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Megafauna from the Late Pleistocene-Holocene deposits of the Upper Ribeira karst area, southeast Brazil

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ABSTRACT

The carbonate caves of the Upper Ribeira Valley, southeastern São Paulo State, Brazil, preserve an abundant fossil record of Pleistocene-Holocene South American megafauna. Nevertheless, in comparison with other localities of the country, its paleontological knowledge still can be considered sparse and in need of further research. This work presents an update taxonomic survey of the megafauna material collected since the beginning of the explorations in the area. Based on this, it discusses paleobiogeographic and paleoecological questions. The fossil megafauna of the Upper Ribeira karst region include: *Eremotherium laurillardi, Nothrotherium maquinense, Lestodon armatus, Catonyx cuvieri, 'Ocnopus gracilis', Ahytherium aff.* aureum, *Glyptodon clavipes, G. reticulatus, Hoplophorus cf., Toxodon* spp., *Stegomastodon waringi,* Equidae (*Hippidion cf.*), *Tapirus terrestris, Panthera onca* and *Smilodon populator*. Only *P. onca* and *T. terrestris* still remain in the region. Despite the occurrence of some typical taxa of the pampean paleobiogeographical province, the fossil assemblage recorded shows greater affinity to the mega-mammal community of the intertropical region. The ecology of species found suggests the previous occurrence of fairly different environmental settings than the existing one in the area. There were more temperate climates – both dry and wet – until the current mesophytic forest was finally established. The studied material does not show any kind of chrono-correlation, given the type of genesis of the cave accumulations. These fossils depict different faunistic moments related to climate changes during the Quaternary. To better understand the information provided by these deposits, efforts on dating and detailed taphonomic investigations should be conducted. The studies of the Quaternary fauna in the state of São Paulo fill an important gap in the intricate biogeographical history of the South American megafauna.

1. Introduction

The first fossil records found in the karst area of the Upper Ribeira Valley are from the late nineteenth century, and can be referred the German-Brazilian naturalist Ricardo Krone. Considered to be the "father of Speleology" in Brazil, Ricardo Krone adopted this region as his main field of work and began his explorations in 1896/97 with the objective of describing and cataloging caves, as well as finding paleontological and archaeological sites. The naturalist studied several caves along the Iguape River Valley, where he found clear records of Pleistocene megafauna. He mentioned it for the first time in his report published in the *Revista do Museu Paulista* (Krone, 1898), entitled *As cavernas calcáreas de Iporanga*. However, the collection gathered by him was only described in 1907 by Florentino Ameghino.

Ameghino (1907) was the first researcher to estimate an age correlation, provide a more precise identification and a detailed description of the material belonging to this region. Similar work would only be performed later by Carlos de Paula Couto, in the second half of the twentieth century, as he sought to consolidate the knowledge of Quaternary mammals in Brazil (Paula Couto, 1959, 1971, 1973, 1975, 1979, 1980).

From 1962 until the present date, the Ribeira Valley region began to be constantly visited by speleological groups. They revealed more than a hundred new caves and built up a large amount of data concerning its locations and topography. Today, in comparison with other karst regions of Brazil, the Upper Ribeira Valley has one of the greatest knowledge bases available regarding

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the presence and distribution of caves (Karmann and Sánchez, 1979; Karmann, 1994; Karmann and Ferrari, 2001; CECAV, 2010).

As for paleontological exploration, more structured projects only began between 1977 and 1979. In 1977, a careful examination in the Iporanga municipality area, São Paulo State, revealed several abysses with rich fossil deposits. The discovery prompted the planning of systematic excavations and the first site chosen to be explored was known as the "Fossil Abyss". The final results were presented by Lino et al. (1979). In their report they highlighted the importance of other abysses and pointed the necessity of persisting with the regional survey of pits and caves with fossils.

In the following years, other projects involving systematic excavations were carried out, including the Ponta de Flecha Abyss exploration. In the Ponta de Flecha Abyss, archaeological remains were found and some even considered are potential evidence of interaction between ancient humans and the megafauna. Meanwhile, a study of fossil micromammals was conducted in the Iguatemi Abyss to reveal some paleobiological and paleoecological aspects of ancient communities. In the Juvenal Abyss, basically a taxonomic survey was done, and more recently the same was carried out in the Gêmeo Pit (Barros-Barreto et al., 1982a, 1982b, 1984; Chahud, 2001; Ferreira and Karmann, 2002; Hingst-Zaher et al., 2003; Castro, 2005; Castro and Langer, 2005; Spinelli et al., 2005; Castro and Langer, 2006; Menin et al., 2006; Castro and Langer, 2008; Alberto Barbosa de Carvalho, personal communication). Although there is a great number of projects, it is possible to consider the paleontological knowledge of the region limited; especially when its potential is considered as source of new sites, and also the possibility to perform more applied paleoecological investigations (Chahud, 2001; Castro, 2005). Furthermore, the Quaternary fauna of the region can bring revealing paleobiogeographic answers about the distribution of some extinct taxa.

The issue, related to differences between the megafauna of the Brazilian Intertropical Region (northeast and parts of southeast and central-west Brazil *sensu* Cartelle, 1999) and the one found mostly south, has not been deeply explored yet. Thus, any study of the Quaternary biota of São Paulo State can provide fundamental information to elucidate this question, since the state lies in the transition range between these two main biogeographical regions (Paula Couto, 1954, 1979; Bergqvist et al., 1997; Oliveira, 1999; Carlini et al., 2003; Oliveira et al., 2009; Ribeiro and Scherer, 2009).

The purpose of the present study was: 1) to consolidate the paleontological knowledge of the Upper Ribeira karst caves; 2) to review the collected material presenting an updated taxonomic list; 3) to understand the biogeographic affinities of its fossil assemblage and; 4) to perform possible paleoecological insights. Herein are also presented relevant considerations and prospects for upcoming paleontological studies in the area. The primary contribution of this effort is to synthesize knowledge in order to provide support for further work.

2. Regional setting

The region known as the Upper Ribeira comprises the southeastern part of São Paulo State, southeast Brazil (Fig. 1), and is included in the Iguape River Basin. The area is characterized by its geological complexity and karst development, which houses an extensive system of caves. It is included in the conservation units' belt of São Paulo State, which includes among others, the Upper Ribeira State Park (PETAR) and the Intervales State Park (PEI). These are known for containing an important portion of the rich speleological patrimony of the region.

The karst of the Upper Ribeira developed on Precambrian carbonate rocks of the Açungüi Group. This geological unit also extends across the eastern part of Paraná State (Fig. 1), and emerges in discontinuous areas arranged in bands. Its typology is different from any other Brazilian karst areas, regularly continuously conformed. The bands are oriented NE-SW and have variable width, ranging between 1 and 10 km on average, with tens of kilometers long. They are interspersed with pockets of detrital metasediments (e.g. quartizites, phyllites and metaschists) oriented in the same direction (Sánchez, 1984; Campanha, 1991; Karmann, 1994; Ferrari et al., 1999; Instituto Geológico, 1999; Karmann and Ferrari, 2001).

The rocks are strongly folded and cracked, and the limestones arranged in thick packets, which favors the development of karst processes (Sánchez, 1984; Karmann, 1994). The age of formation of caves was estimated between 2 and 1.7 million years (Karmann, 1994; Karmann and Ferrari, 2001).

The whole area is under the influence of a humid subtropical climate (Köppen Cfb and Cfa) and it is covered by forests with elevated biomass and high and dense physiognomy, the Atlantic

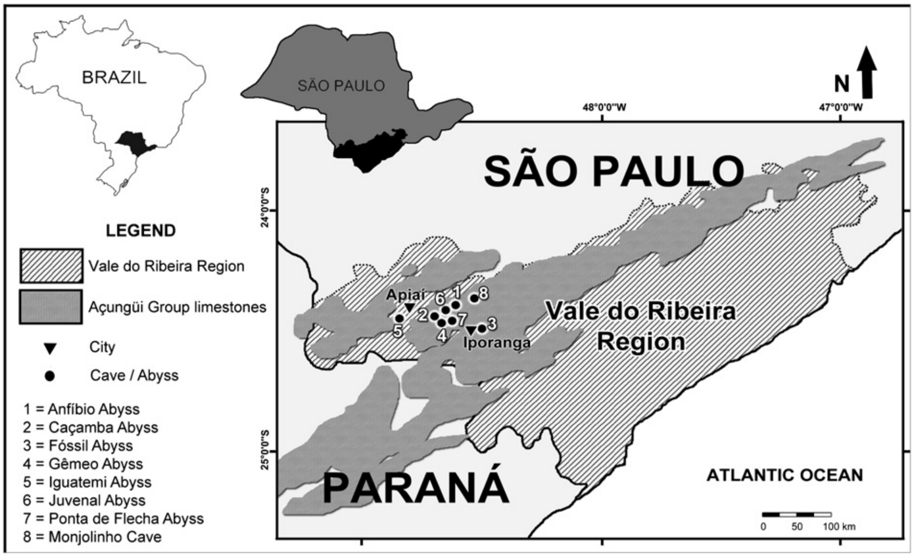

Fig. 1. Upper Ribeira region map showing the Açungüi Group karst area, the main fossiliferous localities and the Apiaí and Iporanga municipalities.

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rainforest. Today this plant layer contributes to the corrosive process of limestone through the production of carbonic acid, which enriches the percolating water (Sánchez, 1984; Karmann, 1994).

In a Brazilian perspective, another aspect that distinguishes the Upper Ribeira karst area from others of the country is the pronounced occurrence of abysses (caves with predominantly vertical development) (Auler and Farrant, 1996).The depths of the Ribeira Valley are the largest in the country, including that of Juvenal, 241 m deep (Spinelli et al., 2005; Menin et al., 2006).

Quaternary sediments, Pleistocene-Holocene in age, are found associated with the extensive cave system (Ameghino, 1907; Paula Couto, 1973, 1975; Cartelle, 1995, 1999; Karmann et al., 1999; Hingst-Zaher et al., 2003; Baffa et al., 2000).These sediments can occasionally form shallow superficial accumulations, but are usually associated with the underground cavities, especially the abysses. In these underground environments, they gather in different levels of the vertical conduits or stagnate in stretches along the horizontal passages (Barros Barreto et al., 1982a, 1982b; Karmann and Ferrari, 2001).

In general, the sediments found in caves show reworking by floods, which destroy the stratigraphic stacking and mix the fossiliferous horizons. This is caused by the flooding of underground rivers and the abundant surficial drainage, recurrent through the months of high rainfall volume. The accumulated sediments in general are characterized by immaturity and poor sorting, with diverse granulometry, in addition to their high organic matter content, dark color and carbonate cementation on some levels (Lino et al., 1979; Barros-Barreto et al., 1984; Karmann and Ferrari, 2001).The fossils found are usually disarticulated and fragmented due to reworking, making identification difficult. Articulated elements are rare, bone beds being common, sometimes with temporally unrelated elements cemented adjacently. In the abysses, the deeper deposits are typically those with larger volumes of sediment and bones, a consequence of the intense transportation and revolving processes (Lino et al., 1979; Barros-Barreto et al., 1982, 1984; Chahud, 2001).

3. Materials and methods

This work was based first on an historical survey of the Upper Ribeira paleontological studies, from which the main repositories harboring fossils from this area were traced. The intent was to visit the collections and review the gathered material concerning their identification. Specimens not contained in these repositories were evaluated through pictures and illustrations of original articles. Attempts were made to find affinities to new specimens collected during 2009 and 2010, as well as old samples not yet formally catalogued.

Based on this assessment, an updated list was made concerning the recurring megafauna taxa of the fossil cave deposits of Upper Ribeira region, along with a table with references to the type of record for each taxonomic group (parts of the appendicular or axial skeleton with specifications considering the presence of cranial material and/or teeth), its provenance and current repository. Notes on particularities of the studied specimens were detailed separately.

Considering the obtained taxa, a survey was conducted of their occurrence throughout Brazil, to find affinities to the Upper Ribeira's faunal assemblage, considering the two main adjacent paleobiogeographic regions, the Intertropical in the north, and the southernmost Pampean. Paleoecological inferences were obtained using the available information on distribution, aspects of biology and paleoautoecology of each species. The concept of megafauna employed in this paper considers as belonging to this set, large animals over 44 kg (Martin and Klein, 1984; Barnosky et al., 2004; Barnosky, 2008).

4. Results

4.1. Repositories

The oldest collections assembled by Krone, most of them obtained in the Monjolinho Cave, were originally sheltered in the so called "*Museu Paulista*", located in São Paulo City, São Paulo State. However, for the "*Museu Paulista*" was just a historical institute, its collections were divided and relocated. The material gathered in the end of the nineteenth century was sent to the University of São Paulo Zoology Museum (MZ-USP), also located in São Paulo City, while that assembled in 1908 was taken to the National Museum of Rio de Janeiro (MN-RJ), in Rio de Janeiro City, Rio de Janeiro State.

Nowadays, MZ-USP houses the greater part of the paleontological material until now collected in the Upper Ribeira region. Besides Krone's material, it also shelters what was recovered from the Fossil, Juvenal and Gêmeo abysses, as well as part of what was collected in the Iguatemi Pit. There are, in addition, isolated bones rescued from the Amphibian, Caçamba, das Ossadas and Megalomilênio abysses, and the Evarista and Areias caves.

The University of São Paulo Geosciences Institute (IGc-USP), São Paulo City, also shelters some recent collected Upper Ribeira's paleontological material. Its collection presents specimens related to the Ponta de Flecha and Iguatemi Pits. Minor collections are harbored in the Museum of the Geology Institute of São Paulo (MUGEO), São Paulo City, and in the Museum Prof. Dr. Mário Tolentino of the Federal University of São Carlos (MUFSCar), São Carlos municipality, São Paulo State.

4.2. Fossil material and taxonomic listing

The Upper Ribeira's megafauna material is characterized by its disarticulation and fragmentary state, integral and undamaged elements being relatively rare. Skulls are scarce, while other parts of the axial (e.g. ribs, vertebrae and teeth) and appendicular skeleton are reasonably frequently found. Tardigrada (Xenarthra) has the most abundant amount of material gathered, followed by that of Toxodontidae (Notoungulata).

The survey has identified the following taxonomic groups: Xenarthra Tardigrada (Megatheriidae, Nothrotheriidae, Mylodontidae and Megalonychidae) and Cingulata (Glyptodontidae), Notoungulata (Toxodontidae), Proboscidea (Gomphotheriidae), Perissodactyla (Equidae and Tapiridae) and Carnivora (Felidae). Table 1 gives a detailed depiction of the identified taxa and Table 2 includes references on both the nature of record for each taxonomic group, and specifications of their place of origin and repository.

4.2.1. Tardigrada

Tardigrada materials are the most abundant, from nearly complete and fragmented skulls to various appendicular bones, several ribs, vertebrae and isolated teeth. Both adult and juvenile animals can be identified, and about six genera distributed among four families recognized.

Related to Megatheriidae, remains of *Eremotherium laurillardi* (Lund, 1839) are common, represented by portions of the skull, jaws, vertebrae, ribs and various elements of the appendicular skeleton, including complete claws, some even articulated with the carpals.

Among Nothrotheriidae, two partial skulls of *Nothrotherium maquinense* (Lund, 1839) were recorded, as well as jaw fragments, isolated teeth and postcranial elements, such as vertebrae and limb bones. One of the skulls is almost complete, and it is housed in the MZ-USP (MZSPVP-767/Fig. 2A). It was collected by Krone during his first incursions into the Upper Ribeira caves and after that identified and described by Ameghino (1907) and redescribed by Paula

Table 1
List of the fossil megafauna taxa registered in the Upper Ribeira karst deposits.

- Xenarthra
- Tardigrada
  - Megatheriidae
    - *Eremotherium laurillardi*
  - Nothrotheriidae
    - *Nothrotherium maquinense*
  - Mylodontidae
    - *Lestodon armatus*
    - *Catonyx cuvieri*
    - Mylodontidae indet
  - Megalonichidae
    - *Ahytherium* aff. *aureum*
    - '*Ocnopus gracilis*'
- Cingulata
  - Glyptodontidae
    - *Glyptodon reticulatus*
    - *Glyptodon clavipes*
    - *Hoplophorus* cf.
- Notoungulata
  - Toxodontidae
    - *Toxodon* spp.
- Proboscidea
  - Gomphotheriidae
    - *Stegomastodon waringi*
- Perissodactyla
  - Equidae
    - *Hippidion* ?
  - Tapiridae
    - *Tapirus terrestris*[a]
- Carnivora
  - Felidae

    - *Panthera onca*[a]
    - *Smilodon populator*

[a] Living species still present in the studied area, ?= The specific genus need to be confirmed.

Couto (1956). The other skull reported is more fragmented and has only the anterior portion well-preserved. It is harbored in the IGc-USP collection, and is still unnumbered and under study.

The Mylodontidae apparently embraces the greater species diversity among Tardigrada into this area. Materials belonging to *Catonyx cuvieri* (Lund, 1839) and *Lestodon armatus* Gervais 1855, can be securely identified. There are also elements related to an indeterminate Mylodontidae still under evaluation. Related to this family, skull fragments, mandibles, appendicular elements, isolated teeth and several vertebrae were identified.

The record for Megalonychidae is somewhat confusing. Although the family can be undoubtedly identified, the species still need to be better evaluated and confirmed. There is a nearly complete skull, skull fragments and elements of the appendicular skeleton that were referred as belonging to '*Ocnopus gracilis*' (Lund, 1839) by Paula Couto in an manuscript written in 1980, but never published (Dos Santos, 1991). '*O. gracilis*', however, is a problematic taxon (Cartelle et al., 2008). The standing of its genus has been widely questioned, and it was recently considered invalid and referred as a possible synonym of *Valgipes* Gervais 1874 (de Iullis and Cartelle, 2007; Cartelle et al., 2008, 2009). '*O. gracilis*' was described by Hoffstetter (1954) based only on postcranial remains rescued from the Lagoa Santa, MG, caves. The nearly complete skull found in the Upper Ribeira (MZ-USP 06) was only tentatively related to '*O. gracilis*' by Paula Couto, but such association lack fundaments (Cartelle et al., 2008). This skull was studied again by Dos Santos (1991) in his master's thesis, in which he rejects Paula Couto hypothesis and elects the material as belonging to a new species, named "*Iporangabradys collecti*". Nevertheless, according to the rules of ICZN (International Code of Zoological Nomenclature, 1999), the proposal of this new taxon could not be considered since it was never formally published. Cartelle et al. (2008) re-examined the same material by comparing it with a complete skull of a new Megalonychidae found in the Poço Azul Cave in Bahia State, Brazil. In this work, the authors reject the proposal of Dos Santos (1991) and tentatively relate it to the new species described by them, *Ahytherium aureum* Cartelle et al., 2008. Nonetheless, they do this with reservations, as they refer to a second new species still being described, which could be more related to the Upper Ribeira material.

As the identification of the skull remains inconclusive, it was decided to consider this record as *Ahytherium* aff. *aureum*. Further studies may change this condition. As for the rest of the Megalonychidae material (*i.e.* the appendicular and some axial elements), preference was to maintain the Paula Couto's identification as '*O. gracilis*', until more studies reveal other affinities and/or a possibly established position for this taxon.

4.2.2. *Cingulata*

For Glyptodontidae, only osteoderms were recorded so far. The first evidence of such animals to the Upper Ribeira region was described by Ameghino (1907), and consists of a specimen collected

Table 2
Taxonomic group, type of register and current repository of the Upper Ribeira's megafauna material.

Taxonomic Group	Type of register	Procedence	Repository
Tardigrada	AX (r, v, fCr, iCr, o, t); AP	AC; AF; AG; AI; AJ; AM; APF; EC; MC; Couto Cave; Morro Preto I Cave; Morro Preto II Cave; clay cave-fill deposit in Capão Bonito and Iporanga, SP, municipalities.	MZ-USP; Igc-USP, MUGEO; MN-RJ
Megatheriidae	AX (r, v, fCr, t); AP		MZ-USP; IGc-USP; MN-RJ;
Nothrotheriidae	AX (v, iCr, t); AP;		MZ-USP; IGc-USP
Mylodontidae	AX (r, v, fCr, t); AP		MZ-USP; IGc-USP, MN-RJ
Megalonichidae	AX (iCr); ?AP		MN-RJ
Cingulata		AF; AI; AJ; APF; MC	
Gliptodontidae	Dp		MZ-USP; IGc-USP
Notoungulata	t; AP	AF; AJ; AM; APF; Los Tres Amigos Abyss	
Toxodontidae	t; AP		MZ-USP; IGc-USP
Proboscidea		AJ; Clay cave-fill deposit in the Apiaí, SP, municipality;	
Gomphotheriidae	t; AP		?; MZ-USP
Perissodactyla	AX (fCr); AP	AG; AC; Cave (?) in the Jacupiranga municipality; Chapéu-Mirim I Cave;	MUFSCar; MZ-USP
Equidae	AP		MUFSCar
Tapiridae	AX (fCr); AP		MZ-USP; MUGEO; IGc-USP
Carnivora		AG; AI; MC	
Felidae	AX (r, v, iCr, t); AP		MZ-USP; IGc-USP

AX = elements of the axial skeleton; AP = elements of the appendicular skeleton; r = ribs; v = vertebrae; fCr = cranial fragments; iCr = inclomplete skull; t = isolated teeth or teeth fragments; o = osteoderms; dp = dermal plates. AA = Anfíbio Abyss; AC = Caçamba Abyss; AF = Fossil Abyss; AG = Gêmeo Abyss; AI = Iguatemi Abyss; AJ = Juvenal Abyss; AM = Megalomilênio Abyss; APF = Ponta de Flecha Abyss; EC = Evarista Cave; MC = Monjolinho Cave, AC = Areias Cave, ?= Unknown.

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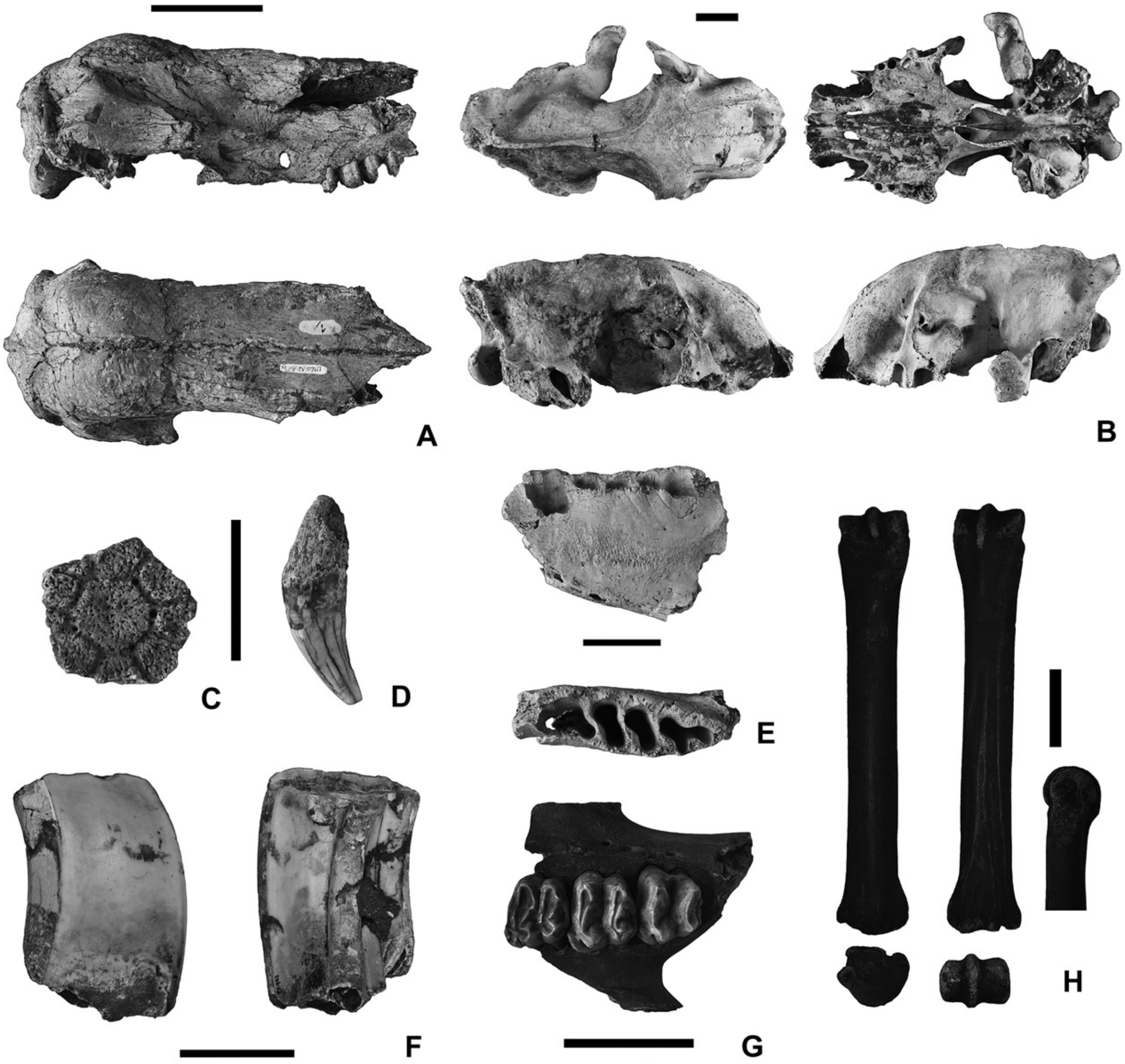

Fig. 2. Some of the megafauna fossil material from the Upper Ribeira region. A = *Nothrotherium maquinense* skull; B = *Smilodon populator* skull; C = *Glyptodon clavipes* dermal plate; D = *Panthera onca* canine; E = *Catonyx cuvieri* mandibular fragment; F = *Toxodon* sp. tooth; G = *Tapirus terrestris* mandibular fragment with inserted teeth; H = Equidae metapodial. Scale bars = 5 cm.

by Krone between 1896 and 1898. Ameghino referred this material as *Sclerocalyptus* Ameghino 1889, but noted that the carbonate incrustations were partially covering the ornaments, making an accurate identification impossible. Paula Couto (1973) redefined this specimen as *Hoplophorus* Lund 1839, as he considered *Sclerocalyptus* as a synonym of it. The general state of this material requires reservations in its identification.

The genus *Glyptodon* Owen 1838 is most certainly represented. There are dermal plates collected in the Fossil, Ponta de Flecha, Iguatemi and Juvenal abysses. They indicate the presence of two different species; *G. clavipes* (Fig. 2C) and *G. reticulatus* Owen 1845. The dermal plates of *G. clavipes* differ from those of *G. reticulatus* by its slender thickness and central ornamentation figure with prominent concavity and similar size to that of peripheral ones (Ameghino, 1889).

4.2.3. Notoungulata

Notoungulata material comprises several isolated teeth (molar, premolars and incisors), plus elements of the appendicular (patella, fragments of scapula, ulna and metapodials elements) and axial skeleton (a fragment of mandible with two juvenile deciduous teeth included, fragments of jaw and mandibles of an adult animal, part of an inner ear, fragmented vertebrae and ribs). Based on the tooth material, it was possible to identify at least two morphotypes into the Toxodontidae Family; certainly one with affinities to *Toxodon* and other possibly related with '*Trigodonops*'. The validity of the genus *Trigodonops*, however, is still under discussion, as it is based on scarce and poorly understood material (Mendonça, 2007). Some even consider it a species within *Toxodon*, naming it *T. lopesi*, taking into account a polymorphic condition for this genus. Given that this question still unsolved, only *Toxodon* sp. was considered in this survey. However, it is worth to note that clear differences exist between the materials.

A *Toxodon* sp. premolar tooth from the Ponta de Flecha Abyss (IGc-USP/PF997) was distinguished by Barros-Barreto et al. (1984) as presenting deep linear and curvilinear incisions into its proximal end. These were arranged preferably in the transverse axis of the tooth. The authors suggested that it could be archeological

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evidence of an attempt to remove the tooth from the arcade. In the same abyss, they also found a long bone of indeterminate large animal with incisions of dismemberment and a silex arrowhead. The premolar was submitted to dating by the Electron Spin Resonance (ESR) technique by Baffa et al. (2000), obtaining the approximate age of 6700–5000 (±1450) years.

4.2.4. Proboscidea

The Order Proboscidea has precarious records. The material referred by Paula Couto (1975) as a molar of *Stegomastodon waringi* Holland, 1920, recovered from a clay cave-fill deposit in the municipality of Apiaí, SP, could not be found. However, the MZ-USP collection has an ulna and a fragment of a tusk.

4.2.5. Perissodactyla

The Perissodactyla are well represented by *Tapirus terrestris* (Tapiridae) material, which was identified by appendicular elements and skull and mandible fragments with inserted teeth.

Equidae is represented only by a metatarsal element (Fig. 2H) whose characteristics fit with those classically described for *Hippidion* Owen 1869 (e.g. metapods shorter and more massive than those of *Equus* (*Amerhippus*), its sister taxon (Alberdi and Prado, 1995; Alberdi et al., 2003)). However, according to Orlando et al. (2003), this can no longer be considered a diagnostic feature, given that ancient DNA analysis have showed that very *Hippidion*-like metapods might also have been possessed by *Equus* (*Amerhippus*). This should be an adaptive convergence that may lead to misidentification. Therefore, only the higher level identification (Equidae) was considered in this study, until more materials are found or further studies realized. The metatarsal bone here in refered was collected in the Chapéu-Mirim II Cave, and consists of the first record of Equidae for this area and also the first formally announced evidence for it from the Late Quaternary of the São Paulo State.

4.2.6. Carnivora

The best record of Carnivora is an almost complete specimen of *Smilodon populator* Lund 1839, which includes a partial skull (Fig. 2B), fragmentary jaws, several vertebrae, the right ulna, the left radius, the left femur, the proximal part of the right femur, the right astragalus, fragmented ribs and a partial pelvis. Its postcranial remains were described by Castro and Langer (2008), and the skull is still under study. The bone elements of this individual were collected at different times; the skull and jaws in a first incursion into the Iguatemi Abyss and the other skeletal parts in a later visit. The skull and jaws are deposited in the IGc-USP and the remaining material in the MZ-USP.

Isolated teeth and some loose bone elements – both appendicular and axial – also indicate the ancient presence of *Panthera onca* Linnaeus (1758) (Fig. 2D). Ameghino (1907) described material belonging to this genus collected by Krone in the late nineteenth century. He emphasized its considerable size and “clear fossil aspect”. There are several other bone elements attributed to this taxon. However, some of them are difficult to determine precisely as to whether they are recent or not, considering the current occurrence of this animal in the region.

5. Discussion

5.1. Paleobiogeographic considerations

Tardigrada Megatheriidae have occurred in all Brazilian regions, especially *Eremotherium laurillardi*. This taxon is widely distributed throughout the north (Acre and Rondônia), northeast (all states), midwest (Goiás, Mato Grosso and Mato Grosso do Sul) and southeast (all states) Brazilian regions, but is less common in the south. *E. laurillardi* is a species with higher affinity to the tropical and intertropical extent, unlike its sister taxon, *Megatherium* Cuvier 1796, whose incidence is restricted to the southern areas of the continent, closely related to the Pampean province(Paula Couto, 1954; Cartelle, 1999, 2000; Cartelle and De Iullis, 1995; Cartelle and De Iullis, 2006; Ribeiro and Scherer, 2009).

Among the Nothrotheriidae, *Nothrotherium maquinense* is recorded for the Pleistocene of Minas Gerais, São Paulo and Bahia. There is still an uncertain occurrence in the Ceará state (Lund, 1839; Cartelle and Fonseca, 1983; Cartelle, 2000; Barleto et al., 2007; Ximenes, 2008).

Lestodon armatus (Mylodontidae) has records only in Rio Grande do Sul and São Paulo states, (Cartelle, 2000; Ribeiro and Scherer, 2009), while *Catonyx cuvieri* was described in Rio Grande do Sul, Minas Gerais, São Paulo, Bahia, Alagoa, Paraíba, Piauí, Ceará and Sergipe. *Catonyx* could be the Mylodontidae best distributed in the Pleistocene of Brazil (Cartelle, 1992; Born et al., 2003; Pereira and Oliveira, 2003; Guérin and Faure, 2004; Dantas and Zucon, 2007; Ximenes, 2008).

The occurrence of Megalonychidae extends through the states of Rio Grande do Sul, São Paulo, Minas Gerais, Bahia, Pernambuco, Ceará, Paraíba and Acre (Oliveira, 1996; Cartelle et al., 2008). ‘*Ocnopus gracilis*’ has marked records in Minas Gerais, São Paulo and Paraíba (Hoffstetter, 1954; Paula Couto, 1980; Cartelle, 1999; Bergqvist, 1993). However, there are also references to Acre State, according to Ranzi (2008), who compared a tibia found in the Juruá region to that collected by Paula Couto (1980) in the Jacupiranga municipality, SP. Ranzi (2008) found similarities in their size and morphology, therefore suggesting the same classification.

Ahytherium is described only in Bahia to date. However, its occurrence can be possibly confirmed in Minas Gerais and São Paulo states (Cartelle et al., 2008). The fact that the description of this genus is still recent implies that more materials have yet to be reviewed, and only then its distribution will be plenty understood.

Within the Glyptodontidae (Xenarthra, Cingulata), the genus *Glyptodon* is the most widely distributed in Brazilian territory. It is represented in the states of Rio Grande do Sul, Minas Gerais, São Paulo, Mato Grosso, Bahia, Sergipe, Pernambuco, Rio Grande do Norte, Piauí, Rondônia and Acre (Winge, 1915; Nascimento et al., 2003; Porpino et al., 2004; Dantas et al., 2005, da Silva et al., 2006; Ximenes, 2008; Oliveira and Pereira, 2009; Oliveira et al., 2009; Ribeiro and Scherer, 2009). *Hoplophorus* has records for Rio Grande do Sul, São Paulo, Minas Gerais, Bahia, Pernambuco and Piauí, although some of these reports probably require revision (Rolim, 1974; Paula Couto, 1973; Cartelle, 1992; Faure et al., 1999).

The occurrence of *Toxodon* (Notoungulata) in Brazil is vast, with reports from Rio Grande do Sul, Paraná, São Paulo, Minas Gerais, Mato Grosso, Bahia, Sergipe, Pernambuco, Rio Grande do Norte, Ceará, Piauí, Paraíba, Rondônia and Acre (Paula Couto, 1956, 1979; Guerin et al., 1993; Cartelle, 1999; Ranzi, 2000; Goes et al., 2002; Nascimento et al., 2003; Porpino and Santos, 2002; da Silva et al., 2006; Dantas and Zucon, 2007; Mendonça, 2007; Ximenes, 2008; Ribeiro and Scherer, 2009).

Stegomastodon waringi (Proboscidea) is also widely distributed throughout all Brazilian regions, with records pointing to Rio Grande do Sul, São Paulo, Minas Gerais, Mato Grosso do Sul, Mato Grosso, Bahia, Pernambuco, Alagoas, Piauí, Rio Grande do Norte, Ceará, Maranhão, Rondônia and Acre (Paula Couto, 1956; Simpson and Paula Couto, 1957; Bergqvist, 1993; Guerin et al., 1993; Goes et al., 2002; Prado et al., 2005; da Silva et al., 2006; Dantas and Zucon, 2007; Nascimento, 2008; Ximenes, 2008).

Among the Perissodactyla, *Tapirus* (Tapiridae) is highlighted as endemic throughout all Brazilian territory. There are fossil records of several species, but fossils of *Tapirus terrestris* are known only in the Pleistocene of Rio Grande do Sul, Paraná, São Paulo, Minas

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Gerais, Bahia, Mato Grosso, Rio Grande do Norte, Rondônia and Acre (Simpson and Paula Couto, 1981; Oliveira, 1992; Hyrooka, 2003; Porpino and Santos, 2002; Sedor et al., 2004; Holanda et al., 2005; Holanda and Cozzuol, 2006; Holanda, 2007).

Equidae, widely recorded in Brazil, were not so far formally known in the Late Quaternary of São Paulo State. The family is mentioned in the Pleistocene of Rio Grande do Sul, Paraná, Minas Gerais, Mato Grosso do Sul, Bahia, Pernambuco, Paraíba, Rio Grande do Norte, Ceará and Piauí (Bergqvist et al., 1997; Oliveira, 1999; Kerber and Oliveira, 2007; Alberdi et al., 2003; Ximenes, 2008). This would be the first officially appointed occurrence to this genus in the São Paulo State, filling a gap in its paleobiogeographical understanding.

Referring to the Carnivora, *Smilodon populator* (Felidae) has been recorded in Rio Grande do Sul, São Paulo, Minas Gerais, Goiás, Mato Grosso do Sul, Bahia, Sergipe, Pernambuco, Rio Grande do Norte, Ceará, Piauí and Paraíba (Gomide et al., 1987; Bergqvist et al., 1997; Lessa et al., 1998; Piló and Neves, 2003; Porpino et al., 2004; Castro and Langer, 2008; Ribeiro and Scherer, 2009). While fossils of *Panthera onca* are known for the Pleistocene of Rio Grande do Sul, São Paulo, Sergipe and Piauí (Dantas and Zucon, 2007; Kerber and Oliveira, 2008; Oliveira and Kerber, 2009), there are gaps in the knowledge about the ancient distribution of this animal.

The Upper Ribeira region encompasses a combination of megafauna species recurrent in both, the pampean and intertropical provinces. The syntopic presence of taxa as *Eremotherium laurillardi* and *Stegomastodon waringi* with *Lestodon armatus* is the best example. The co-occurrence of these animals could indicate that the area in question would be a transition zone between the two biogeographic regions, with characteristic species overlapping. *E. laurillardi* and *S. waringi* are typical species of the intertropical zone, while *L. armatus* is a characteristic taxon of more temperate regions. *Lestodon* fossils are very common in the Southern Cone South American countries. Typical of the Lujanense fauna, it become rare and then absent at lower latitudes. The furthest north occurrence of this species is that of São Paulo State, where it can be found in the Ribeira cave deposits and in clay deposits of Álvares Machado municipality area (Carvalho, 1952; Cartelle, 2000).

The presence of a larger number of taxa typical of the intertropical region (e.g. *E. laurillardi*, *S. waringi*, *Nothrotherium*, *Catonyx*, probably *Ahytherium* and *Tapirus terrestris*), however, suggests a greater affinity to this paleobiogeographic region. The Megatheriidae register reinforce this. *Eremotherium* is a symbolical genus of the intertropical region and apparently a common element in the past ecosystem of Ribeira Valley, where, until now, its sister taxon *Megatherium* - strictly pampean -, has not been recorded.

The unveiling of other indicative taxa with the persistence of paleobiological studies in the Upper Ribeira region may reveal more details about this ancient fauna. It is hoped to better understand the record of Notoungulata, Cingulata and verify the expected occurrence of Litopterna.

5.2. *Paleoecological considerations*

The wide geographic distribution of *Eremotherium* is probably related to a generalized feeding habit, both grazer and browser (McDonald, 2005). According to some authors, they would not be able to feed exclusively on grasses because of its abrasive nature, but megatheriids would be capable of oral processing food, differently from other ground sloths (Ferigolo, 1985; Bargo and Vizcaíno, 2008). *Eremotherium* was adapted to soft types of vegetation and associated to warmer and/or humid climates (Cartelle, 1992).

Nothrotherium maquinense is considered to be a tree climber of peripheral forests. There is evidence that it feed on leaves and fruits of xeric vegetation. It was associated with areas of hot and dry climate and physiognomy similar to the current Cerrado vegetation (Duarte and Souza, 1991; Cartelle, 1999).

Lestodon had the anterior part of its face enlarged, with oval molariform teeth, but two pairs of oversized and laterally projected caniniforms. It probably used them to dig tubercles and snatch leaves and tree barks. *Lestodon* was typically associated with temperate regions, with both dry and humid climates (Cartelle, 2000).

Catonyx, according to Lopes and Pereira (2010), was a mixed or selective feeder. It is found associated with different climatic regimes, but it is more common in warmer areas (Bargo, 2003).

Little is known about the paleobiology of '*Ocnopus gracilis*'. However, it is believed to have life habits similar to those of *Catonyx* (Cartelle, 1999).

Ahytherium aureum had a short and robust skull, with pronounced caniniform teeth. Given its morphology, it is believed to be a browser of shrub vegetation, occasionally digging for roots (Cartelle et al., 2008).

The Glyptodontidae have been related to open areas of grasslands and/or savanna, with temperate or warm climate. Its teeth suggest herbivorous grazing habit, associated with an abrasive diet, which may have included thick branches, leathery leaves and tubercles (Cartelle, 1992; Scillato-Yané et al., 1995).

The ecological requirements of *Toxodon* were not strictly related to climatic aspects, but mainly to its semi-aquatic life, which would require the presence of water bodies. Its feeding habits were wide, including since grasses to shrubs (Oliveira, 1999; Bond, 1999; Miño-Boilini et al., 2006).

Tapirus terrestris is indicative of a hot and humid climate. Its life area requires a mosaic of forested and open areas, used for shelter and pasture. Although primarily cursorial, is generally associated with water bodies. It is typical of mesic environments and/or transitional forests (Salas, 1996). The fact that it still occurs in the Upper Ribeira region shows its close association with the rain forests.

Equidae were grazers commonly associated with steppes, savannas, forested savannas and/or woodlands with temperate and moist climate (*Hippidion*) or hot and dry climate (*Equus*) (Alberdi and Prado, 1995).

Stegomastodon is related to both temperate and hot climates. It presented a mixed and flexible diet, being mainly a shrub browser, although a facultative grass grazer. Their bunodont condition is generally associated with grasslands and dry climates, with vegetal physiognomy typical of that of savannas and woodlands (Alberdi et al., 2002).

Smilodon is commonly associated with warm or temperate savannas. It is constantly referred as a social animal and an active hunter that slaughtered large prey (Turner and Anton, 1997).

Panthera onca has a preference for wooded areas and wetlands, but also occurs in open areas such as floodplains and even savannas. It is a solitary animal, which the feeding behavior is related to small and medium sized prey, occasionally including large animals as the Tapirus. Their foraging generally covers areas near water bodies (Turner and Anton, 1997). This animal stills an existing element in the Upper Ribeira fauna, as the *Tapirus terrestris* does.

There seems to be incongruence between the data retrieved through the paleoecological records of the megafauna assemblage analyzed. Some taxa are typical of hot, humid and forested areas, while others are characteristic of temperate climates and open physiognomies, like woodlands and savannas. The first hypothesis to explain this result is that the entire region was constituted by a mosaic of vegetation and climates, given different conditions of topography and association with water bodies. The second is that the fossil record does not represent a true biocoenose. In this case, the deposition data corroborate the latter hypothesis. What would

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be represented in this assemblage are different moments of a history of constant changes over the Late Pleistocene-Holocene, with the presence of distinct biological communities not temporally related.

The observed chronological distortion would be created by processes involved in the genesis of fossil concentrations in karst deposits. In the Upper Ribeira area, constant reworking by water is the main agent of stratigraphic disorder. The bioclasts are redistributed, and materials related to different deposition events are deposited adjacently. It is not possible, therefore, to establish relationships between the taxa based strictly on the orictocoenose analysis, since it does not represent an unique faunistic scenario, but several. Only taphonomic and more detailed paleoecological studies can retrieve information obscured by the tendency of taphocoenosis.

Most of the material recovered has lost their taphonomic data, but from the paleoecological inquiry at least three distinct faunistic groups can be identified. One is composed of species closely related to open vegetation areas, a second unites the generalists and plastic taxa, and the last is composed of species more connected and/or tolerant to forested environments.

The taxa linked to open vegetation are indicative of the existence of ancient conditions very different of the current one in the Upper Ribeira area. They include some of the Xenarthra, *Stegomastodon*, Equidae and *Smilodon*. These animals must have been organized in distinct communities throughout the Late Pleistocene; those associated with colder and dryer climates, colder and wet, or hot and dry, all with a predominance of open vegetation physiognomies (e.g. fields, savannas and woodlands).

Panthera onca and *Tapirus terretris*, preferably forest species, would have only definitely established and progressed with the expansion of mesophytic forests in a warmer and more humid period during the Holocene, and then remained in the region until today.

The generalistic taxa, as *Toxodon* and *Eremotherium*, may have presented a greater temporal range (*biocron*), due to their higher climatic tolerance and ecological flexibility. Their extinction would have occurred only with the definitive establishment of the rainforest, elapsed by higher temperatures and precipitation in the region during the Middle Holocene.

The Upper Ribeira *Toxodon* tooth dated by Baffa et al. (2000) indicate that the species would have survived until about 6700–5000 years ago in the area. It can be argued, then, that at least some portions of open vegetation were still present in the Ribeira Valley in that period, composing a mosaic with the mesophytic forest.

Megafauna materials dated from other Brazilian regions also suggest that some of the most generalist species have taken over the Pleistocene/Holocene boundary (Auler et al., 2006). Thus, it is understood that the next step in the paleontological studies of the Upper Ribeira Valley should be dating its material, in order to locate events of faunistic changes and characterize distinct faunas in each climatic moment.

The data obtained from the paleofaunistic record agree with those of Ledru (1991), and also Behling and Negrelli (2001), for the Quaternary vegetation changes in southeastern Brazil. These authors showed, using palynology data, the expansion of rain forests from 8500 BP until its final establishment around 5000 BP. The climatic oscillation that caused the great vegetation turn over would have elapsed due to alternate events of greater intensity of solar radiation, which affected the monsoon energy in both hemispheres (Wang et al., 2007; Cruz et al., 2009).

6. Conclusions

Fifteen different megafauna taxa were registered for the Late Quaternary of the Upper Ribeira region, with the recognition of the first formal register of Equidae in the São Paulo state. This synthesis of the paleontological knowledge of the Upper Ribeira Valley serves as a subsidy for further studies. Future efforts should focus on dating the material already collected and in the continuity of prospection, to fill faunistic gaps and acquire more robust data to support the paleoecological and paleobiogeographic studies.

The following surveys should concentrate on getting as much bioestratinomic data as possible to identify selective and destructive processes involved in the genesis of this karst deposit. Moreover, conducting mapping of the fossiliferous localities would be essential to understand the potential of the area and concentrate the prospection efforts. The study of the Quaternary fauna in the State of São Paulo fills a gap in the biogeographic history of the South American megafauna. The occurrence of fossils species common to both Intertropical and Pampean biogeographic provinces, demonstrates that there was a story more complex than expected; and the occurrence of taxa typical to open vegetation physiognomies, that there was a very distinct scenario than the currently present in the region. These questions are to be further examined and understood in a broader perspective.

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