximodistally, while those in the middle of the series tends to be shorter.

The plastral bridge is better preserved on the left side of the carapace (Fig. 4), encompassing peripheral plates 2-8. At the cranial end of the bridge, the axillary process extends medially as a smoothly sigmoid wall that articulates with the internal surface of the first costal plate. Caudally, the articulation facet for the inguinal process extends nearly straight along the distal third of the fifth costal plate. The angle formed between the dorsal and ventral surfaces of the peripheral plates that contribute to the bridge is of about 45° at the third plate, expanding to 90° at the level of plates 5-6. In the seventh plate, the angle is of about 75° at its cranially and of 30° caudally. In the end of the bridge (eighth plate), the angle diminishes to about 5-10°.

Based on the pattern of contact sulci in its carapace, *Cambaremys langertoni* n. gen., n. sp. possessed no cervical scute, and the first marginal scute met its mate at the cranial border of the carapace, where they covered the cranial portion of the nuchal plate. Caudally, the vertebral scutes covered the entire neural series and the medial portions of the costal plates, while the first of them also covered the caudal half of the nuchal plate and the caudomedial corners of the first peripheral pair. On each of these plates, there is a complex sulcus pattern composed of two triradiated junctions including marginal scutes 1 and 2, vertebral scute 1, and pleural scute 1. It is also possible to reconstruct vertebral scutes 2 and 3, while the parts of scutes 4 and 5 that cover the pygal and suprapygal plates are unknown. The preserved sulci between vertebral scutes 1-2, 2-3, and 3-4 respectively divide neural plates 1, 3, and 5. Each bears a marked cranial convexity at the sagittal axis, which is least marked in the sulcus between scutes 1 and 2. Among the examined podocnemids, this differs from the condition in forms like *Peltocephalus* (MZUSP-3137), *Portezueloemys* (De la Fuente 2003), and *Bauruemys elegans* (Suárez 1969), which has a caudally convex sulcus between vertebral scutes 1 and 2; *Peltocephalus*, *Roxochelys wanderleyi* (Price 1953), ?*Roxochelys vilavilensis* (Broin 1971), and *Podocnemis negrii* (Carvalho *et al.* 2002), the sulcus between vertebral scutes 2 and 3 of which is not markedly convex cranially; and *Podocnemis negrii* that has a caudally convex sulcus between vertebral scutes 3 and 4.

The four pleural scutes covered the distal two-thirds of the costal series, and the sulci between them extend transversely along costal plates 2, 4, and 6. The marginal series covered most of the peripheral plates, each scute occupying adjacent halves of two neighboring plates. The sulci between the marginal and pleural scutes extends along the proximalmost portion of the peripheral plates at the cranial (plates 1-3) and caudal (plates 7-11) segments of the series, while it is displaced proximally at the middle of the series, and superimposed to the peripheral-costal plates contact. This is also seen in most examined podocnemids, but not *Bauruemys elegans* (Suárez 1969), and ?*Roxochelys vilavilensis* (Broin 1971).

Plastron (Fig. 6)

Most of the plastron is missing, probably due to *post-mortem* disarticulation and transport, but the right mesoplastron and both xiphiplastra were found inside the carapace, which was preserved upside-down. The former is round, restricted to the lateral portion of the plastron. This configuration is typical of podocnemoids (*sensu* Lapparent de Broin 2000), also seen in other Pelomedusoides (Broin 1980; Gaffney & Meylan 1991), but distinct from the more lateromedially elongated mesoplastron of basal eupleurodires (De la Fuente & Iturralde-Vinent 2001) and basal chelids (De la Fuente *et al.* 2001; De la Fuente 2003). In this context, the mesoplastra were most probably apomorphically connected in *Pelusios* and independently lost in recent Chelidae and *Araripemys* (Meylan 1996). The mesoplastron of *Uberamemys* has no sign of interscute sulci. On the contrary, the pectoro-abdominal sulcus of most basal pleurodires (Broin 1980; Gaffney & Meylan 1991; De la Fuente *et al.*

2001; De la Fuente & Iturralde-Vinent 2001; De la Fuente 2003) extends along the cranial portion of that plate. Among podocnemoids, the pectoro-abdominal sulcus usually enters the cranial border of the mesoplastron in bothremydids (Antunes *et al.* 1988; Gaffney *et al.* 2001; MacPhee *et al.* 2003), but not in either fossil (Cattoi & Freiberg 1958; Suárez 1969; Broin 1971; Wood 1976; Carvalho *et al.* 2002; De la Fuente 2003), or recent podocnemids, although there are exceptions within both groups (De la Fuente 1993; Tong *et al.* 1998).

The right xiphiplastron (Fig. 6A, B) is well preserved, sub-orthogonal, and broader cranially. Its cranial and lateral edges form oblique angles to the sagittal line, while the caudolateral corner is rounded. The caudal margin is gently inclined, so that a shallow anal incisure is formed. Among South American Cretaceous podocnemids, this approaches the condition of *Bauruemys elegans* (Suárez 1969; URC-R47, R58) and ?*Roxochelys vilavilensis* (Broin 1991), differing from the more conspicuous incisure of "*Podocnemis*" *brasiliensis* (Price 1953). Yet, significant intraspecific variation regarding this character was reported among podocnemids (Wood & Gamero 1971). The visceral surface of the xiphiplastron bears the articulation facets for the pubis and ischium. The pubic articulation is ovoid as in ?*Roxochelys vilavilensis* (Broin 1971), and not as elongated as in *Bauruemys elegans* (Suárez 1969) and "*Podocnemis*" *brasiliensis* (Price 1953). This does not seem to be fused, since suture scars are apparent. According to Kischlat *et al.* (1994), this condition is seen in *Bauruemys elegans*, but not in *Roxochelys*. The ischiadic articulation is subtriangular, with craniomedial, craniolateral, and caudolateral apexes. This resembles the condition in ?*Roxochelys vilavilensis* (Broin 1971), and differs from the more medially expanded suture of *Bauruemys elegans* (Suárez 1969) and "*Podocnemis*" *brasiliensis* (Price 1953). However, important variation in the shape of the pubic and ischiadid sutures to the plastron occurs among recent podocnemids. The external surface of the xiphiplastron bears the femoro-anal sulcus, extending obliquely at the level of the pubic articulation scar, well within the cranial half of the xiphiplastron.

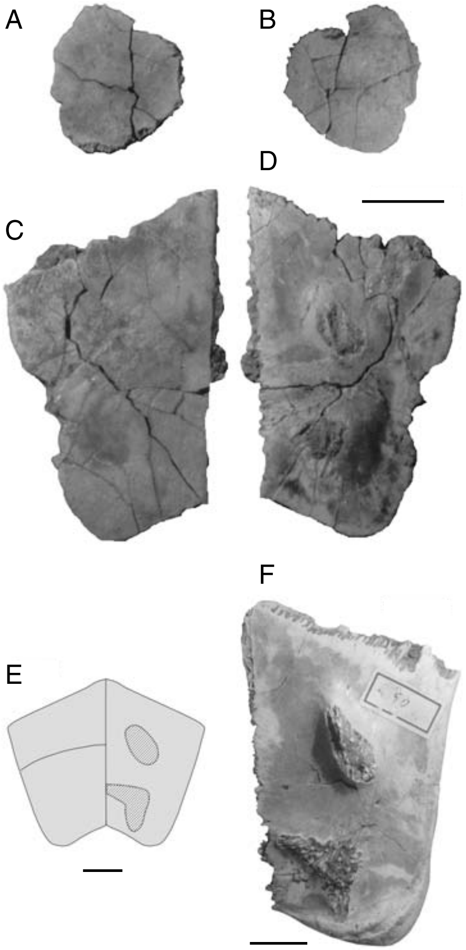

Fig. 6. — **A**-**E**, plastral elements of *Cambaremys langertoni* n. gen., n. sp. (CPP-0252); **A**, **B**, right mesoplastron; **A**, ventral aspect; **B**, visceral aspect; **C**, **D**, right xifiplastron; **C**, ventral aspect; **D**, visceral aspect; **E**, composite reconstruction of the xiphiplastra in ventral and visceral aspects; **F**, right xifiplastron of cf. *Cambaremys langertoni* n. gen., n. sp. (CPP-0290) in visceral aspect. Scale bars: 20 mm.

Pectoral girdle and forelimb (Fig. 7; Table 2)

The scapula has elongated rod-like dorsal and acromial processes. These form an angle of about 80° and no bony wall extends distally connecting them. This is typical of podocnemids, and differs from the condition in modern chelids. The dorsal

FIG. 7. — Pectoral girdle and forelimb elements of *Cambaremys langertoni* n. gen., n. sp. (CPP-0252); **A**, **B**, right scapula; **A**, cranial aspect; **B**, caudal aspect; **C**, **D**, right coracoid; **C**, dorsal aspect; **D**, ventral aspect; **E**-**I**, right humerus; **E**, dorsal aspect; **F**, ventral aspect; **G**, caudal aspect; **H**, cranial aspect; **I**, proximal aspect; **J**, **K**, left radius; **J**, ventral aspect; **K**, lateral aspect; **L**, right radius, ventral aspect; **M**-**P**, right ulna; **M**, dorsal aspect; **N**, ventral aspect; **O**, medial aspect; **P**, lateral aspect. Non-preserved parts indicated by stippled lines. Scale bar: 20 mm.

process curves slightly medially, and bears no clearly defined longitudinal ridges or grooves. This differs markedly from the strongly curved and short process of *Stupendemys* (Gaffney *et al.* 1998), but approaches the condition of recent podocnemids. Its proximal portion is craniocaudally flattened and have an ovoid cross section. The distal tip is incomplete, but seems to be slightly expanded. The shorter acromial process also has an oval proximal cross section. At this point, its craniodorsal corner is composed of a marked longitudinal ridge, bounded ventrally by an elongated excavation. Distally, the cross section of the acromial process gets subtriangular, due to the presence of craniodorsal and ventral grooves, and a longitudinal ridge at the caudal surface. Among modern podocnemids, the development of these elements varies, and different specimens show more transversally rounded or triangular acromia. The scapular part of the glenoid cavity faces laterally as in most podocnemids, and not ventrolaterally as in *Stupendemys* (Gaffney *et al.* 1998). It is slightly projected from the main part of the bone, and has prominent borders, but no proper glenoid neck is seen. The articulation is subtriangular, with the cranial face the longest, and concave. The coracoid articulation is ovoid, not clearly marked, and placed caudoventrally to the glenoid cavity.

The coracoid is composed of a proximal articulation and a distal body. The former is rounded, but flattened craniodorsally. This is where the scapula articulates, while the rest of that area forms the glenoid cavity. The main body of the bone is cylindrical proximally, but expands distally to form a dorsoventrally flattened lamina. Its dorsal surface is slightly convex as in *Peltocephalus*, lacking the sharp longitudinal ridge typical of *Podocnemis*. The ventral surface is concave, more deeply excavated laterally, and the distal margin is flattened. Kischlat *et al.* (1994) characterized two distinct coracoid morphotypes among fossil and recent podocnemids. *Cambaremys* n. gen. shares the plesiomorphic type with *Bauruemys elegans* and ?*Roxochelys vilavilensis*. This is expanded and slim (= dorsoventrally flat), as also seen in chelids (De la Fuente 1993), *Araripemys* (Meylan 1996), and pelomedusids (Wood 1976). The apomorphic condition, on the other hand, is an unexpanded and deep coracoid, as seen in modern podocnemids, *Erymnochelys*, *Stupendemys*, and apparently *Roxochelys wanderleyi* (Kischlat *et al.* 1994).

TABLE 2. — *Cambaremys langertoni* n. gen., n. sp. (CPP-0252), measurements of the pectoral girdle and forelimb elements (mm). Abbreviations: **cc**, craniocaudal; **dv**, dorsoventral; **lm**, lateromedial. Measurements given under brackets correspond to the preserved portions of incomplete bones.

Measurements	Right side	Left side
Scapula		
Length	(51.3)	–
Middle width (lm × cc)	3.9 × 5.3	–
Glenoid cavity width (dv × cc)	8.9 × 6.7	–
Acromion length	27.4	–
Acromion distal width (lm × cc)	6.3 × 5.4	–
Coracoid		
Length	33.6	34.0
Glenoid cavity width (dv × lm)	5.7 × 5.5	5.6 × (4.8)
Minimal width (dv × lm)	3.2 × 2.9	3.2 × 3.0
Distal width (dv × lm)	1.7 × 11.2	1.4 × 10.9
Humerus		
Length	33.7	(26.8)
Proximal width (cc)	19.7	18.5
Middle width (cc × dv)	6.4 × 6.9	–
Distal width (cc × dv)	12.3 × 7.9	–
Head width (lm × cc)	8.3 × 7.5	8.2 × 7.3
Radius		
Length	20.7	(14.9)
Proximal width (dv × lm)	3.6 × 3.9	3.8 × 2.6
Middle width (dv × lm)	2.1 × 2.3	2.0 × 2.4
Distal width (lm)	7.3	–
Ulna		
Length	20.1	–
Proximal width (dv × lm)	6.2 × 4.6	–
Middle width (dv × lm)	2.4 × 3.5	–
Distal width (dv × lm)	3.1 × 5.0	–

Both humeri were preserved, although the distal half of the left bone is missing. The head forms a nearly equidimensional hemisphere, and the lateral and medial processes expand at the same ventral plane. These are connected to the dorsally projecting head by bony expansions, forming a ventrally concave surface. Shallow excavations mark the proximal limits between both processes and the head. The lateral process projects cranioproximally as in other podocnemids, and differs from the more laterally directed process of chelids. At its distal margin, lies a dorsocranial ovoid excavation for the insertion of the M. deltoideus. An equally marked muscle scar is seen in *Podocnemis*, but not in *Peltocephalus* or the examined recent chelids. The medial process is caudoproximally directed and somewhat larger than the lateral. Its proximal tip extends slightly proximal to the head. This condition is shared by

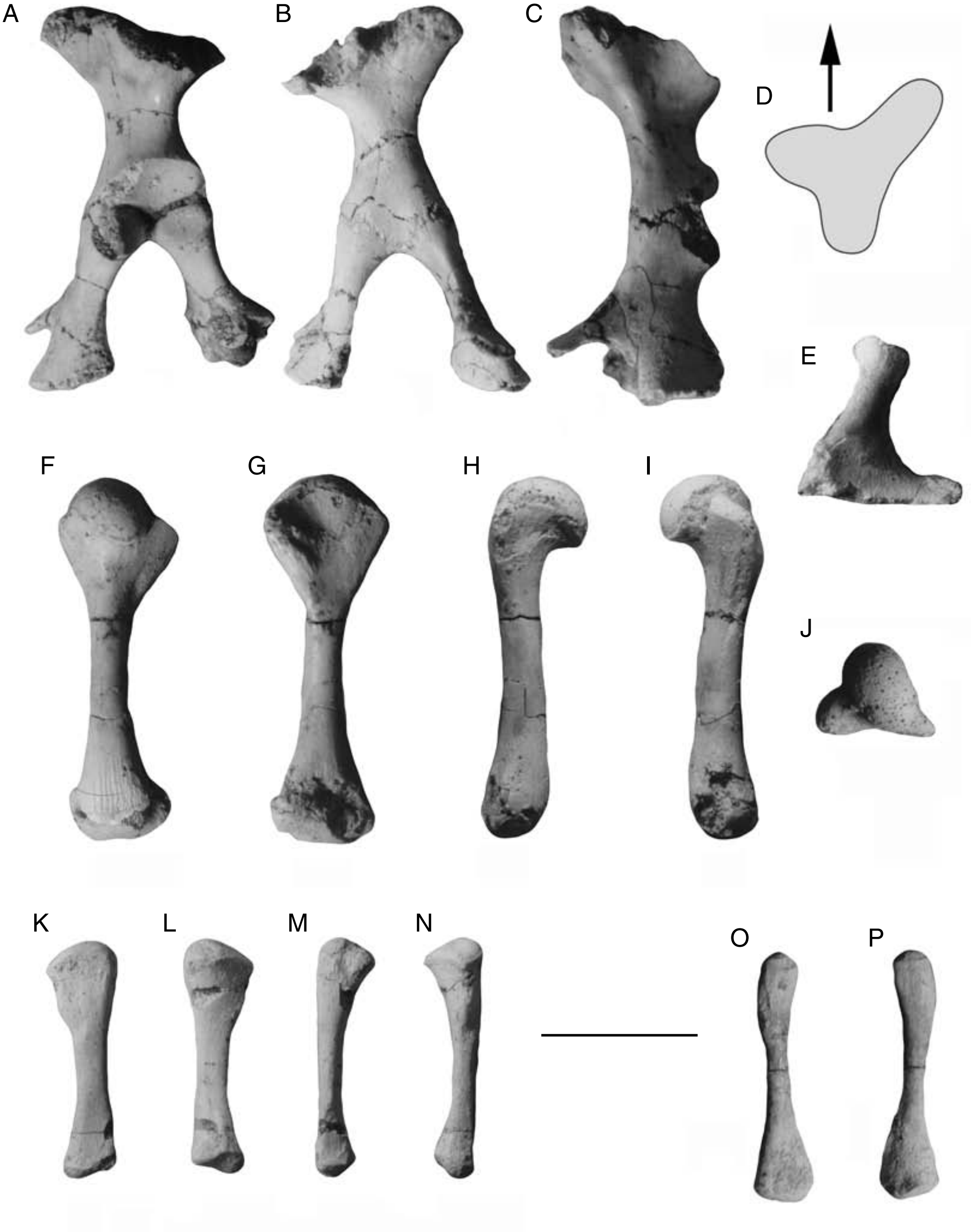

FIG. 8. — Pelvic girdle and hind limb elements of *Cambaremys langertoni* n. gen., n. sp. (CPP-0252); **A**-**D**, left pelvic girdle; **A**, lateral aspect; **B**, medial aspect; **C**, cranial aspect; **D**, outline of iliac articulation to the carapace, dorsal aspect, arrow points cranially; **E**, right ischium, medial aspect; **F**-**J**, right femur; **F**, dorsal aspect; **G**, ventral aspect; **H**, caudal aspect; **I**, cranial aspect; **J**, proximal aspect; **K**-**N**, left tibia; **K**, dorsal aspect; **L**, ventral aspect; **M**, lateral aspect; **N**, medial aspect; **O**, **P**, left fibula; **O**, dorsal aspect; **P**, ventral aspect. Scale bar: 20 mm.

Stupendemys (Broin *et al.* 1993) and recent Chelidae, while the humeral head of *Podocnemis* tends to project more proximally than that process. According to Walker (1973) the medial process is more developed in highly aquatic Testudines such as marine turtles and trionychids. Accordingly, this condition in *Cambaremys* n. gen. might, at the same time, represent a plesiomorphy and an adaptation to its aquatic lifestyle. Also differently from recent *Podocnemis*, no clear scar for the M. subscapularis is seen on the medial process, which lacks marked crests or grooves.

The humeral shaft of *Cambaremys* n. gen. is dorsally arched and ovoid in cross section. As in recent podocnemids, the proximal and distal expansions of the bone are longitudinally restricted, so that the shaft is proportionally longer than that of chelids. At the distal end of the humerus, the radial and ulnar condyles are ventrally directed. These are of about the same size and there is no strong incisure between them. The entepicondyle and ectepicondyle are inconspicuous, but the latter is slightly larger and bears a deeply excavated groove. This extends longitudinally along the dorsomedial surface of the bone, and is homologous to the ectepicondylar foramen (Romer 1956; Gaffney 1990), but does not perforate the humerus.

Both radia are incompletely preserved, the left bone lacks most of its distal expansion, while the right radius lacks portions of both the proximal and distal ends. The latter can, however, be reconstructed based on the impression with fragments it left on the matrix. The proximal articulation is nearly flat and roughly semicircular: longer dorsoventrally than lateromedially and flatter laterally to contact the ulna. Right distal to this contact there is a rugosity that represents the attachment of the proximal branch of the radio-ulnar ligament (Haines 1942). The distal end of the radius is dorsoventrally flattened and lateromedially expanded to contact the intermedium and medial centrale. This expansion is more remarkable in *Cambaremys* n. gen. than in recent *Podocnemis*, and its lateral portion projects further distally in the former, so that its distal margin is less obliquely inclined, as also seen in *Araripemys* (Meylan 1996).

Only the right ulna of *Cambaremys* n. gen. was preserved, and its laterodistal corner is missing. The proximal surface is subrectangular, longer dorsoventrally than lateromedially. This is given by the ventral projection of the articulation surface, as seen in *Podocnemis* but not in *Peltocephalus*. The dorsal part of this surface is proximally projected, forming the inconspicuous olecranon process. The medial ulnar surface bears a well developed bicipital tubercle. It lays at the middle of the proximal half of the bone, clearly separated from its proximal articulation. Distal to this tendon attachment area, the medial margin of the ulna is composed of a pinched crest. At its distal third, the bone gets dorsoventrally flattened, with an elongated cross section. The ulna expands markedly at its distal margin, bearing a oblique and flat medial articulation facet for the intermedium.

Pelvic girdle and hind limb (Fig. 8; Table 3)

Both pelvic girdles were preserved disarticulated from the shell and are nearly complete, although the right one is partially covered by matrix. As typical of eupleurodires (Lapparent de Broin & Murelaga 1999; Lapparent de Broin 2000; De la Fuente & Iturralde-Vinent 2001), the pelvis of *Cambaremys* n. gen. has a mainly vertical orientation, and the thyroid fenestrae are united as a single large aperture. This condition is shared by other fossil podocnemoids (Wood 1972, 1976; De la Fuente 1993, 2003; Lapparent de Broin & Werner 1998; Carvalho *et al.* 2002). The pelvic bones are firmly attached, and their medial contact is represented by a serrated suture. Laterally, there is a small gap between the bones that was probably filled by cartilage of the acetabular capsule. Each ilium is formed of a central waist, with dorsal and ventral expansions. The former articulated to costal plates 7-8, only the first of which is preserved in *Cambaremys* n. gen. This articulation is triradiated in dorsal aspect, with cranial, caudal, and caudolateral projections, the first of which is longer and more pinched. This differs from the condition of non-Pelomedusoides (*sensu*

TABLE 3. — *Cambaremys langertoni* n. gen., n. sp. (CPP-0252), measurements of the pelvic girdle and hind limb elements (mm). Abbreviations: **cc**, craniocaudal; **dv**, dorsoventral; **lm**, lateromedial. Measurements given under brackets correspond to the preserved portions of incomplete bones.

Measurements	**Right side**	**Left side**
Ilium		
Length	–	27.7
Proximal width (cc × lm)	–	22.5 × 1.8
Middle width (cc × lm)	–	6.5 × 6.4
Distal width (cc × lm)	–	13.2 × 10.2
Pubis		
Length	–	25.2
Proximal width (cc × lm)	–	6.4 × 10.4
Middle width (cc × lm)	–	3.2 × 9.6
Distal width (cc × lm)	–	6.6 × 8.5
Ischium		
Length	–	21.4
Proximal width (cc × lm)	–	6.7 × 8.7
Middle width (cc × lm)	–	3.5 × 7.6
Distal width (cc × lm)	–	8.6 × (14.5)
Acetabulum width (dv × cc)	–	12.3 × 10.1
Femur		
Length	–	44.1
Distal width (cc × dv)	–	12.3 × 7.5
Middle width (cc × dv)	–	4.8 × 5.3
Proximal width (cc)	–	17.6
Head width (lm × cc)	–	9.8 × 9.1
Tibia		
Length	30.3	30.6
Proximal width (dv × lm)	7.6 × 9.3	7.6 × 9.3
Middle width (dv × lm)	2.8 × 4.3	2.9 × 4.3
Distal width (dv × lm)	5.4 × 6.8	5.3 × 6.8
Fibula		
Length	(27.9)	30.1
Proximal width (dv × lm)	2.7 × 4.6	2.9 × 4.5
Middle width (dv × lm)	2.3 × 2.9	2.1 × 2.8
Distal width (dv × lm)	–	4.5 × 7.3

Lapparent de Broin 2000) pleurodires, the iliac articulation of which seems to lack well developed projections (Meylan 1996; Lapparent de Broin & Murelaga 1999; De la Fuente & Iturralde-Vinent 2001). The iliac articulation of pelomedusids has a less developed cranial projection (Lapparent de Broin & Murelaga 1999), which is better defined in other Pelomedusoides (Broin 1991; Broin & Werner 1998; Lapparent de Broin & Murelaga 1999). In *Cambaremys* n. gen., from the more conspicuous cranial and caudolateral projections of the dorsal iliac margin, two crests extend ventrally along the main body of the bone, demarcating two surfaces: a more excavated laterocranial, and a rounded medial to caudal surface. The iliac acetabulum is ovoid, an there is no visible excavation on its dorsal edge.

The pubis has expanded dorsal and ventral portions, and is craniocaudally constricted in the middle. Its dorsal segment forms the cranioventral portion of the acetabulum, connecting the ilium dorsally and the ischium caudally. Distally, the bone bifurcates into medial epipubis and the lateral process. The latter is craniocaudally flattened, but expands in all directions for the articulation to the plastron. The much thinner epipubis is incomplete distally. It extends craniomedially, but it is not possible to determine if there was an expanded distal end. These two processes diverge at an almost right angle, forming a typical embayment between them. The ischium also has expanding dorsal and ventral portions. The shaft is oval in cross section, emphasizing the general craniocaudal compression of the bone. The distal portion of the better preserved left bone has a subtriangular cross section, but is incomplete distally, lacking the typical podocnemid caudal and medial projections. The former can, however, be identified in the right side.

The right femur was the only preserved. It is slightly longer than the humerus, as common for freshwater turtles (Walker 1973). The shaft is cylindrical and discreetly arched dorsally, while the head projects dorsally. This forms a proximally opened and strongly concave intertrochanteric fossa, and a dorsoproximally directed rounded articulation. The latter is ovoid, as typical of aquatic Testudines (Walker 1973): caudoproximally to craniodistally elongated in dorsal aspect. The minor trochanter extends cranioproximally. Its connection to the head is damaged, but it seems to be marked by a constriction. On its distal margin, at the dorsocranial surface of the femur, there is a marked longitudinally elongated groove for the insertion of the M. puboischiofemoralis externus. The major trochanter does not split so markedly from the main body of the bone, and forms a nearly continuous proximal articulation to the femoral head. Its medial surface bears strong longitudinal striations, possibly related to the insertion of the iliofemoral musculature. The distal part of the femur is obliterated on its cranioventral portion, but the ventrodistally directed condyles, and a subtle intercondylar fossa can be distinguished. On the caudal surface of the femur, proximal to the slightly larger fibular condyle, lays a small striated area that corresponds to the origin of the M. flexor digitorum longus. Dorsally, the distal part of the bone bears strong longitudinal striations, possibly related to the patelar tendon.

Both tibiae of *Cambaremys* n. gen. are well preserved. Each of them is nearly straight, although concave ventrally. Both proximal and caudal portions are expanded in relation to the shaft, but the former is much broader, so that the bone has a distally tapering outline. The proximal articulation is subtriangular, with a sharp medial corner. It bears a shallow mediocaudal excavation that receives the femoral condyle, and is convex for the rest of its surface. Starting at the dorsal corner of the proximal articulation, the cnemial crest extends distally along the dorsal surface of the bone for about one third of its length, and bears strong longitudinal striations on its medial surface. Medial to this, the tibia is pinched, with dorsal and ventral shallow longitudinal excavation that leads to an elongated protuberance at the medial margin of the bone. This is somewhat continuous to the sharp medial angle of the proximal articulation, and represents the insertion of the M. gastrocnemius. Distally, the shaft is dorsoventrally compressed and slightly excavated at the lateral and medial margins. The distal articulation surface bear two condyles separated by a notch. The medial condyle is larger, more convex, and more distally projected. The lateral condyle is flatter, but expands ventrally to its medial counterpart.

Both fibulae are preserved, but the right is distally incomplete. This is a slender bone, dorsoventrally flattened for its entire length. Its proximal portion is slightly expanded, with an ovoid and convex articulation: lateromedially broader than dorsoventrally deep. Slightly distal to that articulation, the lateral margin of the fibula bears a longitudinally elongated rugose area. This represents the typically projected origin area of the M. iliofibularis. The fibular shaft is relatively straight and ovoid in cross section. The distal end is lateromedially expanded and dorsoventrally broadened. It is laterally pinched, forming a sharp border. The distal articulation is convex and subtriangular. Two subtle condyles can be identified, and that correspondent to the calcaneum is slightly larger.

DISCUSSION AND CONCLUSION

The pleurodire affinity of *Cambaremys langertoni* n. gen., n. sp. is given by its pelvic girdle that is suturated to the shell, and narrower than the bifid caudal lobe of the plastron (Lapparent de Broin 2000; De la Fuente & Iturralde-Vinent 2001). *Cambaremys* n. gen. is also more derived that the Jurassic representatives of the group for its cervical vertebra with a postzygapophyses-bearing pedicel, narrow nuchal plate, inguinal process contacting the fifth costal plate, and vertically oriented pelvis with a single large thyroid fenestra, all of which are features that characterize Eupleurodira (Lapparent de Broin & Murelaga 1999; De la Fuente & Iturralde-Vinent 2001). Within that clade, *Cambaremys* n. gen. belongs into the stem-lineage to Pelomedusoidea (*sensu* Meylan 1996), which is generally characterized (see Lapparent de Broin 2000; De la Fuente 2003) by traits such as the absence of the cervical scute, a nuchal plate longer than broad, a neural series that does not reach the suprapygal plate, and rounded mesoplastra. Yet, none of these characters has an unambiguous distribution, to clearly diagnose a particular eupleurodire group. This is often due to polymorphism/homoplasy within major clades such as Chelidae and Pelomedusidae, which show variation in the completeness of the neural series and/or the shape/presence-absence of the mesoplastra. That uncertainty can also reflect the extreme modification of the shell, as seen in *Araripemys* (Meylan 1996), or simply the occurrence of plesiomorphies within supposedly derived taxa, such as the broader nuchal plate of *Roxochelys* (Broin 1971).

TABLE 4. — Comparison of named pleurodire carapaces of the Bauru Group (Late Cretaceous). Traits probably related to the same complex of morphologic changes indicated by an asterisk.

	***Cambaremys langertoni* n. gen., n. sp.**	***Roxochelys wanderleyi* Price, 1953**	***Bauruemys elegans* Suárez, 1969**
Shell bones	thin	thick	thin
Nuchal plate	longer than broad	broader than long	as broad as long
Contact nuchal costal plates 1 *	short	short	long
Number of neural plates	7	?	6
Neural plate 1 *	ovoid	ovoid	subtriangular
Contact neural plate 1 costal plates 2 *	absent	absent	present
Neural plate 2 *	hexagonal	hexagonal	squared
Marginal scute 1	longer than broad	much broader than long	broader than long

Nonetheless, the presence of all those features in *Cambaremys* n. gen. seems enough to assure its pelomedusoid affinity. Within that clade, De la Fuente (2003) defined an elongated plastral bridge as synapomorphic for Podocnemoidae (*sensu* Meylan 1996). Besides, a pectoro-abdominal sulcus that does not encroach the mesoplastron is more typical of Podocnemidae, than of Pelomedusidae or Bothremydidae (Gaffney *et al.* 2001; De la Fuente 2003), and *Cambaremys* n. gen. seems to belong to that group of pelomedusoids.

The phylogeny of podocnemids is still a controversial issue (Noonan 2000), especially when it comes to fossil forms (Broin 1988; Lapparent de Broin 2000; De la Fuente 2003), and no unambiguous framework can be employed to assess the position of *Cambaremys langertoni* n. gen., n. sp. Nonetheless, this new species differs from recent podocnemids for its thin and expanded coracoid and proximally projected medial process of the humerus, suggesting a basal position in relation to the crown-Podocnemidae. In addition, its coracoid shape also indicates a basal position in relation to *Stupendemys*. No autapomorphic feature was recognised for *Cambaremys* n. gen., but it differs from all well known South American Cretaceous podocnemids based on a unique suite of shell features. It is distinct from *Roxochelys wanderleyi* (Table 4) and ?*Roxochelys vilavilensis* for its thinner shell bones and narrower nuchal plate, from *Portezueloemys patagonica* for the presence of a seventh neural plate, from *Bauruemys elegans* (Table 4) for that same character and the contact between the first costal and second neural plates, and from the undetermined podocnemid described by De la Fuente (1993) for a pectoro-abdominal sulcus that does not touch the mesoplastron.

The differentiation of *Cambaremys langertoni* n. gen., n. sp. from "*Podocnemis*" *brasiliensis* is not so straightforward, due to the small overlapping of elements preserved in both taxa. Yet, the anal notch of *Cambaremys* n. gen. is shallower, and the pelvic sutures to its plastron less transversely expanded. This is clearer in the ischiadic suture, which only briefly contacts its mate medially. Wood & Gamero (1971) demonstrated that among three specimens of *Bairdemys venezuelensis* (gen. Gaffney & Wood 2002) the larger ones have a more incised "U-shaped" anal notch. Likewise, it is expected of older individuals to have a more extensive suture of pelvic bones to the shell. Accordingly, both features that putatively distinguish *Cambaremys* n. gen. from "*Podocnemis*" *brasiliensis* could be explained if the former was considered a younger individual. This fits the larger size of "*Podocnemis*" *brasiliensis*, the xiphiplastron of which is 2.4 times longer than that of *Cambaremys* n. gen., and the round-shaped carapace of the latter, which is more typical of juvenile podocnemids (Broin 1991). Accordingly, based on these features, the possibility that *C. langertoni* n. gen., n. sp. represents a juvenile of "*P.*" *brasiliensis* cannot be dismissed until more complete specimens of both taxa are recovered. On the other hand, the type locality of *C. langertoni* n. gen., n. sp. has yielded a larger (1.4 times longer and almost two times broader) isolated xiphiplastron of uncertain affinities, but possibly referable to that taxon by topotypy (Fig. 6F). This resembles the type specimen of *C. langertoni* n. gen., n. sp. in the shape of the anal notch and ischiadic suture, pointing to the taxonomic uniqueness of that taxon, and to its distinction from "*P.*" *brasiliensis*.

In terms of palaeoecology, *Cambaremys langertoni* n. gen., n. sp. was surely an aquatic turtle, as given by its flat shell and parameters such as the more distally projected medial process of the humerus and elongated femoral head (Walker 1973). This fits into the depositional environment proposed for the Sarra da Galga Member in the area of Uberaba (Fernandes & Coimbra 2000), which was dominated by braided fluvial systems and medial to distal alluvial fans, in a semi-arid climate.

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REFERENCES

ANTUNES M. T., BECQUART D. & BROIN F. L. 1988. — Le Crétacé de Beira Litoral, Portugal : remarques stratigraphiques et écologiques, étude complémentaire de *Rosasia soutoi* (Chelonii, Bothremydidae). *Ciências da Terra* 9: 153-200.

ARID F. M. & VIZOTTO L. D. 1966. — Um quelônio fóssil de São José do Rio Preto. *Ciência e Cultura* 18: 422-428.

BAEZ A. M. & PERÍ S. 1989. — *Baurubatrachus pricei* nov. gen., nov. sp., un anuro del Cretácico Superior de Minas Gerais, Brasil. *Anais da Academia Brasileira de Ciências* 61: 447-458.

BAUR G. 1893. — Notes on the classification of the Cryptodira. *American Naturalist* 27: 672-675.

BROIN F. 1971. — Une espèce nouvelle de tortue pleurodire (aff. *Roxochelys vilavilensis* n. sp.) dans le Crétacé supérieur de Bolivie. *Bulletin de la Société géologique de France* 7^{e} sér., 13: 445-452.

BROIN F. 1980. — Les tortues de Godoufaoua (Aptien du Niger) ; aperçu 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 le fractionnement du Gondwana et la dispersion géographique des tortues pleurodires à partir du Crétacé. *Studia Geologica Salmanticensia, Studia Paleocheloniologica* 2: 103-142.

BROIN F. 1991. — Fossil turtles from Bolivia, *in* SUAREZ-SORUCO R. (ed.), Fósiles y facies de Bolivia. Volume 1. Vertebrados. *Revista Técnica Yacimientos Petrolíferos Fiscutes de Bolivia* 12: 509-527.

BROIN F., BOCQUENTIN J. & NEGRI F. R. 1993. — Gigantic turtles (Pleurodira, Podocnemididae) from the Late Miocene-Early Pliocene of South Western Amazon. *Bulletin de l'Institut français d'Études andines* 22: 657-670.

CAMPOS D. DE A. & KELLNER A. W. A. 1999. — On some sauropod (Titanosauridae) pelves from the continental cretaceous of Brazil. *National Science Museum Monographs*, Tokyo 15: 143-166.

CARVALHO P., BOCQUENTIN J. & BROIN F. L. 2002. — A new species of *Podocnemis* (Pleurodira, Podocnemididae) from the Neogene of the Solimoes Formation, Acre, Brazil. *Geobios* 35: 677-686.

CARVALHO I. S., RIBEIRO L. C. B. & ÁVILA L. S. 2004. — *Uberabasuchus terrificus* sp. nov., a new crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. *Gondwana Research* 7: 975-1002.

CATTOI J. & FREIBERG M. 1958. — Una nueva especie de "*Podocnemis*" del Cretáceo argentino. *Physis* 21: 58-67.

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., Broin F. L. & Bianco T. M. De 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 la Fuente M. S. & Iturralde-Vinent M. 2001. — A new pleurodiran turtle from the Jagua Formation (Oxfordian) of western Cuba. *Journal of Paleontology* 75: 860-869.

Dias-Brito D., Musacchio E. A., Castro J. C. De, Maranhão M. S. A. S., Suárez J. M. & Rodrigues R. 2001. — Grupo Bauru: uma unidade continental do Cretáceo no Brasil – concepções baseadas em dados micropaleontológicos, isotópicos e estratigráficos. *Revue de Paléobiologie*, Genève 20: 245-304.

Estes R. & Price L. I. 1973. — Iguanid lizard from the Upper Cretaceous beds of Brazil. *Science* 180: 748-751.

Fernandes L. A. & Coimbra A. M. 1996. — A Bacia Bauru (Cretáceo Superior, Brasil). *Anais da Academia Brasileira de Ciências* 68: 195-205.

Fernandes L. A. & Coimbra A. M. 2000. — Revisão estratigráfica da parte oriental da Bacia Bauru (Neocretáceo). *Revista Brasileira de Geociências* 30: 717-728.

França M. A. G. de & Langer M. C. 2003. — Novas informações sobre um quelônio fóssil do cretáceo superior de Minas Gerais. *XVIII Congresso Brasileiro de Paleontologia, Boletim de Resumos* 1: 136-137.

Fúlfaro V. J. & Barcelos J. H. 1991. — Grupo Bauru no Triângulo Mineiro: uma nova visão Litoestratigráfica. *II Simpósio de Geologia do Sudeste, Anais* 1: 59-66.

Gaffney E. S. 1990. — The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History* 194: 1-263.

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. 1991. — Primitive Pelomedusid Turtle, *in* Maisey J. G. (ed.), *Santana Fossils: an Illustrated Atlas*. TFH Publications, New Jersey: 335-339.

Gaffney E. S., Tong H. & Buffetaut É. 1998. — *Foxemys*, a new side-necked turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. *American Museum Novitates* 3251: 1-19.

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.

Gobbo-Rodrigues S. R., Coimbra J. C., Petri S. & Bertini R. J. 2003. — Kwango series (Congo), Bauru group (Brasil) and Neuquen basin (Argentina) ages, based on ostracodes and vertebrates. *XVIII Congresso Brasileiro de Paleontologia, Boletim de Resumos* 1: 152.

Goldberg K. & Garcia A. J. V. 1995. — Faciologia dos calcários do Grupo Bauru na região de Uberaba (MG). *Geociências* 14: 121-131.

Haines R. W. 1942. — The tetrapod knee joint. *Journal of Anatomy* 76: 270-301.

ICZN 1999. — *International Code of Zoological Nomenclature*. 4th ed. International Trust for Zoological Nomenclature, London, xxix + 306 p.

Joyce W. A. 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.

Kellner A. W. A. 1996. — Remarks on Brazilian dinosaurs. *Memoirs of the Queensland Museum* 39: 611-626.

Kischlat E.-E., Barberena M. C. & Timm L. L. 1994. — Considerações sobre a queloniofauna do Grupo Bauru, Neocretáceo do Brasil. *3º Simpósio sobre o Cretáceo do Brasil, Boletim* 1: 105-107.

Langer M. C. 1996. — A possible Podocnemididae (Testudines, Pelomedusoides) from the Marília Formation (Bauru Group), Upper Cretaceous of the Triângulo Mineiro (Minas Gerais, Brazil). *Anais da Academia Brasileira de Ciências* 68: 1-298.

Lapparent de Broin F. 2000. — The oldest prepodocnemidid 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 Paléontologie* 84: 131-214.

Lindholm W. A. 1929. — Revidiertes Verzeichnis der Gattungen der rezenten Schildkröten nebst Notizen zur Nomenklatur einiger Arten. *Zoologischer Anzeiger* 81: 275-295.

MacPhee R. D. E., Iturralde-Vinent M. A. & Gaffney E. S. 2003. — Domo de Zaza, an early Miocene vertebrate locality in south central Cuba: with notes on the tectonic evolution of Puerto Rico and the Mona Passage. *American Museum Novitates* 3394: 1-42.

Meylan P. A. 1996. — Morphology and relationships of the Early Cretaceous side-necked turtle, *Araripemys barretoi* (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 Paranahyba, *in* DOURADOS J. (ed.), Exploração do Rio Grande e de seus afluentes. *Comissão de Geografia e Geologia, São Paulo*: 33-38.

POWELL J. E. 2003. — Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum* 111: 1-173.

PRICE L. I. 1951. — Um ovo de dinossáurio na Formação Bauru, do Cretácico do Estado de Minas Gerais. *Notas Preliminares do Estududos do Departamento Nacional de Produção Mineral* 53: 1-6.

PRICE L. I. 1953. — Os quelônios da Formação Bauru, Cretáceo terrestre do Brasil Meridional. *Boletim da Divisão de Geologia e Mineralogia Departamento Nacional de Produção Mineral* 147: 1-34.

PRICE L. I. 1955. — Novos crocodilídeos dos areniros da Série Bauru, Cretáceo do Estado de Minas Gerais. *Anais da Academia Brasileira de Ciências* 27: 487-501.

PRICE L. I. 1961. — Sobre os dinossáurios do Brasil. *Anais da Academia Brasileira de Ciências* 33: 28-29.

ROMER A. S. 1956. — *Osteology of the Reptiles*. University of Chicago Press, Chicago, 772 p.

SANTUCCI R. M. & BERTINI R. J. 2001. — Distribuição Paleogeográfica e Biocronológica dos Titanossauros (Saurischia, Sauropoda) do Grupo Bauru, Cretáceo Superior do Sudeste brasileiro. *Revista Brasileira de Geociências* 31: 307-314.

STAESCHE K. 1937. — *Podocnemis brasiliensis* n. sp. aus der Oberen Kreide Brasiliens. *Neues Jahrbuch für Mineralogie, Geologie und Paläntologie B*, 77: 291-309.

SUÁREZ J. M. 1969. — Um quelônio da Formação Bauru. *XXIII Congresso Brasileiro de Geologia, Anais* 3: 168-176.

SUÁREZ J. M. 2002. — O sítio fossilífero de Pirapozinho, SP, *in* SCHOBBENHAUS C., CAMPOS D. DE A., QUEIROZ E. T., WINGE M. & BERBERT-BORN M. (eds), *Sítios Geológicos e Paleontológicos do Brasil*. DNPM/CPRM, Brasília: 49-56.

TONG H., GAFFNEY E. S. & BUFFETAUT É. 1998. — *Foxemys*, a new side-necked turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. *American Museum Novitates* 3251: 1-19.

WALKER W. F. 1973. — The locomotor apparatus of Testudines, *in* GANS C. & PARSON T. S. (eds), *Biology of Reptilia* 4: 1-100.

WOOD R. C. 1972. — A fossil pelomedusid turtle from Puerto Rico. *Breviora* 392: 1-13.

WOOD R. C. 1976. — *Stupendemys geographicus*, the world's largest turtle. *Breviora* 438: 1-31.

WOOD R. C. & GAMERO M. L. D. DE 1971. — *Podocnemis venezuelensis*, a new fossil pelomedusid (Testudines, Pleurodira) from the Pliocene of Venezuela and a review of the history of *Podocnemis* in South America. *Brevoria* 376: 1-23.

ZANGERL R. 1969. — The turtle shell, *in* GANS C., BELLAIRS A. D'A. & PARSONS T. S. (eds), *Biology of the Reptilia*. Volume 1. Academic Press, London: 311-339.

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