

## Tetrapods from the Upper Cretaceous (Turonian–Maastrichtian) Bauru Group of Brazil: a reappraisal

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### Abstract

An updated, annotated list of all tetrapods from the Adamantina, Uberaba and Marília formations (Bauru Group), which constitute some of the best studied Upper Cretaceous units in Brazil, is presented. Tetrapod diversity in the Bauru Group is remarkable, including an admixture of typically austral Gondwanan taxa (e.g., abelisaurids, notosuchians) and boreal Gondwanan forms (e.g., carcharodontosaurids). Of note is the absence of Laurasian taxa in the upper portion of the Bauru Group. With the exception of some turtles, an anuran, mesoeucrocodylians and one titanosaur, most taxa from the Bauru Group are based on fragmentary and isolated bones, and as such many specimens can be identified only to a higher taxonomic level. Fishes, turtles, anurans, mesoeucrocodylians, dinosaurs, birds and mammals from the Adamantina and Marília formations resemble the latest Late Cretaceous vertebrate faunas from southern South America, except for the absence of ornithischian dinosaurs.

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### 1. Introduction

Recent collections of Late Cretaceous vertebrates in South America have provided new insights into the fauna of this part of the world, as well as additional data on palaeogeography and biostratigraphy. A great taxonomic diversity of tetrapods have now come from South America and other Gondwanan localities (e.g., India, Madagascar, Australia and Antarctica),

which, although in many cases incomplete, shows that during the Late Cretaceous the biota was undergoing a complex evolutionary history.

In Brazil, there are several localities exposing Upper Cretaceous strata that have yielded numerous specimens, representing a wide array of species; all terrestrial rocks from this time interval are found in the Bauru Basin. The sequence is divided into two units, the Caiuá Group and the Bauru Group (Fernandes and Coimbra, 1996). The former comprises the Santo Anastácio (Aptian–Cenomanian), Rio Paraná (Santonian–Maastrichtian) and Goio Erê (Santonian–Maastrichtian) formations (Fernandes and Coimbra, 1996; Fernandes, 1998;

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Dias-Brito et al., 2001), while the Bauru Group consists of the Adamantina (Turonian–Santonian), Uberaba (Turonian–Coniacian) and Marília (late Maastrichtian) formations. Derby (1896) was the first author to note remains of tetrapods, turtles and dinosaurs in the Bauru Group. Later, von Ihering (1911) mentioned crocodyliform teeth from this unit, followed by contributions by Pacheco (1913), von Huene (1931), Roxo (1936, 1937) and von Staesche (1937), among others. At that time, crocodyliforms and turtles were the most abundant and complete fossils from the Bauru Group of São Paulo State to be reported, but, subsequently, through the extraordinary efforts of Llewellyn Ivor Price (1945, 1950a, b, 1951, 1953, 1955; Estes and Price, 1973), the dinosaur-bearing deposits of the Marília Formation in the Triângulo Mineiro region yielded a great number of specimens. This material considerably increased the tetrapod fossil record of the Bauru Group, revealing not only new crocodyliform and turtle taxa, but also some dinosaurs. In recent decades, the Bauru Group has been extensively explored and numerous papers have appeared (e.g., Arid and Vizzotto, 1971; Báez and Perí, 1989; Bertini et al., 1993; Kellner and Azevedo, 1999; Kellner and Campos, 2000, 2002; Candeiro, 2002; Santucci, 2002; Carvalho et al., 2003, 2004; Candeiro et al., 2004a,b, 2006; Alvarenga and Nava, 2005; Avilla et al., 2005).

The aim of the present contribution is to provide an updated, annotated systematic list of all tetrapods recognized

so far from the Bauru Group (Fig. 1). In addition, comparisons with other Upper Cretaceous tetrapod-bearing formations in South America, as well as in other parts of Gondwana, are presented.

## 2. Localities and geological setting

The Bauru Basin (Fig. 2) has furnished one of the richest Late Cretaceous tetrapod assemblages known to date from Brazil. The basin covers about 370,000 km<sup>2</sup> of southern and central Brazil, including the states of Goiás, Mato Grosso do Sul, Minas Gerais, Paraná and São Paulo, and the sequence exposed is composed mainly of fluvial, aeolian and lacustrine sediments. Fernandes and Coimbra (1996) recognised the Caiuá Group (Goio Ére, Rio Paraná and Santo Anastácio formations; e.g., Fernandes, 1998) and the Bauru Group (Adamantina, Uberaba and Marília formations) (Figs. 2, 3).

Aeolian and fluvial-lacustrine sediments of the Bauru Group have yielded abundant tetrapod bones, teeth and eggs, commonly found associated with the remains of other vertebrates and invertebrates. The best known tetrapod taxa are from the Adamantina and Marília formations in the states of Goiás, Minas Gerais and São Paulo. It was the discovery of fossils in these two formations that first made scientists realise the palaeontological potential of this area. These two units have been correlated with Upper Cretaceous strata in Argentina

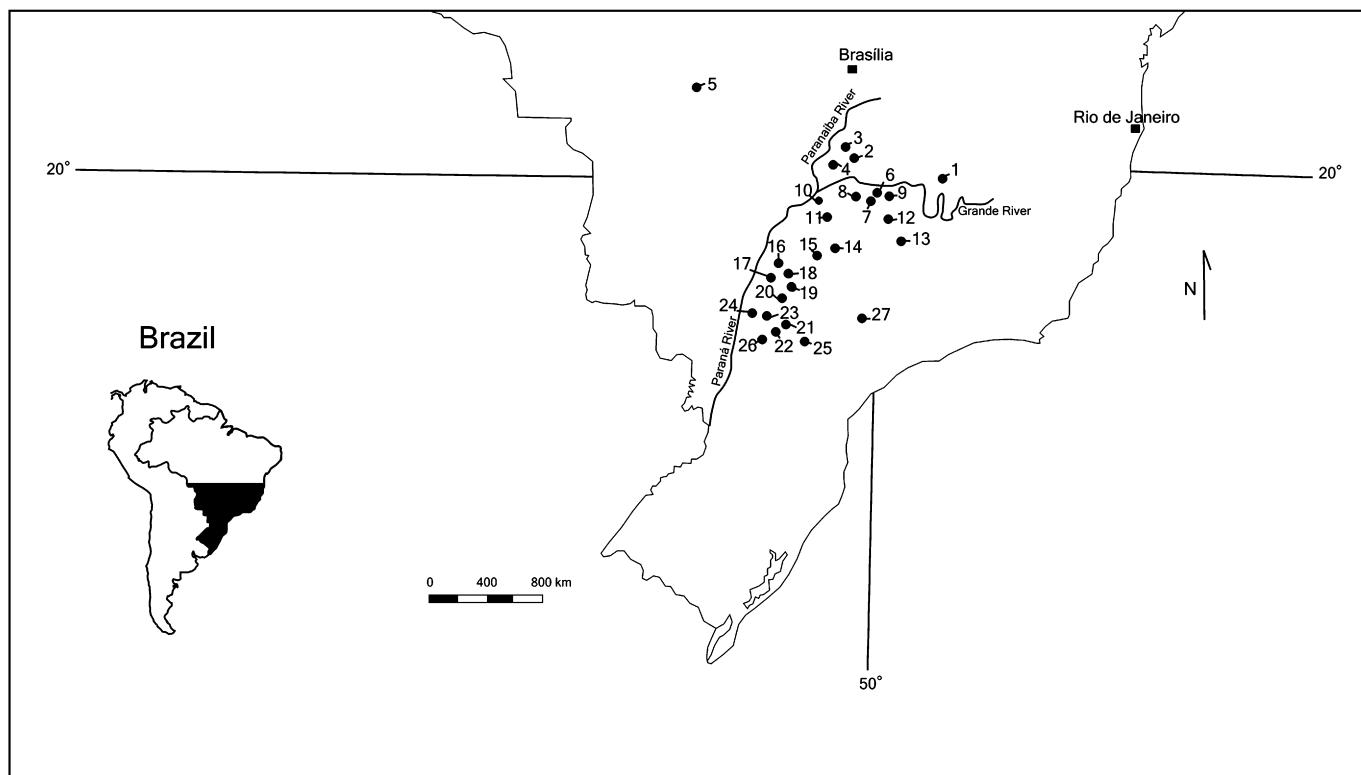


Fig. 1. Map showing the most important tetrapod-bearing localities in the Bauru Group of southern Brazil. Minas Gerais State: 1, Peirópolis, Uberaba; 2, Prata; 3, Monte Alegre de Minas; 4, Campina Verde. Mato Grosso State: 5, Cambebe. São Paulo State: 6, Paulo de Faria; 7, São José de Rio Preto; 8, Monte Aprazível; 9, Colina; 10, Jales; 11, General Salgado; 12, Ibirá; 13, Monte Alto; 14, Araçatuba; 15, Guararapes; 16, Pacaembu; 17, Irapuru; 18, Flórida Paulista; 19, Adamantina; 20, Alfredo Marcondes; 21, Presidente Prudente; 22, Guajuçara; 23, Presidente Bernardes; 24, Santo Anastácio; 25, Álvares Machado; 26, Pirapozinho; 27, Marília.

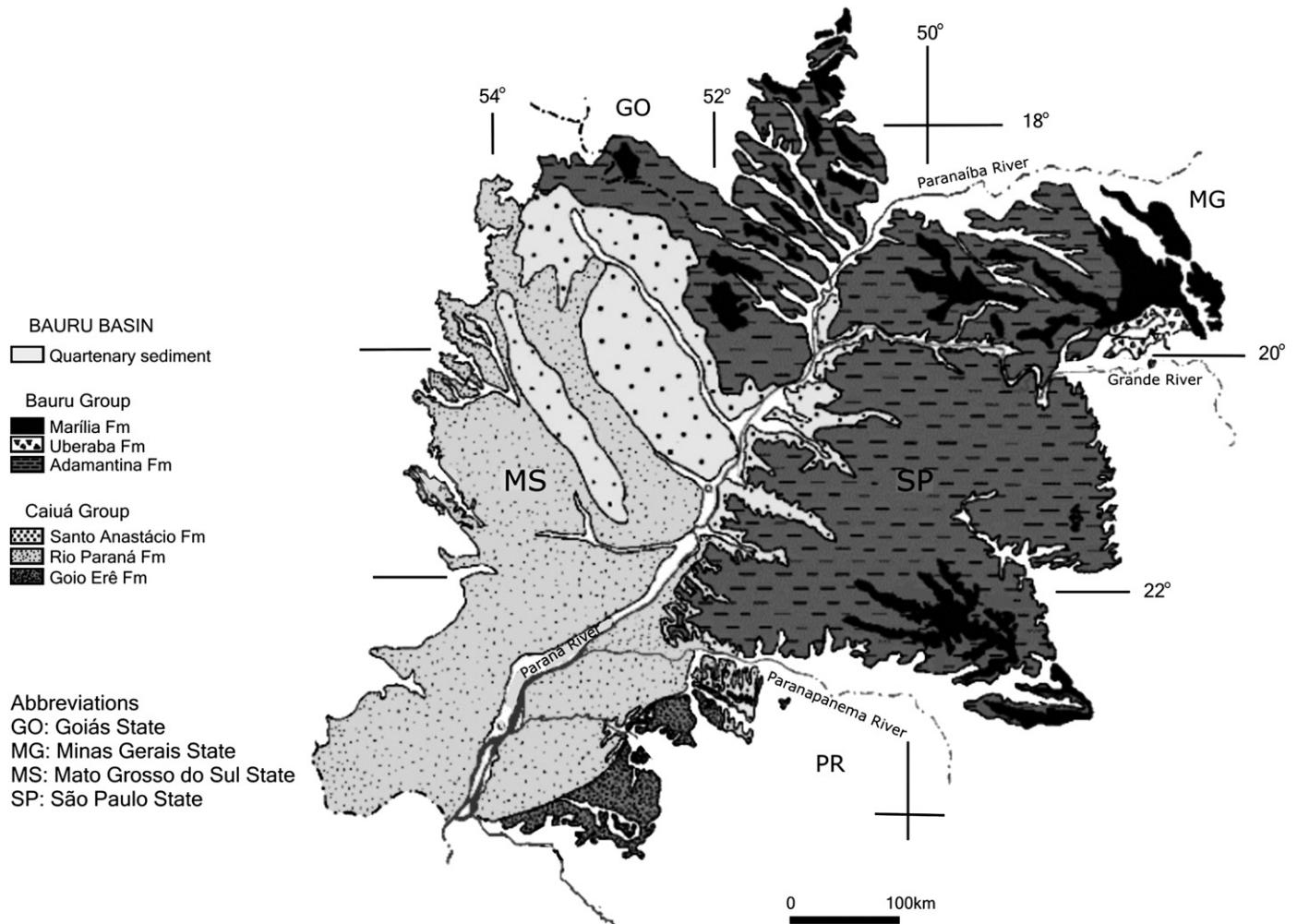


Fig. 2. Geological map of the Bauru Basin (modified from Fernandes and Coimbra, 1996).

(e.g., von Huene, 1929). Until recently, the Uberaba Formation (found only in the Triângulo Mineiro region) yielded just a few isolated tetrapod remains. In the Caiuá Group, the vertebrate record is poor, being represented mainly by footprints and isolated bones (Kellner, 1996; Candeiro et al., 2004b).

Sediments in the Bauru Basin have a complex nomenclatural history (Fernandes and Coimbra, 1996), in part due to the artificial division of Upper Cretaceous strata in the flat regions of Goiás, Mato Grosso do Sul, Minas Gerais (Triângulo Mineiro), Paraná and São Paulo states. Thus, strata of the Adamantina and Marília formations (*sensu* Fernandes and Coimbra, 1996) were formerly described as Sandstone (Gonzaga de Campos, 1905) Series (Freitas, 1955), Formation (Arid, 1967) or Group (Soares et al., 1980), or even assumed to belong to the Paraná Basin (Barcelos, 1984; Ferreira Júnior, 1996). Here we follow the stratigraphic scheme of Fernandes and Coimbra (1996), Fernandes (1998) and Dias-Brito et al. (2001).

Our current understanding of stratigraphic relationships within the Bauru Basin units has allowed us to be more precise in describing the numerous fossil-bearing localities exposing strata of the Caiuá and Bauru groups, particularly during the last two decades. However, stratigraphic problems are still

| SYSTEMS | STAGES (With age boundaries in Ma) | BAURU GROUP          |
|---------|------------------------------------|----------------------|
|         | 65,0±0,1                           | Marília Formation    |
|         | MAASTRICHTIAN                      |                      |
|         | 71,3±0,5                           |                      |
|         | CAMPAHIAN                          |                      |
|         | 83,5±0,3                           |                      |
|         | SANTONIAN                          |                      |
|         | 85,8±0,5                           | Adamantina Formation |
|         | CONIACIAN                          |                      |
|         | 89,0±0,5                           |                      |
|         | TURONIAN                           |                      |
|         | 93,5±0,2                           |                      |
|         | CENOMANIAN                         |                      |
|         | 98,9±0,6                           |                      |

Fig. 3. Chrono- and lithostratigraphy of the Bauru Group (modified from Dias-Brito et al., 2001).

far from being resolved and new studies should be conducted in order to clarify the relationships of these units, and their fossil content compared to other invertebrate and vertebrate-bearing formations of Gondwana.

*Institutional abbreviations.* AMNH, American Museum of Natural History, New York; CPP, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Peirópolis, Minas Gerais, Brazil; DGM, Departamento Nacional da Produção Mineral, Museu de Ciências da Terra, Rio de Janeiro, Brazil; GPRD, Coleção do Museu de Geologia, Universidade Estadual Paulista, São José do Rio Preto, São Paulo, Brazil; IG, Instituto Geológico de São Paulo, São Paulo, Brazil; MACN, Museo Argentino Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MCF-PVPH, Museo Municipal “Carmen Funes”, Paleontología de Vertebrados, Plaza Huincul, Argentina; MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MMR/UFU-PV, Museu de Minerais e Rochas, Paleontología de Vertebrados, Universidade Federal de Uberlândia, Minas Gerais, Brazil; MN-V, Museu Nacional, Coleção de Paleovertebrados, Universidade Federal do Rio de Janeiro, Brazil; MPMA, Museu de Paleontología de Monte Alto, Monte Alto, São Paulo, Brazil; MUGEO, Museu Água Branca, Água Branca, São Paulo, Brazil; MZ, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; RCL, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UFRJ-DG-R, Departamento de Geología, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, fossil reptilian collection; UFRJ-DG-R(d), fossil reptilian teeth collection; URC-M, Universidade Estadual Paulista, Coleção de Mamíferos, Rio Claro, São Paulo, Brazil; URC-R, Universidade Estadual Paulista, Coleção Répteis, Rio Claro, São Paulo, Brazil.

### 3. Tetrapod systematics

#### 3.1. Anurans

In the Bauru Group, anurans are poorly represented, with only *Baurubatrachus pricei* Báez and Perí, 1989 known, plus several other specimens of possible “leptodactylid” affinity, all of which were briefly described by Carvalho et al. (2003). Contrary to other Cretaceous vertebrate-bearing formations in South America, Pipoidea (sensu Báez and Pugener, 2003) are unknown from the Bauru Group; this clade is widely distributed in the Upper Cretaceous of Argentina (Reig, 1959; Báez, 1981, 1987; Báez et al., 2000; Martinelli and Forasiepi, 2004).

Genus *Baurubatrachus* Báez and Perí, 1989

*Baurubatrachus pricei* Báez and Perí, 1989

Fig. 4

*Type.* Holotype is MCT 1412-R, A and B, a partially articulated, incomplete skeleton, in two blocks of sandstone, from

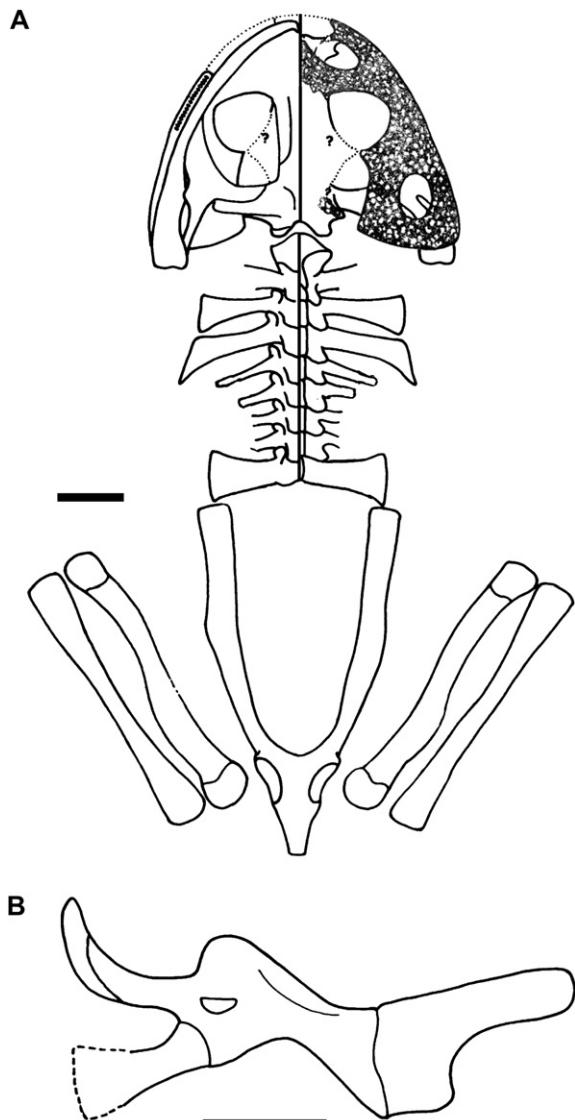


Fig. 4. *Baurubatrachus pricei* Báez and Perí, 1989. A, tentative partial reconstruction of skeleton; skull and vertebrae in dorsal (right-hand half) and ventral (left-hand half) views; pelvis and hindlimbs in ventral view. B, right pectoral girdle in dorsal view (modified from Báez and Perí, 1989). Scale bars represent 10 mm.

Peirópolis (Uberaba, Minas Gerais State, Brazil); Marília Formation, upper Maastrichtian.

*Remarks.* Báez and Perí (1989) suggested ceratophryine affinities for this “leptodactylid” taxon. The record of Cretaceous “Leptodactylidae” (currently considered to be a paraphyletic assemblage; see e.g., Ford and Cannatella, 1993) in southern South America is based on fragmentary and isolated remains from the Los Alamitos (Báez, 1987), Loncoche (Gonzalez Riga, 1999) and Allen (Martinelli and Forasiepi, 2004) formations. Unfortunately, a revision of these records has not been carried out yet, mainly in view of the incompleteness of the material. Some of the specimens from Argentina were interpreted to be more closely related to the living genus *Caudivera* (Telmanotobinae) than to the Ceratophryinae (Báez, 1987).

Indeterminate genus and species (sensu Carvalho et al., 2003)

**Material.** MZ, unnumbered, from the municipality of Marília (Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** Several partial skeletons of an unnamed “leptodactylid” from western São Paulo State were briefly reported by Carvalho et al. (2003), who noted that these remains belonged to a new species, thus providing further evidence of neobatrachian diversity in the Upper Cretaceous of Brazil. This form has procoelous presacral vertebrae, an arciferal pectoral girdle and a neopalatine bone, indicating that it belongs within the Neobatrachia (Carvalho et al., 2003). In addition, this taxon shares with “leptodactylids” the fusion of the frontoparietals with the occipital bones and a distinctive morphology of the ilium (Carvalho et al., 2003). It differs from *Baurubatrachus pricei* in having a high degree of exostosis in the dermal skull bones and tubular-shaped sacral diapophyses. However, we note that the degree of exostosis can change during ontogeny, as has been reported in some extant “leptodactylids” (Lynch, 1971). A careful restudy of these specimens is needed in order to evaluate their taxonomic position.

### 3.2. Turtles

The Adamantina and Marília formations have yielded well-preserved and near-complete turtles belonging to the pleurodire clade Pelomedusoides (e.g., von Staesche, 1937; Price, 1953; Kischlat, 1994, 1996; Kischlat et al., 1994; França and Langer, 2003). The oldest pelomedusoids are from the upper Aptian of Gadoufaoua, Niger (e.g., de Broin, 1980) and the Aptian–Albian Santana Formation of Chapada do Araripe, Brazil (Price, 1973; de Broin, 2000). Pelomedusoids diversified mainly in northern Gondwana but, during the Late Cretaceous, they also occurred in Bolivia (El Molino Formation; de Broin, 1991) and Argentina (Portezuelo and Anacleto formations; de la Fuente, 1993, 2003). Members of Chelidae are unknown from the Bauru Group; this family is restricted to Patagonia (Argentina) during the Late Cretaceous (de Broin and de la Fuente, 1993).

### Genus *Roxochelys* Price, 1953

*Roxochelys wanderleyi* Price, 1953 and *R. harrisi* (Pacheco, 1913)

**Types.** Holotype of *R. wanderleyi* is DGM 216-R, an anterior portion of the dorsal shell and an anterior plastral lobe, and holotype of *R. harrisi* is DGM 287, a right xiphiplastron and three peripheral plates, all of which appear to be lost at present. DGM 216-R is from Araçatuba Jupia (municipality of Mirandópolis, São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian; DGM 287 is from Colina, São Paulo State (Brazil); same unit.

**Remarks.** Price (1953) noted that the holotype of *Podocnemis brasiliensis* (now *Bauruemys brasiliensis*; see below), described by von Staesche (1937), in fact comprised two taxa, and erected *Roxochelys wanderleyi* to accommodate the other one. *Roxochelys harrisi* was first described as *Podocnemis harrisi* by Pacheco (1913), but Price (1953) noted that the carapace ornament of that species was closely similar to that of *R. wanderleyi*, and referred to the taxonomic problem this raised. Subsequently, de Broin (1988, 1991) and Kischlat (1994) assigned *P. harrisi* to *Roxochelys*.

Just how many species of *Roxochelys* are present in the Upper Cretaceous beds of Brazil is uncertain. There were probably more than two species, in view of the wide spatial and temporal distribution of the genus. Extra-Brazilian records include the lower Paleocene (Santa Lucia Formation) of Bolivia (*R. vilavilensis*; de Broin, 1971), but it should be noted that this species has subsequently been interpreted as being a closer relative of *Bauruemys* (de Broin, 1991; Kischlat et al., 1994).

### Genus *Bauruemys* Kischlat, 1994

*Bauruemys brasiliensis* (von Staesche, 1937) and *B. elegans* (Suárez, 1969)

Fig. 5A–F

**Types.** Holotype of *B. brasiliensis* is DGM 2980, an incomplete plastron; holotype of *B. elegans* is UFRGS 148 and MN-V 4487, a postcranium, from Araçatuba Jupia (municipality of Mirandópolis, São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** After von Staesche (1937) had described *Podocnemis brasiliensis*, Price (1953) noted that the holotype of that species in fact comprised two taxa that differed in size and carapace morphology. For the other species he proposed the name *Roxochelys wanderleyi* (see above), and for *P. brasiliensis* he provided a new diagnosis. Recently, Kischlat (1994) transferred *Podocnemis brasiliensis* to *Bauruemys*, but noted that this reassignment was provisional.

Suárez (1969) described *Podocnemis elegans*; de Broin (1988, 1991) later referred to it provisionally as *Roxochelys?* *elegans*, but Kischlat (1994) erected the new genus *Bauruemys* for this taxon. Subsequently, Tong and Buffetaut (1996) reassigned *B. elegans* to *Hamadachelys*, a genus known from the Albian–Cenomanian of Hamada du Guir, Morocco. However, the derived cranial features of *B. elegans* allow it to be distinguished from that taxon (de Broin, 2000; de la Fuente, 2003).

### Genus *Cambaremys* França and Langer, 2005

*Cambaremys langertoni* França and Langer, 2005

Fig. 5G–I

**Type.** Holotype is CPP-0252, a cervical vertebra, a partial carapace and plastron, both coracoids, the right scapula, both humeri, the left radius, both ulnae, both pelvic girdles, the right femur, both tibiae, both fibulae and other appendicular

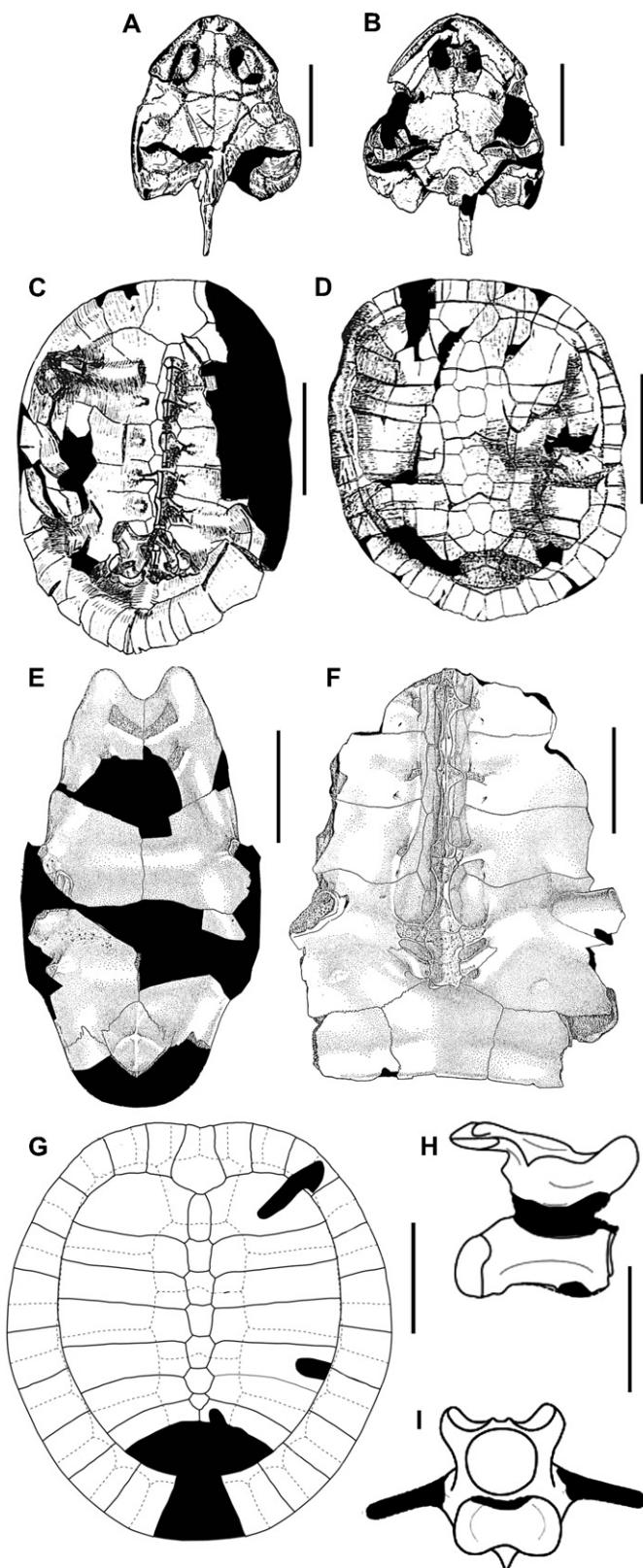


Fig. 5. A–D, *Bauruemys elegans* (Suárez, 1969). A, B, skull in dorsal and ventral views. C, carapace in dorsal view. D, carapace in ventral view. E, F, *Bauruemys brasiliensis* (von Staesche, 1937), plastron and carapace in ventral view, respectively (modified from Suárez, 1969). G–I, *Cambaremys langertoni* de França and Langer, 2005. G, carapace in dorsal view. H, I, cervical vertebra in right lateral and cranial views, respectively (modified from França and Langer, 2005). Scale bars represent 10 mm in A–F, 60 mm in G, and 15 mm in H and I.

bones, from the Serra do Veadinho area near the village of Peirópolis (municipality of Uberaba, Minas Gerais State, Brazil); Marília Formation, upper Maastrichtian.

**Remarks.** *Cambaremys* differs from other South American Cretaceous podocnemids in having the following combination of characters: thin shell bones, narrow nuchal plate, seven neural plates and contact between first costal and second neural plates (de França and Langer, 2005). This taxon is clearly differentiated from other Brazilian podocnemids, except for *Bauruemys brasiliensis* (“*Podocnemis*” *brasiliensis* sensu de França and Langer, 2005). The only features to differentiate *Cambaremys* from *B. brasiliensis* are the presence of a shallower anal notch and the fact that the pelvic sutures in its plastron are less transversely expanded. These features appear to change during ontogeny; therefore, as noted by França and Langer (2005), the possible conspecificity can only be hinted at and awaits the discovery of more, and better-preserved, material. Of note is the fact that *Cambaremys* represents the first named and well-preserved turtle from the Marília Formation; *B. brasiliensis* occurs in the older Adamantina Formation.

Indeterminate genus and species (sensu Azevedo et al., 2000)

**Material.** MN-V 4315, a chelonian egg, from the municipality of Alvares Machado (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** Based on similarities in eggshell rugosity pattern displayed by extant *Podocnemis expansa*, and on the abundance of remains of Podocnemididae in beds that yielded this egg, it was tentatively assigned to the genus *Podocnemis* (Azevedo et al., 2000). However, this generic assignment remains uncertain because the genus *Podocnemis* is as yet unknown in Brazil, and Cretaceous records of the genus are not corroborated (Kischlat, 1994).

### 3.3. Squamata

The squamate record in Upper Cretaceous beds of Brazil is still extremely poor, and currently comprises but a single lizard and a single snake. Overall, Mesozoic lizards in South America are rare; to date, the single formally named Late Cretaceous taxon is *Pristiguana brasiliensis* Estes and Price, 1973 from the Bauru Group. Added to this is a fragment of a dentary with subpleurodont dentition, possibly of teioid affinity, reported from the Campanian Anacleto Formation of the province of Río Negro, Argentina by Albino (2002), as well as an incomplete frontal bone, possibly of iguanid affinity, from the Cenomanian Candeleros Formation of the same province (Apesteguía et al., 2005). Unstudied lizard material is also known from the Peirópolis locality in Minas Gerais State, Brazil (Marília Formation) and from the province of Río Negro, Argentina (Los Alamitos Formation).

Contrary to other localities in South America where Upper Cretaceous strata are exposed, the snake record of Brazil is poor, consisting of a possible member of the Anilioidea (Zaher et al., 2003) only. From Bolivia (El Molino Formation; Gayet et al., 2001) and Patagonia (Argentina), a high diversity of Dipsidiidae and Madtsoiidae has been reported (e.g., Bonaparte, 1991a; Albino, 1996, 2000; Caldwell and Albino, 2002; Martinelli and Forasiepi, 2004).

It is noteworthy that the Paleogene record of Squamata in Brazil differs significantly from that from the Cretaceous. A wide array of squamates, including Iguanidae, Teiidae, Gekkonidae, Aniliidae, Madtsoiidae, Boidae, Tropidophiidae, Russelophiidae and, possibly, Scincidae, has been recovered from upper Paleocene strata at São José de Itaboraí (Rio de Janeiro, Brazil; e.g., Paula Couto, 1970; Estes, 1983; Albino, 1990; Rage, 2001). At that locality, snake diversity is extremely high, much higher than that of lizards. It may be assumed, on the basis of this disparity, that the Cretaceous record of snakes in Brazil is incomplete.

#### Genus *Pristiguana* Estes and Price, 1973

##### *Pristiguana brasiliensis* Estes and Price, 1973

Fig. 6

**Type.** Holotype is DGM 552, part of a disarticulated skeleton of a single individual, from Peirópolis (municipality of Uberaba, Minas Gerais State, Brazil); Marília Formation, upper Maastrichtian.

**Remarks.** *Pristiguana brasiliensis* is the first Mesozoic lizard to have been described from South America. Estes and Price (1973), Estes (1983), Estes and Báez (1985), Reynolds (1998), and Apesteguía et al. (2005) all noted that *Pristiguana* might have iguanian affinities. However, such an assignment was questioned by Borsuk-Bialynicka and Moody (1984), who suggested that it might be a teiid. A restudy of the type specimen is thus called for.

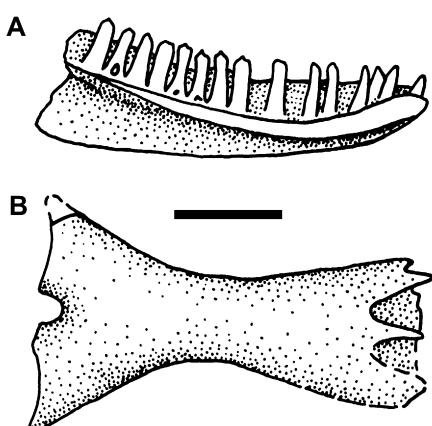


Fig. 6. *Pristiguana brasiliensis* Estes and Price, 1973. A, dentary in lingual view. B, frontals in dorsal view (modified from Estes, 1983). Scale bar represents 2.5 mm.

Indeterminate genus and species (sensu Zaher et al., 2003)

**Material.** MZ unnumbered, a few articulated vertebrae and ribs, from the municipality of General Salgado (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** The snake record from the Bauru Group comprises only this recent discovery by Zaher et al. (2003); the material, of two specimens, includes a few articulated vertebrae and ribs, notable for their small size, and narrow, rather depressed, elongated vertebrae. The neural arches are dorsoventrally compressed, the neural spine is reduced, the zygosphenic bar is thin, and both the diapophysis and parapophysis are present (Zaher et al., 2003). According to Albino (1996), aniliids are characterised principally by flat neural arches and poorly developed neural spines; both of these features are observed in the Bauru specimens. If the assignment is correct, this unnamed taxon represents the first and earliest record of the Aniliidae in South America. In the Paleocene of Brazil, where snake diversity is high, there are at least two members of the Aniliidae, namely *Coniophis* cf. *C. predeudens* and *Hoffstetterella brasiliensis* (Rage, 1998), both from Itaboraí.

#### 3.4. Crocodyliforms

Terrestrial crocodyliforms are abundant in Upper Cretaceous rocks of South America, and their record comprises a diverse mesoeucrocodylian assemblage that developed a wide range of adaptations, some of which involved extremely bizarre features in skull, dentition and postcranium. Despite differences of opinion concerning the phylogenetic position of these taxa, mainly notosuchians (e.g., Price, 1950a; Gasparini, 1971; Bonaparte, 1991a; Carvalho and Bertini, 1999; Martinelli, 2003; Pol, 2003), baurusuchids (e.g., Price, 1945, 1959; Gasparini, 1972; Campos et al., 2001; Avilla, 2002; Carvalho et al., 2005), sebecids (e.g., Gasparini, 1972; Turner and Calvo, 2005), sarcosuchids (e.g., Buffetaut and Taquet, 1977), “araripesuchids” (e.g., Price, 1959; Gasparini, 1971; Ortega et al., 2000), and peirosaurids (e.g., Price, 1955; Gasparini et al., 1991; Carvalho et al., 2004) are represented. Crocodyliform remains occur in the Bauru Group in the states of Minas Gerais and São Paulo.

#### Genus *Sphagesaurus* Price, 1950a

##### *Sphagesaurus huenei* Price, 1950a

Fig. 7A

**Type.** Holotype is DGM 332, a posterior maxillary tooth from the municipality of Presidente Prudente (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Other material.** DGM 333-R, an isolated tooth from the municipality of Santo Anastácio; Adamantina Formation, Turonian–Santonian; URC-R 015, an isolated tooth (Bertini et al., 1993); DGM 1411-R, the anterior portion of the snout

(Kellner et al., 1995); RCL-100, a near-complete skull and fragment of the dentary symphysis (Pol, 2003).

**Remarks.** Prior to Pol's (2003) description of the skull and lower jaw, *Sphagesaurus* was known only from isolated teeth of uncertain affinity. On the basis of the new material, this taxon is now thought to be nested within the notosuchian clade and, more specifically, to represent the sister-taxon of *Chimaerasuchus paradoxus* from the Lower Cretaceous of China (Wu et al., 1995; Wu and Sues, 1996). The *Sphagesaurus*/*Chimaerasuchus* clade is closely related to a clade that includes baurusuchids plus sebecids (Pol, 2003). *Sphagesaurus* shows a combination of derived features, such as the presence of posterior teeth within an occlusal of reversed triangle-shape and extensive wear facets. These features suggest the presence of both lateral and fore-aft movement of the jaws (Pol, 2003).

#### Genus *Mariliasuchus* Carvalho and Bertini, 1999

*Mariliasuchus amarali* Carvalho and Bertini, 1999  
Fig. 7B

**Type.** Holotype is UFRJ-DG-R 50, an almost complete skeleton with skull, from the municipality of Marília (São

Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** *Mariliasuchus amarali* is a notosuchian, closely related to *Notosuchus terrestris* from the Upper Cretaceous of Patagonia (Carvalho and Bertini, 1999). It is a small species, with an anteroposteriorly short snout in comparison to other crocodyliforms. As in *Notosuchus*, the third premaxillary tooth is hypertrophied, whereas most of the preserved cheek teeth are bulbous, striated, and have well-differentiated crowns. The relatively large size of the orbits, and comparisons made with other specimens found at the same site, indicate that the holotype was a young individual. Our knowledge of the palaeobiology and palaeoecology of *M. amarali* has increased substantially in recent years, as a complete ontogenetic series (eggs, young and adult individuals) is now known. In addition, new techniques (such as three-dimensional scanners) have been applied in studies of the internal cranial anatomy (Santos et al., 2003).

#### Genus *Baurusuchus* Price, 1945

*Baurusuchus pachecoi* Price, 1945 and *B. salgadoensis* Carvalho et al., 2005  
Fig. 7C, D

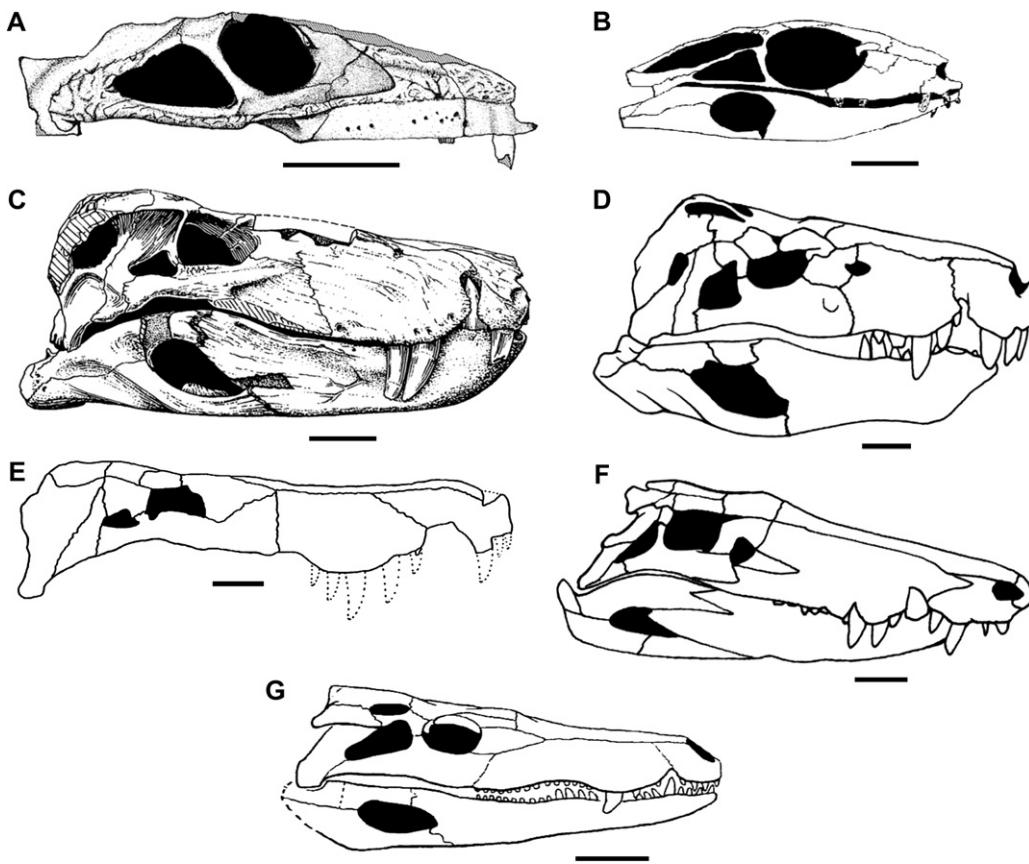


Fig. 7. Crocodyliform skulls in lateral view. A, *Sphagesaurus huenei* Price, 1950a (modified from Pol, 2003). B, *Mariliasuchus amarali* Carvalho and Bertini, 1999 (modified from Carvalho and Bertini, 1999). C, *Baurusuchus pachecoi* Price, 1945 (modified from Price, 1945). D, *Baurusuchus salgadoensis* Carvalho et al., 2005 (modified from Carvalho et al., 2005). E, *Stratiotosuchus maxhechti* Campos et al., 2001 (modified from Campos et al., 2001). F, *Uberabasuchus terrificus* Carvalho et al., 2004 (modified from Carvalho et al., 2004). G, *Itasuchus jesuinoi* Price, 1955 (modified from Buffetaut, 1991). Scale bars represent 10 mm.

**Types.** Holotype of *B. pachecoi* is DGM 299-R, an almost complete skull from Vila do Veadinho, municipality of Paulo de Faria (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian; holotype of *B. salgadoensis* is MPMA 62-0001-02, a skull and lower jaws, from General Salgado Country (São Paulo State, Brazil); same unit.

**Remarks.** *Baurusuchus pachecoi* is an extremely specialized crocodyliform, described by Price (1945) on the basis of a skull and lower jaws. This material has recently been revised by Riff and Kellner (2001), who added substantial data on dental formula and tooth morphology. Avilla (2003) described postcranial remains of *Baurusuchus*, referred to as cf. *B. pachecoi*, and discussed its phylogenetic position within the Notosuchia. Recently, a new species of *Baurusuchus*, *B. salgadoensis*, has been erected by Carvalho et al. (2005); this differs from *B. pachecoi* in having a low crest between the supratemporal fenestrae, a septum dividing the external nares and more rounded and less crenulate teeth (Carvalho et al., 2005), among other features. Both taxa were highly specialized terrestrial predators, and group as sister-taxon of *Stratiotosuchus maxhechti* (see below), thus adding support to the monophyly of the Baurusuchidae.

#### Genus *Stratiotosuchus* Campos et al., 2001

##### *Stratiotosuchus maxhechti* Campos et al., 2001

Fig. 7E

**Type.** Holotype is DGM 1477-R, an almost complete skull, lacking the lower jaws, from Irapuru (São Paulo State, Brazil); Adamantina Formation, Turonian-Santonian.

**Remarks.** *Stratiotosuchus* was assigned to the Baurusuchidae on account of the presence of ziphodont teeth, a reduced number of maxillary teeth, the high anterior region of the skull, and the presence of a shallow depression lateral to the external nares (Campos et al., 2001).

#### Genus *Peirosaurus* Price, 1955

##### *Peirosaurus tormini* Price, 1955

**Type.** Holotype is DGM 433-R, cranial and postcranial bones, from Peirópolis (municipality of Uberaba, Minas Gerais State, Brazil); Marília Formation, upper Maastrichtian.

**Remarks.** The relationships of *P. tormini* have always been controversial; it has been considered to be either a sebecosuchian (Price, 1955), a sebecid (Romer, 1966), a baurusuchid (Langston, 1965), a uruguaysuchid (Bonaparte, 1978) or a trematochampsid (Buffetaut, 1988). Gasparini (1982) coined the family name Peirosauridae to accommodate *P. tormini*, and subsequently, a new species, *Lomasuchus palpebrosus*, from Loma de la Lata (Neuquén, Argentina; Gasparini et al., 1991). These authors also supported the monophyly of the

family, providing several synapomorphies shared between *Peirosaurus* and *Lomasuchus*. Nevertheless, peirosaurid relationships among mesoeucrocodyliforms are still not clear; different hypotheses have been proposed in recent years (e.g., Gasparini et al., 1991; Buckley et al., 2000; Ortega et al., 2000; Sereno et al., 2001). Recently, peirosaurids have been included in the Notosuchia (Carvalho et al., 2004), but it should be noted that this analysis lacked inclusion of a large number of notosuchians, araripesuchids and crown group taxa (including eusuchians) that have the potential to change the topology of the tree drastically, as well as conclusions drawn from it.

#### Genus *Uberabasuchus* Carvalho et al., 2004

##### *Uberabasuchus terrificus* Carvalho et al., 2004

Fig. 7F

**Type.** Holotype is CPP 630, a skull, mandible and part of the axial and appendicular skeleton, from Peirópolis (municipality of Uberaba, Minas Gerais State, Brazil); Marilia Formation, upper Maastrichtian.

**Remarks.** *Uberabasuchus terrificus* is one of the most complete crocodyliforms found to date in any Brazilian locality. Its relationship within the peirosaurids appears to be well established, and it is in a sister-group relationship with the Madagascan *Mahajangasuchus* (Carvalho et al., 2004). In our view, however, the phylogenetic relationships proposed for Gondwanan crocodyliforms by Carvalho et al. (2004) remain controversial, mostly because their analysis did not incorporate a sufficient number of non-Gondwanan taxa. We consider it likely that the inclusion of such taxa could have had a substantial impact on their conclusions about phylogeny.

#### Genus *Itasuchus* Price, 1955

##### *Itasuchus jesuinoi* Price, 1955

Fig. 7G

**Type.** Holotype is DGM 434-R, cranial and postcranial bones, from Peirópolis (municipality of Uberaba, Minas Gerais State, Brazil); Serra da Gaga Member, Marília Formation, upper Maastrichtian.

**Remarks.** *Itasuchus jesuinoi* was originally assigned to the family Goniopholididae by Price (1955), although later it was considered either to be a member of the Trematochampsidae (e.g., Buffetaut, 1985, 1988), to be closely related to peirosaurids (Avilla, 2002) or to be nested with *Malawisuchus* in “Itasuchidae” (Carvalho et al., 2004). *Itasuchus jesuinoi* shares with *I. campani* from the Albian (Santana Formation) of Ceará State (Brazil), a closely similar skull, teeth and lower jaw morphology. Both *I. jesuinoi* and *I. campani* have a characteristic swelling formed by the nasals and prefrontals. In *I. jesuinoi* the anterior maxillary teeth are sharp and conical,

whereas the posterior ones are rounded. Tooth crowns are transversely compressed and bear a dense ornament. According to Rasmussen (2002), the dentary of *I. camposi* has approximately 21 maxillary teeth.

#### Indeterminate genus and species (sensu Garcia et al., 2005)

**Material.** IG 250, a fragmentary skull and mandible in occlusion, from western São Paulo State, Brazil; Adamantina Formation, Turonian–Santonian.

**Remarks.** Tooth crowns in this specimen have their longest axis obliquely orientated relative to the long axis of the skull, a feature also seen in *Sphagesaurus huenei* (Pol, 2003). However, a possible autapomorphy of IG 250 is the presence of a carina, positioned on the lingual surface, which suggests the presence of a new mesoeucrocodylian taxon in western São Paulo State (Garcia et al., 2005).

### 3.5. Dinosaurs

The Bauru Group has yielded the majority of significant dinosaur remains from the Upper Cretaceous of Brazil. Sauropods and theropods have been recorded from the Adamantina and Marília formations in Goiás, Mato Grosso, Minas Gerais and São Paulo states.

#### 3.5.1. Sauropods

Titanosaurs are the only sauropod dinosaurs from the Bauru Group, with numerous specimens having been reported from Minas Gerais and São Paulo, and a few records from Goiás and Mato Grosso states. This group was widely distributed in the Cretaceous of Gondwana and Laurasia, yet much more abundant and diverse on the Gondwanan landmasses (e.g., Bonaparte, 1996; Novas, 1997a; Powell, 2003).

The first record of titanosaur remains from Brazil was made by Friedrich von Huene (1927a-c), who recognised a caudal vertebra and referred it to “*Titanosaurus australis*” (von Huene, 1927c). Arid and Vizzoto (1971) described the first Brazilian titanosaur species, *Antarctosaurus brasiliensis*, from the municipality of São José do Rio Preto (São Paulo State). Most titanosaurs from the Bauru Group, including *A. brasiliensis*, were described on the basis of disarticulated skeletons, isolated postcranial remains or even isolated teeth, with the exception of *Gondwanatitan faustoi* from the Adamantina Formation. This is the most complete titanosaur known from Brazil (Kellner and Azevedo, 1999).

#### Genus *Antarctosaurus* von Huene, 1929

##### “*Antarctosaurus*” *brasiliensis* (Arid and Vizzoto, 1971)

Fig. 8

**Type.** Holotype is GP-RD-2-4, a left femur, a right humerus and a fragmentary posterior dorsal vertebra, from the

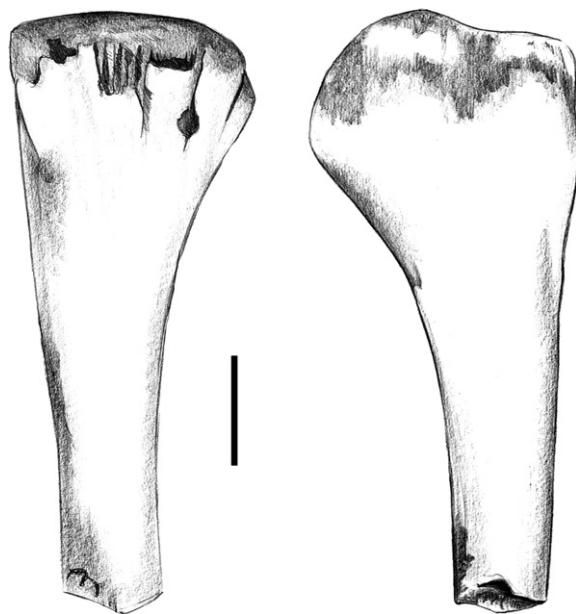


Fig. 8. “*Antarctosaurus*” *brasiliensis* (Arid and Vizzoto, 1971); right humerus in anterior and posterior views (modified from Arid and Vizzoto, 1971). Scale bar represents 50 mm.

municipality of São José do Rio Preto (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** “*Antarctosaurus*” *brasiliensis* was described by Arid and Vizzoto (1971), who mostly compared this taxon with titanosaurs from Argentina. Of those species, the closest similarities are to *Antarctosaurus wichiannianus* von Huene, 1929, in the relative position of the fourth trochanter of the femur and the overall morphology of the proximal portion of the humerus. Nevertheless, the femur of *A. wichiannianus* is slender and slightly twisted, and these features are not definitely present in the Brazilian specimen. In contrast to “*A.*” *brasiliensis*, the fourth trochanter in *A. wichiannianus* is located near the median border approximately midway along the shaft. Unfortunately, the fragmentary condition of the holotype of “*A.*” *brasiliensis* means that assignment to the genus *Antarctosaurus* cannot be but provisional, and because of the lack of autapomorphies this taxon is best considered a “nomen dubium” (Upchurch et al., 2004).

#### Genus *Gondwanatitan* Kellner and Azevedo, 1999

##### *Gondwanatitan faustoi* Kellner and Azevedo, 1999

Fig. 9

**Type.** Holotype is MN-V 4111, a near-complete skeleton, from the Yoshitoshi Myzobuchi farm, municipality of Álvares Machado (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** Kellner and Azevedo (1999) described *G. faustoi* on the basis of a near-complete skeleton recovered from the Adamantina Formation (Turonian–Santonian) of the

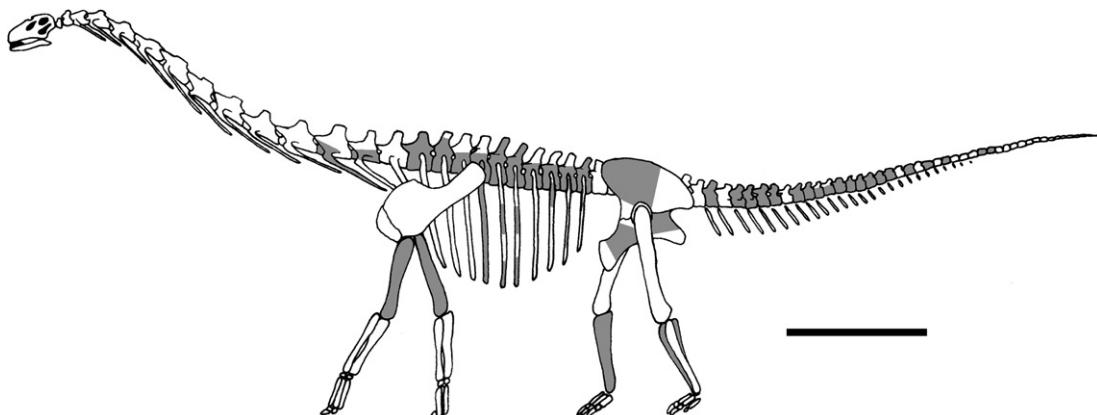


Fig. 9. Reconstruction of *Gondwanatitan faustoi* (modified from Kellner and Azevedo, 1999). Grey areas indicate recovered bones.

municipality of Álvares Machado, São Paulo State. It was interpreted as a member of the Titanosauridae by these authors, and by Salgado and Garcia (2002). Bertini et al. (2000) were of the opinion that this species should be assigned to *Aeolosaurus*, based on the anterodorsally projecting neural spines of proximal caudal vertebrae and other characters of the appendicular skeleton. However, the original description of *Gondwanatitan* makes clear that it differs from *Aeolosaurus* in several features: the centrum of the sixth sacral vertebra has a concave posterior articular surface; there are heart-shaped posterior articular surfaces on proximal and mid-caudal vertebrae; and a prominent lateral ridge is present on the basal portion of the neural arch of mid-caudal vertebrae in *Gondwanatitan*. Prezygapophyses of *Aeolosaurus* have a large articular surface but this is absent in *Gondwanatitan*. There is a lateral tuberosity on the ischium of *Gondwanatitan*, and the iliac peduncle of the ischium is less expanded; the medial ischial plate is less expanded in *Aeolosaurus*, and the humerus is more slender. In view of these differences, we consider them to be distinct taxa.

#### Genus *Aeolosaurus* Powell, 2003

##### *Aeolosaurus* sp.

Fig. 10A

**Material.** MPMA “S/N-1”, postcranial bones from the municipality of Monte Alto (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian; CPP 0248, a caudal vertebra, from Peirópolis (municipality of Uberaba, Minas Gerais State, Brazil); Marília Formation, upper Maastrichtian.

**Remarks.** Almeida et al. (2004), on the basis of UFRJ-DG 270-R, a caudal vertebra (Fig. 10A), and Marinho (2003) recorded the presence of *Aeolosaurus* in Brazil, a genus first described from the Upper Cretaceous of Patagonia (Argentina; Powell, 1986, 2003; Salgado and Coria, 1993). Postcranial remains assignable to this genus are common in the Bauru Group. The vertebral centrum is deep and relatively low, procoelous, and bears a heart-shaped anterior articular facet (Fig. 10A). The transverse process is well developed and

positioned at the centro-neural suture, while the base of the neural arch is positioned anteriorly in relation to the centrum. The neural canal is oval: the lateral diameter is the larger. The neural spine is large and posteriorly orientated, showing well-developed prespinal laminae (PRSL) (Fig. 10A). The spinoprezygapophyseal laminae are also well developed and both are joined to the base of the PRSL. The postzygapophysis is well marked. The haemal arch is straight and laterally compressed. Although its proximal region is fragmentary, its Y-shaped nature is readily seen. The open haemal canal indicates that this caudal vertebra belongs to the Camarasauromorpha. Within that group, the procoelous condition of this caudal

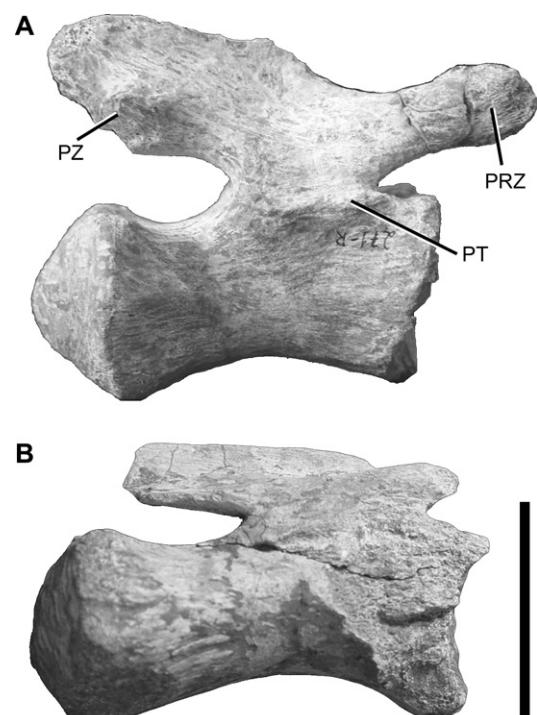


Fig. 10. A, procoelous caudal vertebra of *Aeolosaurus* sp. (UFRJ-DG 270-R) in lateral view: PZ, postzygapophysis; PRZ, prezygapophysis; PT, transverse process. B, procoelous caudal vertebra of Titanosaura indet. (MMR/UFU-PV 0001) in lateral view. Scale bar represents 10 mm.

vertebrate is a synapomorphic feature that allies it with the Titanosauria (Bonaparte and Coria, 1993; Wilson and Upchurch, 2003).

Recently, a titanosaur (MN-V 5013) has been documented from the same locality, the Boa Vista Hill. Almeida et al. (2004) noted the absence of diagnostic features of both *Gondwanatitan* and *Aeolosaurus* (see above) from this specimen. Henriques et al. (2002) also pointed out the possibility of a new taxon closely related to either *Gondwanatitan* or *Aeolosaurus*.

#### Indeterminate genus and species (sensu Avilla et al., 2005)

**Material.** MZ unnumbered, cranial and postcranial remains, from the municipality of Presidente Prudente (Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** The Nemegtosauridae, once included in the Diplococoidea (Upchurch, 1995), is a group of basal Titanosauria (Wilson, 2002, 2005), phylogenetically defined as all titanosaurs more closely related to *Nemegtosaurus* than to *Saltasaurus* (Wilson, 2005). Recently, cranial fragments found in strata of Santonian age (Bajo de la Carpa Formation) in Río Negro (Argentina) have been assigned to a new taxon, *Bonitasaura salgadoi*; see Apesteguía (2004). This author noted that *B. salgadoi* was a titanosaur closely related to the Nemegtosauridae, but did not attribute it to any existing family. Avilla et al. (2005) have briefly described a new nemegtosaurid from the Turonian–Santonian (Adamantina Formation) in the municipality of Presidente Prudente, São Paulo State. The dentary described shows a dentary symphysis perpendicular to the jaw ramus, as in *Bonitasaura salgadoi* and *Nemegtosaurus mongoliensis* (Nemegt Formation, Maastrichtian; Mongolia; see Nowiński, 1971). This new discovery suggests a link between Laurasian and South American tetrapod faunas during the Late Cretaceous.

#### Indeterminate genus and species

Fig. 10B

**Material.** CPP 036-037, 102-103, 110, 217, 297, 360, 393-402, 458, 674, “S/N-1”; GP-RD-6; MCT 1487-R (série A), 1488-R (série B), 1489-R, 1490-R (série C), 1536-R; MPMA 0072-0093; MUGEO 1282, 1295; Pedro Gallo Collection (private); “URC S/N-1”. Most of these specimens are isolated fragments of postcranial elements, not yet catalogued but housed at CPP, UR-RC and MPMA. CPP 217 and 360 are from Bairro de Lourdes, municipality of Uberaba, Minas Gerais State (Brazil); Uberaba Formation, Coniacian-Santonian; CPP 036-037, 102-103, 110, 217, 297, 360, 393-402, 458, 674, “S/N-1”, GP-RD-6, MCT 1487-R (série A), 1488-R (série B), 1489-R, MCT 1490-R (série C), 1536-R and MPMA 0072-0093 are from Peirópolis, municipality of Uberaba (Minas Gerais State, Brazil); Marília Formation, upper Maastrichtian. MUGEO 1282 and 1295 are from the municipality of Flórida Paulista (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian; GP-RD-6 (Pedro Gallo Colln) is from Vila Ventura, municipality of Uchoa (São Paulo

State, Brazil); Adamantina Formation, Turonian–Santonian; RC “S/N-1” is from the municipality of Ibirá (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** As noted above, most Bauru Group titanosaur specimens are isolated bones or teeth, a notable exception being the individual described by Powell (1986, 2003), which consists of several articulated cervical and dorsal vertebrae. These were assigned to “*Titanosaurus*”, while other isolated remains were considered Titanosauridae “incertae sedis” (Powell, 2003). Santucci (2002) claimed that some of the Bauru specimens housed in the CPP, MPMA and DGM collections, and the material described by Powell (2003), corresponded to the genus “*Titanosaurus*”. However, Wilson and Upchurch (2003) argued that the specimen described by Powell (1986) represented a new taxon, and stressed the need for a detailed revision.

#### 3.5.2. Theropods

Theropod remains are extremely rare in the Bauru Group and, to date, only isolated and incomplete specimens have been found. In other Gondwanan localities, especially in South America, theropods are relatively well known and include abelisaurid ceratosaurs (e.g., Bonaparte et al., 1990; Bonaparte, 1991b, 1996; Novas, 1997b; Sampson et al., 1998; Coria et al., 2002), carcharodontosaurid and spinosaurid tetanurans (e.g., Coria and Salgado, 1995; Kellner and Campos, 1996; Sereno et al., 1996, 1998; Sues et al., 2002) and comparatively rare coelurosaurians (e.g., Novas, 1997b, c; Novas and Puerta, 1997; Naish et al., 2004; Novas and Pol, 2005).

#### Genus *Pycnonemosaurus* Kellner and Campos, 2002

##### *Pycnonemosaurus nevesi* Kellner and Campos, 2002

Fig. 11

**Type.** Holotype is DGM 859-R, five teeth, portions of seven caudal vertebrae, fragments of ribs, and an incomplete right tibia and fibula, from the Roncador farm, Cambebe area (Mato Grosso State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** *Pycnonemosaurus nevesi* represents the first Brazilian abelisaurid to have been formally named. Teeth (Bittencourt and Kellner, 2002; see Fig. 12A here), described prior to postcranial remains (Fig. 11B, C), are strongly transversely compressed, with an elliptical cross section. Diapophyses of caudal vertebrae have expanded lateral ends, as seen in other abelisaurs (e.g., *Ilokelesia*, *Carnotaurus*, and *Aucasaurus*). According to Novas et al. (2004), *P. nevesi* and *Lametasaurus indicus* have a short tibia in common, in contrast to other Abelisauroidea (e.g., *Aucasaurus*, *Masiakasaurus*, and *Xenotarsosaurus*).

#### Indeterminate genus and species

**Material.** URC 44-R, a fragmentary premaxilla with a single tooth from an abandoned quarry in the southern outskirts of

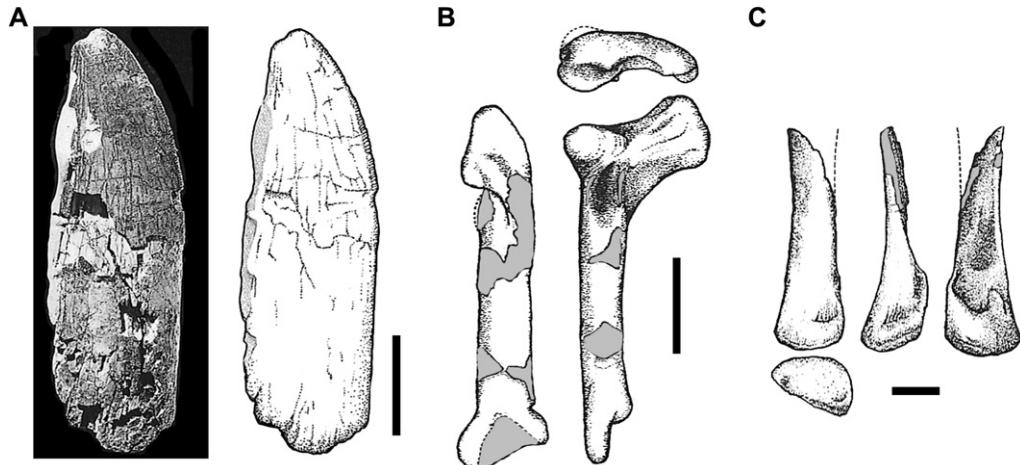


Fig. 11. *Pycononemosaurus nevesi* Kellner and Campos, 2002. A, tooth in lateral view with explanatory drawing (modified from Bittencourt and Kellner, 2002). B, right tibia in anterior (left), lateral (right) and proximal (top) views. C, distal portion of right fibula in lateral (left), anterior (centre), posterior (right) and distal (base) views (B and C, modified after Kellner and Campos, 2002). Scale bar represents 20 mm.

the city of Santo Anastácio (southeastern São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** Bertini (1996) attributed this fragmentary premaxilla to an abelisaurid on account of the irregular surface texture and ventrally facing small tubercles grouped near the naris, recalling the condition in *Abelisaurus comahuensis* Bonaparte and Novas. Among abelisaurids, URC 44-R is closely related to *A. comahuensis* than to *Carnotaurus sastrei* Bonaparte. However, *Carnotaurus* is unusual among basal theropods in possessing a premaxilla-nasal contact; other neoceratosaurids and coelophysoids lack it. The similarity of URC 44-R to *Abelisaurus* is therefore not informative, but plesiomorphic. URC 44-R and other unnamed Adamantina Formation abelisaurids have four premaxillary teeth; this feature was considered by Currie and Zhao (1993) to be the plesiomorphic condition of abelisaurids. URC 44-R has a deep premaxillary body with numerous small foramina on the dorsal portion of its external surface, in common with *Indosuchus* (AMNH 1733) from the Upper Cretaceous of India.

The preserved tooth, associated with the premaxilla, is labiolingually elongate with an oval cross section; both features are present in Gondwanan members of the Abelisauria and Allosauroidae. In contrast, most Laurasian theropods and members of the Spinosauridae have a “D”-shaped or conical cross section. Even though the material is fragmentary, it is possible to consider URC 44-R as an abelisaurid given the numerous derived traits shared with other members of this group; however, a more detailed comparison of URC 44-R with other abelisaurids is called for.

#### Indeterminate genus and species

Fig. 12A

**Material.** CPP 002, 020-021, 121, 123, 129b, c, 131, 132, 134-136, 144, 150, 154, 158, 161/1, 198, 205-207, 211, 242, 372, 375/2, 446, 451/1, 452/1, 463, 476-478; MMR/UFU-PV 0006; UFRJ-DG 371-Rd, 374-Rd and 378-Rd, all isolated

teeth. CPP specimens are from Peirópolis, municipality of Uberaba; Marília Formation, upper Maastrichtian; material held at MMR/UFU-PV is from Prata, municipality of Prata (Minas Gerais State); Adamantina Formation, Turonian–Santonian; UFRJ-DG 371-Rd and UFRJ-DG 374-Rd are from the municipality of Florida Paulista (São Paulo State); Adamantina Formation, Turonian–Santonian, and UFRJ-DG 378-Rd is from the municipality of Alfredo Marcondes (São Paulo State); Adamantina Formation, Turonian–Santonian.

**Remarks.** Theropod teeth are the commonest tetrapod fossils in the Adamantina and Marília formations; they are labiolingually compressed with a low crown and denticles on carinae (Fig. 12A). These features are also observed in *Carnotaurus sastrei* (MACN-CH 894), *Aucasaurus garridoi* (MCF-PVPH 236), *Indosuchus raptorius* (AMNH 1733) and *Majungatholus atopus* (Candeiro, 2002; Lamanna et al., 2002). Other theropod teeth (e.g., of Tyrannosauridae,

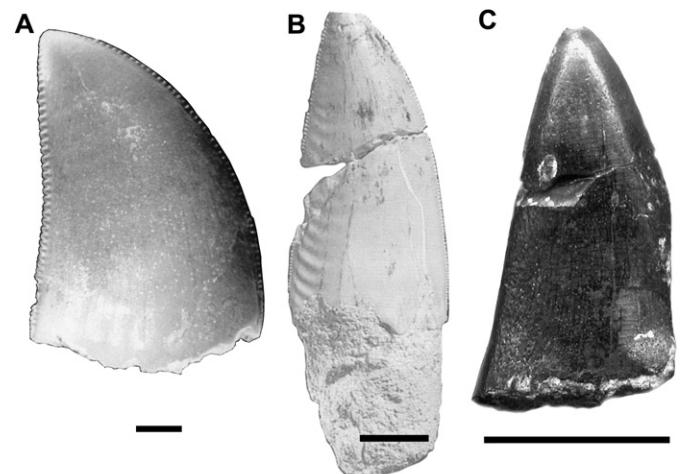


Fig. 12. Isolated teeth of A, Abelisauridae (CCP 123), B, Carcharodontosauridae (modified from Kellner and Campos, 2000), and C, Spinosauridae (UFRJ-DG 372-Rd). Scale bars represent 2 mm in A, and 10 mm in B and C.

Dromaeosauridae and Spinosauridae) are more conical, with relatively higher crowns, and relatively more rounded cross sections.

#### Indeterminate genus and species

Fig. 12B

**Material.** CPP 124, 127, 129a, 152, 156, 197, 199, 200, 208, 216, 241, 375/1, 376, 447-449, 474, 475; MMR/UFU-PV 005 and UFRJ-DG 379-Rd, all isolated teeth. CPP specimens are from Peirópolis, municipality of Uberaba; Marília Formation, upper Maastrichtian; MMR/UFU-PV 005 is from the municipality of Prata (Minas Gerais State); Adamantina Formation, Turonian–Santonian; while UFRJ-DG 379-Rd is from the municipality of Alfredo Marcondes (São Paulo State); Adamantina Formation, Turonian–Santonian.

**Remarks.** Carcharodontosaurids were possibly distributed worldwide, but probably became restricted to Gondwana during the early Late Cretaceous (Forster, 1999). Carcharodontosaurid teeth have been recorded from some southern continents and, recently, also from the Bauru Group (Fig. 12B). These specimens differ from other theropod teeth in having lower crowns (more so than abelisaurids) and characteristic wrinkles on both labial and lingual surfaces (Coria and Salgado, 1995; Larsson, 1996; Sereno et al., 1996). Strata of the Adamantina and Marília formations have yielded a large number of carcharodontosaurid teeth (Candeiro, 2002). These teeth, as well as a single record from the Allen Formation in Patagonia, possibly represent the last occurrences of the group (Martinelli and Forasiepi, 2004).

#### Indeterminate genus and species (sensu Novas et al., 2005)

**Material.** CPP 659, an isolated manual ungual with the distalmost portion broken off, from Serra do Veadinho, Peirópolis, municipality of Uberaba (Minas Gerais State, Brazil); Marília Formation, upper Maastrichtian.

**Remarks.** This specimen was assigned to the Maniraptora on account of the presence of a proximodistal lip such as in oviraptorosaurs, troodontids, dromaeosaurids and basal birds (Novas et al., 2005). Of note is the fact that this ungual shows a combination of features not found in other maniraptorans (e.g., dorsoventrally low and proximodistally elongated, block-like flexor tuberosity, proximal articular surface more dorsally orientated than in other theropods, and cutting keel located distally on ventral surface), suggesting the presence of an unknown, derived group of non-paravian maniraptorans in the Upper Cretaceous of Brazil (Novas et al., 2005).

#### Indeterminate genus and species (sensu Alvarenga and Nava, 2005)

**Material.** MZ unnumbered, some articulated vertebrae and ribs, from the municipality of Presidente Prudente (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** Alvarenga and Nava (2005) briefly described, from the Adamantina Formation, the first avian remains from the Upper Cretaceous of Brazil. The enantiornithine identification of the material is based mainly on the anatomy of postcranial fragments, which are similar to those of *Enantiornis leali* from the Maastrichtian (Lecho Formation) of the province of Salta, Argentina.

#### Indeterminate genus and species

Fig. 12C

**Material.** UFRJ-DG 354-Rd and 372-Rd, isolated teeth, from the municipalities of Flórida Paulista and Santo Anastácio (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** These specimens were first referred to the Spinosauridae (Candeiro et al., 2004a), on account of similarities with teeth of *Irritator challengeri*, *Spinosaurus aegyptiacus*, *Baryonyx walkeri* and *B. tenerensis* (Martill et al., 1996; Martill and Hutt, 1996; Sereno et al., 1998; Sues et al., 2002), and of the absence of denticles and smooth striations on the tooth crowns (as in *Irritator challengeri*; Sues et al., 2002). However, it should be noted that the absence of denticles on tooth crowns has also been reported for other theropods, e.g. Dromaeosauridae (Currie et al., 1990), and smooth striations on crowns also occur in other tetrapods (e.g., *Champsosaurus* RTMP 1991.36.446; *Albertochamps* RTMP 1990.36.439; *Leidyosuchus* RTMP 1983.98.53; Crocodylidae RTMP 1983(52-1), 1991.61.11, 1991.102.2; Hypsilophodontidae RTMP 1994.12.558, 1998.68.177, 2003.12.94; and Plesiosauridae RTMP 87.48.42, 2001.12.151); therefore, these features should not be used as synapomorphies of Spinosauridae as suggested by Sereno et al. (1998) and Sues et al. (2002). Thus, specimens UFRJ-DG 354-Rd and 372-Rd should be regarded as Theropoda indet.

#### 3.6. Mammals

The evolutionary relationships of Gondwanan Mesozoic mammals have become more complex in recent decades due to numerous new discoveries that have revealed a high degree of endemism and/or a combination of features that do not fit the classic evolutionary model constructed on the basis of Laurasian taxa (e.g., Luo et al., 2002). In South America, and particularly in Argentina, our knowledge of Cretaceous mammals has increased significantly in recent years. From the Lower Cretaceous, an exceptionally well-preserved cladotherian mammal, *Vincelestes neuquianus*, was recorded from the La Amarga Formation of Neuquén (Argentina) by Bonaparte (1986a), whereas from Upper Cretaceous strata, about 15 species have now been recognised, based mainly on fragmentary skulls, lower jaws and isolated teeth. The most diverse and abundant Mesozoic mammal assemblage in Argentina is from the Los Alamitos (e.g., Bonaparte, 1986a, 1987, 1990, 1992, 1994, 1996, 2002) and La Colonia formations (e.g., Pascual et al., 2000). Furthermore, isolated mammal remains, not yet

studied in detail, have been recovered from the El Molino (Gayet et al., 2001) and Allen (Rouvier et al., 2003) formations.

In Brazil, mammals are still poorly known. Only an isolated jaw fragment with a premolar is on record from the Bauru Group (Bertini et al., 1993).

Indeterminate genus and species

Fig. 13

**Material.** URC-M001, the anterior part of a right dentary with a premolar (Bertini et al., 1993) from 1.8 km south of Santo Anastácio (São Paulo State, Brazil); Adamantina Formation, Turonian–Santonian.

**Remarks.** Bertini et al. (1993) suggested placental affinities for the fragmentary lower jaw found in the Bauru Basin, based on the presence of four premolars. Unfortunately, the posterior edge of the alveolus of the canine and the alveolus for p1 were not illustrated. While the presence of at least four premolars can be determined, it is impossible to establish whether p4 represents the last premolar or if there were more premolars, as is commonly the case in basal cladotherians, dryolestids and basal eutherians (e.g., *Eomaia*, *Prokennalestes*) of Laurasia (e.g., Kielan-Jaworowska and Dashzeveg, 1989; Ji et al., 2002). In view of the incomplete nature of URC-M001 (Fig. 13), we regard this specimen as Mammalia “incertae sedis”. Because the history of Gondwanan mammals is far from being adequately understood, we expect that new discoveries will clarify its taxonomic affinities.

#### 4. Discussion

##### 4.1. Biogeographical implications of Bauru Group tetrapods

The abundant vertebrate remains described by Bertini et al. (1993) from the Bauru Group, and similarities to



Fig. 13. Fragment of lower jaw of Mammalia “incertae sedis” in lingual and occlusal views (modified from Bertini et al., 1993). Scale bar represents 1 mm.

titanosaur remains from other latitudes (Santucci, 2002; Candeiro et al., 2006), justify the Late Cretaceous age assignment of the Bauru Group. In addition, the recent report of palynological assemblages by Dias-Brito et al. (2001) provides further support for a Late Cretaceous date for this unit.

The rich tetrapod assemblages from this group have been known since the early twentieth century (e.g., von Ihering, 1911; Petri, 2001). However, only during the last 15 years have these fossiliferous beds been studied in detail, and this has resulted in a large number of studies on tetrapods (see Appendix). In terms of taxonomic diversity and abundance, turtles, crocodyliforms and dinosaurs constitute the best represented groups. The predominance of large terrestrial mesoeucrocodylian taxa is noteworthy. In most cases, these were highly predatory animals, as indicated by the presence of ziphodont teeth. In addition, postcranial features such as the presence of a more parasagittal femur than in other mesoeucrocodylians may provide data on behaviour. In strata of Campanian–Maastrichtian age in Argentina, terrestrial mesoeucrocodylians are not abundant; instead, several theropod groups such as abelisaurids and coelurosaurs are on record. Terrestrial crocodyliforms were frequent in Argentina until the Santonian–Campanian, but in younger strata they have not been recorded. It appears that Campanian–Maastrichtian crocodyliforms had a more important ecological role to play as the main carnivorous group in Brazil than did theropods. Among mesoeucrocodylians, *Peirosaurus* has been recovered from the Marília Formation (upper Maastrichtian) of the Bauru Group as well as from the Santonian of Patagonia (Gasparini et al., 1991; Gasparini, 1996). Thus, crocodyliforms have a remarkable record in the Bauru Basin, not only in terms of morphological diversity but also in number of taxa, with at least eight species formally described.

Remains of titanosaur, abelisaurid and carcharodontosaurid dinosaurs are frequently encountered in the Bauru Group (e.g., Kellner, 1996; Candeiro, 2002; Magalhães-Ribeiro, 2002a,b; Santucci, 2002; Santucci and Bertini, 2002; Candeiro et al., 2004a,b, 2006) (Table 1). However, it seems that dinosaurs are much less diverse than crocodyliforms, possibly because of the extremely fragmentary nature of most dinosaur specimens, which makes characterisation of different taxa impossible, and thus accounts for a less diverse dinosaur assemblage.

The Bauru Group has yielded several specimens assigned to the Titanosauria, indicating a close similarity to the fossil record in Argentina (Powell, 2003; Wilson and Upchurch, 2003; Almeida et al., 2004; Candeiro et al., 2006). Santucci and Bertini (2002) and Almeida et al. (2004) recorded *Aeolosaurus*, previously known only from the Upper Cretaceous of Argentina (Salgado and Coria, 1993; Salgado et al., 1997; Powell, 2003).

Dromaeosaurids and *Richardoestesia gilmorei* have been recorded from Minas Gerais and São Paulo states, suggesting the possible occurrence of Laurasian theropod taxa (“invaders”) in the Bauru Group (Franco and Bertini, 1997;





Fig. 14. Reconstruction of landscape and tetrapod fauna of the Adamantina Formation in São Paulo State, Brazil (drawing by J.L. Blanco).

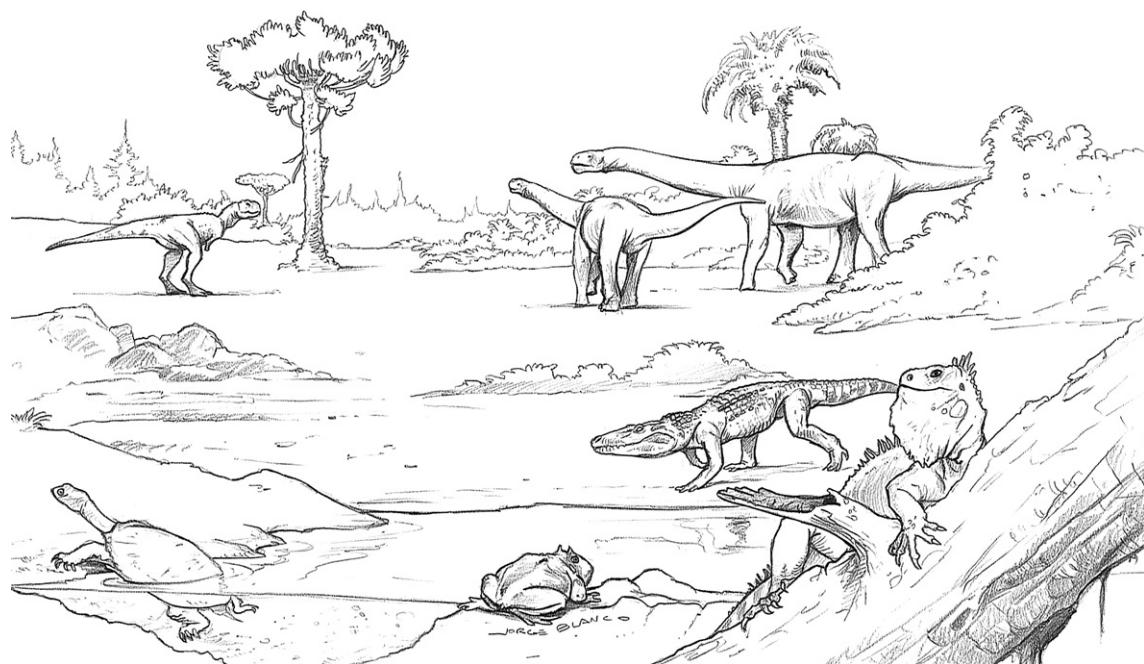


Fig. 15. Reconstruction of landscape and tetrapod fauna of the Marília Formation at Minas Gerais State, Brazil (drawing by J.L. Blanco).

#### 4.2. Comparisons with other Gondwanan faunas and a palaeobiogeographical approach

Bauru Group tetrapods are closer to those from the Upper Cretaceous of Argentina than to any other Gondwanan tetrapod assemblage (Table 1). Late Cretaceous tetrapods in Argentina have been described from several units, among which are the Bajo de la Carpa, Angostura Colorada, Los Alamitos, Allen, Loncoche and La Colonia formations, while in Madagascar the Maevarano Formation, and in India the Lameta Formation have furnished comparable assemblages.

The Maevarano Formation, of Maastrichtian age, is exposed in northern Madagascar (e.g., Rogers et al., 2000). Recent studies have reported a great variety of tetrapods (e.g., Sampson et al., 1998; Krause et al., 1999) including Mesobatrachia, Neobatrachia, ?Pelomedusoides, Madtsoiidae, Peirosauridae, ?Notosuchidae, ?Eusuchia, ?Nemegtosauridae, Abelisauridae, Aves, Ornithothoraces, Enantiornithes, ?Tribosphenida, Multituberculata, and Gondwanatheria.

The Lameta Formation, also of Maastrichtian age, is exposed in central India (e.g., Matley, 1921; Loyal et al., 1996; Bonaparte, 1999, and references therein), and tetrapod assemblages include “Leptodactylidae”, Pelobatidae, Discoglossidae, Myobatrachinae, Anguidae, Nigerophiidae, Pelo-medusidae, Alligatoridae, Nodosauridae, Titanosauridae, Abelisauridae, Aves, and mammals.

In Bolivia, the El Molino Formation (Puca Group; Maastrichtian–Danian) has provided the most representative Late Cretaceous tetrapod fauna; it was studied by Gayet et al. (1991, 2001, and references therein).

In Argentina, the recently proposed Allenian assemblage is represented by tetrapods recorded from the Campanian–Maastrichtian Angostura Colorada, Loncoche, Allen, Los Alamitos and La Colonia formations (Leanza et al., 2004, and references therein). This association includes “Leptodactylidae”, Pipidae, Chelidae, Sphenodontia, Madtsoiidae, Eutitanosauria, Titanosauria, Abelisauridae, Ornithothoraces, Carinatae, Hadrosauridae, Nodosauridae, Abelisauridae, Carcharodontosauridae, Dryolestoidea, “Symmetrodonta”, “Triconodonta”, and Gondwanatheria. In addition, some northwesterly Argentinian Campanian–Maastrichtian units (Salta Group) have produced a high diversity of tetrapods (Bonaparte, 1996, and references therein). The Los Blanquitos Formation has yielded Titanosauria and Maniraptora, while from the Yacoraite Formation eusuchians have been reported, as well as dinosaur and bird tracks. In the Lecho Formation (Salta Group), representatives of Saltasaurinae, Noasauridae, Enantiornithines and ?Oviraptorosauria have been discovered, as have indeterminate nonavian theropod teeth.

A comparison of tetrapod faunas thus suggests strong affinities among the Argentinian tetrapod-bearing units (Table 1). Within South America, some Laurasian groups (e.g., Ornithopoda, Nodosauridae) are restricted to Argentinian formations. Possible differences in composition of Laurasian ornithischian and theropod taxa represented in Argentinian faunas are unknown. Possible explanations for the absence of such taxa from the Bauru Group include the possibility that they never

lived in other areas, that they inhabited the relevant area but became extinct, or that they did live there but have yet to be discovered.

The Bauru Group tetrapod fauna is important for several reasons. These fossil assemblages (e.g., eutitanosaurian *Aeolosaurus* and mesoeucrocodylian *Peirosaurus*) correlate with the Coloradoan and Allenian associations proposed by Leanza et al. (2004), and thus directly match the record of *Aeolosaurus* and *Peirosaurus* to the standard southern South American Gondwanan chronostratigraphic time scale. These links reinforce earlier correlations proposed by von Huene (1931), which indicated that both the Bauru Group and Patagonian units (e.g., Neuquén Group) are of Late Cretaceous age.

#### 5. Conclusions

Bauru Group tetrapods recorded from the Adamantina and Marília formations in central Brazil are represented mainly by frogs, turtles, crocodyliforms, dinosaurs, birds and mammals. The highly fossiliferous, yet poorly known, Bauru Group succession accumulated in the northwesterly Bauru Basin during the Late Cretaceous, and represents fluvio-lacustrine settings. The Late Cretaceous age of the group suggested by previous authors has several important palaeobiogeographical and palaeontological implications. Firstly, it indicates that the Bauru Group assemblage is approximately coeval with faunas recovered from southern South America (e.g., Argentina) and western Gondwana (India and Madagascar). Secondly, the Bauru Group tetrapod fauna, when considered within the larger framework of Late Cretaceous faunal assemblages, is notable for its lack of ornithischians, in contrast to the Argentinian record.

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## Appendix

Late Cretaceous tetrapods from the Bauru Group, Brazil. For the most important tetrapod-bearing localities, see Fig. 1.

| Taxon                            | Locality  | Stratigraphy  | Selected References                       |
|----------------------------------|---|---|---|
| <b>Anura</b>                     |   |   |   |
| <i>Baurubatrachus pricei</i>     | Peirópolis, Uberaba,<br>Minas Gerais  | Serra da Galga Member   | Báez and Perí (1989)                      |
| ?“Leptodactylidae”               | Marília, São Paulo  | Marília Formation<br>Adamantina Formation   | Carvalho et al. (2003)                    |
| <b>Chelonia</b>                  |   |   |   |
| Chelonia indet.                  | Peirópolis, Uberaba,<br>Minas Gerais  | Serra da Galga Member,<br>Marília Formation   | França and Langer (2003)                  |
| Podoceminiidae                   | Peirópolis, Uberaba, Minas Gerais;<br>Álvares Machado, São Paulo                    | Serra da Galga Member, Marília<br>Formation; Adamantina Formation                     | Azevedo et al. (2000)                     |
| <i>Roxochelys harrisi</i>        | Presidente Prudente-Pirapozinho,<br>São Paulo                                       | Adamantina Formation  | Pacheco (1913);<br>Kischlat et al. (1994) |
| <i>Roxochelys wanderlyi</i>      | ?Araçatuba Jupia, São Paulo   | Adamantina Formation  | Price (1953)                              |
| <i>Bauruemys elegans</i>         | Presidente Prudente-Pirapozinho,<br>São Paulo                                       | Adamantina Formation  | Suárez (1969); Kischlat (1994)            |
| <i>Bauruemys brasiliensis</i>    | Araçatuba, São Paulo  | Adamantina Formation  | Bertini et al. (1993)                     |
| <i>Cambaremys langertoni</i>     | Peirópolis, Uberaba, Minas Gerais   | Serra da Galga Member,<br>Marília Formation   | França and Langer (2005)                  |
| <b>Squamates</b>                 |   |   |   |
| <i>Pristiguana brasiliensis</i>  | Peirópolis, Uberaba, Minas Gerais   | Serra da Galga Member,<br>Marília Formation   | Estes and Price (1973)                    |
| Anilioidea                       | General Salgado, São Paulo  | Adamantina Formation  | Zaher et al. (2003)                       |
| <b>Crocodyliformes</b>           |   |   |   |
| <i>Itasuchus jesuinoi</i>        | Peirópolis, Uberaba, Minas Gerais   | Serra da Galga Member,<br>Marília Formation   | Price (1955)                              |
| <i>Peirosaurus tormini</i>       | Peirópolis, Uberaba, Minas Gerais   | Serra da Galga Member,<br>Marília Formation   | Price (1955); Gasparini et al. (1991)     |
| <i>Uberabasuchus terrificus</i>  | Peirópolis, Uberaba, Minas Gerais   | Serra da Galga Member,<br>Marília Formation   | Carvalho et al. (2004)                    |
| <i>Baurusuchus pachecoi</i>      | General Salgado, Jales, Monte Aprazível,<br>Paulo de Faria, São Paulo               | Adamantina Formation  | Price (1945); Avilla (2003)               |
| <i>Baurusuchus salgadoensis</i>  | General Salgado, São Paulo  | Adamantina Formation  | Carvalho et al. (2005)                    |
| <i>Mariliasuchus amarali</i>     | Marília, São Paulo  | Adamantina Formation  | Carvalho and Bertini (1999)               |
| <i>Sphagesaurus huenei</i>       | Guajuçara, Presidente Prudente, Presidente<br>Bernardes, Santo Anastácio, São Paulo | Adamantina Formation  | Price (1950a); Pol (2003)                 |
| <i>Stratiotosuchus maxhechti</i> | Irapuru, São Paulo  | Adamantina Formation  | Campos et al., (2001); Avilla (2002)      |
| <b>Dinosauria</b>                |   |   |   |
| Sauropoda                        |   |   |   |
| “Antarctosaurus” brasiliensis    | São José do Rio Preto, São Paulo  | Adamantina Formation  | Arid and Vizzoto (1971);<br>Powell (2003) |
| <i>Gondwanatitan faustoi</i>     | Álvares Machado, São Paulo  | Adamantina Formation  | Kellner and Azevedo (1999)                |
| <i>Aeolosaurus</i> sp.           | Peirópolis, Uberaba, Prata, Minas Gerais;<br>Monte Alto, São Paulo                  | Echaporã and Serra da<br>Galga Members,<br>Marília Formation; Adamantina<br>Formation | Candeiro et al. (2004b)                   |

(continued on next page)

## Appendix (continued)

| Taxon                         | Locality  | Stratigraphy  | Selected References                                       |
|-------------------------------|---|---|---|
| Nemegtosauridae               | Presidente Prudente, São Paulo  | Adamantina Formation  | Avilla et al. (2005)                                      |
| Titanosauria indet.           | Peirópolis, Uberaba, Prata, Monte Alegre de Minas, Minas Gerais; Flórida Paulista, Guararapes, Monte Alto, São José do Rio Preto, São Paulo | Serra da Galga Member, Marília Formation; Uberaba Formation; Adamantina Formation | Powell (1986, 2003)                                       |
| Sauropoda indet.              | Peirópolis, Uberaba, Prata, Minas Gerais; Adamantina, Colina Pacaembu, São Paulo  | Serra da Galga Member, Marília Formation; Uberaba Formation; Adamantina Formation | Candeiro et al. (2004b)                                   |
| <b>Theropoda</b>              |   |   |   |
| <i>Pycnonemosaurus nevesi</i> | Cambebe, Mato Grosso  | Adamantina Formation  | Bittencourt and Kellner (2002); Kellner and Campos (2002) |
| Abelisauridae                 | Peirópolis, Uberaba, Prata, Minas Gerais; Alfredo Marcondes, Flórida Paulista, Santo Anastácio, São Paulo                                   | Serra da Galga Member, Marília Formation; Adamantina Formation                    | Candeiro et al. (2004b)                                   |
| Carcharodontosauridae         | Peirópolis, Uberaba, Prata, Minas Gerais; Alfredo Marcondes, São Paulo  | Serra da Galga Member, Marília Formation; Adamantina Formation                    | Candeiro et al. (2004b)                                   |
| Maniraptora                   | Peirópolis, Uberaba, Minas Gerais   | Serra da Galga Member, Marília Formation  | Novas et al. (2005)                                       |
| Enantiornithine indet.        | Presidente Prudente, São Paulo  | Adamantina Formation  | Alvarenga and Nava (2005)                                 |
| Theropoda indet.              | Peirópolis, Uberaba, Prata, Minas Gerais; Ibirá, Florida Paulista, Alfredo Marcondes, São José do Rio Preto, São Paulo                      | Serra da Galga Member, Marília Formation; Adamantina Formation                    | Candeiro et al. (2004b)                                   |
| <b>Mammalia</b>               |   |   |   |
| Mammalia indet.               | Santo Anastácio, São Paulo  | Adamantina Formation  | Bertini et al., (1993)                                    |