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RESEARCH PAPER

The Baurusuchidae vs Theropoda record in the Bauru Group (Upper Cretaceous, Brazil): a taphonomic perspective

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Abstract

Purpose The Bauru Group is worldwide known due to its high diversity of archosaurs, especially that of Crocodyliformes. Recently, it has been suggested that the Crocodyliformes, especially the Baurusuchidae, were the top predators of the Bauru Group, based on their anatomical convergence with theropods and the dearth of those last ones in the fossil record of this geological group.

Methods Here, we erect the hypothesis that assumption is taphonomically biased. For this purpose, we made a literature survey on all the published specimens of Theropoda, Baurusuchidae and Titanosauria from all geological units from the Bauru Group. Also, we gathered data from the available literature, and we classified each fossil find under a taphonomic class proposed on this work.

Results We show that those groups have different degrees of bone representativeness and different qualities of preservation pattern. Also, we suggest that baurusuchids lived close to or in the abundant flood plains, which explains the good preservation of their remains. Theropods and titanosaurs did not live in association with such environments and the quality of their preservation has thus been negatively affected.

Conclusions We support the idea that the Baurusuchidae played an important role in the food chain of the ecological niches of the Late Cretaceous Bauru Group, but the possible biases in their fossil record relative to Theropoda do not support the conclusion that baurusuchids outcompeted theropods. Rather, this taphonomic bias must be tackled first, which previous studies have not regarded.

Keywords Bauru Group · Baurusuchidae · Theropoda · Titanosauria · Taphonomy · Palaeoecology

Resumen

Objetivo El Grupo Bauru es mundialmente conocido debido a su diversidad de arcosaurios, especialmente Crocodyliformes. Recientemente, se ha sugerido que los Crocodyliformes –y, particularmente los Baurusuchidae– fueron superdepredadores del Grupo Bauru debido a sus convergencias anatómicas con los terópodos y a la escasez de estos últimos en el registro fósil de este grupo geológico.

Métodos En el presente trabajo presentamos la posibilidad que esta hipótesis esté tafonómicamente sesgada. Para lograr este objetivo, realizamos una evaluación bibliográfica sobre todos los especímenes publicados de Theropoda, Baurusuchidae y Titanosauria de todas las unidades geológicas del Grupo Bauru. Asimismo, también recopilamos datos de la literatura disponible y clasificamos cada hallazgo fósil dentro de una clase tafonómica propuesta en este estudio.

Resultados Mostramos que tales grupos tienen grados muy diferentes de representatividad ósea y calidad en los patrones de preservación. Además, sugerimos que los baurusúquidos vivieron bien cerca o en llanuras de inundación, lo que podría explicar la buena preservación de sus restos. Terópodos y titanosaurios no vivieron en asociación a tales ambientes y la calidad de su preservación se vería así negativamente afectada.

Conclusiones Apoyamos la idea que los Baurusuchidae jugaron un papel importante en la cadena trófica de los nichos ecológicos del Cretácico Superior del Grupo Bauru, pero los posibles sesgos en su registro fósil referentes a los Theropoda no

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apoya la conclusión que los baurusúquidos desplazaron a los terópodos. Más bien, este sesgo tafonómico debe ser encarado primero, lo que hasta ahora estudios previos al presente no han contemplado.

Palabras clave Grupo Bauru · Baurusuchidae · Theropoda · Titanosauria · Tafonomía · Paleoecología

1 Introduction

The Bauru Group is one of the most fossiliferous geologic units from Brazil, comprising an area of 370.000 km^2 (Fernandes and Coimbra 1996) and constituting the largest Cretaceous continental unit in South America (Bertini et al. 1993). This unit was formed by the deposition of sandstones in lacustrine, fluvial and aeolian environments, which implies in the existence of different formations among the unit (e.g., Fernandes and Coimbra 1996; Azevedo et al. 2013a).

The palaeoenvironment of the Bauru Group was inhabited by a plethora of animals, with vertebrates being its most abundant record, including fish (e.g., Martinelli et al. 2013), Lissamphibia (e.g., Baez and Peri 1989), Squamata (Estes and Price 1973; Nava and Martinelli 2011), turtles (e.g., Romano et al. 2013), birds (e.g., Alvarenga and Nava 2005) and mammals (e.g., Bertini et al. 1993). Despite this diversity, in terms of species abundance, the Crocodyliformes are predominant (with 26 species; Roxo 1936; Price 1945, 1950, 1955; Carvalho and Bertini 1999; Campos et al. 2001; Arruda et al. 2004; Carvalho et al. 2005; Nobre and Carvalho 2006; Carvalho et al. 2004, 2007; Nobre et al. 2007; Andrade and Bertini 2008; Iori and Carvalho 2009; Marinho and Carvalho 2009; Nascimento and Zaher 2010; Kellner et al. 2011a, b; Campos et al. 2011; Carvalho et al. 2011; Montefeltro et al. 2011; Iori and Carvalho 2011; Iori and Garcia 2012; Marinho et al. 2013; Godoy et al. 2014; Pol et al. 2014; and excluding *Brasileosaurus pachecoi* Huenei 1931 due to the fragmentary nature of the specimen and its dubious systematic positioning, see Riff et al. 2012), with non-avian dinosaurs being the second more diverse clade (with nine species; Kellner and Azevedo 1999; Campos et al. 2005; Kellner et al. 2005; Santucci and Bertini 2006a; Kellner et al. 2006; Salgado and Carvalho 2008; Santucci and Arruda-Campos 2011; Machado et al. 2013; Bandeira et al. 2016).

Among the Crocodyliformes, eight of those species are baurusuchids, all of which exhibit some degree of anatomical convergence with non-avian theropods (e.g., Riff and Kellner 2011). Regarding Sauropoda, all known species from the Bauru Group are titanosaurs (e.g., Bandeira et al. 2016). Theropods (including birds) are represented only by sparse and isolated remains and no nominal species has been proposed yet for the group (Brum et al. 2016, 2017; *contra* Kellner and Campos 2002). The abelisaurid species *Pycnonemosaurus nevesi* Kellner and Campos 2002 was originally attributed to the Bauru Group, but is nowadays considered as belonging to the Parecis Group after geological revisions on those strata (Weska 2006; Bittencourt and Langer 2011; Delcourt 2017).

Regarding the low diversity of theropods in the Bauru Group, some authors have argued that this scenario does not represent the original Bauru's biocoenosis (Martinelli et al. 2013; Godoy et al. 2016), thus preferring a taphonomic explanation (e.g., Souza et al. 2014). Other authors prefer a palaeoecological explanation, assuming that Titanosauria and Theropoda have a similar taphonomic signature and then that the high abundance of titanosaurs and the lower diversity of theropods is a real representation of the Bauru's biocoenosis, as opposed to a taphonomic artefact (Riff and Kellner 2011). As such, the diversification of Baurusuchidae is justified as an occupation of the top terrestrial predatory niche in the Bauru Group, replacing small and medium-sized theropods (Riff and Kellner 2011).

The palaeoecological hypothesis as an explanation for the Baurusuchidae diversification in the Bauru Group suggests that there is no taphonomic bias regarding the preservation of theropods. However, no taphonomic analysis has ever been performed to corroborate this affirmation. Therefore, the present work aims at describing quantitatively and qualitatively the non-avian Theropoda, Titanosauria and Baurusuchidae record in the Bauru Group. This data will serve as evidence for the analyses of taphonomic patterns and possible preservation signatures in those groups, which will provide new subjects to the discussion and test the palaeoecological scenario for the Baurusuchidae diversification.

Institutional abbreviations: CPP/CPPLIP, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Peirópolis, Minas Gerais state, Brazil; DGM-R, Departamento Nacional da Produção Mineral, Museu de Ciências da Terra, Rio de Janeiro state, Brazil; GP-RD, Departamento de Geociências da Faculdade de Filosofia, Ciências e Letras de São José do Rio Preto, São Paulo state, Brazil; LF-R, Grupo de Ciências Luckesi, Escola Estadual José Firpo, Lucélia City, São Paulo state, Brazil; LGP-D Laboratório de Geologia e Paleontologia of Fundação Universidade Federal do Rio Grande; Rio Grande do Sul state, Brazil LPRP/USP, Laboratório de Paleontologia de Ribeirão Preto, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, São Paulo state, Brazil; MBC-PV, Coleção Zoológica do INBIO/Universidade Federal de Uberlândia, Uberlândia city, Minas Gerais state, Brazil; MCT, Museu de Ciências da Terra–Companhia de Pesquisas de Recursos Minerais, Rio de Janeiro state, Brazil; MN, Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro state, Brazil; MP, Museu Geológico Valdemar Lefèvre, São Paulo state, Brazil; MPM, Museu de Paleontologia de Marília, São Paulo state, Brazil; MUGEO, Museu Geológico Valdemar Lefèvre, São Paulo state, Brazil; MZSP-PV, Coleção de Paleovertebrados do Museu de Zoologia da Universidade de São Paulo, São Paulo state, Brazil; MPMA, Museu de Paleontologia de Monte Alto, São Paulo state, Brazil; UFRJ DG-R, fossil reptilian collection from Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro state, Brazil; URC-R, Museu de Paleontologia e Estratigrafia da Universidade do Estado de São Paulo *campus* Rio Claro, São Paulo state, Brazil.

Anatomical abbreviations: cd,coracoid; ch, chevrons; fe, femur; fi, fibula; hu, humerus; hy, hyoid; il, ilium; is, ischium; man, manus; mdb, mandible; os, osteoderm; pb, pubis; pes, pes ph, phalanx; pt, proatlas; ra, radius; rb, rib; sc, scapula; sk, skull; st, sternum; ti, tibia; ul, ulna; vb, vertebrae.

2 Geological background

The Bauru Group (sensu Soares et al. 1980) is an Upper Cretaceous sequence which filled up the same geotechtonic and layed over the strata of the Paraná Basin (Soares et al. 1980; Fernandes and Coimbra 2000; Brusatte et al. 2017). This unit was deposited in a depression developed during the Late Cretaceous, resulting from the Gondwana break-up (Fernandes and Coimbra 2000), being deposited immediately above the Serra Geral basaltic rocks (Fernandes and Coimbra 2000). Here, we follow the geological unit proposition for the Bauru Group, originally described by Soares et al. (1980) and later updated (Fernandes and Coimbra 2000; Fernandes 2004), with the major formations (from the oldest to the most recent): Vale do Rio do Peixe, Araçatuba, Uberaba, Presidente Prudente, São José do Rio Preto and Marília. The propostion of Fernandes and Coimbra (2000) divided the Adamantina Formation into the Vale do Rio do Peixe, Araçatuba and Presidente Prudente formations, although the Vale do Rio do Peixe and São José do Rio Preto do not exhibit distinctive features among them, with the rare differences often being regional variations, especially in São Paulo state (Brusatte et al. 2017). In this way, we do not adopt these designations, using the former designation Adamantina Formation instead.

The Adamantina Formation corresponds mainly to fine sandstones with ripple cross-lamination or planar to trough-cross stratification, with some intraclasts of mudstones at the base of the troughs. Those sedimentary matrices are interbedded with heterolithic facies with matrix-supported intraformational conglomerates, being considered as fluvial braided palaeoenvironment (Menegazzo et al. 2016, Brusatte et al. 2017). Dias-Brito et al. (2001) suggested a Turonian-Santonian age for the Adamantina Formation in strata.

The Uberaba Formation is comprised by fine-to-medium sandstones with planar to trough-cross stratification. The sandstones with ripple cross-lamination are also frequent, together with the cross-bedded and massive conglomerates with fragments of volcanic rocks (Brusatte et al. 2017), being interpreted as a fluvial braided environment (e.g., Menegazzo et al. 2016). The Presidente Prudente Formation contains thick mudstone beds interbedded with sandstone lenses at the base (Simbras 2009; Azevedo et al. 2013b; Brusatte et al. 2017), with channelized deposits comprising a fining-upward sequence which conglomerates are at the base, sandstone on the middle and mudstones at the top. This formation has been interpreted as a large overbank fine deposits as well as amounts of filled channel, flood plains and crevasse splays, typical of a meandering fluvial system. Finally, the Marília Formation is traditionally divided in three Members: Serra da Galga, Ponte Alta and Echaporã. The Serra da Galga Member has coarse to fine sandstones, with some conglomerates interpreted as fluvial braided system. The Ponte Alta Member also comprise course coarse to fine sandstones but these are more cemented. Lastly, the Echaporã Member is composed by sand sheets deposits, which are interpreted as residual lakes.

3 Materials and methods

3.1 Studied materials

In order to test the palaeoecological hypothesis proposed by Riff and Kellner (2011) as an explanation for baurusuchid morphology and its specimen abundance, we must search for evidences (i.e. morphology of the specimens and species abundance on fossil record) that have the same causal origin as the hypothesis in test (see Jeffares 2008). We regard here the taphonomic pattern of small to medium sized specimens of Baurusuchidae and Theropoda to argue whether the species diversity of those groups has a palaeoecological explanation as opposed to a preservational bias hypothesis. If the Baurusuchidae and Theropoda specimens represent different taphonomic patterns, implying on different causes, the taphonomic bias will be preferred rather than the palaeoecological explanation. Following the reasoning of Riff and Kellner (2011), we also study the taphonomic pattern observed among Sauropoda (Titanosauria) as an outgroup comparison. The teeth (associated or isolated) of both dinosaurs clades and of the crocodyliforms were not considered in this study, due the high quantity of teeth than any other type of bone. In this way, to understand the taphonomic process regarding the fossilization of Baurusuchidae, Theropoda and Titanosauria specimens from the Bauru Group, we perfomed an extensive literature survey on all the published specimens from these groups. A total of 21 Baurusuchidae, 26 Theropoda and 71 Titanosauria specimens were catalogued (see Table 1 for parameters of the taphonomic class and the results in Table 2).

3.2 Taphonomic remarks

The completeness, articulation and quality of preservation (Table 1) are evidences for the inference of the biostratinomic processes and its respective duration. The approach taken in this paper aims to reveal the preservation bias of each studied group, and not the specific taphonomic history of each specimen itself. Therefore, these taphonomic classes and their frequencies are a gauge for overall preservational biases in overall preservation, both in terms of quality and quantity of material.

Therefore, our classes are based on the biased potential for taphonomic grade from Behrensmeyer (1978) which qualitatively seeks to assess the degrees of weathering in the bones. As a result, all 115 specimens are scored on eight classes (Table 1), with the bone surface damage being consequently distributed on five levels (Behrensmeyer 1978). The best preserved specimens are scored at the initial letters (e.g., A, B) from Table 1 and smallest numbers of the Table 2 (e.g., level 1), and the most damaged specimens are scored at the most largest ones (e.g., level 5). Those classes indirectly indicate an estimation of how long the exposure of the bone lasted.

4 Results

4.1 Bone representativeness

The Titanosauria are the best represented clade recovered from the Bauru Group in comparison with the other analysed groups, with 9 nominal species described up to date. Baurusuchidae is the second, with eight species, while Theropoda exhibit no nominal species. In terms of specimen representativeness, titanosaurian remains totalize 71 specimens, followed by the theropods with 26 while baurusuchids are represented at least with 21 specimens (Table 2, Fig. 1, see also Table 3). Vertebrae and ribs are the most sampled bones for the three clades. However, the titanosaurs exhibit the highest comparative frequency of those axial remains. Skull bones (including the mandible) are well-represented in Baurusuchidae with two complete and twelve associated skull bones, while those ones are rare in the dinosaurian clades recovered from the Bauru Group (two for Theropoda and five elements for Sauropoda). Taking the most frequent bones among the compared groups, the predominance of hindlimb elements is remarkable.

The baurusuchid is the more representative taxa when compared with theropods and titanosaurs. This is a direct consequence of the most numerous kinds of bones (e.g., skull, vertebrae, femora, etc.; see Fig. 1 and Table 2). This trend has similarities with titanosaurs, the second group with high degree of representativeness of bones, despite the vertebrae and ribs being the most abundant bones for this group. Although titanosaurs and baurusuchids share similar number of described species, this tendency could be related to the low number of specimen sampling for Titanosauria, rather than a more general taphonomic tendency.

4.2 Biostratinomic comments

Our taphonomical remarks concerning the preservation aspects of baurusuchids, theropods and titanosaurs in the Bauru Group suggest different biostratinomic patterns for individuals of each group. Baurusuchid fossils are those with the highest degrees of completeness and articulation (13 out of 21 individuals show at least some degree of articulation; see Table 2), which include almost complete skulls and almost complete postcranial skeletons, with only faint signs of weathering (e.g., Araújo-Júnior and Marinho 2013). We interpreted that these fossils suffered a relatively short process of subaerial exposure and transportation prior to burial of those bone elements.

Although titanosaurs are represented by 71 specimens, only 5 exhibit some degree of articulation, while other 25 specimens are represented only by associated elements (10 of class F and 15 of class G; Table 2), and 41 are isolated remains. Though some titanosaur specimens exhibit good preservation of bone surface, most specimens exhibit more signs of weathering (e.g., Santucci and Arruda-Campos 2011) than baurusuchids. Additionally, a considerable number of titanosaurs (29) exhibit elements with minor loss of superficial bone tissue (e.g., Bandeira et al. 2016), while 4 specimens show an extensive loss, such as DGM 497-R which lost an almost entire bone surface (Trotta et al. 2002).

On the other hand, theropods are represented almost entirely by isolated, incomplete material, with only two specimens (out of 26) represented by associated remains (Table 2). Most theropod remains (7 out of 26) show at least slight signs of superficial damage, with 7 specimens having more advanced weathering signs. In this way, theropods show more taphonomic loss of quality than baurusuchids, but without the expressive loss of the bone surface seen in some sauropods—which in turn, could be correlated to a longer time exposed to the weathering and abrasion factors, as expected to sauropods due to their larger size.

4.3 Taphonomic patterns

The majority of Baurusuchidae specimens can be classified as belonging to classes A, B, C and D (Table 2). No baurusuchid specimen consists of isolated bones. All theropod specimens can be classified as belonging to classes F, G, and H. No theropod specimens are articulated or nearly completely associated. The titanosaurian specimens can be classified as belonging to classes E, F, G, and H (Table 2). However sporting similar classes as theropods, titanosaurs from the Bauru Group tend to be somewhat more complete and to be found in closer association than Theropoda.

Overall, in terms of completeness a comparison between these three groups indicates that baurusuchid remains tend to be more complete than either of the two other groups, and titanosaur specimens tend to be more complete than theropods. In terms of articulation and association, the Baurusuchidae individuals are found in articulation in greater quantity than the other two groups. In contrast, most theropod remains consist of isolated bone material, with no articulated specimens being found. The Titanosauria are rarely found in articulation but are often in association, while the Theropoda remains are scarce.

In terms of bone representativeness, baurusuchid remains have a tendency to be reasonably complete or, failing that, to be well represented by their cranial elements. In comparison, Theropoda tend to be woefully incomplete: the most commonly found elements are vertebrae and long bones. Characteristically, very little in terms of cranial elements has been recovered. Sauropod bone representativeness varies, with some elements being reasonably complete though seldom as complete as the least complete baurusuchid. Most of the specimens are incomplete (54.13%; Table 3) with long bones and vertebrae being the main elements recovered. Lastly, 57 (80, 28%) titanosaurs are represented by single isolated elements, mostly vertebrae or long bones.

4.3.1 Diversity distribution among formations of Bauru Group

The distribution of the diversity of the fossil record of Baurusuchidae, Theropoda and Titanosauria among the formations of the Bauru Group is compiled in Table 2. The Adamantina Formation is the most diverse unit of the Bauru Group regarding the groups surveyed in this study: all baurusuchid crocodyliforms specimens (21), with eight species, as well as 13 out of 26 theropod specimens and 22 out of 71 titanosaur specimens (with three species) yielded from the Adamantina Formation. As the unique unit with baurusuchid fossils, the Adamantina Formation is the only one to yield all the three groups of the survey provided herein. The baurusuchid fauna of this Formation includes the species *Baurusuchus albertoi*, *B. pachecoi* and *B. salgadoensis*, *Aplestosuchus sordidus*, *Campinasuchus dinizi*, *Gondwanasuchus scabrosus*, *Pissarrachampsa sera* and *Stratiotosuchus maxhetchi*, as well as a specimen assigned to *Baurusuchus* cf. *B. salgadoensis* and another to *Baurusuchus* sp. The theropod fauna of the Adamantina Formation includes records of Unenlagiinae (Dromaeosauridae) and of indeterminate Abelisauroidea, Noasauridae, Megaraptora, Maniraptora and Aves. The Titanosauria record includes the species *Adamantisaurus mezzalirai, Maxakalisaurus topai* and *Aeolosaurus maximus*. The holotype of "*Antarctosaurus brasiliensis*" was described as a distinct species by Arid and Vizotto (1971), but it later considered to be a *nomen dubium* (Upchurch et al. 2004). Furthermore, there are also records of several Aeolosaurini and of indeterminate Titanosauria remains recovered in the Adamantina Formation.

The Marília Formation is the second most diverse by having 10 specimens of theropods and 44 of Titanosauria

Table 1 Taphonomic classes proposed here and their respective degree of articulation and association

Taphonomic class (T.C.)	Name	Description
A	Complete articulated	Complete or nearly complete specimen, in articulation
B	Complete associated	Complete or nearly complete specimen, in association
C	Skull and mandible articulated	Cranium and mandible in articulation
D	Skull and mandible associated	Cranium and mandible in association
E	Headless articulated postcranium	No cranium or mandible, wealth of postcranial elements, in articulation
F	Headless associated postcranium	No cranium or mandible, wealth of postcranial elements, in association
G	Headless postcranium	No cranium or mandible, wealth of postcranial elements, dispersed but belonging to the same individual
H	Isolated bone	Skeletal material in isolation

Table 2 The specimens of Baurusuchidae, Theropoda and Titanosauria analysed on present work, regarding their identification as species (‘SPECIES’) or less inclusive clade (‘CLADE’, see table), as the known body portions (‘SPECIMEN’), and all specimens are discriminated with their respective bones recovered (‘MATERIAL’)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
Baurusuchidae	*Aplestosuchus sordidus*	LPRP/USP 0229*	sk, mdb, pt, hy, vb, rb, sc?, cd?, hu, ra, ul, man, il, is?, pb?, fe, ti, fi	A	Fine-grained sandstones and siltstones with intercalations of red oxidized mudstones	AF	Extensive alluvial plain reworked by fluvial systems alongside scattered shallow ephemeral lakes in an arid or semi-arid seasonal climate	1	Marinho et al. (2013) (lith.settings); Godoy et al. (2014)
	Baurusuchus albertoi	MZSP-PV 140*	sk, mdb, hy, vb, rb, ch, sc, cd, hu, ra, ul, man, il, pb, fe, ti, fi, pes	B	Fine-grained sandstones and siltstones with intercalations of red oxidized mudstones	AF	Extensive alluvial plain reworked by fluvial systems alongside scattered shallow ephemeral lakes in an arid or semi-arid seasonal climate	1	Marinho et al. (2013) (lith.settings); Nascimento and Zaher (2010); Nascimento and Zaher (2011)
	Baurusuchus pachecoi	DGM 299-R*	Sk, mdb	C	Fine-grained red sandstone with cross lamination (pers.obs)	AF	Floodplain in arid climate	1	Price (1945)
	Baurusuchus cf. B. pachecoi	MCT 1724	Sk, mdb	C	Fine to medium grained sandstones with cross lamination (pers.obs)	AF	Floodplain in arid climate	3	Geroto and Bertini (2012)
	Baurusuchus salgadoensis	MPMA 62-0001-02*	Sk,mdb	C	Fine-grained sandstones and siltstones with intercalations of red oxidized mudstones	AF	Predominantly lacustrine environment, increasing in aridity and relief, leading to formation of alluvial plains, braided rivers, and temporary pools. Specimen found in alluvial plain formed through sudden floods. Eggs and eggshells on correlated nearby levels	1	Carvalho et al. (2005)
	Baurusuchus cf. *B. salgadoensis*	UFRJ DG 288-R	vb, rb, ch, cd, hu, ra, ul, man, il, is, pb, fe, ti, fi, pes	E	Fine to medium grained sandstones	AF	Floodplain in arid climate	1	Arruda et al. (2004); Riff and Kellner (2011)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Baurusuchus sp.	UFRJ-DG 418 R	vb,rb, pb, os	E	Set of intercalations between very fine sandstones with carbonate cementation and very fine sandstones with planar cross-bedding.	AF	Floodplain in arid climate	3	Araújo-Junior and Marinho (2013)
	Campinasuchus dinizi	CPPLIP 1235*	sk, mdb, pt	C	Fine to coarse grained sandstones with calcrete surfaces (most complete specimen); conglomeratic sandstones with alkali pebbles and sandstone intraclasts (bones disarticulated)	AF	(Formation) Alluvial plain reworked by fluvial systems, alongside shallow ephemeral lakes, in arid or semi-arid seasonal climate. (Fossil Occurrence) Distal alluvial fans and alluvial plains subjected to sudden floods in a dry and hot climate. Further down, the authors seemingly contradict themselves, stating that the environment is marked by “relatively deep lakes”	3	Carvalho et al. (2011)
		CPPLIP 1234	sk, mdb	C				3	Carvalho et al. (2011)
		CPPLIP 1236	sk, mb	C				3	Carvalho et al. (2011)
		CPPLIP 1237	sk, mdb, pt, vb, rb, ch, sc, cd, hu, man, il, is, fe, ti, pes, os	A				3	Carvalho et al. (2011); Cotts et al. 2016
		CPPLIP 1435	vb, ch	F			Distal alluvial fans and alluvial plains subjected to sudden floods in a dry and hot climate	4	Cotts et al. (2016)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
		CPPLIP 1436	hu, ra, ul, man, ti, pes	F			Distal alluvial fans and alluvial plains subjected to sudden floods in a dry and hot climate	2	Cotts et al. (2016)
		CPPLIP 1437	pt, rb, sc, cd hu, pb, ti, fi	F			Distal alluvial fans and alluvial plains subjected to sudden floods in a dry and hot climate	2	Cotts et al. (2016)
	Gondwanasuchus scabrosus	UFRJ DG 408-R*	sk, mdb, vb, rb	B	Fine-grained sandstones and siltstones with intercalations of red oxidized mudstones	AF	Alluvial plain reworked by fluvial systems alongside shallow ephemeral lakes, arid or semi-arid seasonal climate	2	Marinho et al. (2013)
	Pissarrachampsa sera	LPRP/USP 0019*	sk, mdb	C	Fine-grained sandstones with sandy-mudstone contributions	AF	Continental, semi-arid climate	2	Montefeltro et al. (2011)
		LPRP/USP 0018	sk, mdb	C	Fine-grained sandstones with sandy-mudstone contributions		Continental, semi-arid climate	2	Montefeltro et al. (2011)
		LPRP/USP 0739, LPRP/USP 0740, LPRP/USP 0741, LPRP/USP 0742, LPRP/USP 0743, LPRP/USP 0744, LPRP/USP 0745, LPRP/USP 0746	ul, man, il, fe, ti, fi, pes,	G	Fine-grained sandstones with sandy-mudstone contributions		Continental, semi-arid climate	1	Godoy et al. (2016)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Stratiotosuchus maxhechti	DGM 1477-R*	sk, mdb, vb, rb, cd, hu, ra, ul, man, il, is, fe, ti, fi, pes	B	Sequence of fine-grained sandstones, intercalated by mudstones, siltstones and clayish-sandstones	AF	Fluvial meandering or braided, semi-arid conditions (unclear whether this proposed depositional paleoenvironment is for the Formation as a whole or the locality where the specimen was found)	1	Campos et al. (2001); Riff and Kellner (2011)
		URC R-73	sk, mdb	D	–		Fluvial meandering or braided, semi-arid conditions (unclear whether this proposed depositional paleoenvironment is for the Formation as a whole or the locality where the specimen was found)		4 Pinheiro et al. (2008)
Theropoda	Unenlagiinae indet.	MPM 011	vb	H	–	AF	–		3 Candeiro et al. (2012b)
	Aves indet.	UFRJ-DG 06-Av	ph	H	–	AF	–	2?	Azevedo et al. (2007)
	Aves indet.	UFRJ-DG 07-Av	ti + fi + pes	H	–	AF	–	4?	Azevedo et al. (2007)
	Aves indet.	CPP 481	ph	H	White limestone and conglomerate, also composed by thin to medium-grained limestones, with bleached coloration in an arkosic matrix	MF	–		3 Candeiro et al. (2012a)
	Aves indet.	CPP 470	ph	H	White limestone and conglomerate, also composed by thin to medium-grained limestones, with bleached coloration in an arkosic matrix	MF	–		2 Candeiro et al. (2012a)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Enanthiornithes indet.	CPP 482	pes	H	White limestone and conglomerate, also composed by thin to medium-grained limestones, with bleached coloration in an arkosic matrix	MF	–	2	Candeiro et al. (2012a)
	Theropoda indet.	DGM 935-R	mdb	H	–	AF	–	–	Bertini et al. (1993)
	Abelisauroidea indet.	UFRJ-DG 254-R	il	H	Channelized deposits comprising fining-upward vertical profiles with conglomerates at the base, sandstones in the middle and mudstones at the top	PPF	Meandering fluvial of high sinuosity system	4	Azevedo et al. (2013a)
	Abelisauroidea indet.	MPMA 08-0016-95	vb	H	–	AF	–	4	Méndez et al. (2014)
	Abelisauroidea indet.	MPMA 08-0069-13	fi	H	–	AF	–	4	Méndez et al. (2014)
	Abelisauroidea indet.	MCT 1783-R	ti	H	–	MF	–	2	Machado et al. (2013)
	Abelisauroidea indet.	MPMA 27-0001-02	il, is, pb	F	–	MF	–	4	Méndez et al. (2014)
	Abelisauroidea indet.	URC R-44, URC R-45	sk	H	Medium to thick sandstones and conglomerate beds, colored blue and moderately red, with silty-clay matrix and associated pebbles of colored clay	AF	Intensely energetic water environment	5	Bertini (1996)
	Megaraptora indet.	MPMA 08-003094	vb	H	–	AF	–	1	Méndez et al. (2014)
	Megaraptora indet.	CPPLIP-1324	vb	H	Green fine sandstones	UF	Braided fluvial system	5	Martinelli et al. (2013)
	Carcharodontosauridae indet	UFRJ-DG 379-Rd.	sk	H	Channelized deposits comprising fining-upward vertical profiles with conglomerates at the base, sandstones in the middle and mudstones at the top	PPF	Meandering fluvial of high sinuosity system	2	Azevedo et al. (2013b)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Coelurosauria indet.	UFRJ-DG 390-R	fi	H	Channelized deposits comprising fining-upward vertical profiles with conglomerates at the base, sandstones in the middle and mudstones at the top	PPF	Meandering fluvial of high sinuosity system	2	Azevedo et al. (2013b)
	Maniraptora indet.	CPPLIP 659	ph	H	–	MF	–	4	Novas et al. (2005)
	Maniraptora indet.	MCT 1718-R	sc	H	–	MF	–	2	Machado et al. (2008)
	Maniraptora indet.	DGM 930-R	vb, rb, fe, pes	G	Sandstones intercalated with siltstones and sandy mudstones	AF	Aeolian deposits and depressions in shallow and ephemeral aqueous bodies, created during periods of higher water level	2	Delcourt and Grillo (2014)
	Abelisauroidea indet.	CPP 893	vb	H	Carbonated sandstones associated with impure limestones, overlain by coarse to conglomeratic sandstones and fine sandstones interbedded with clayish sandstones in tabular geometry although cross bedding and planar cross-stratification are also common. There are fining-upwards cycles finished by fine quartz-rich sandstones with planar cross-stratification. Interbedded are pelites, clayish sandstones and coarse sandstones, with mud intraclasts	MF	(Basin) Fluvial and lacustrine deposits (Formation, locally) Flash-flood deposits that reworked previously exposed soil sediments (caliche) in a seasonally arid environment (Fossil Occurrence) Sudden floods over the alluvial plains	2	Novas et al. (2008)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Abelisauroidea indet	CPP 174	fe	H	Carbonated sandstones associated with impure limestones, overlain by coarse to conglomeratic sandstones and fine sandstones interbedded with clayish sandstones in tabular geometry although cross bedding and planar cross-stratification are also common. There are fining-upwards cycles finished by fine quartz-rich sandstones with planar cross-stratification. Interbedded are pelites, clayish sandstones and coarse sandstones, with mud intraclasts	MF	(Basin) Fluvial and lacustrine deposits (Formation, locally) Flash-flood deposits that reworked previously exposed soil sediments (caliche) in a seasonally arid environment (Fossil Occurrence) Sudden floods over the alluvial plains	4	Novas et al. (2008)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Abelisauroidea indet.	CPP 692	ph	H	Carbonated sandstones associated with impure limestones, overlain by coarse to conglomeratic sandstones and fine sandstones interbedded with clayish sandstones in tabular geometry although cross bedding and planar cross-stratification are also common. There are fining-upwards cycles finished by fine quartz-rich sandstones with planar cross-stratification. Interbedded are pelites, clayish sandstones and coarse sandstones, with mud intraclasts.	MF	Fluvial and lacustrine deposits (Flash-flood deposits that reworked previously exposed soil sediments (caliche) in a seasonally arid environment (Fossil Occurrence) Sudden floods over the alluvial plains)	4	Novas et al. (2008)
	Abelisauridae indet.	DGM 927-R	il	G	–	AF	–	2	Brum et al. (2016)
	Abelisauroidea indet.	MCT 1857-R	fe	G	–	AF	–	2	Brum et al. (2016)
	Noasauridae indet.	DGM 929-R	vb	G	–	AF	–	2	Brum et al. (2017)
Titanosauria	“*Antarctosaurus brasiliensis*”	GP-RD-2, GP-RD-D3, GP-RD-4	vb, hu, fe	G	Reddish fine-grained sandstone with some layers of siltstones	AF	–	4	Arid and Vizotto (1971)
	Gondwanatitan faustoi	MN 4111-V	vb, rb, sc, hu, il, pu, is, ti	E	Mudstone layer in a fining upward with cross laminated sandstone overlain by a conglomeratic layer	PPF	Fluvial	4 (vb), 2 (long bones)	Kellner and Azevedo (1999)
	“Série A”	MCT 1487-R	vb	E	–	MF	–	2	Powell (1987, 2003)
	Trigonosaurus pricei	MCT 1488-R, MCT 1719-R	vb, il	E	Fine to medium grained white and yellow sandstones	MF	–	2	Campos et al. (2005)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Baurutitan britoi	MCT 1490-R	vb, hp	E	Fine to medium grained white and yellow sandstones	MF	–	3	Kellner et al. (2005)
	Adamantisaurus mezzalirai	MUGEO 1282, MUGEO 1289, MUGEO 1295	vb, hp	F	Cross-stratified reddish sandstones that gradually change to beige siltstones	AF	–	3	Santucci and Bertini (2006a)
	Maxakalisaurus topai	MN 5013-V, MN 7048-V, MN 7049-V, MN 7050-V, MN 7051-V	vb, hp, sc, st	F	Fine to medium grained reddish sandstone above a thin conglomeratic layer	AF	Fluvial depositional environment with semi-arid condition, with dry and wet alternate periods predominated	5	Kellner et al. (2006)
	Maxakalisaurus topai	MBC-42-PV	mdb	G	Fine to medium grained reddish sandstone above a thin conglomeratic layer	AF	Fluvial depositional environment with semi-arid condition, with dry and wet alternate periods predominated	3	França et al. (2016)
	Uberabatitan riberoi	CPP-UrHoA, CPP-UrHoB, CPP-UrHoC	vb, rb, cd, hu, ra, man, pb, is, fe, fi, pes	F	Conglomerates and coarse-grained sandstones to fine-grained sandstones in fining-upwards cycles (fine sandstones interbedded with pelites, clayish sandstones and coarse sandstones with mud intraclasts)	MF	Alluvial fans, braided fluvial systems, alluvial plains and ephemeral lakes under hot and dry climate (Formation); Braided fluvial systems (possibly ephemeral, caused by torrential rains after drought) (Member); Channel (Fossil Occurrence)	3	Salgado and Carvalho (2008)
	Aeolosaurus maximus	MPMA 12-0001-97	vb, rb, sc, hu, ra, is, fe	E	Reddish, massive sandstones locally with carbonatic cementationand conglomeratic and lamitic lenses and cross-bedded sandstones are present	AF	Semi-arid floodplain	4	Santucci and Arruda-Campos (2011)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Brasilotitan nemophagus	MPM 125R	mdb, vb, il, is	F	Reddish fine-grained sandstone	PPF	–	4	Machado et al. (2013)
	Austroposeidon magnificus	MCT 1628-R	vb, rb	F	Fine red sandstone with cross lamination	PPF	Floodplain	4	Bandeira et al. (2016)
	cf *Maxakalisaurus topai*	UFRJ-DG 270-R	vb, ch	G (vb), H (ch)	Very fine to fine grained, well-sorted, cross-bedded red sandstones. Furthermore, these authors recognized intraformational conglomerates and subordinate red shales, which are massive or laminar. The top of this unit is characterized by the interbedding of (1) conglomerates, (2) fine- to medium-grained crossbedded sandstones and (3) abundant nodular and horizontal carbonate concretions, which coarsen and thicken upward	MF	Fluvial?	3	Almeida et al. (2004); Candeiro et al. (2006); Martinelli et al. (2011)
	Aeolosaurini indet.	LGP-D0001-5	co	H	Fine to medium pink sandstone layer	MF	Fluvial?	4	Lopes and Bunchmann (2008)
	Aeolosaurini indet.	LGP-D0002	vb	H	Fine to medium pink sandstone layer	MF	Fluvial?	3	Lopes and Bunchmann (2008)
	Aeolosaurini indet.	LGP-D003	vb	H	Fine to medium pink sandstone layer	MF	Fluvial?	3	Lopes and Bunchmann (2008)
	Aeolosaurini indet.	LGP-D0004	ph	H	fine to medium pink sandstone layer	MF	Fluvial?	5	Lopes and Bunchmann (2008)
	Aeolosaurini indet.	LGP-D0005	ti	H	Fine to medium pink sandstone layer	MF	Fluvial?	3	Lopes and Bunchmann (2008)
	Aeolosaurini indet.	CPP 248	vb	H	–	MF	–	2	Santucci and Bertini (2001); Martinelli et al. (2011)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Titanosauria indet	MPMA-01	fe	H	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-02	fe	H	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-04	rb	G	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-05	fe	H	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-06	rb	G	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-07	fi	H	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-08	b	H	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-09	st	H	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-10	ra	H	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-11	ul	H	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-13	il	H	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-14	ch	H	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-15	vb	G	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-16	rb	G	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-17	ul	H	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-18	hu	H	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-22	rb	G	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-26	rb	G	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-27	ti	H	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-28	ra	H	–	MF	–	4	Bertini and Franco-Rosas (2001)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Titanosauria indet	MPMA-29	is, il	F	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-31	rb	G	–	MF	–	3	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MPMA-63	vb	G	–	MF	–	4	Bertini and Franco-Rosas (2001)
	Titanosauria indet	MMR/UFU-PV 0001	vb, rb	H	Very fine to fine grained, well-sorted, cross-bedded red sandstones. Furthermore, these authors recognized intraformational conglomerates and subordinate red shales, which are massive or laminar. The top of this unit is characterized by the interbedding of (1) conglomerates, (2) fine- to medium-grained crossbedded sandstones and (3) abundant nodular and horizontal carbonate concretions, which coarsen and thicken upward	AF	Fluvial?	3	Candeiro et al. (2006a); Martinelli et al. (2015)
	Titanosauria indet	UFRJ DG 326-R	ti	H	Fine reddish sandstones with plan-parallel lamination and with some conglomerate layer	AF	Fluvial-lacustrine origin	4	de Azevedo et al. (2007)
	Titanosauria indet	UFRJ DG 327-R	fe	H	Fine reddish sandstones with plan-parallel lamination and with some conglomerate layer	AF	Fluvial-lacustrine origin	5 (post-diagenetic due to exposure)	de Azevedo et al. (2007)
	Titanosauria indet	LF-007-R	vb	H	Collected by local people	AF	–	4	Geroto and Bertini 2014
	Titanosauria indet	LF-008-R	vb	H	Collected by local people	AF	–	3	Geroto and Bertini (2014)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Titanosauria indet	LF-009-R	vb	H	Collected by local people	AF	–		3 Geroto and Bertini (2014)
	Titanosauria indet	LF-011-R	pb	H	Massive or laminated (parallel stratification) very fine beige sandstones, with sub-rounded to subangular grains, a strong silty matrix, and carbonate cementation	AF	–	4	Geroto and Bertini (2014)
	Titanosauria indet	LF-012-R	is	H	Massive or laminated (parallel stratification) very fine beige sandstones, with sub-rounded to subangular grains, a strong silty matrix, and carbonate cementation	AF	–	4	Geroto and Bertini (2014)
	Titanosauria indet	LF-1V	rb	H	Massive or laminated (parallel stratification) very fine beige sandstones, with sub-rounded to subangular grains, a strong silty matrix, and carbonate cementation	AF	–	4	Geroto and Bertini 2014
	Titanosauria indet	LF-2V	rb	H	Massive or laminated (parallel stratification) very fine beige sandstones, with sub-rounded to subangular grains, a strong silty matrix, and carbonate cementation	AF	–	3	Geroto and Bertini (2014)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Titanosauria indet	LF-3V	rb	H	Massive or laminated (parallel stratification) very fine beige sandstones, with sub-rounded to subangular grains, a strong silty matrix, and carbonate cementation	AF	–	3	Geroto and Bertini (2014)
	Titanosauria indet	LF-4V	rb	H	Massive or laminated (parallel stratification) very fine beige sandstones, with sub-rounded to subangular grains, a strong silty matrix, and carbonate cementation	AF	–	2	Geroto and Bertini (2014)
	Titanosauria indet	LF-001-R	hu	H	Collected by local people	AF	–	2	Geroto and Bertini (2014)
	Titanosauria indet	LF-002-R	hu	H	Collected by local people	AF	–	4	Geroto and Bertini (2014)
	Titanosauria indet	LF-006-R	hu	H	collected by local people	AF	–	4	Geroto and Bertini (2014)
	Titanosauria indet	LF-003-R	fe	H	collected by local people	AF	–	3	Geroto and Bertini (2014)
	Titanosauria indet	LF-005-R	ti	H	Collected by local people	AF	–	3	Geroto and Bertini (2014)
	Titanosauria indet	DGM 497-R	vb	F	–	MF	–	4	Trotta et al. (2002)
	Titanosauria indet	MCT 1536-R	vb, il, sc	F	Conglomeratic sandstones	MF	Under fluviatile condition	2	Kellner and Campos (1999)
	Titanosauria indet	MCT 1489-R	vb, il,sc	F	Conglomeratic sandstones	MF	Under fluviatile condition	2	Kellner and Campos (1999)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Titanosauria indet	CPPLIP 0032, CPPLIP 0115, CPPLIP 0031, CPPLIP 0086, CPPLIP 0114,CPPLIP 0029, CPPLIP 0034	vb, il, is	F	Conglomerates and coarse-grained sandstones to fine-grained sandstones in fining-upwards cycles (fine sandstones interbedded with pelites, clayish sandstones and coarse sandstones with mud intraclasts)	MF	Braided fluvial system	3	Silva Jr. et al. (2017)
	Titanosauria indet	CPPLIP 12141	vb*	H	Conglomerates and coarse-grained sandstones to fine-grained sandstones in fining-upwards cycles (fine sandstones interbedded with pelites, clayish sandstones and coarse sandstones with mud intraclasts)	MF	Braided fluvial system	1	Martinelli et al. (2015)
	Titanosauria indet	CPPLIP 296, CPPLIP 247	sk*	H	Conglomerates and coarse-grained sandstones to fine-grained sandstones in fining-upwards cycles (fine sandstones interbedded with pelites, clayish sandstones and coarse sandstones with mud intraclasts)	MF	Braided fluvial system	1	Martinelli et al. (2015)
	Titanosauria indet	CPP-297	os	H	Calciferous sandstone, deposited in a fluvio-lacustrine environment, showing cross-stratification and conglomeratic sequences	MF	–	4	Marinho and Candeiro (2005)

Table 2 (continued)

Clade	Species	Specimen	Material	T. C.	LIT.	FM	D. E.	B.S.	References
	Titanosauria indet	CPP-674	os	G	Calciferous sandstone, deposited in a fluvio-lacustrine environment, showing cross-stratification and conglomeratic sequences	MF	–	1	Marinho and Candeiro (2005)
	Titanosauria indet	MPMA 08-0058-11	os	G	Sand deposits, frequently conglomeratic	AF	Fluvial bars of broad and shallow braided systems	2	Marinho and Iori (2011)
	Eutitanosauria indet	CPP 261	vb	G	White to beige cross-bedded sandstones and conglomeratic sandstones, intercalated with thin massive mudstones beds	MF	Braided fluvial system and distal alluvial fan	5	Santucci and Bertini (2006b)
	Eutitanosauria indet	CPP 491	vb	G	White to beige cross-bedded sandstones and conglomeratic sandstones, intercalated with thin massive mudstones beds	MF	Braided fluvial system and distal alluvial fan	4	Santucci and Bertini (2006b)
	Eutitanosauria indet	CPP 494	vb	G	White to beige cross-bedded sandstones and conglomeratic sandstones, intercalated with thin massive mudstones beds	MF	Braided fluvial system and distal alluvial fan	4	Santucci and Bertini (2006b)

The taphonomic information is scored based on its taphonomic class (‘T.C.’) as well as on the degrees of weathering and maintenance of the bone surface that were observed (‘BONE SURFACE’, B.S.). Lastly, the lithology of the facies from where the material was collected (‘LIT.’), the geological formation (‘FM’) attributed to include the facies and the interpreted depositional palaeoenvironment (‘D.E.’), with the references in which the specimens are described or revised

? missing information, – inconclusive, * holotype specimen, *Af* Adamantina Formation (includes the São José do Rio Preto Formation and the Vale do Rio do Peixe Formation sensu Fernandes and Coimbra 2000), *FM* Formation, *MF* Marilia Formation, *PPF* Presidente Prudente Formation, *UF* Uberaba Formation

(with three species). The theropod fauna includes indeterminate Abelisauroidea, Maniraptora, Enanthiornithes and Aves, which indicates at least a great representativeness of the clade. The titanosaurian fauna includes the species *Trigonosaurus pricei*, *Baurutitan britoi* and *Uberabatitan ribeiroi*, aside from records of supposed *Aeolosaurus* sp. (see Martinelli et al. 2011 for a discussion) and of indeterminate Titanosauria bones. The last three formations present a low diversity, which may be a reflection of both the taphonomic factors and the short time in which these formations have been investigated in detail. The Presidente Prudente Formation diversity is represented by three specimens for each dinosaurian group. Each of the Titanosauria specimens represent a different species (*Gondwanatitan faustoi*, *Brasilotitan nemophagus* and *Austroposeidon magnificus*), while the theropod record is comprised by occurrences of indeterminate Abelisauroidea, Carcharodontosauridae and Coelurosauria. Lastly, the Uberaba Formation has a single theropod record assigned to an indeterminate megaraptoran, and the Araçatuba Formation has an occurrence of notosuchian remains (Simbras et al. 2017).

5 Discussion

The Bauru Group is considered one of the most important geological units from Brazil due the occurrence of many vertebrate fossils (Azevedo and Simbras 2009; Candeiro et al. 2008; Candeiro et al. 2006a). Despite this context, virtually no work has focused in applying a taphonomic approach to the vertebrate fossils found in it (e.g., Araújo-Júnior and Marinho 2013). Generally, the taphonomic inferences are presented as notes or observations in osteological descriptions. The precariousness of works focusing on taphonomic approaches in the Bauru Group reflects the low rates of bone preservation along environmental gradients, which in turn influences the data acquisition for better understanding of depositional rates and biogenic processes.

5.1 Proposition of taphonomic patterns for studied groups

There is a marked tendency for baurusuchid remains of the Bauru Group to be relatively complete, well preserved and to be found either in articulation or in association. Indeed, nearly every Baurusuchidae specimen belongs to the first four taphonomic classes, therefore including at least partial cranial elements. Furthermore, some specimens display remarkable preservation, as is the case of *Aplestosuchus sordidus*, a most superb specimen (see Godoy et al. 2014). For the purposes of this paper, the rarity of detailed lithological information for many specimens is lamentable. The rare exceptions are those researches with focus on the Baurusuchidae, where the lithological information could be found. The majority of baurusuchids have been recovered from psammitic sediments, particularly fine sandstones. We possess even less information regarding the depositional environment of theropods as quite often the information is either missing or unclear.

When we focus on the theropods of the Bauru Group, the completeness, quality and amount of material are entirely reversed. Nearly all of the findings consist of isolated bones, with a couple of specimens consisting of associated postcranial elements. Characteristically, very little cranial material has been recovered, and most of the isolated bones are broken and fragmented. Unfortunately, we do not possess detailed lithological information for all finds, and as for the Baurusuchidae environmental information is scarce. Where we do have such information, as is the case for the specimens UFRJ-DG 254 R, UFRJ-DG 379 R and UFRJ-DG 390 R, the finds come from the bedload of a meandering fluvial system, while being worthwhile to note that the material is fragmented and broken.

The absence of detailed environmental information difficults a direct comparison between the records of Baurusuchidae and Theropoda for the Bauru Group in terms of their biostratinomic paths and places of final burial. We must rely on the taphonomic classes and general environmental information to provide us some insight into the conditions about the formation of these deposits and the nature of the processes that influenced them. The abundance of skeletal elements coupled with the ubiquity of articulated and associated specimens, as is the case for Baurusuchidae, suggest relatively little transportation and exposure prior to burial. The degree of preservation of the skulls and the fact that some of them have been found in articulation are also indicative of little destructive action, either through transportation or scavengers. All of this does not necessarily mean lack of transportation, given that "bloat and float" is a quite common mode of transportation of crocodyliform carcasses (e.g., Salisbury et al. 2003; Syme and Salisbury 2014), but it does mean that there was very little subaerial exposure prior to burial in a level enough to allow the degree of articulation and preservation of fragile elements.

As stated previously, the situation of theropods is the opposite, with most specimens being represented by broken isolated bones, with very few of them being associated. These taphonomic characteristics are indicative of destructive taphonomic agents and processes. Whether the bones were broken due to the action of scavengers, during transportation or the diagenesis cannot be determined from the literature alone and is largely irrelevant for the present discussion. All that matters is to acknowledge the fact that, as a rule, theropod fossils have undergone very destructive taphonomic processes, in comparison with the Baurusuchidae.

If we consider the widely accepted environmental interpretation of the Bauru Group as warm and dry, the derivation pathways for the distinct preservation of Baurusuchidae and Theropoda become more evident. Some aspects also help to clarify the different preservations related to those taxa. As expected to semi-arid environments, whose remains are subjected to sudden floods or outpouring of the floodplains (Behrensmeyer 1978), and the carcasses could potentially lie scattered throughout the plains for a long time before being washed away, all the while undergoing the rigors of bone weathering, abrasion, trampling and scavenging (e.g., Behrensmeyer 1978). Under these conditions, it is expected that carcasses which have been left close to where they died will have some elements destroyed or carried away. When the sporadic flash flood carried the scattered elements, washing away the plains into the streams and temporary lakes, it formed a deposit that might contain the eventual skeletal material separated from the rest of the original carcass, and also sorting with the carcasses of other animals that died at more distant points—those ones represented by the isolated bones, like the theropods remains.

Such scenario plausibly explains most of the Theropoda finds in the Bauru Group. In contrast, the Baurusuchidae remains to be preserved in articulation under the same environmental conditions, with so much material being found, in good conditions and with fragile cranial elements also preserved, we conclude that the taphonomic processes that operated on the genesis of their depositions were not nearly as destructive, as a whole, as they were for Theropoda. Whether the Baurusuchidae arrived at their place of final burial as "bloat and float" carcasses or they lived and died close to them, they were not subject to extensive subaerial exposure or transportation after the end of the biological decay.

5.2 Palaeoecological considerations

Palaeoecological observations over the species diversity of baurusuchids and dinosaurs from the Bauru Group are here discussed based on our taphonomical considerations. Riff and Kellner (2011, p. 50) assumed that Baurusuchidae and Theropoda exhibit similar preservation patterns in the Bauru Group and that the proportional diversity of those groups in the taphocoenosis reflects the original diversity of its biocoenosis. However, the taphonomic results found here support a different scenario where the proportional diversity of this group is parsimoniously explained by a taphonomic bias. Therefore, this works supports that the hypothesis of the Bauru Group taphocoenosis does not correspond to the real diversity of the biocoenosis (as traditionally expected in palaeontology, e.g., Behrensmeyer et al. 2000).

An ecomorphological hypothesis presented by Riff and Kellner (2011) regards evolutionary convergences on the skull, teeth and limbs between baurusuchid crocodyliforms and theropod dinosaurs (see Riff and Kellner 2011). These authors thus suggested that baurusuchids and small to medium-sized theropods of the Adamantina Formation occupied similar ecological niches and exhibited a competition relationship. Moreover, based on the assumption that the small to medium-sized theropods are scarce and the large-sized ones are rare, Riff and Kellner (2011, p. 50) proposed that baurusuchids dominated their niche over theropods. Nonetheless, as already pointed out, there is no strong evidence regarding the scarcity of small to medium size theropods in the Bauru Group, with the fossil record of this clade being recovered from both Adamantina and Marília Formations. Anyhow, Riff and Kellner (2011) did not leave it clear whether baurusuchids had dominated their niche over theropods because they would have competitively excluded those dinosaurs or if they would have occupied a niche left open by the purported scarcity of theropods.

Competitive exclusion occurs when, given a case of competition, a certain species has an advantage over the other(s) and ends up dominating its niche (Gause 1932). If this were to be the case, the hypothesis by Riff and Kellner (2011) of baurusuchid dominance would have to explain why baurusuchids were better fit to occupy their niche than small to medium-sized theropods. However, no evidences exist for a supposed best fit of baurusuchids over theropods, such as best predatory adaptations in the first over the later. In fact, Riff and Kellner (2011) actually defended the hypothesis that baurusuchids could have been up to as competent as theropods as predators of small to medium-sized prey, and not superior. Furthermore, if a competitive exclusion hypothesis were to be considered anyway, then the extinction or a significant reduction on theropod diversity would have to be expected for the Adamantina Formation (to which baurusuchids are exclusive in the Bauru Group). However, despite the negative preservational bias of theropod dinosaurs, there is no evidence supporting their reduction in diversity associated with the presence of baurusuchids. This is also corroborating with our observation that, to date, no Baurusuchidae has been found outside the Adamantina Formation.

On the other case, if an open niche were to be considered, then the scarcity of theropods would have to be explained by some other event, what has not been done in the literature. Notwithstanding, an open niche hypothesis could be considered if an absence of large-sized theropods in the Adamantina Formation is observed on the future. In such case (as opposed to what has been proposed for Argentine palaeoenvironments, see Gasparini et al. 1993), the absence of potential theropods as the top predators would enable the diversification of those crocodyliforms and the sharing of their niche with the small to medium sized theropods rivalling the latter as competitors. Therefore, the purported dominance of baurusuchids in the food web of the Adamantina Formation proposed by Riff and Kellner (2011) and the concurrent hypothesis of open niche would still require the following answers: (1) How diverse were theropods in the Adamantina and Marília Formations?; (2) Is there any diversity modification regarding theropod species between the Adamantina and Marília Formations?; (3) Does exist in fact an absence of large-sized theropods in the Adamantina Formation? And if so, what caused it?; (4) Why are baurusuchids absent in the Marília Formation?; and, (5) How baurusuchids conquered and diversified in the Adamantina Formation?

We agree here that the morphological and biomechanical similarities between baurusuchids and theropods demonstrated by Riff and Kellner (2011) must imply in similar ecomorphologies concerning at least dietary habits (that is, consuming small to medium-sized prey). Nonetheless, similar dietary habits does not necessarily imply in a relationship of competition, which these authors suggested to occur (Riff and Kellner 2011). Based on these considerations and on our proposed taphonomic bias in the Bauru Group, we argue that baurusuchids and theropods did not completely compete for prey at least partially due to spatial niche partitioning. Niche partitioning explains how two or multiple species can coexist without directly competing and preventing competitive exclusion. Spatial niche partitioning refers specifically to cases where two predators forage for similar prey in different spaces. This occurs for example with some arboreal lizards of the genus *Anolis*, which comprises sympatric species that feed on similar arthropods but forage on different layers of vegetation (Pacala and Roughgarden 1985). This also occurs with the felid top-predators, hyper-carnivores *Panthera onca* (the jaguar) and *Puma concolor* (the puma) which, in Central Brazil, consume similar prey in different habitats (Sollmann et al. 2011). While jaguars prefer to occupy areas closer to water-bodies, pumas occupy jaguar-free areas more distant from water-bodies (Sollmann et al. 2011).

In a similar way, we suggest that baurusuchids and theropods preferred different ecosystems: being baurusuchid fossils correlated with floodplains and with theropods with drylands (Fig. 2). It is important to notice, however, that an association between baurusuchids and floodplains does not imply in semi-aquatic habits, especially by the morphology that indicates a terrestrial lifestyle (e.g. Riff and Kellner 2011). Though semi-aquatic crocodyliforms are present in the Marília (e.g. *Itasuchus jesuinoi* Price 1955) and Presidente Prudente formations (*Pepesuchus deisae* Campos et al. 2005), they are yet unconfirmed in the Adamantina Formation. It is important to note that non-baurusuchid crocodyliforms (omnivorous notosuchians such as *Mariliasuchus amarali*, *Morrinhosuchus luziae*, *Armadillosuchus arrudai* and *Caipirasuchus paulistanus*) exhibit taphonomic patterns of good preservation and facies occurrence similar to baurusuchids (Carvalho and Bertini 1999; Iori and Carvalho 2009; Marinho and Carvalho 2009; Iori and Carvalho 2011). On the other hand, the taphonomic aspects of sauropods are closer to those of theropods. In this way, we interpret that non-baurusuchid notosuchians most likely shared more similar habitats with baurusuchids than with dinosaurs, especially regarding theropods, while theropods and sauropods had a preferred occupation of drylands (Fig. 2).

Godoy et al. (2016) had already suggested that baurusuchids could not have completely dominated the Adamantina food web, if assumed as solitary predators, and they would be incapable of preying on large adult sauropods (*contra* Riff and Kellner 2011). These authors thus suggested that there should have been a prey item niche partitioning, that is, a case of niche partitioning in which predators that share an ecosystem do not share the same species for prey (Godoy et al. 2016). However, the only direct evidence so far of baurusuchid diet consists of a small sphagesaurid notosuchian in the stomach content of the *Aplestosuchus sordidus* holotype (Godoy et al. 2014). This single case of stomach content in baurusuchids only partially supports this hypothesis, especially given the absence of evidence of theropod predation so far. In fact, another point that supports our hypothesis is the presence of teeth marks found in some *Maxakalisaurus topai* bones (Kellner et al. 2006). These marks were attributed to the theropods, due to the presence of several theropod teeth closely associated to the *Maxakalisaurus topai* holotype. Therefore, until more evidence is found, it still remains possible that, as Riff and Kellner (2011) suggested, baurusuchids and small to medium-sized theropods consumed similar prey (that is, small sized prey such as small crocodyliforms, small dinosaurs and mammals). We consider that none of these possibilities can be confidently corroborated yet, though we can consider the occurrence of at least spatial niche partitioning. However, we agree that, most likely, only large theropods could have preyed on large sauropods (assuming baurusuchids as solitary hunters; Godoy et al. 2016).

The abundance of baurusuchid fossils greatly exceeds the abundance of theropod fossils, what does not necessarily imply in an original larger abundance of baurusuchid individuals over theropod individuals in the biocoenosis of the palaeoecosystem. As proposed here, the larger number of baurusuchids remains can be explained by a taphonomic bias, once again due to the different habitats of baurusuchids and theropods in the Bauru Group. In addition to being represented in larger numbers, baurusuchid remains are also more complete, articulated and better preserved.

Another aspect regarding the abundance and good preservation quality of baurusuchids and other Crocodyliformes was tentatively explained by a burrowing behaviour (e.g., Marinho and Carvalho 2009) that would be absent in saurischian dinosaurs. Based on the documented burrowing behaviour observed in extant Crocodylia (Smith 1979), this behaviour was inferred as plausible for some crocodyliform

Fig. 1 Graphic bars of the bone representative for Baurusuchidae, Theropoda and Titanosauria. *cd* coracoid, *ch* chevrons, *fe* femur, *fi* fibula, *hu* humerus, *hy* hyoid, *il* ilium, *is* ischium, *man* manus, *mdb* mandible, *os* osteoderm, *pb* pubis, *pes* pes, *ph* phalanx, *pt* proatlas, *ra* radius, *rb* rib, *sc* scapula, *sk* skull, *st* sternum, *ti* tibia, *ul* ulna, *vb* vertebrae

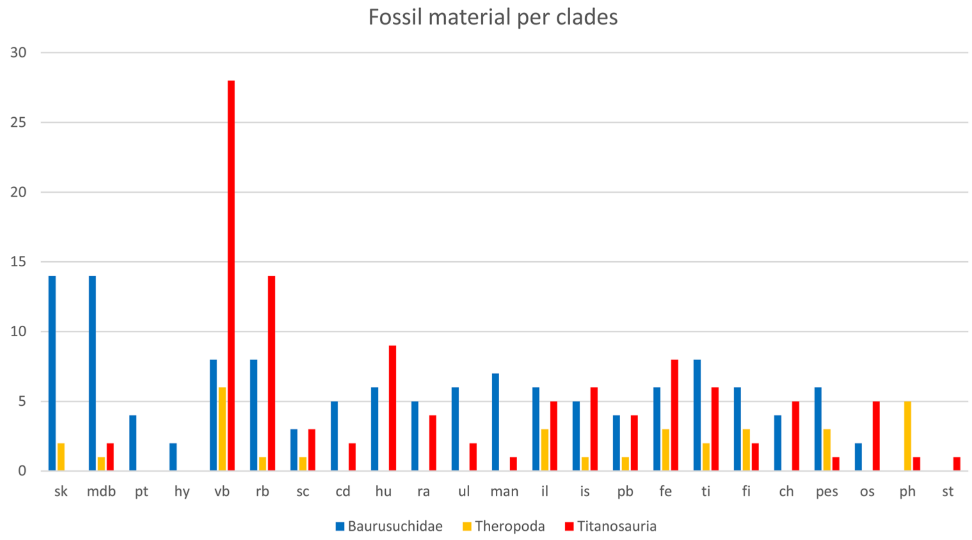

Table 3 Summarized table of the fossil material and distribution per clade, with the relative frequency, mean and deviation

B	Ba	F	T	F	Ti	F	TF	To
sk	14	0.108527132	2	0.064516129	0	0	0.0576811	16
mdb	14	0.108527132	1	0.032258065	2	0.0183486	0.0530446	17
pt	4	0.031007752	0	0	0	0	0.0103359	4
hy	2	0.015503876	0	0	0	0	0.005168	2
vb	8	0.062015504	6	0.193548387	28	0.2568807	0.1600622	42
rb	8	0.062015504	1	0.032258065	14	0.1284404	0.074238	23
sc	3	0.023255814	1	0.032258065	3	0.0275229	0.0276789	7
cd	5	0.03875969	0	0	2	0.0183486	0.0190361	7
hu	6	0.046511628	0	0	9	0.0825688	0.0430268	15
ra	5	0.03875969	0	0	4	0.0366972	0.0251523	9
ul	6	0.046511628	0	0	2	0.0183486	0.0216201	8
man	7	0.054263566	0	0	1	0.0091743	0.021146	8
il	6	0.046511628	3	0.096774194	5	0.0458716	0.0630525	14
is	5	0.03875969	1	0.032258065	6	0.0550459	0.0420212	12
pb	4	0.031007752	1	0.032258065	4	0.0366972	0.033321	9
fe	6	0.046511628	3	0.096774194	8	0.0733945	0.0722268	17
ti	8	0.062015504	2	0.064516129	6	0.0550459	0.0605258	16
fi	6	0.046511628	3	0.096774194	2	0.0183486	0.0538781	11
ch	4	0.031007752	0	0	5	0.0458716	0.0256264	9
pes	6	0.046511628	3	0.096774194	1	0.0091743	0.05082	10
os	2	0.015503876	0	0	5	0.0458716	0.0204585	7
ph	0	0	5	0.161290323	1	0.0091743	0.0568215	6
st	0	0	0	0	1	0.0091743	0.0030581	1
Sum	129		32		109			270
Mean	5.6087		2.9783		4.7391			11.7391
s	3.4792		1.7258		6.0919			5.0142

B. bone, *Ba* Baurusuchidae, *F* frequency, *s* sample standard deviation, *T* Theropoda, *Ti* Titanosauria, *TF* total frequency, *To* total

species such as *Malawisuchus* (Gomani 1997) and *Armadillosuchus* (Marinho and Carvalho 2009; also see more extensive discussion in Sertich and Groenke 2010). Some could argue that the burrowing behaviourism were widely distributed among the Crocodyliformes, including Baurusuchidae, and that this behaviour could explain the abundance

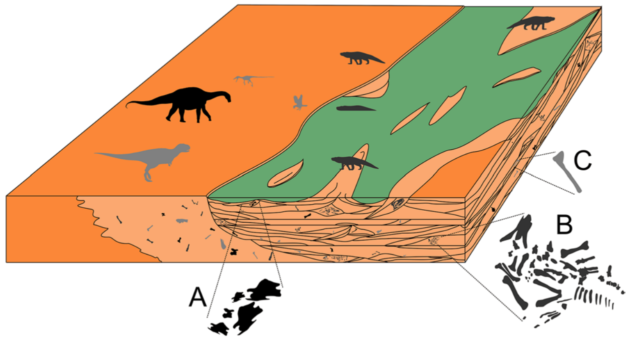

Fig. 2 Scheme representing our proposed depositional context for Adamantina Formation correlation to the tafonomic hypotheses of the titanosaur (A), baurusuchid (B) and theropod (C) remains. Depositional model based on Model 3 from Miall (1985). Vertebrate silhouettes modified from Godoy et al. (2014) and Curry Rogers (2009)

and quality of the crocodyliform fossil record in the Bauru Group. However, this argument only becomes plausible if the animal burrowed itself and naturally died while buried or if it was suddenly caught by a collapse of the burrow. The present work does not discard the possibility of a widespread burrowing behaviour for Crocodyliformes, which could potentially help in thermoregulation (Pooley 1969). However, based on our taphonomic results (as the absence of some skeletal parts and the weathering and abrasion marks among the fossils),we consider more plausible a scenario of mummification plus water carcass (Hill 1979; Weigelt 1989; Araújo-Júnior and Marinho 2013) instead of assuming the burrowing hypothesis for distinct groups of crocodyliforms in the Bauru Group. The absence of geological marks such as holes (e.g., the fossil preserved on a rock different form the remaining facies) or fossils without mummification and transport signals also corroborates our assumption.

6 Conclusions

The specimens of Baurusuchidae from the Bauru Group, which are relatively complete, articulated, or in close articulation and well preserved corroborate our hypothesis of a taphonomic tendency for this clade. This was indicated by the high bone representativeness and better quality on preservation pattern of available specimens in comparison with theropod bones. Although poor lithological and stratigraphic information was given by previous authors, our work also shows that baurusuchids lived (or at least died) close to the abundant flood plains, with those animals probably being quickly buried after death, which favoured the process of preservation. Theropods and titanosaurs probably did not live close to such environments, which implied in their low sampling on those facies (almost absent at all for theropods), with the quality of their preservation being negatively affected as a result. We support that the Baurusuchidae played an important role in the food chain in the ecological niches of the Late Cretaceous Bauru Group of Brazil, but the possible biases in their fossil record, as well as in that of the theropods, do not support the conclusion that baurusuchids outcompeted theropods as previously regarded. Rather, this taphonomic bias must be tackled first, what previous studies have failed to do. Also, the different palaeoenvironments among the Bauru Group exhibit an abundance of predatory and herbivorous archosaurs occupying those spaces, and the numbers here presented do not warrant decisive conclusions for taphonomic patterns of any group of vertebrates in the Bauru Group. Finally, we recommend that authors who will eventually come to describe new specimens also offer a more rigorous taphonomic control on future works. With most specimens collected near large roads and previously exploited sites, we recognize that our work is still an early assessment, and that future evidence can shed light on the hypotheses elaborated here.

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