



## PALEONTOLOGY

# Georeferencing fossiliferous localities from Solimões and Acre Basins (Brazil) - what we know so far about Solimões Formation and future perspectives

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**Abstract:** The Solimões and Acre basins are complex geological units related to the Andean uplift, covering the Northwestern region of Brazil, being one of the most important units due to their fossil diversity. In order to produce a document that integrates part of the fossil records of this region, we compiled/georeferenced localities from literature on which tetrapods are described, focusing on Solimões Formation but not restricted to this unit. We were able to recognize 208 localities, documented in over two centuries of reports of fossils from several taxonomic groups from the proto-Amazonia, 199 new entries in Paleobiology Database. We summarize, for each locality, its geographical position, geological information, age, and data of the paleodiversity. Most outcrops in the Amazonia region are located on river banks (~96%), while road cuts and other non-riverside outcrops represent the remainder (~4%). Most tetrapod are Mammalia, followed by Testudinata, and Crocodyliformes. This work reinforces the need for a more controlled and refined prospecting at the Solimões/Acre Basins, especially in the Solimões Formation, which represents the majority of fossiliferous records, to help answer old questions, such as dating, and new ones, here discussed, such as the paleodiversity patterns and temporal distribution among the mapped localities.

**Key words:** Acre region, Proto-Amazonia, RadamBrasil Project, river banks, South America, Tetrapod paleodiversity.

## INTRODUCTION

The Amazon biome currently represents one of the largest biodiversity hotspots on the planet (Kerber et al. 2016a, Hoorn et al. 2017). The evolution of the plethora of endemic organisms in this region is related to the Andean orogeny, which dates back to Neogene, influencing the environmental dynamics and the proto-Amazonian landscape (Hoorn et al. 2010, 2017, Kerber et al. 2016a, Kern et al. 2020). However, the evolution of Amazonian organisms and their current diversity take root with the Paleogene/

Neogene biota and the past paleoecosystems of the proto-Amazonia (Hoorn et al. 2010, 2017, Ribeiro et al. 2013, Bicudo et al. 2019).

Currently, in addition to being an unquestionable hotspot and sanctuary of a wide diversity of biological forms, the Amazonian region (or Acre region, see Cozzuol 2006) shows some of the most prominent fossiliferous assemblages in South America, presenting a range of the proto-Amazonian paleodiversity; both in terms of fauna and flora (Cozzuol 2006, Hoorn et al. 2010, 2017, Latrubesse et al. 2010, Negri et al. 2010, Kloster et al. 2017). In fact, many

modern families of plants found in the Upper Miocene are still present in the tropical region of the Amazonian biome (Latrubesse et al. 2010).

Most outcrops located in the Brazilian Amazonian region (Acre and Amazonas States – Brazil, and nearby regions in Bolivia and Peru), are attributed to rocks from the intracontinental sedimentary deposition of the Solimões Formation (*sensu* Rego 1930). This lithostratigraphic unit has the highest exposed levels in northern Brazil, mainly on river banks and road cuts in the southwestern Amazon rainforest (Cozzuol 2006, Latrubesse et al. 2010, Negri et al. 2010, Czaplewski & Campbell Jr 2017). These rocks that cover a great part of the northwestern region of Brazil, mainly those associated with the Solimões Formation, have preserved an important representation of the proto–Amazonia, with records of South American biota preceding the faunal migration from North America (i.e. Great American Biot Interchange – GABI; Latrubesse et al. 2010, Negri et al. 2010, Bissaro-Júnior et al. 2019).

In order to produce a document that integrates a large part of the fossil records of the Southwestern Amazonian region, we have compiled the available literature in which tetrapod fossils were described or figured, focusing on records from Acre and Solimões Basins (Brazil and frontiers with Peru and Bolivia). To our knowledge, all published data regarding the geology, distribution (within Acre and Solimões Basins), and taxonomy of the described tetrapods from both Basins were compiled and made available in a KML file (a free multiplatform extension used to show geographic data in Google Maps and other map applications – see the Supplementary Geographic Annotation (KML file, Google Earth Pro ©2020) available by FigShare DOI: 10.6084/m9.figshare.14046959. All mapped outcrops were updated in the Paleobiology Database. All the

literature that supports our data compilation is presented and the distribution of tetrapod groups and aspects of their diversity are discussed. Based on such complicated data of diversity, age, and geographical distribution, we discuss gaps in the current research conducted specifically in the Solimões Formation, aiming to guide future works to thread and fulfill such gaps.

## HISTORICAL OVERVIEW

The first field collections and literature records of fossil materials collected in Solimões and Acre Basins, as well as the first descriptions of fossil species from northern Brazil date from the 19th century and the first half of the 20th century (e.g. Agassiz 1868, Gervais 1876, Barbosa Rodrigues 1892, Gürich 1912). From the first to the second half of the 20th century, several surveys of geological data, including controlled excavations and new descriptions of fossil taxa from Neogene/Quaternary began to be carried out more systematically, coinciding with the development of paleontology research (e.g. Paula Couto 1944, Simpson & Paula Couto 1957, Price 1964).

Between the 1970s and 1980s there was a great advance in knowledge about the region's natural resources and its geomorphological and paleontological aspects. In addition to several publications by C. Paula Couto, there were expeditions from the Los Angeles County Museum that would culminate in later contributions (e.g. Frailey 1986). Still in the 1970s, an important project called RadamBrasil was developed, with the goal of acquiring knowledge regarding the natural resources of Brazil, and providing a large amount of information about geomorphology, geodiversity and paleontology (see Brasil 1976). Regarding the paleontological

studies developed from the RadamBrasil project, the main contributions were carried out by researchers of broad notoriety for Brazilian paleontology - Llewellyn Ivor Price and Diogenes Almeida Campos, from expeditions carried out in Southwestern Amazonia, starting in the year of 1974. Together, the works of Campos et al. (1976) and Price et al. (1977) mapped 180 fossiliferous localities across the Acre, southern region of Amazonas, and Rondônia states, at that time performing the collection of several fossil organisms and compiling information on previous expeditions in the region (e.g. Price 1957, 1964, Simpson & Paula-Couto 1957).

The dozens of specimens collected by and described in Campos et al. (1976) and Price et al. (1977) are currently housed in Paleontological Collection of the Museu de Ciências da Terra (MCT) under responsibility of Serviço Geológico do Brasil, Companhia de Produção de Recursos Naturais (CPRM), the institution that promoted several contributions concerning the geodiversity and paleontological knowledge of Acre and Amazonas states (see Brasil 1976, Adamy 2015). Nevertheless, many of these fossils (catalogued in Campos et al. 1976 and Price et al. 1977), remain without formal studies and descriptions until date (Latrubesse & Rancy 1998). However, a few efforts are being made to review some of these findings (e.g. Souza et al. 2016).

Although other institutions have allowed the initial development of research in this region, since the 1980s onward, the Laboratório de Pesquisas Paleontológicas (LPP) of the Universidade Federal do Acre (UFAC) was established, becoming an important regional research establishment. The LPP-UFAC enables the advance of paleontology research, including new expeditions and fossil findings (Souza-Filho & Guilherme 2015). Nowadays, the UFAC paleontological collection (lead by

J. Souza-Filho) consists of more than 4, 576 specimens collected in more than 70 different fossiliferous sites of the Solimões Formation (Haag & Henriques 2016). This collection is of great importance due to its expressive number of fossils, especially considering the difficult access to the outcrops where fossils, in general, are collected - margins of rivers and cuts of the BR 364 highway (Souza-Filho & Guilherme 2015, Haag & Henriques 2016). Nevertheless, the paleontology laboratory of UFAC Cruzeiro do Sul (lead by F. Negri) represents one of the strategic research centers in the region. Besides that, the paleontological research carried out by different groups of researchers has been advancing in the region of Acre, such as the “Prof. Rosalie Benchimol” expedition developed by UFAC and Museu da Amazônia in recent years and reported by Loboda et al. (2019b); notwithstanding, FFCLRP/USP’s paleontological expeditions have been carried out since 2012 (lead by A. Hsiou), or the recent communications and contributions of researchers in the field (e.g. Hsiou et al. 2016, Silveira & Souza 2016, Souza et al. 2016, 2018, Kerber et al. 2016a,b, 2018, 2019, Kloster et al. 2017, Sá & Carvalho 2017, Sá et al. 2020, Guimarães et al. 2018, Bissaro-Júnior et al. 2019, Cidade et al. 2019b,c, Loboda et al. 2019a,b, Lopes et al. 2019, Souza-Filho et al. 2019, 2020, Guilherme et al. 2020, Kern et al. 2020, Lacerda et al. 2020).

As a result of the history of paleontological research in the Amazon region briefly described above, there are currently several paleontological sites recorded, mainly from the Solimões Formation, and a well-established fossil collection program in the region. However, no comprehensive survey of those localities and fossils have been done to date. Our objective is to provide such data compilation in order to establish not only a bibliographic survey for the region but also a discussion of the paleodiversity

patterns and temporal distribution among the known localities.

There is a plethora of described fossils, such as paleovegetation and palynomorphs (e.g. Silveira & Souza 2016, Kloster et al. 2017, Kern et al. 2020, Sá & Carvalho 2017, 2020), invertebrate groups (e.g. Gross et al. 2013, Guimarães et al. 2018, Kern et al. 2020), ‘fishes’ (e.g. Aguilera et al. 2008, Lundberg et al. 2010) and rare anurans records (reported by Muniz et al. 2016). When we consider amniote clades, the Solimões Formation has more than 70 recorded taxa (Fortier et al. 2014), composing a great diversity of snakes and lizards (e.g. Hsiou & Albino 2009, 2010, Hsiou et al. 2009, 2010), turtles and crocodylians (e.g. Oliveira & Romano 2007, Riff et al. 2010, de la Fuente et al. 2018, Souza-Filho et al. 2020), birds (e.g. Alvarenga & Guilherme 2003, Guilherme et al. 2020), and a large diversity of mammalian clades (e.g. Frailey 1986, Cozzuol 2006, Negri et al. 2010, Ribeiro et al. 2013, Kerber et al. 2016a,b). The most diverse tetrapod clades are Crocodylia, Rodentia, Xenarthra, and Notoungulata (Cozzuol 2006, Fortier et al. 2014), and, recently, ichnotaxa were described based on traces in crocodylian materials (*Nihilichnus* - Di Gregorio & Araújo-Júnior 2020).

## GEOLOGICAL AND PALEOENVIRONMENTAL SETTINGS

The northwestern region of Brazil has extensive sedimentary cover deposited in intracratonic basins located in the continental area of the South American Platform with a complex geological history (Bahia 2015). The two main sedimentary basins in the southwest portion of the Brazilian Amazon region are the Solimões and Acre Basins.

The Solimões Basin is located in the western Amazon ecoregion, corresponding to a Paleozoic

intracratonic depression covering 440,000 km<sup>2</sup> (Caputo 2014). This Basin is limited by two arches and two shields: the Guiana Shield in the north and by the Brazilian Shield in the south; and by the Iquitos Arch in the west and by the Purus Arch in the east being subdivided in two sub-basins, Juruá and Jandiatuba respectively (Wanderley Filho et al. 2007, 2010, Caputo 2014). The Solimões Basin contains the Paleozoic and Meso-Cenozoic sedimentary sequences; the Meso-Cenozoic sequence is represented by the Javari Group, which in turn is composed by strata dated as Neogene and Pleistocene (Solimões and Iça Formations respectively, Rossetti et al. 2005, Wanderley Filho et al. 2007, 2010).

The Acre Basin is a small sedimentary basin located mainly in the Acre state at the border with Peru and Bolivia, covering 40,000 km<sup>2</sup> (Caputo 2014). It is limited on the western side by the Cenozoic basement-involved Divisor Reverse Fault and on the eastern side by the Late Jurassic Envira Arch (Caputo 2014, Bahia 2015). This Basin is also divided into the Jaquirana Group (composed of the Moa, Rio Azul, Divisor and Ramon Formations) trough in the north and the Central trough in the south with several formations comprising this member, namely: Formosa, Cruzeiro do Sul, Apuí, Juruá-Mirim, Rio do Moura, Solimões and Içã Formations (Price et al. 1977, Bahia 2015, Souza-Filho & Guilherme 2015).

The Solimões Formation is a multi-basin formation, being recognized both in Solimões and Acre Basins, as well in seven other northwestern South American basins (Rego 1930, Caputo et al. 1971, Eakin et al. 2014), outcropping mainly in the uppermost part of Acre State (extending over 80% of the state - Souza-Filho & Guilherme 2015), and southern Amazonas State, and also in Bolivia and Peru (Latrubesse et al. 2007, Duarte 2011). The Andean Orogeny tectonic influence compressed the Solimões Formation

by overlapping its eastern limits and presenting several reverse faults (Brasil 1976, Bahia 2015). In addition, Kronberg et al. (1989) based on geochemistry, suggested that the depositional environment of the Solimões Formation constitutes a chaotic system influenced by tectonic pulses.

The deposits of Solimões Formation comprise mainly mudstones, silty and sandy mudstones, and clayey siltstones that vary from fine to medium-grained sandstones; these levels are usually intercalated with lignite rich in plant remains, as well as carbonaceous clays and limestones (Price et al. 1977, Caputo 2014, Sá et al. 2020). The works by Latrubesse et al. (2007, 2010) recognized two main lithological facies: (i) a fossiliferous assembly represented by a channel; and (ii) a floodplain – lacustrine assemblage - being the level of the floodplain-lacustrine lower energy sedimentary depositions that better preserved tetrapod records (Latrubesse et al. 2007, 2010, Kerber et al. 2016a).

The depositional paleoenvironment of the Solimões Formation has been interpreted as a fluvio-lacustrine system which, in general, consisted of meandering and anastomosed rivers, associated with flood plains, abandoned meanders, and marshes surrounded by open vegetation interspersed with forests, similar to the Brazilian biome of the Pantanal (Alvarenga & Guilherme 2003, Negri et al. 2010, Silva-Caminha et al. 2010, Gross et al. 2011). However, paleoenvironmental changes during the Miocene and Early Pliocene changed the landscape from a mega-wetland to a strict fluvial system influenced by the Andean orogeny in this 'chaotic depositional system' (Kronberg et al. 1989, Alvarenga & Guilherme 2003, Latrubesse et al. 2010, Negri et al. 2010, Silva-Caminha et al. 2010, Gross et al. 2011, Nogueira et al. 2013, Horbe et al. 2019, Kern et al. 2020, Sá et al. 2020).

Traditionally, the outcrops of the Solimões Formation have been attributed to Huayquerian–Montehermosan South America Land Mammal Age (SALMA) system, corresponding to the late Miocene to Pliocene based on the mammalian diversity and palynostratigraphy, which suggest a correlation with paleofaunas from the Mesopotamian region of Argentina, Uruguay, and Venezuela (Cozzuol 2006, Latrubesse et al. 2007, Negri et al. 2010). However, it may be a little older, reaching the Chasicuan SALMA Age (Campbell Jr et al. 2001). Although the age of most outcrops of the Solimões Formation are certainly attributed to the Neogene (Cozzuol 2006), the first effort to refine the age of some localities from this Formation (in Talismã and Niterói sites) was conducted by Bissaro-Júnior et al. (2019) via U-Pb dating of detrital zircons. These authors suggested the maximum age of the sedimentation of the two studied outcrops of the Solimões Formation is Tortonian (Late Miocene). Similar results were obtained by Kern et al. (2020), also based on U-Pb dating of detrital zircons, leading to the conclusion that the maximum deposition age is  $11.42 \pm 0.66$  Ma (Tortonian, Late Miocene) at one point in the western Brazilian Amazonia. Both inferences about the age of the upper levels of the Solimões Formation (from biochronology and zircon dating) suggest that it dates to the Miocene Epoch (10.89 Ma - 8.5 Ma, Bissaro-Júnior et al. 2019;  $11.42 \pm 0.66$  Ma, Kern et al. 2020), or at least to Upper Miocene to Pliocene age (Cozzuol 2006, Latrubesse et al. 2010).

In addition, Pleistocene outcrops have already been recognized (Price et al. 1977, Latrubesse & Rancy 1998). According to Latrubesse & Rancy (1998) and highlighted by Cozzuol (2006), some Pleistocene vertebrates occur in the Amazon region associated with pre-Quaternary faunas being time-averaged. As these authors explained, the Pleistocene terraces went

through the diagenesis process, reworking the older Cenozoic sediments (Cozzuol 2006). This time-averaging is mainly affected by dynamics of the rivers cutting the sediments, leading to mixing of fossils from the middle Miocene to Holocene (Cozzuol 2006). As noted by Latrubesse & Rancy (1998), reworked Neogene fossil trunks (probably from the Solimões Formation), are found associated with Pleistocene records of wood. Nevertheless, considering the Solimões Formation in its entirety, we follow the dating proposed by Cunha (2007), which corresponds to the Eocene – Pliocene age. Even though some biostratigraphic inferences (see Cozzuol 2006, and Latrubesse et al. 2010) and absolute dating (see Bissaro-Júnior et al. 2019, and Kern et al. 2020) suggest Miocene age, we prefer not to assume that this holds true for the entire Solimões Formation, as most of the outcrops in the Amazonia region have not been dated. This broader age (Eocene – Pliocene *sensu* Cunha 2007) was adopted in previous studies that did not have a stratigraphic control of the collection of the described fossils (e.g. Souza et al. 2016, 2018, Lacerda et al. 2020).

## MATERIAL AND METHODS

### Outcrops acquisition data

Using Google Earth Pro version 7.3.3.7786 (©2020 Google), we mapped several known fossiliferous localities from Solimões and Acre basins, in Acre, southern part of Amazonas and Rondônia states, as well as the limits of these basins in Peru and Bolivia (Acre and Abunã River).

For each fossiliferous locality, the following information was recovered: (1) geographical positioning (when available); (2) geological information (when available); (3) inferred age; (4) taxonomic identification of the collected fossil specimens; and (5) references. In the discussions and compiled data, we kept nomenclatures and

outcrop names or numbers as mentioned on the original source literature. However, some taxonomic reviews and updates were considered (e.g. Kay & Frailey 1993, Negri & Ferigolo 2004, Goillot et al. 2011, Mothé et al. 2012, Kerber et al. 2016a, Cadena et al. 2020; see Supplementary Geographic Annotation and Table SI to access more detailed information).

In addition to the outcrops listed and mapped by the RadamBrasil Project (Campos et al. 1976, Price et al. 1977), the following references were verified to support this data compilation: Gürich (1912), Paula-Couto (1944), Simpson & Paula Couto (1957), Price (1964), Frailey (1986), Souza-Filho (1987), (1993), Souza-Filho & Bocquentin-Villanueva (1989), Villanueva & Santos (1989), Broin et al. (1993), Kay & Frailey (1993), Santos et al. (1993), Bocquentin & Silva (1994), Czaplewski (1996), Bocquentin & Guilherme (1997), Bergqvist et al. (1998), Gaffney et al. (1998), Bocquentin et al. (2001), Carvalho et al. (2002), Alvarenga & Guilherme (2003), Negri & Ferigolo (2004), Bocquentin & Melo (2006), Cozzuol et al. (2006), Holanda & Cozzuol (2006), Kay & Cozzuol (2006), Hsiou & Albino (2009), (2010), Hsiou et al. (2009), (2010), Meylan et al. (2009), Negri et al. (2010), Guilherme et al. (2011), (2020), Souza-Filho & Guilherme (2011), Frailey & Campbell Jr (2012), Fortier et al. (2014), Prothero et al. (2014), Kerber et al. (2016a,b), (2018), (2019), Muniz et al. (2016), Souza et al. (2016), (2018), Czaplewski & Campbell Jr (2017), de la Fuente et al. (2018), Souza-Filho et al. (2019), (2020), Cidade et al. (2019b,c), Loboda et al. (2019a,b), Lopes et al. (2019), and Lacerda et al. (2020).

Although this work is intended to be a comprehensive review, compiling data and presenting the ‘state-of-the-art’ on paleontological research in the proto-Amazonian region, we state that this is not an exhaustive search. Generally, old literature and gray-literature were not accessed because

they are not easily available and/or do not consist of reviewed contributions (e.g. meeting abstracts with preliminary results). That being said, we intend to provide a basis for further improvements and refinements on this fossiliferous dataset as a continuous and collective enterprise. We tried to include all possible occurrences, but some materials from an uncertain location (e.g. Villanueva & Santos 1989) and with identification numbers associated with more than one taxonomic level (e.g. Souza et al. 2016), or materials considered dubious and of unknown whereabouts (e.g. those fossil materials from the locality F-47 Oco do Mundo - see Campos et al. 1976) were disregarded. In cases where the authors indicated a specific location for a specimen (e.g. a specific river or a municipality), but without the exact point of collection (e.g. Simpson & Paula Couto 1957, Lopes et al. 2019, Souza-Filho et al. 2019), we tried to unify these records at a point along the river or municipality where the materials come from, avoiding the creation of “new” localities in Supplementary Geographic Annotation. The outcrops were mapped using FL (=Fossil Locality) followed by a exclusive number (see Supplementary Geographic Annotation and Table S1). Our georeferenced localities were linked with the Paleobiology Database (paleobiodb.org) and taxonomic informations could be accessed from the database and/or from our Supplementary Material (Supplementary Geographic Annotation and Table S1).

### **Geographical distribution**

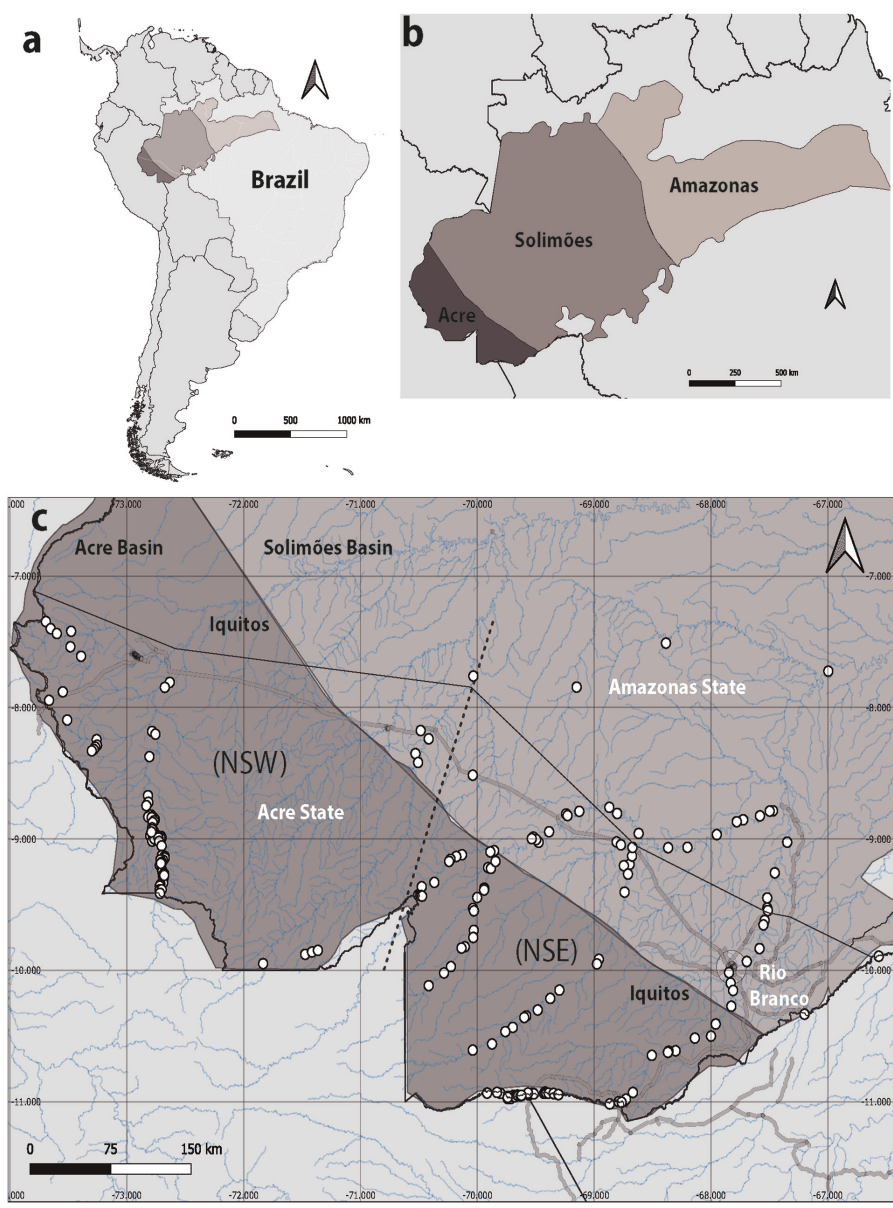
For a matter of locality distribution, we have arbitrarily divided the Acre and southmost part of Amazonas, and Rondônia states into two informal regions (west portion and east portion) in order to facilitate discussions. The delimitation between the two areas is drawn north of the Amazon region (Amazonas state)

from the Envira river, already in the south of Acre state, towards the Santa Rosa do Purus river, in Peru (Supplementary Geographic Annotation, and figure 1). These localities were divided into: (1) Northeast and Southeast (NSE), including mainly Rio Branco, Sena Madureira, Manuel Urbano, Bujari, and Senador Guimard, Xapuri, Capixaba, Brasiléia, and Santa Rosa do Purus municipalities; and (2) Northwest and Southwest (NSW), including mainly Mâncio Lima, Cruzeiro do Sul, Feijó, Tarauacá, Porto Walter municipalities, and the north portion of Serra do Divisor National Park, as well as Jordão and Marechal Thaumaturgo municipalities, besides the south portion of Serra do Divisor National Park.

All the major rivers where outcrops are found can be consulted on Supplementary Geographic Annotation, or in subsequent discussions on geographic distribution. Regarding geographic distribution, it is important to highlight two limitations on the compiled geographic data: (1) many authors did not provide GPS data or precise geographic reference. Even when they did, the information may be out of date. Thus, the inserted location in Supplementary Geographic Annotation and matches the original coordinate/geographic reference presented in the original manuscripts, but might be slightly wrong. (2) Many outcrops may no longer exist (at least the original rock exposure) due to the environmental dynamism (e.g. weathering and erosion) or anthropic damage. These limitations were reported in the literature, for example, by Kerber et al. (2016a, in supplementary material), where the authors showed that some outcrop previously described in the literature was not successfully located in subsequent field work.

### **Paleodiversity and outcrops age**

Based on the aforementioned literature revision (see references in section Outcrops Acquisition



**Figure 1.** Southwestern Amazonian map in Brazilian region. (a) South America; (b) Detached northern region of Brazil, with emphasis on the main geological coverings, namely, from left to right, Acre, Solimões, and Amazonas Basin; (c) Highlight for the most southwestern region (states of Acre and Amazonas). Black dot with circle, capital Rio Branco; White dots, fossiliferous localities georeferenced in this work; dashed line, hypothetical division into two zones: Northwest and Southwest (NSW), and Northeast and Southeast (NSE). Other map elements, highways, rivers, streams, and political-geographic division. **Supplementary Geographic Annotation (KML file, Google Earth Pro ©2020) is available by FigShare DOI: 10.6084/m9.figshare.14046959.**

Data), the paleodiversity of tetrapod groups from Solimões and Acre Basins have been compiled. It was not our main purpose to review the taxonomic identifications made by several authors and therefore we will solely discuss the paleodiversity aspects of the surveyed outcrops. Thus, for those interested in any aspect related to taxonomy of the listed species, we strongly suggest that the original references and further revisions compiled in this paper

be consulted. Moreover, we assumed the age of fossils according to the original dating for a given outcrop. Generally, the age inferences for the outcrops were made based on SALMA (e.g. Cozzuol 2006, Latrubesse et al. 2010), but also through pollen grains correlations (e.g. Latrubesse et al. 2010) and zircon dating (e.g. Bissaro-Júnior et al. 2019). We restricted our discussion on this subject based exclusively on



the results obtained from the data compilation performed here.

## RESULTS

### Distribution of fossiliferous localities

We were able to map two hundred and eight (208) outcrops in the southwestern part of the Amazon region (see Supplementary Geographic Annotation and figure 1). From our compilation of fossiliferous outcrops, 199 of these points have been updated in the Paleobiology Database as new entries. These locations include not only tetrapods, but other fossil organisms. Of this total, at least 123 outcrops (~59%) are positioned in the arbitrarily defined Northesat and Southeast (NSE) region whereas 85 (~41%) are distributed in the Northwest and Southwest (NSW) region. At least 54 (~26%) fossiliferous localities are distributed at the north of the Iquitos Arch. Meanwhile, 154 (~74%) outcrops are located in the Acre Basin at the south of the Iquitos Arch (figure 1).

Considering the distribution along Brazilian states, as expected, most fossiliferous localities are located in the Acre State (185 outcrops – equivalent to 89% of the outcrops mapped), followed by Amazonas State (21 outcrops – 10%), and Rondônia State (2 outcrops – 1%), with outcrops located on the eastern edge of Solimões Basin.

Most localities which have collection data are located on river banks, from 194 outcrops (i.e. 96% of the mapped sites). Only 13 (4%) sites are located in other areas (e.g. farms or highways). In the NSW region, the outcrops are mainly distributed on the Juruá, Moa, Tejo and Envira rivers. Nevertheless, it is worth noting that the Juruá River has the largest number of outcrops along its course. In the NSE region, the outcrops are mainly distributed on the Purus, Chandless, Macauã, Iaco, and Acre

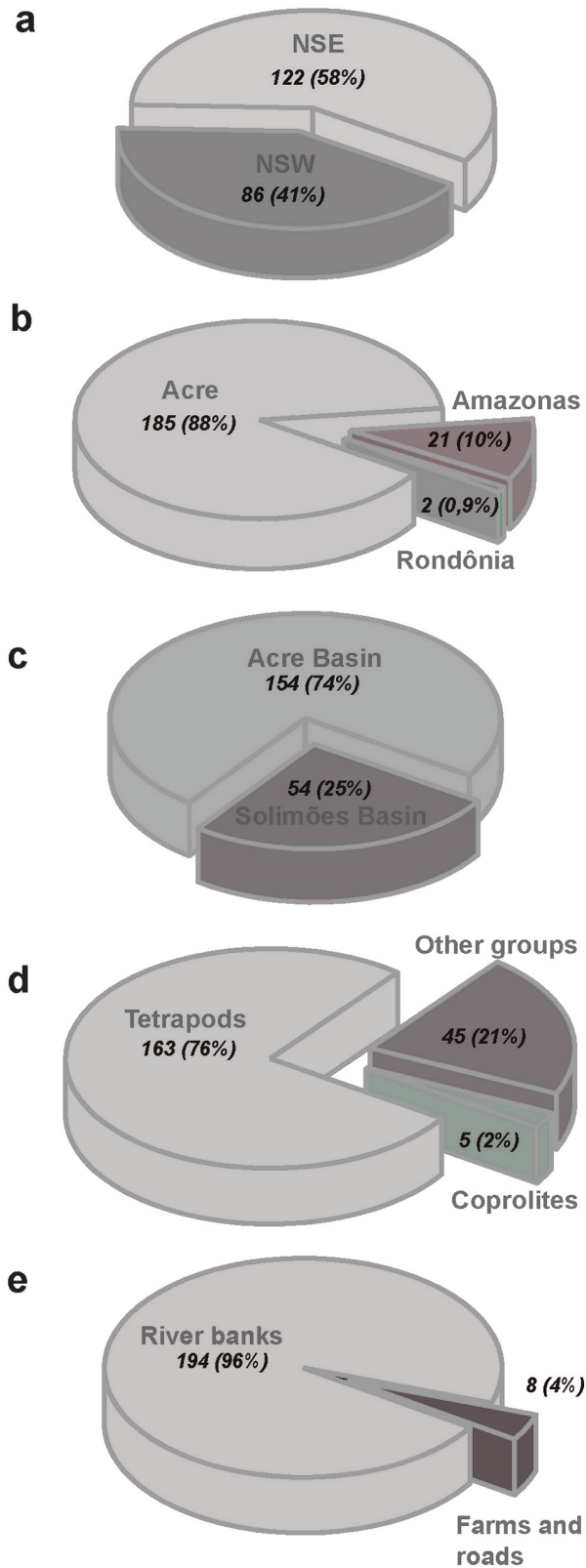
rivers, with a concentration of points in the south limits of Acre, near the Assis Brasil, and Brasiléia municipalities along the Acre river course. The areas with less known outcrops are those included in indigenous reserves or have extensive vegetation covering, which naturally limits the anthropogenic destructive influences (e.g. roads and highways) and fossil collecting efforts. It is already known that due to the forest cover and adverse geological conditions, most outcrops are exposed in river banks (in accordance with Souza-Filho & Guilherme 2015); in this sense our data support this statement, since only 4% of the outcrops we mapped are in areas unrelated to river banks (figure 2).

### Tetrapods paleodiversity and geographical distribution

One hundred and sixty two (163) outcrops mapped in this work, or ~78% of the 208 recorded locations, yielded fossil tetrapods. The summary of records are presented in figures 1-4 and all compiled information, including literature citations and georeferenced records, are condensed in the supplementary KML file (Supplementary Geographic Annotation).

### Records at higher taxonomic levels

Several fossils are identified at more inclusive taxonomic levels (i.e. Class, Order), in some cases because they represent very fragmented materials (e.g. *Crocodyliformes* indeterminate specimens described in Lacerda et al. 2020). Poorly identified specimens (i.e. identified to Class or Order level) summed up to 205 records. The most abundant clade with poorly identified specimens is *Crocodyliformes*, with records in 71 fossiliferous localities, followed by *Testudines*, with 47 occurrences (including 14 fossiliferous localities with pleurodiran indeterminate materials). Other reptilian (i.e. *Diapsida*) records



are assigned to Squamata, in three localities, including one record attributed to Serpentes. Moreover, seven localities include fossils identified as “Reptilia”. Uncertain mammalian fossils are recorded in 29 localities, including 20 Rodentia, 14 Xenarthra, two Cingulata, and one Artiodactyla occurrences. Indeterminate Aves are reported in two localities. Non-amniote records include one Anuran report. Finally, at least 31 localities have fossil occurrence identified as indeterminate Craniata (figure 3).

**Records at Superfamily, Family and Subfamily levels**

Besides those higher level imprecise taxonomic identifications, several specimens could be identified at the family level by the original authors. Among these fossils, the Family Toxodontidae (Mammalia) comprise most of the records, occurring in 28 localities. Other mammalian families are included in Xenarthran Orders Cingulata (14 occurrences) and Pilosa (seven occurrences). The former are attributed to the families Glyptodontidae (11 localities), Pampatheriidae (two localities), and Dasypodidae (one locality). The second include records identified as Megatheriidae (six localities) and Megalonychidae (one locality) (figure 3).

**Figure 2.** Pie chart referring to the southwestern fossiliferous localities of the Brazilian Amazonia. (a) Number of fossiliferous localities per hypothetical region; (b) Number of fossiliferous localities per sedimentary basin; (c) Number of fossiliferous localities per Brazilian state in the Amazonian region; (d) Number of fossiliferous localities according to their location (roads vs. river banks); (e) Taxonomic groups (tetrapods vs. other groups - plants, invertebrates) and coprolites registered by fossiliferous localities.

South American ungulates identified up to family level include indeterminate Astrapotheriidae occurrences in five localities and four Litopterna records: two attributed to Proterotheriidae, and two records of Macraucheniiidae.

Other occurrences belong to Order Rodentia, with 12 localities recovered. Caviomorpha and Erethizontidae were registered in two localities whereas the families Cuniculidae, Dasyproctidae, Ocotodontoidea, Neopiblemidae, and the Subfamilies Cardiomyinae, Dolichotinae, Heteropsomyinae, and Potamarchinae, were reported in one locality each (figure 3).

Besides rodents, other less representative mammals groups include bats of the Family Molossidae (two occurrences), dolphins of the family Delphinidae (one occurrence), and primates of the families Atelidae and Cebinae, both with one record.

The herpetological record includes one locality where anurans of the family Pipidae were registered. The non-avian Sauropsida record include four occurrences of turtles of the families Testudinidae (1 record), Pelomedusidae indet (1 record) [certainly referable to Pelomedusoides in the classical sense, Oliveira & Romano 2007], and Podocnemididae (2 record). Snakes of the family Colubridae were recorded in one fossiliferous outcrop. The records of Sebecidae (Mesoeucrocodylia) summed up two occurrences, whereas the Crocodylia record presents Gavialoidea (1 record), Caimaninae (2 records), and Brevirostres (1 record) (figure 3).

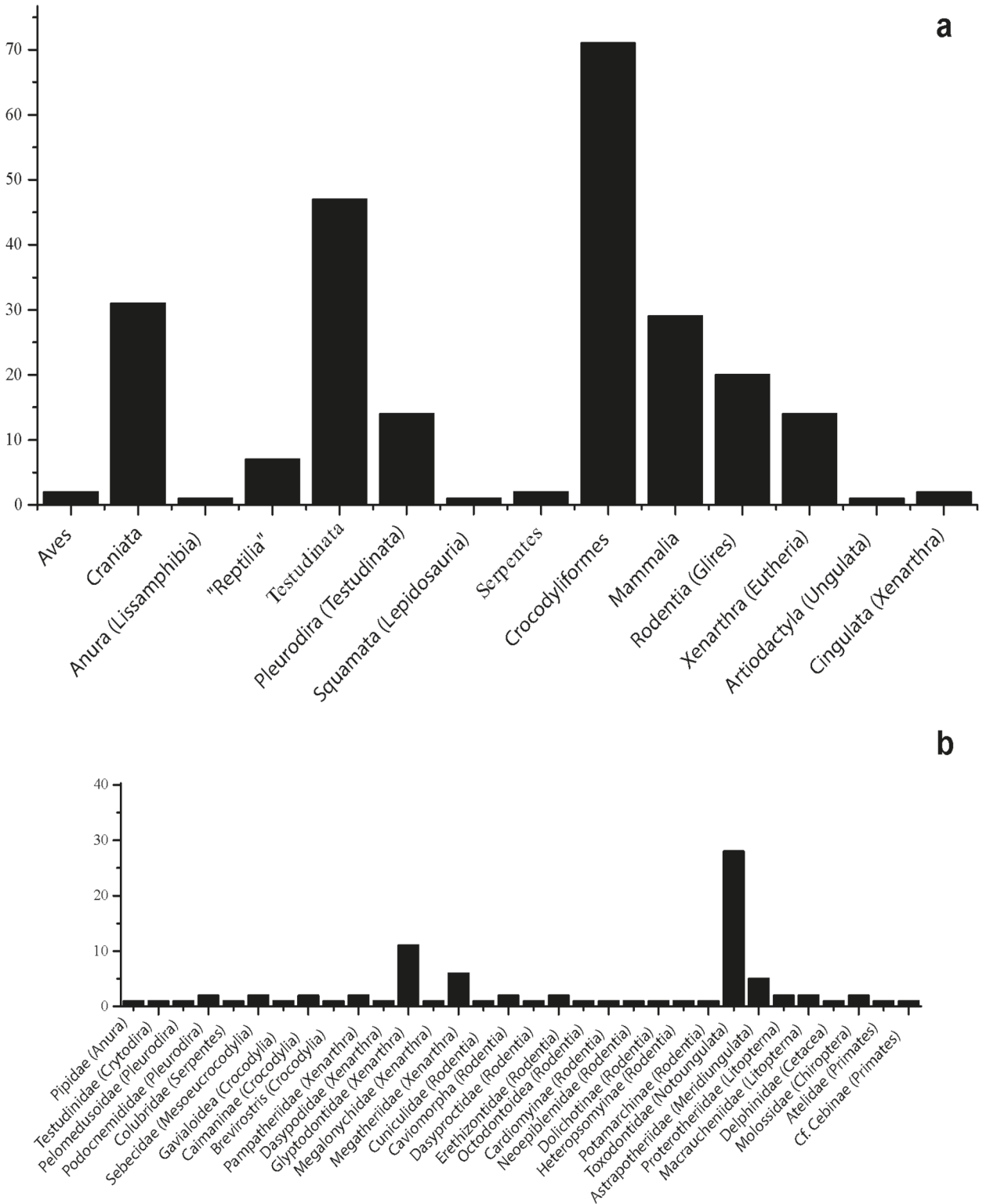
### **Records at lower taxonomic levels (genus and species)**

Considering specimens that could be identified at a specific or generic level by the original authors, we compiled 164 tetrapods records.

The turtles of the Family Chelidae comprise the highest number of records (28 records) all to the matamata genus *Chelus*: *Chelus lewisi* (3 records), *Chelus colombiana* (6 records), and 19 records of indeterminate *Chelus*. Other 13 records are attributed to Podocnemididae: *Podocnemis negrii* (1 record), *Stupendemys geographicus* (9 records including those originally attributed to *Stupendemys souzai* and *Caninemys tridentata*, currently known as junior synonyms of *S. geographicus*, sensu Cadena et al. 2020), and three records to indeterminate *Podocnemis*. The Cryptodira turtles were the least represented with 5 records of Testudinidae assigned as *Testudo* sp (figure 4) and one record of *Testudo elata*.

Squamata genera and species are represented by snakes and lizards remains, that include the families: Boidae (Serpentes), and Teiidae. The snakes specimens records are *Colombophis spinosus* (3 records), *Waincophis* sp, *Eunectes* sp (1 record) and aff. *Epicrates* (1 record). Lizards represented by Teiidae records are, cf. *Paradracaena* sp and *Dracaena* sp, both with one record (figure 4).

Considering Crocodyliformes, Caimaninae are the most representative, with at least 27 occurrences. The *Caiman* genus is represented by *Caiman brevirostris* (2 records), and *Caiman* aff. *crocodilus* (1 record). In two localities occur fossils of *Melanosuchus Mourasuchus* specimens have been described for at least six outcrops, *Mourasuchus* sp (3 records), *Mourasuchus arendsi* (1 record), and *M. amazonensis* (2 records). Eight outcrops recorded specimens of *Purussaurus*, *Purussaurus* sp (6 records), and *Purussaurus brasiliensis* (2 records). Other Caimaninae species, *Acrasuchus pachytemporalis* has been recorded in at least 6 sites. The gavialid *Gryposuchus* was registered in three localities: *Gryposuchus* sp (1 record) and *Grypossuchus jessei* (2 records).



**Figure 3.** Column chart showing the number of fossil tetrapod records identified at more inclusive taxonomic levels. (a) Class or Order level; (b) Superfamily, Family and Subfamily levels.

The Crocodyloidea *Brasilosuchus mendesi* and *Charactosuchus fieldsi* have been registered in at least 2 of the mapped sites (figure 4), being one record of each genus.

There are at least four records of birds, all attributed to Anhingidae species (one record each): *Anhinga minuta*, *Anhinga* cf. *fraileyi*, *Anhinga* cf. *grandis* with *Macranhinga ranzii* having at least two occurrences (figure 4).

Fossil mammal genera and species were the most diversified among the mapped materials, adding up to 76 occurrences. The marsupial *Didelphis solimoensis*, the trichechid cf. *Ribodon* sp, the mustelid *Eira barbara* and the astrapothere *Xenastropotherium amazonensis* had records in one location each. In two locations were recorded Chiroptera species: *Amazonycteris divisus* and *Noctilio lacrimaelunaris*. The gomphotheriids *Notiomastodon platensis* were sampled in 14 outcrops. Three primates are recorded, the cebid *Acrecebus fraileyi*, and the atelids *Stirtonia* sp, and *Solimoea acrensensis*. Among Notoungulata, Toxodontidae were represented by *Trigodon* sp and cf. *Gyrinodon* sp with one record each; and *Toxodon* sp with two records. Regarding Haplodontheriidae, *Trigodonops lopesi* and *Abothrodon pricei* were registered, both with one record. There were five records of Mylodontidae sloths: *Pseudopreoptherium venezuelanum* (1 record), *Octodontobradys* sp (1 record), *Octodontobradys puruensis* (1 record), and *Urumacotherium campbelli* (2 records). The giant-sloths (Megatheriidae), were registered in two localities, one for each taxon: *Megatherium* sp and *Nothropus priscus*. The Palaeomyeridae species *Surameryx acrensensis* were recorded in one locality (however, this taxon needs a reappraisal to confirm their taxonomic validity (Perini et al. 2016, Gasparini et al. 2021)), as well as the Tayassuidae *Sylvochoerus woodburnei* (this taxon also has your doubtful taxonomic and stratigraphic (Perini et al. 2016, Gasparini et

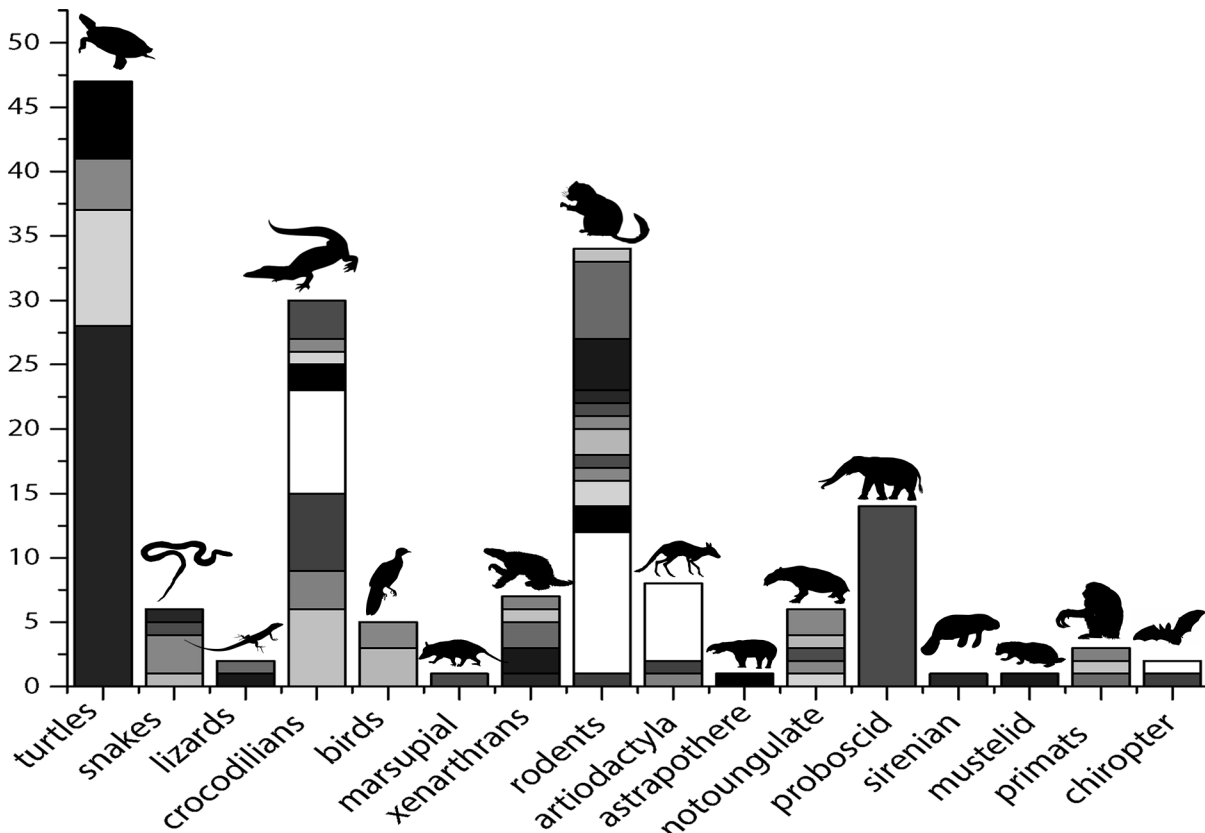
al. 2021)). *Tapirus* sp (Tapiridae) were found in six localities (figure 4).

Rodentia sums up 34 records, being the most diverse mammal order in fossil record of Solimões and Acre Basins. The Dinomyidae family has 20 occurrences of the taxa identified at genus or species level, namely: *Drytomomys* sp, *Potamarchus* sp, *Potamarchus adamae*, *Pseudopotamarchus vallanuevai*, *Potamarchus murinus*, *Telycomys amazonensis*, “*Scleromys*” cf. *colombianus*, *Ferigolomys pacarana*, *Tetrastylus* sp. There were two records of Caviomorpha: *Eoincamys* sp and cf. *Eobranisamys* sp. Hydrochoeridae rodents had at least 5 records, with *Caviodon* sp (1 record), *Cardiatherium* sp (2 records), and *Cardiatherium orientalis* (2 records). Finally, the Neoepiblemidae family has at least seven records: *Phoberomys* sp (1 record), *Neoepiblema* sp (2 records), *N. horridula* (2 records), *N. ambrosettianus* (1 record) and *N. acrensensis* (1 record) (figure 4).

## DISCUSSION

### Most representative tetrapod groups

By adding the records of Mammalia indet with other occurrences of the group we found a total of 217 records. Five outcrops in Acre and south of Amazonas State, concentrate most of the mammalian paleobiodiversity at: (1) Locality Talismã; Pilosa (Orophodontidae, Megalonychidae, and Megatheriidae), Rodentia (Cuniculidae, Neoepiblemidae, and Dinomyidae), Liptoterna (Protheroheriidae), Cingulata (Pampatheriidae), and Primates (Atelidae), this outcrop is located on the south of the border between the State of Amazonas and north of the State of Acre; (2) Locality Bandeira; Rodentia (Neoepiblemidae), Notoungulata (Toxodontidae), Primates (Atelidae and Cebidae), and Cetacea (Platanistidae and Pontoporiidae), outcrop located on the southern border of the State of



**Figure 4.** Column chart showing the number of tetrapod records identified by genera. **Turtles:** *Chelus* (Chelidae) (28 records), *Stupendemys* (Podocnemididae) (9), *Podocnemis* (Podocnemididae) (4), *Testudo* (Testudinidae) (6); **snakes:** *Waincophis* (Boidae) (1), *Colombophis* (Alethinophidia) (3), *Eunectes* (Boidae) (1), *Aff. Epicrates* (Boidae) (1); **lizards:** *Cf. Paradracena* (Teiidae) (1), *Dracaena* (Teiidae) (1); **crocodylians:** *Acresuchus* (Caimaninae) (6), *Caiman* (Caimaninae) (3), *Mourasuchus* (Caimaninae) (6), *Purussaurus* (Caimaninae) (8), *Melanosuchus* (Caimaninae) (2), *Brasilosuchus* (Crocodyloidea) (1), *Charactosuchus* (Crocodyloidea) (1), *Gryposuchus* (Gavialoidea) (3); **birds:** *Anhinga* (Anhingidae) (3), *Macranhinga* (Anhingidae) (2); **marsupial:** *Didelphis* (Didelphidae) (1); **xenarthrans:** *Pseudopreoptherium* (Mylodontidae) (1), *Octodontobradys* (Mylodontidae) (2), *Urumacotherium* (Mylodontidae) (2), *Megatherium* (Megatheriidae) (1), *Nothropus* (Megatheriidae) (1); **rodents:** *Drytomomys* (Dinomyidae) (1), *Potamarchus* (Dinomyidae) (11), *Pseudopotamarchus* (Dinomyidae) (2), *Telycomys* (Dinomyidae) (2), “*Scleromys*” (Dinomyidae) (1), *Ferigolomys* (Dinomyidae) (1), *Tetrastylus* (Dinomyidae) (2), *Eoincamys* (Caviodea) (1), *Cf. Eobranisamys* (Caviomorpha) (1), *Caviodon* (Hydrochoeridae) (1), *Cardiatherium* (Hydrochoeridae) (4), *Neoepiblema* (Neoepiblemidae) (6), *Phoberomys* (Neoepiblemidae) (1); **artiodactyla:** *Suramerix* (Palaeomerycidae) (1), *Sylvochoerus* (Tayassuidae) (1), *Tapirus* (Tapiridae) (6); **astrapothere:** *Xenastrapotherium* (Astrapotheriidae) (1); **notoungulates:** *Trigodonops* (Haplodontheriidae) (1), *Abothrodon* (Haplodontheriidae) (1), *Trigodon* (Toxodontidae) (1), *Cf. Gyrodon* (Toxodontidae) (1), *Toxodon* (Toxodontidae) (2); **proboscid:** *Notiomastodon* (Gomphoteriidae) (14); **sirenian:** *Cf. Ribodon* (Trichechidae) (1); **mustelid:** *Eira* (Mustelidae) (1); **primats:** *Acrecebus* (Cebidae) (1), *Stirtonia* (Atelidae) (1), *Solimoea* (Atelidae) (1); **chiropters:** *Amazononycteris* (Thyropteridae) (1), *Noctilio* (Noctilionidae) (1). The silhouettes were extracted from PhyloPic.

Acre, the SE region; (3) Locality Patos; Rodentia (Dinomyidae and Neopiblemidae), Chiroptera (Molossidae and Noctilionidae), Notoungulata (Toxodontidae), Marsupialia (Didelphidae), and Primates (Atelidae), this locality is situated in

south of the State of Acre, the SW region (see Supplementary Geographic Annotation and Table SI for details).

Crocodyliformes also is a highly documented group, with records in all regions

of Acre and south of Amazonas State, summing up 101 occurrences. Three outcrops stand out in Crocodyliform registers: (1) Talismã locality; Crocodyloidea (*Charactosuchus*, *Brasilosuchus*), *Caiman brevirostris*, *Mourasuchus*, Gavialoidea, *Aresuchus pachytemporalis*, and *Melanosuchus latrubessei*; (2) BR 364 locality; *Caiman*, *Mourasuchus*, and *Melanosuchus* cf. *niger*, this locality is in the north of the State of Acre, the NE region; (3) Locality Bandeira; indeterminate Crocodyliformes, Breviostres indet, Gavialoidea, and the caimanine taxa (*Purussaurus* and *Mourasuchus*). However, in relation to the Talismã site, there is a hidden diversity gap for small vertebrates groups (see Muniz & Hsiou 2018 master thesis). Although it is not the scope of the discussions in this article, it is important to note that several georeferenced outcrops also provide a fossil record of plants, invertebrates and coprolites (Figure 2) (see Supplementary Geographic Annotation, Table SI and references of this work).

### Age

Based on the aging inference provided by the original authors that first described each locality as well as subsequent authors who have worked on the same localities, we mapped a temporal and geographic distribution of the studied localities for the region. The complete information about locality-age is presented in the supplementary materials (Supplementary Geographic Annotation and Table SI).

The NW zone contains twenty-seven (27) fossiliferous localities described in the literature, being the less represented Acre region. This zone is the only one with localities dated as Cretaceous, a total of five localities Igarapé Água Quente, Igarapé Capanuana, Capanuana, Marco 82, and Serra do Jaquirana. Those localities are in the northwest portion of the NW zone, between the AC 402 and BR 364 highways associated to

the Rio Moa stream. There is one locality on the Serra do Divisor referred to Pliocene age: Igarapé Jesumira. A total of seven Pleistocene localities are located in NW region. Those localities are distributed mainly in the course of the Moa and Juruá rivers. A total of eight Holocene localities are distributed mainly in the Juruá and Envira rivers. The outcrop called Alto Juruá is dated as Late Miocene, and the locality Igarapé Cardoso is generally recognized as Cenozoic in age. Three NW localities have more than one inferred age, they are: Estirão Tabocal; Corredeira Velho Chico; and Morro do Careca. The localities Estirão Tabocal and Corredeira Velho Chico have two inferred ages: Pleistocene and Holocene. The inferred ages for the locality Morro do Careca are Late Miocene and Miocene/Pliocene.

The NE zone contains fifty-eight (58) described outcrops, and most of them (39 outcrops) are considered here as Cenozoic in age. The majority of the localities in the NE region are distributed along the Purus and Acre rivers. A total of seven Holocene localities are described for the NE region. Two localities are referred to Pleistocene, they are: Igarapé da Onça and Camarajibe. Two localities are Pliocene in age: Rio Unauini and Pauini. The localities: Seringal Amapá and BR 364 Road are dated as Miocene-Pliocene. Two outcrops are dated as Late Miocene: Lula and Perseverância. The locality in Sena Madureira municipality is referred to has Eocene - Pliocene (since there is no evidence for a more refined age). The Talismã locality is referred to Late Miocene and Late Miocene-Pliocene, and recently Bissaro-Júnior et al. (2019) based on dating via U-Pb of detrital zircon, dated Talismã as upper Miocene (Tortonian age,  $10.89 \pm 0.13$  Ma), which was previously anticipated considering biostratigraphy and faunal comparisons (Cozzuol 2006, Latrubesse et al. 2010, Bissaro-Júnior et al. 2019). Some of the localities in NE region described by Campos et al. (1976) do not

present any specific age assignment and are here, conservatively, considered as Cenozoic in age (as the temporal range proposed by Cunha (2007) to Solimões Formation).

The region SW has at least fifty-six (56) localities described. In this region, most of the localities are dated as Pleistocene (31). Eleven localities are Holocene in age. Six localities in the SW region described by Campos et al. (1976) are here considered Cenozoic (*sensu* Cunha 2007). A total of five localities have two or more age proposals, they are: Volta da Pedra Pintada, Miocene and Pliocene; Cachoeira da Pedreira, Holocene and Pleistocene; Minas Gerais, Pliocene and Pleistocene; Cantagalo, Late Miocene and Pleistocene; and Pedra Preta, Late Miocene, Holocene and Pleistocene in age. The majority of the localities in the SW region are distributed along the Juruá river.

The SE region has fifty-five (55) outcrops described, most of them (41) dated as Cenozoic. Three localities are dated as Holocene: Minas Gerais; Reintegra; and Oriente. One locality is Late Miocene in age: Cavalcante. One locality is Pleistocene in age: Florescência. A total of nine localities have two or more age proposals. The localities dating as Cenozoic and Eocene-Pliocene are: Chapiama; Ipiranga; Pedreira; Guajará; and Morada Nova. The Niterói site was also dated via U-Pb (see Bissaro-Júnior et al. 2019) as  $8.5 \pm 0.5$  Ma. Seringal Sacado is dated as Cenozoic and Lower Eocene - Pliocene. The locality Patos is dated as Cenozoic, Miocene - Pliocene and Late Miocene. The Bandeira locality is dated as Cenozoic, Eocene - Pliocene and Late Miocene - Pliocene. The majority of localities are along the Purus, Iaco, and Acre rivers.

The Solimões Formation is routinely weathered by several rivers of different sizes (Latrubesse et al. 2010). This natural erosion is responsible to rework and redeposit fossils of different Solimões Formation layers, causing

the dating of fossils found freely in river margins not to be very reliable (Hsiou AS, personal communication). Also, it is important to recognize, due to the river dynamic, the distinction between the original and unconsolidated sedimentary rocks from the Holocene deposition. As the Solimões Formation sediments are deposited in a fluviolacustrine system (Caputo et al. 1971) there is evidence of time averaging during its original deposition (Latrubesse & Rancy 1998). Behrensmeyer (1982) provided some tentative time resolution for fluvial vertebrate assemblages being around some thousands of years, which is not a great temporal mix in the context of million years of the Cenozoic ages. Souza et al. (2016) argued that this original time averaging of Solimões Formation deposits must be always considered, but in the localities studied by those authors (see Souza et al. 2016), this temporal mix was not considered an unavoidable problem for aging and ecological interpretations.

Generally, the ages suggested for the mentioned localities are mainly based on biochronostratigraphy of other better understood South American formations, such as those with South American Land Mammal Age (see Cozzuol 2006, Latrubesse et al. 2010), including as principal proxy for inference pollens and fossil mammals. In the absence of a controlled and refined stratigraphy as well as a poor understanding of the temporal distribution of biodiversity in the Solimões Formation, those age inferences must be viewed with caution. It is common in some localities to find Crocodylia species that are regarded as Miocene-Pliocene together with Pleistocene mammals (e.g. localities Museu and Morro do Careca). This is remarkable for the supposed Holocene localities Pedra Pintada and Igarapé Parição, which produced Sebecidae teeth. Sebecidae is a Crocodyliform group known for the Paleocene



and Early Miocene of South America that become extinct in the Middle Miocene (Price et al. 1977, Cidade et al. 2019a). Therefore, more studies are needed to assure if those species were chronocorrelates or if some of the discussed time averaging occurred at those localities. The first effort at absolute dating for outcrops for Solimões Formation was provided by Bissaro-Júnior et al. (2019), who argued that Niterói locality (SE) and Talismã (SW) are Tortonian age (Miocene; 10.89 Ma - 8.5 Ma, Bissaro-Júnior et al. 2019), based on dating angular detrital zircons via U-Pb. Similar age (Tortonian age,  $11.42 \pm 0.66$  Ma) was obtained by Kern et al. (2020) for the western Amazonia region. Dozens of localities in Acre State, mainly described by Campos et al. (1976) and Price et al. (1977), continue without a proper dating refinement. However, efforts to revisit previously described localities exist and allow to evaluate interpretations on dating and environment described previously (e.g. Kerber et al. 2016a).

The influence in the time averaging of the reverse faults in Solimões Formation is poorly understood and could result in wrong correlations of facies and ages between the different localities (Bissaro-Júnior et al. 2019). This kind of fault can close distances between older facies and those of the uppermost portion of the Solimões Formation. The time averaging effect of reverse faults could be magnified by erosion of the exposed strata due to rivers dynamics in the region.

Time averaging in outcrops of Solimões Formation is a real problem due to the fluvial origin of its sediments (Hsiou AS, personal communication). As observed by Souza et al. (2016) the time averaging for fluvial environments for Solimões Formation is not an exception compared with other similar outcrops (e.g. Behrensmeyer 1982). Therefore, despite the probably allochthonous origin and reworking

from different depositional events the maximum temporal mix is around some thousand years, which enables a hypothesis of coexistence between several recorded fossil species (Souza et al. 2016). An additional problem, not well-discussed in the literature, is that most of the localities are from river margins, enabling the river to rework fossil materials from one locality and redeposit it in another locality (see Price et al. 1977 and Latrubesse & Rancy 1998 for examples). However, there is no empirical data discussing how this local and temporal mixing acts. Also, the lack of high resolution stratigraphic studies from the recorded localities makes it difficult to assess a more time-refined data. Also, the medley of different facies ages increases the problem.

Only in the NW region are described outcrops dating as Cretaceous, in the Serra do Divisor in the course of the Moá river source west of the Acre State with Peru. The majority of outcrops that have the inferred age Pleistocene and Holocene are known from the SW region. Nevertheless, SW is the region with the highest occurrence of Pleistocene mammals (e.g. *Tapirus*, Proboscidea). These localities are mainly positioned along the course of the Juruá river. The SE region has the majority of the outcrops considered here as Cenozoic in age, in the SE region, the only locality with absolute aging proposed is Niterói (Tortonian) located along the Acre River, also, several localities are considered Miocene in SE region bringing a new view on some pleistocene mammals (e.g. Frailey & Campbell Jr 2012, Prothero et al. 2014), however these interpretations have been revised (e.g. Perini et al. 2016, Parisi-Dutra et al. 2017). The NE region also has the majority of its outcrops considered as Cenozoic in age, but it also has outcrops that are dated as Pleistocene, and the Talismã that is proposed Tortonian in age. Thus, there is not a clear pattern of the geographical distribution of

the outcrops that are consistent with a temporal range except that outcrops dated as Cretaceous which are restricted to the NW region. On the other hand, the most of the outcrops dating as Pleistocene and outcrops with temporally mixed fossils are known from the SW region (Price et al. 1977, Latrubesse & Rancy 1998). Campos et al. (1976) mapped only two outcrops in the state of Rondônia (Abunã river) considered to be of holocene age, probably these outcrops are more related to other geological formations than the Solimões Formation. Finally, the regions NE and SE do not reveal a pattern of age distribution. Although these regions include two localities with more precise dating (Talismã and Niterói), the majority of outcrops has a wide temporal range (Cenozoic) identification, pending studies that focus on mixing temporal age.

Even though some precise dating has already been carried out in some Amazonian locations (e.g. Campbell Jr et al. 2001, Bissaro-Júnior et al. 2019, Kern et al. 2020), along with biochronological studies (e.g. Cozzuol 2006, Latrubesse et al. 2010), we discourage age projections and inferences for fossiliferous locations to be based only by proximity to better-dated outcrops or even regionalisms. Such actions should be avoided until we have more precise and better sampled stratigraphic studies, considering that a wide area lacks this type of study. Furthermore, it is important to keep in mind that both basins (Acre and Solimões basins) have numerous reverse faults (e.g. Campos et al 1976, Caputo 2014) that can raise older lithological layers, thus being able to generate chronological discrepancies even among close outcrops.

### **Paleodiversity**

Generally speaking, some regional patterns of fauna distribution and age can be identified. The NW region has fewer fossils with the

better-sampled reptile specimens identified as Crocodylia and Testudinata, whereas the most common mammal records in the region are Toxodontidae (Notoungulata), nevertheless, some collection bias related to these groups cannot be ruled out (Hsiou AS, personal communication). The Cretaceous localities are restricted to NW region and the only specimens collected from those outcrops are plants.

The NE region, in contrast, is the best sampled from the Amazonian region. There are at least 58 outcrops described, including the higher known paleobiodiversity of Squamata (e.g. Boidae, Alethinophidia, and Teiidae) and the sole anurans recorded until now. Several specimens from the NE region have not been formally described and identifications at higher taxonomic levels – as Craniata indet and Crocodylia indet – are the most common reports in the mapped outcrops. The inferred dating for most of these localities is Cenozoic. Notwithstanding the presented compilation, it is important to take into account aspects of taphonomy to establish a reliable fossil diversity rate, considering that, as demonstrated by Muniz & Hsiou (2018) master thesis, there is a sample bias around groups of large tetrapods.

The SW region is also well sampled, with the most representative taxa being Crocodylia and Testudines. The most diverse taxon from this region is Testudines, with the occurrence of Pleurodira (Podocnemididae and Chelidae), and Cryptodira (Testudinidae). Among mammals, Toxodontidae, Rodentia, and *Notiomastodon platensis* are the most numerous (however there is an intense debate about *Notiomastodon*, see Mothé et al. 2012, Lucas et al. 2013). The most common inferred dating from this region is Pleistocene along the Juruá river. Besides that, the upper part of the Juruá River is the area that has the largest quantity of Pleistocene mammals (Latrubesse & Rancy 1998). It is important to

note that most of the localities identified as Pliocene and Holocene by Price et al. (1977) had records of Toxodontidae.

The SE region is the most paleobiodiverse, with occurrences of turtles, crocodiles and mammals. The Crocodylia taxa include records of Alligatoroidea, Gavialoidea, and Crocodyloidea. Several Mammalia records have not been decently identified, but include representatives of distinct higher taxa: Rodentia, Notoungulata, Primates, and Chiroptera; the last one, to date, restricted to this region. This region also has a considerable number of occurrences of Aves (Anhingidae). The inferred dating widely from this region is Cenozoic, but some sites in it have been considered temporally restricted to Eocene-Pliocene by Souza et al. (2016).

We must be aware that many of the observed paleobiodiversity patterns may suffer from a taphonomic/sample bias (Muniz & Hsiou 2018). Thus, both the biodiversity and the inferences of dating and time of Great American Biotic Interchange (Negri et al. 2010, Bissaro-Júnior et al. 2019) can have implications that are related to taxonomy, taphonomy, and age of some Amazonian specimens (Frailey 1986, Latrubesse & Rancy 1998, Campbell Jr et al. 2001, Cozzuol 2006, Frailey & Campbell Jr 2012, Prothero et al. 2014; Kerber et al. 2016a, Perini et al. 2016, Parisi-Dutra et al. 2017, Muniz & Hsiou 2018, Bissaro-Júnior et al. 2019).

### **Suggestions for future work on amazonian region**

Based on the current compilation of data, we make some suggestions for future work in Solimões and Acre basins, especially in the extent of Solimões Formation. Questions regarding the overall knowledge about paleodiversity, aging, and distribution of fossil taxa in Solimões and Acre basins should address the following problems:

(1) Providing a reliable stratigraphic sequence for Solimões Formation; until that, one should avoid the oversimplification of estimating the age for localities that is not based on clear evidence. Thus, whenever it is impossible to infer supported age for a given locality, the authors should avoid general age identification based on overall similarity of taxa, suggesting instead a less accurate (i.e. conservative) age and being explicit on the inaccuracy of dating information.

(2) The problem of weathering can start to be solved if fossils that are not in their primary sedimentary context, have at least this contextual information with them (e.g. Campos et al. 1976) as well as the stratigraphic control to distinguish original sedimentary rocks from secondary Holocene sedimentary deposition. The appropriate collecting control increases the chance of avoiding temporal and faunal mixing between localities.

(3) The temporal averaging during the original deposition of Solimões Formation rocks is a real problem that must always be addressed before providing age and ecological hypotheses for them. As a solution, a taphonomic study on the collected materials must be conducted to evaluate the depositional influence during the biostratigraphic phase of the studied localities. Also, as an additional line of evidence the execution of a refined stratigraphic study will elucidate in which architectural element the fossils were deposited and if those facies present evidence of reworking from the older facies.

(4) The effect of reverse faults must be considered in stratigraphic and biostratigraphic correlations. The mapping and identification of them are essential for future refined sequence stratigraphy. Thus a stratigraphic chart must be provided for the localities and must indicate where each fossil was collected.

(5) Search for different lines of evidence before proposing an age for the localities. Also, use care in inferring biochronostratigraphic ages from other geological formations and basins. The proposition of biochronostratigraphic levels for Solimões Formation is mandatory and can be made with auxiliary absolute dating methodologies that are available for the studied areas.

(6) As previously proposed (Lacerda et al. 2020), controlled excavations in areas that do not belong to river banks can increase our knowledge regarding Solimões Formation, allowing field works in any season.

## CONCLUSIONS

Our extensive bibliographic survey of the previous works on Solimões and Acre Basins, mainly for Solimões Formation, enabled the recognition of 208 fossiliferous localities in the southwestern region of the Amazon. To help future studies, those localities are identified and the inferred age and their fossils content are summarized. The time averaging is a well-known problem in fluvial depositis, but no generalizations can be made for the entire Solimões Formation, because cautious case-by-case study is necessary comparing geographically close localities.

Regarding estimating the age of the studied localities, the only distributional pattern recognized was the presence of Cretaceous rocks in the NW zone, which can be explained by the orogenesis of the Serra do Divisor that exposed those rocks. It is important to note that the absence of a temporal distributional pattern of the localities could be the result of the reverse faults and/or the limited studies of stratigraphy and data on geochronologic age at

those localities, being in general recognized as Cenozoic.

In general terms, all sectors from the northwestern region of the Brazilian Amazonia preserve fossil mammals, Crocodyliformes, and turtles. Many of the fossil localities, especially those with Crocodyliformes and turtles fossils, are derived from the work of RadamBrasil Project (Campos et al. 1976, Price et al. 1977). The differences in localities' diversity seems to be more related to the degree of prospecting effort than due to preservation bias of a particular taphonomic process. This conclusion is corroborated by the fact that the localities with the higher data acquisition and paleodiversity are those where most of the ancillary supportive studies were carried out (e.g. at Bandeira, Niterói and Talismã). Thus, the knowledge shortfalls are probably due to the difficulty of access to some fossil localities, limitations on field time, funding restrictions, and the possibilities to see, recognize, and measure local strata and regional or formational stratigraphic sections. Therefore, the increase in funding to support long-term controlled excavations in distant or new sites can greatly improve our knowledge on the Solimões Formation paleodiversity.

The identification refinement of some indeterminate materials, including both cranial and postcranial elements, are feasible as shown by Souza et al. (2016), focusing on crocodiles, and Kerber et al. (2016a) focusing on some mammal groups. Such revisions on sampled sites can provide more complete knowledge of the taphocenosis and provide key evidence for better inferences about biocenosis for the Solimões Formation.

This work reinforces the need for more controlled and refined prospecting in the Solimões Formation in order to help answer old questions regarding this geological unit, such as its precise dating and its paleodiversity

and, therefore, increase the knowledge on the evolution of Amazonian ecosystem.

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## SUPPLEMENTARY MATERIAL

**Table S1. Worksheet with age proposed and paleodiversity for mapped outcrops can be accessed via FigShare (DOI: 10.6084/m9.figshare.14046959).**

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