

VERTEBRATE TAPHONOMY OF TWO UPPER MIOCENE BONEBEDS IN WESTERN PROTO-AMAZONIA (SOLIMÕES FORMATION, BRAZIL): INSIGHTS FROM MACROVERTEBRATE AND MICROVERTEBRATE FOSSILS

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ABSTRACT: The Niterói and Talismã sites comprise two of the most important fossiliferous deposits of the Neogene in Brazil. After 30 years of research, these sites have revealed rich assemblages of vertebrates and provided a glimpse of the Amazonian fauna and environment during the Miocene. Despite this, detailed studies that attempt to explain the genesis of these bonebeds are still scarce and hamper more robust paleoenvironmental and paleoecological reconstructions. Here we provide the first in-depth taphonomic analysis for both locations. Sedimentological and taphonomic evidence suggest that the depositional environments of Niterói and Talismã were similarly represented by shallow and calm waters in lacustrine/swampy contexts. We propose that the accumulation of bones and teeth is the result of attritional (day-to-day) mortality of organisms of the local community in a low sedimentation environment. The thanatocoenosis was exposed to biostratinomic processes for longer periods of time, which explains the high disarticulation, disassociation, fragmentation and loss of skeletal elements. The almost absence of weathering indicates that the aquatic environment slowed down the organic degradation of bioclasts, while the rarity of abrasion shows a limited influence of hydraulic flows in transporting and remobilizing bioclasts. Thus, both sites preserve mostly autochthonous to parautochthonous bioclasts, with a moderate level of time-averaging. Our results corroborate the hypothesis that lentic environments can present remarkable preservational conditions for the formation of attritional accumulations of vertebrate remains. Moreover, we show how the different collecting methods affect the description of preservational features and taphonomic interpretations of both fossil assemblages.

INTRODUCTION

Microfossil bonebeds preserve large numbers of mostly small and disarticulated bones and teeth often derived from various micro- and macrovertebrate groups. In addition to their importance for taxonomic studies, they are a valuable source of information for paleoenvironmental and paleoecological inferences in continental contexts (e.g., Brinkman et al. 2004; Baszio 2008; Wilson 2008; Rogers and Brady 2010). Careful sampling of fossils in these localities through surface collection, excavation and screen-washing may lead to the discovery of rare taxa and shed light on many paleontological issues, including trophic relationships and community structure (e.g., Brinkman et al. 2007; Carrano et al. 2016).

Much of our knowledge of western Brazilian Amazonia ecosystems during the upper Miocene comes from the study of vertebrate bonebeds of the Solimões Formation, in the Acre Basin. These deposits are exposed mainly along riverbanks and road cuts, in Acre and Amazonas states (Cozzuol 2006; Latrubesse et al. 2010; Souza-Filho and Guilherme 2015). A diverse vertebrate fauna has been reported and includes all major living clades: cartilaginous and bony fishes, frogs, turtles, birds, crocodylians, lizards, snakes and mammals (e.g., Cozzuol 2006; Lundberg et al. 2010; Riff et al. 2010; Negri et al. 2010; Hsiou 2010). The fauna consisted of an interesting mixture of taxa with old Gondwanan affinities and South American endemics, many of these closely related to the extant lineages that inhabit the South American Neotropical region. Similar Miocene faunas have been found in several other localities in the northern region of

South America, with fossil material known from Colombia, Venezuela, Peru, and Bolivia (e.g., Lundberg et al. 2010; Negri et al. 2010; Riff et al. 2010; Antoine et al. 2016). Although the taxonomic composition of the Solimões Formation has been studied extensively, taphonomical considerations of the vertebrate-bearing assemblages are scarce (Souza et al. 2016; Lacerda et al. 2020) and detailed taphonomic investigations are still lacking (Bissaro-Júnior et al. 2018). In fact, only a few continental vertebrate assemblages from the Miocene of South America have been taphonomically analyzed (Forasiepi et al. 2004; Montalvo et al. 2008; Verzi et al. 2008; Montalvo et al. 2019).

The aim of this study is to describe the taphonomic processes involved in the accumulation and deposition of the vertebrate remains recovered from Niterói and Talismã localities. These two microfossil bonebeds are among the most important fossil deposits in the upper Miocene of the Solimões Formation. Thousands of bones have been excavated from the sites since their discovery in the 1980s (Negri 2004; Latrubesse et al. 2010; Bissaro-Júnior et al. 2018). In addition to the unusually high concentration of bones, the sites have yielded diverse vertebrate assemblages that include not only rare taxa (e.g., lizards, snakes, anurans, primates, litopterns), but also type specimens of species of fishes, mammals and crocodylians (e.g., Bergqvist et al. 1998; Alvarenga and Guilherme 2003; Gayet et al. 2003; Hsiou et al. 2009; Kerber et al. 2017; Souza-Filho et al. 2020). This work will contribute to the understanding of preservational patterns in the

Solimões Formation and likely serve as a useful reference for further comparisons with other localities that have similar fossiliferous deposits.

GEOLOGICAL CONTEXT

The Acre Basin is in the southwestern region of the Brazilian Amazonia and encompasses part of the Acre and Amazonas states (Latrubesse et al. 2010). The basin was strongly influenced by pre-Andean and Andean tectonic events that occurred along the west margin of South America and the basin fill includes rocks ranging in age from the Paleozoic (Permian) to the Neogene (Pliocene) (Cunha 2007; Wanderley et al. 2010).

The Solimões Formation records the Cenozoic geological history of the basin and is composed by mudstones, siltstones, muddy sandstones, fine to medium sandstones, with gypsum veins (probably of diagenetic origin as stated by Latrubesse et al. 2010), lignite and calcareous concretions (RadamBrasil 1976; Maia et al. 1977; Hoorn 1993; Eiras et al. 1994). The sediments were deposited mainly under fluvio-lacustrine conditions and can be divided into a floodplain-lacustrine facies and a channel facies (Latrubesse et al. 1997, 2010). The high-energy facies represent channel deposits and include reddish-brown to brown, cross-bedded sandstones, siltstones, muddy sandstones, and intraformational conglomerates composed of small pebbles. The low energy facies consist of green, grayish-green and red mudstones and siltstones that are massive or laminated, and are interpreted as floodplain, lacustrine or swampy deposits.

The specimens studied in this work come from two of the most prolific fossiliferous bonebeds of the Solimões Formation, the Niterói and Talismã sites (Fig. 1, Table 1). The Niterói site (19L 629983E/8879539S, datum WGS84) is on the right bank of the Acre River, near Senador Guiomard municipality, in southeastern Acre State (Negri 2004). Many vertebrate fossils have been discovered, including freshwater rays, lungfishes (*Lepidosiren*), characiform and siluriform fishes, crocodylians (e.g., *Purussaurus*, *Mourasuchus*, *Acreosuchus*, *Gryposuchus*), turtles (*Chelus*) and birds (*Macranhinga*). The mammal record is represented by tardigrade xenarthrans (e.g., *Urumacotherium*) and rodents (e.g., *Neopiblema*, *Phoberomys*) (see Online Supplemental File Table S1 for complete references).

Latrubesse (1992) described an 11-meter thick section for Niterói consisting of green to grayish-green massive mudstones and containing two fossiliferous levels. During fieldwork in 2015, only two layers of the outcrop were exposed while dense vegetation covered the remaining area (Fig. 2). One of these layers was 1 m above low-water level and consists of a 40 cm thick grayish-green mudstone, with mudballs, gypsum crystals and carbonaceous plant remains. One bivalve mold was found, along with coprolites and a high abundance of isolated vertebrate remains. This layer corresponds to the inferior fossiliferous level described by Latrubesse (1992) and Latrubesse et al. (2007) and represents the typical floodplain-lacustrine facies.

The Talismã site (19L 510475E/90297415S, datum WGS84) is on the right bank of the upper Purus River, in the south of Amazonas State, near the limit with Acre State (Negri 2004). A rich vertebrate fauna has been recovered including lungfishes (*Lepidosiren*), characiform (*Colossoma*) and siluriform fishes, crocodylians (e.g., *Purussaurus*, *Caiman*, *Acreosuchus*), turtles (*Chelus*), lizards (*Paradracena*) and snakes (e.g., *Eunectes*, *Colombophis*). Remains of mammals were also discovered and revealed tardigrade and cingulate xenarthrans, rodents (*Neopiblema*, *Potamarchus*), litopterns and primates (Table 1).

A stratigraphic profile of the locality was described by Cozzuol (2006) and comprises an 8-meter thick sequence, dominated by grayish-green to red massive mudstones and siltstones, with occasional gypsum crystals and calcite veins. These beds represent a succession of poorly and well-drained floodplain deposits with weak pedogenetic overprinting. During fieldwork in 2015 and 2016, three fossiliferous levels were identified (Fig. 2). The collecting efforts focused on the level corresponding to the upper level

described by Cozzuol (2006) which is the richest source of fossils from the locality. This layer comprises a 20-cm thick grayish-green massive mudstone with gypsum crystals and carbonate concretions, representing a swampy/lacustrine deposit. Carbonaceous plant remains, coprolites, crustacean claws and vertebrate fossils are common in the deposit.

The outcropping strata of the Solimões Formation are dated as upper Miocene (Huayquerian–Mesopotamian; SALMA, 9–6.5 My) based on palynology and mammal faunas (Cozzuol 2006; Latrubesse et al. 2007). This age is consistent with the recent U–Pb dating of detrital zircons from the fossiliferous beds of Niterói and Talismã (Bissaro-Júnior et al. 2019). The analyses suggest a maximum depositional age of 8.5 ± 0.5 Ma for Niterói and 10.89 ± 0.13 Ma for Talismã, both within the Tortonian (Bissaro-Júnior et al. 2019). Based on the different maximum depositional ages and some differences in the composition of the rodent fauna, Bissaro-Júnior et al. (2019) suggest that Talismã might be ~1.5–2 million years older than Niterói.

MATERIAL AND METHODS

The examined fossil remains were collected in Niterói (Acre River, Acre State) and Talismã (Purus River, Amazonas State) during fieldwork in 2015 and 2015–2016, respectively. All fossils were obtained through excavation (Bissaro-Júnior et al. 2018) or screen-washing, regardless of size, degree of preservation and taxonomic identification. At the laboratory, approximately 15 kg of sediment from Niterói and 18 kg from Talismã were dried and then soaked in 10% hydrogen peroxide solution for a few minutes. The resulting disaggregated sediment was screen-washed in water through sieves of 1 mm and 0.5 mm.

Taphonomic assessments were based on standard methods (e.g., Behrensmeyer 1991; Lyman 1994; Eberth et al. 2007a). The following taphonomic features were documented for each sample: (1) taxonomic group; (2) disarticulation; (3) degree (absent/present) of fragmentation; (4) bone representation; (5) shape; (6) weathering; (7) abrasion; (8) size; (9) corrosion; (10) bioerosion; and (11) tooth marks. The hydraulic equivalence of the specimens and their host matrix was assessed using the equivalency graph of Behrensmeyer (1975, p. 496). The presence or absence of parallel striations, often interpreted as evidence for trampling, were also noted.

The relative abundance of taxa was estimated from counts of the number of identifiable specimens (NISP) (Badgley 1986; Lyman 1994). Fish scales were removed from the abundance estimates due to their fragility and proneness to breaking during screen-washing. The relative abundance data were compared to the relative taxonomic abundances determined from previously collected specimens, housed in the paleontology collection of the Federal University of Acre.

The minimum number of individuals (MNI) was used to estimate the survival rate of crocodylian bones. This index (MNI) was calculated for crocodylians by counting the most abundant skeletal element in the assemblage (Blob and Badgley 2007). Crocodylians are represented by only a few specimens in Niterói, and the MNI was 1. In Talismã, the MNI was 3 based on the number of femora.

The long axis of specimens was measured using digital calipers. The size distribution of specimens collected by excavation was determined by measuring all specimens that did not undergo fragmentation after collection (101 specimens, Niterói; 741 specimens, Talismã). The size distributions of specimens obtained by screen-washing were produced by measuring all specimens from Niterói (3,672 specimens), whereas in Talismã, it was estimated from a subsample of 15,792 measured specimens. The shape of specimens was classified according to the four categories of Blob and Fiorillo (1996): tabular, elongate, equidimensional and conical. Degree of abrasion was measured on a 0–3 scale (Fiorillo 1988; Wilson 2008) in which 0 represents unabraded bones and 3 represents extremely rounded bones (Fig. 3). Weathering of bones was

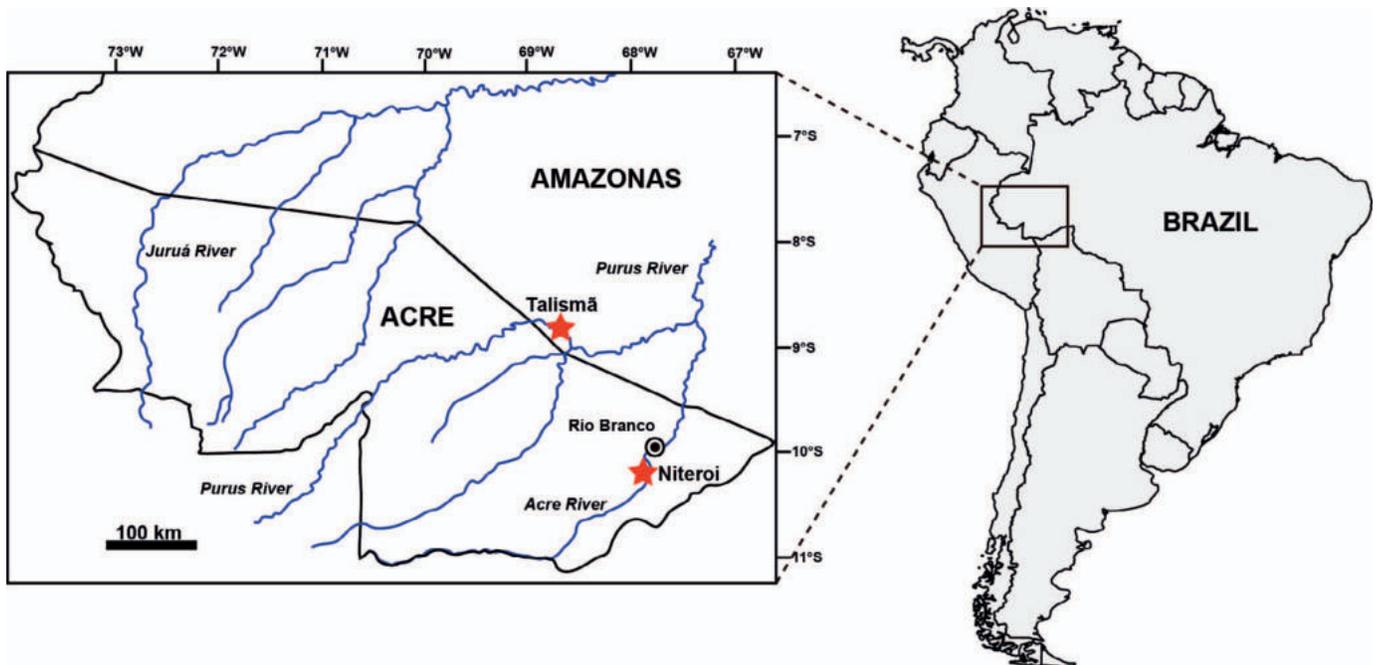


Fig. 1.—Location of Talismã (Amazonas State) and Niterói (Acre State) sites.

measured using a 0–3 scale based on Behrensmeier's weathering stages (1978) as modified by Fiorillo (1988) with 0 indicating no alteration, 1 showing surface cracking, 2 flaking and more profound cracking and 3 deep cracking and flaking resulting in loss of exterior bone (Fig. 3).

Crocodylian bones were classified according to the Voorhies groups to investigate the potential of dispersal under the influence of hydraulic transport (Voorhies 1969). The Voorhies classification is assumed to be applicable exclusively to crocodylians in the present study because they are the only vertebrate group in which the recovered skeletal elements are both abundant and comparable in size to that of the medium to large mammals studied by Voorhies (1969). Because the Group III of Voorhies was originally based on the fused skulls of mammals, it was not considered applicable to the disarticulated skulls and mandibles studied here. Therefore, these elements were attributed to Group II, following Gates (2005), Lauters et al. (2008) and Ullman et al. (2017). Osteoderms were included in Group I based on the experiments of Behrensmeier (1975). As it is not possible to attribute crocodylian teeth confidently to any of Voorhies Groups, they were not classified in this analysis. The vertical distribution of excavated specimens was assessed based on the record of their precise three-dimensional location by the Total Station (TST, model Topcon GTS 236W; details in Bissaro-Júnior et al. 2018). The Chi-square tests were used to determine if the taphonomic signatures (shape, abrasion, weathering) between the two locations differed significantly. Adjusted residuals were calculated to identify which individual cells in the chi-square tests are statistically overrepresented or underrepresented. Values greater than ± 1.96 are significant at a 0.05 confidence level.

The Niterói and Talismã assemblages were compared with other vertebrate assemblages that were formed under similar conditions and for which there is taphonomic data available. Comparative data were compiled from published records from the Permian of USA and Miocene of Pakistan (Behrensmeier 1988), the Cretaceous of USA (Rogers and Brady 2010), the Cretaceous of Spain (Buscalioni et al. 2008), the Cretaceous of Hungary (Botfalvai et al. 2015), the Eocene of Spain (Badiola et al. 2009), and the Miocene (Montalvo et al. 2019) and Quaternary (Méndez et al. 2017) of Argentina. The taphonomic features of these assemblages are summarized in the Online Supplemental File (Table S2).

RESULTS

General Aspects

A total of 907 vertebrate fossil specimens were collected by excavation, in which 113 specimens came from Niterói and 794 from Talismã. Screen-washing of the sediments produced 52,785 vertebrate microfossil specimens, 3,676 from Niterói and 49,109 from Talismã (Table 2). The percentage of excavated specimens that could be attributed to a taxonomic group was 49.5% in Niterói and 62.5% in Talismã. Sieved specimens were less identifiable in Niterói (28.3%), but more identifiable in Talismã (65.85%).

Taxonomic Representation

The specimens found in this study add four new taxa to the known diversity of vertebrates from both sites, increasing from 38 to 42 taxa (Online Supplemental File Table S1). The new findings include anurans, octodontoid rodents, a dasypodid armadillo, and a characid fish, all representing small-sized animals. For the first time, a boid snake and the rodent *Potamarchus* are recorded in Niterói. Excavation and sieving efforts in both sites during the 2015–2016 field seasons resulted in the identification of 18 taxa, including aquatic, semi-aquatic and terrestrial forms (Online Supplemental File Table S1).

Considering the total number of identifiable specimens (NISP) collected by screen-washing and excavation in the present study, fishes are the most abundant vertebrates in both localities (89.8% in Niterói, 67.6% in Talismã) (Fig. 4A). The second most abundant group in both localities are crocodylians (8.8% in Niterói, 22.1% in Talismã). In Niterói, turtles (1.6%) and mammals (0.2%) are also encountered, while the assemblage of Talismã is more diverse and includes turtles (8.0%), mammals (1.3%), frogs (0.7%), snakes (0.3%), and a bird (0.1%).

The taxonomic composition changes remarkably when collecting methods are considered separately (Fig. 4, Online Supplemental File Table S3). Based on the previously collected specimens, cataloged and housed in the paleontology collection of the Federal University of Acre (Rio Branco, Acre State), crocodylians are the most abundant group

TABLE 1.—Vertebrate fossil fauna from Niterói and Talismã sites (references are listed in Online Supplemental File Table S1). The “+” denotes the presence and the “-” the absence of the taxon.

Taxa	Niterói	Talismã
CHONDRICHTHYES		
Potamotrygonidae indet.	+	-
OSTEICHTHYES		
<i>Lepidosiren megalos</i>	+	-
<i>Lepidosiren</i> sp.	-	+
Characidae indet.	-	+
Serrasalminae indet.	-	+
<i>Colossoma</i> sp.	-	+
<i>Paleohoplias assisbrasilensis</i>	+	-
Siluriformes indet.	+	+
<i>Phractocephalus acreornatus</i>	+	-
ANURA		
Pipidae indet.	-	+
Bufonidae indet.	-	+
CROCODYLIA		
Alligatoroidea indet.	+	+
<i>Purussaurus brasiliensis</i>	+	+
<i>Purussaurus</i> sp.	+	+
<i>Caiman breviostris</i>	-	+
“ <i>Caiman pachytemporalis</i> ”	+	-
<i>Mourasuchus nativus</i>	+	-
<i>Acrasuchus pachytemporalis</i>	-	+
<i>Melanosuchus latrubessei</i>	-	+
<i>Charactosuchus fieldsi</i>	+	+
<i>Charactosuchus mendensi</i>	+	+
Gavialoidea indet.	+	+
<i>Gryposuchus jessei</i>	+	-
TESTUDINES		
<i>Chelus lewisi</i>	+	-
<i>Chelus</i> sp.	+	+
? <i>Chelonoidis</i> sp.	-	+
SQUAMATA		
Boidae indet.	+	+
<i>Eumectes</i> sp.	-	+
aff. <i>Epicrates</i>	-	+
“Colubridae” indet.	-	+
<i>Colombophis portai</i>	-	+
<i>Colombophis spinosus</i>	-	+
cf. <i>Paradracaena</i>	-	+
AVES		
Aves indet.	-	+
<i>Macranhinga ranzii</i>	+	-
MAMMALIA		
<i>Pseudopreotherium venezuelanum</i>	+	-
<i>Urumacotherium</i> “ <i>campbelli</i> ”	+	-
<i>Urumacotherium</i> sp.	+	-
Mylodontidae indet.	-	+
Megalonychidae indet.	-	+
cf. <i>Hapalops</i>	-	+
Nothrotheriinae indet.	-	+
cf. <i>Planops</i>	-	+
<i>Octodontobradys</i> sp.	-	+
<i>Octodontobradys puruensis</i>	-	+
Pampatheriidae indet.	-	+
Dasyopodidae indet.	-	+
<i>Phoberomys bordasi</i>	+	-
<i>Phoberomys burmeisteri</i>	+	-
<i>Neopiblema ambrosettianus</i>	+	-
<i>Neopiblema horridula</i>	-	+
<i>Potamarchus</i> cf. <i>murinus</i>	+	-
<i>Potamarchus</i> sp.	-	+
<i>Drytomomys</i> sp.	-	+

TABLE 1.—Continued.

Taxa	Niterói	Talismã
<i>Ferigolomys pacarana</i>	+	-
Octodontoidea indet.	-	+
Agoutidae (Cuniculidae?) indet.	-	+
Protheroheriidae indet.	-	+
Atelidae indet.	-	+

(74.8% in Niterói; 42.9% in Talismã), whereas fishes appear to be rare (0.3% in Niterói; 6.1% in Talismã; Fig. 4B). Most of these specimens were recovered by surface collecting and quarrying. When only the specimens that were excavated in the present study are considered, fishes are also underrepresented (10.9% in Niterói; 15.3% in Talismã), while crocodylians are still the dominant group in both sites (70.9% in Niterói; 44.7% in Talismã; Fig. 4C). However, sieved collections from both sites show significantly higher fish abundances (97.8% in Talismã; 84.5% in Niterói), and a decrease in abundance of all other vertebrate groups (Fig. 4D).

Vertical Distribution of Specimens

Fossils are continuously distributed throughout the vertical sections in both localities, without considerable gaps, but with distinct denser intervals. In Niterói (Fig. 5A) and Talismã (Fig. 5B), fossils are more concentrated towards the middle of the deposit. However, at a different square in Talismã (Fig. 5C), specimens are more abundant near the base of the bed. There is no clear evidence for a relationship between the size of the specimens and their vertical distribution, i.e., that specimens are vertically graded. All these features are in agreement with the gradual accumulation of skeletal elements over a long-time span.

Articulation, Fragmentation, and Skeletal Element Abundances

All fossils from Niterói and Talismã sites are disarticulated and dissociated. Most specimens have some degree of fragmentation, and only 3.4% of them are complete in Niterói and 2.2% in Talismã (Table 2). However, the number of fragmented specimens may be inflated by recent breakage caused during excavation and screen-washing. The lower proportion of complete specimens in the sieved samples (2.7%, Niterói; 1.9%, Talismã) in comparison to excavated samples (27.5% Niterói; 9.6% Talismã) might reflect the greater breakage of fossil elements during screen-washing. Smooth transverse fractures are observed on some fragmented bones, suggesting post-fossilization damage. The most complete elements are small and physically resistant, such as fish spines, dermal plates and teeth found in Niterói, and osteoderms, vertebrae, phalanges, fish spines and teeth found in Talismã.

Fish skeletal remains are by far more abundant than the remains of any other vertebrate group in both fossil assemblages (Fig. 6A, Online Supplemental File Table S3). The scales are the most common elements recovered in Niterói and Talismã, but the abundance of other fish elements vary in the two localities. Crocodylians are represented mainly by teeth and osteoderms, but other cranial and postcranial isolated elements were also found in both sites. The mammal remains include isolated teeth in the two localities, although osteoderms and vertebrae were also collected in Talismã. Snakes are represented by isolated vertebrae in the two localities. Turtle fossils consist entirely of isolated shells found in both sites, except for a humerus collected in Talismã. A tarsometatarsus of a bird and postcranial remains of frogs were recovered from Talismã.

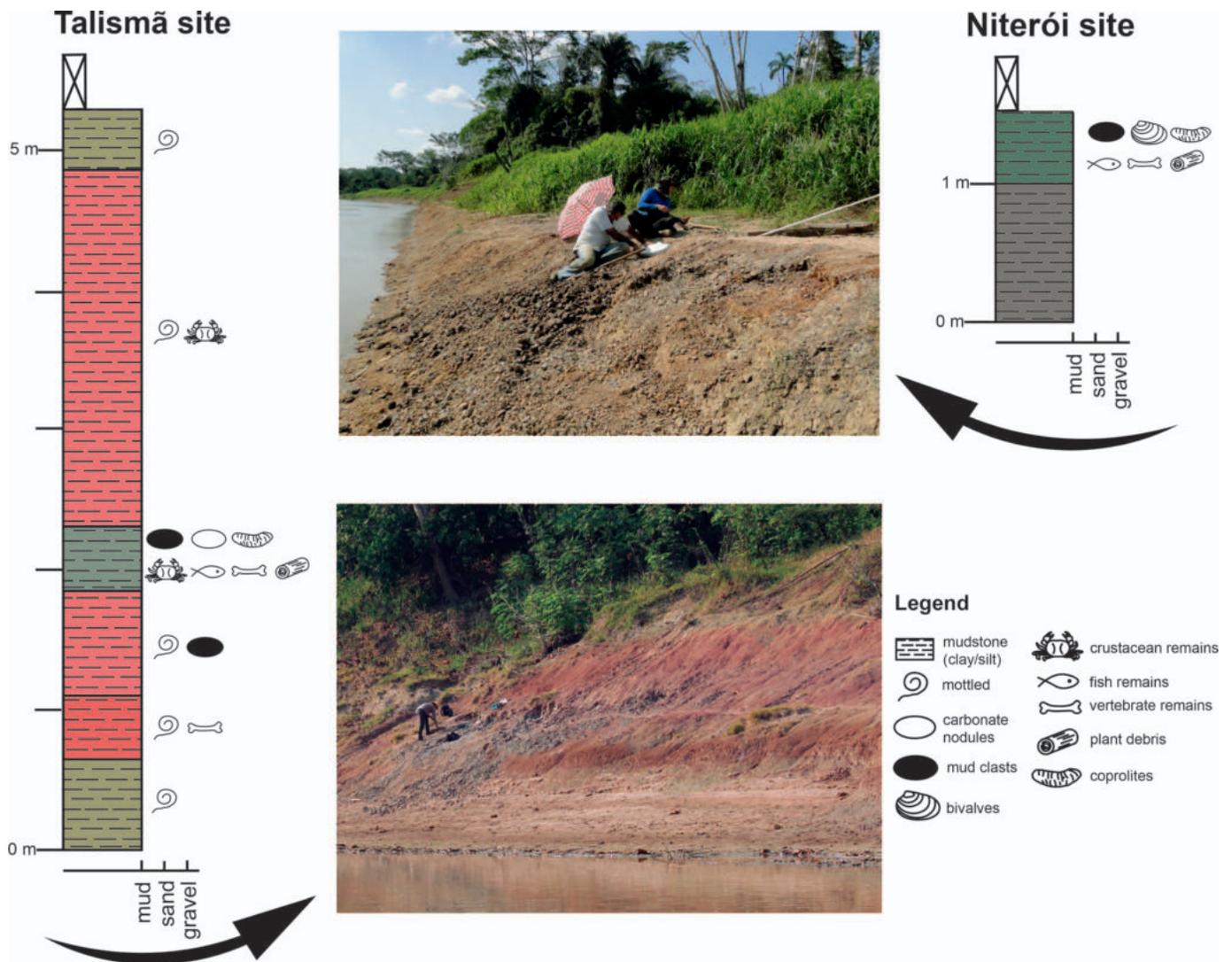


FIG. 2.—Stratigraphic sections and field photos of Niterói and Talismã sites (modified from Bissaro-Júnior et al. 2018).

Size

The mean long axis of excavated specimens is 49.4 mm in Niterói and 40.0 mm in Talismã. The size distribution pattern of Niterói specimens is less clear than that of Talismã because of the fewer number of specimens recovered, therefore it is likely that the mean length would considerably shift with the inclusion of new specimens (Fig. 7). The mode of the size distribution of sieved fossils is 1–2 mm in both localities, but the frequency is higher in Talismã. While sieved bioclasts are commonly in the 1–2 mm size range, the smaller interval (0–1 mm) is underrepresented. The same pattern is observed in size distributions of other bonebeds (e.g., Brinkman et al. 2004; Cullen et al. 2016; Rogers et al. 2017). Rogers et al. (2017) speculated that the abrupt decrease of specimens recovered in the smallest size interval was related to their higher susceptibility to chemical dissolution in the depositional environmental or a structural limitation to preservation imposed by their small size. Other factors that could also account for this pattern are (1) the traditional use of sieves with openings not smaller than 0.5 mm, limiting the recovery of fossils in the 0–1 mm size interval; (2) the increased difficulty of identifying and collecting tiny specimens under stereomicroscope; (3) fragmentation and removal of

bioclasts caused by screen-washing; and (4) natural minimal size limitations of skeletal elements.

The vast majority of skeletal remains are less than 5 cm in maximum length, representing 97.7% of Niterói specimens and 93.2% of Talismã specimens. Following the bonebed criteria outlined by Eberth et al. (2007a), both localities can be considered microfossil bonebeds because over 75% of specimens are ≤ 5 cm in maximum length. The higher representativeness of small specimens results mainly from the numerous fish elements in the assemblages.

Shape

Considering the total samples, the tabular specimens are the most abundant in both assemblages (71.0%, Niterói; 91.1%, Talismã), followed by elongate, compact and conical specimens (Fig. 6B, Table 2), although the shape proportions are statistically different (Online Supplemental File Table S4). Adjusted residuals indicate that Talismã collections are significantly overrepresented by tabular specimens and underrepresented by elongate, compact and conical specimens, while the opposite pattern occurs in Niterói (Online Supplemental File Table S4).

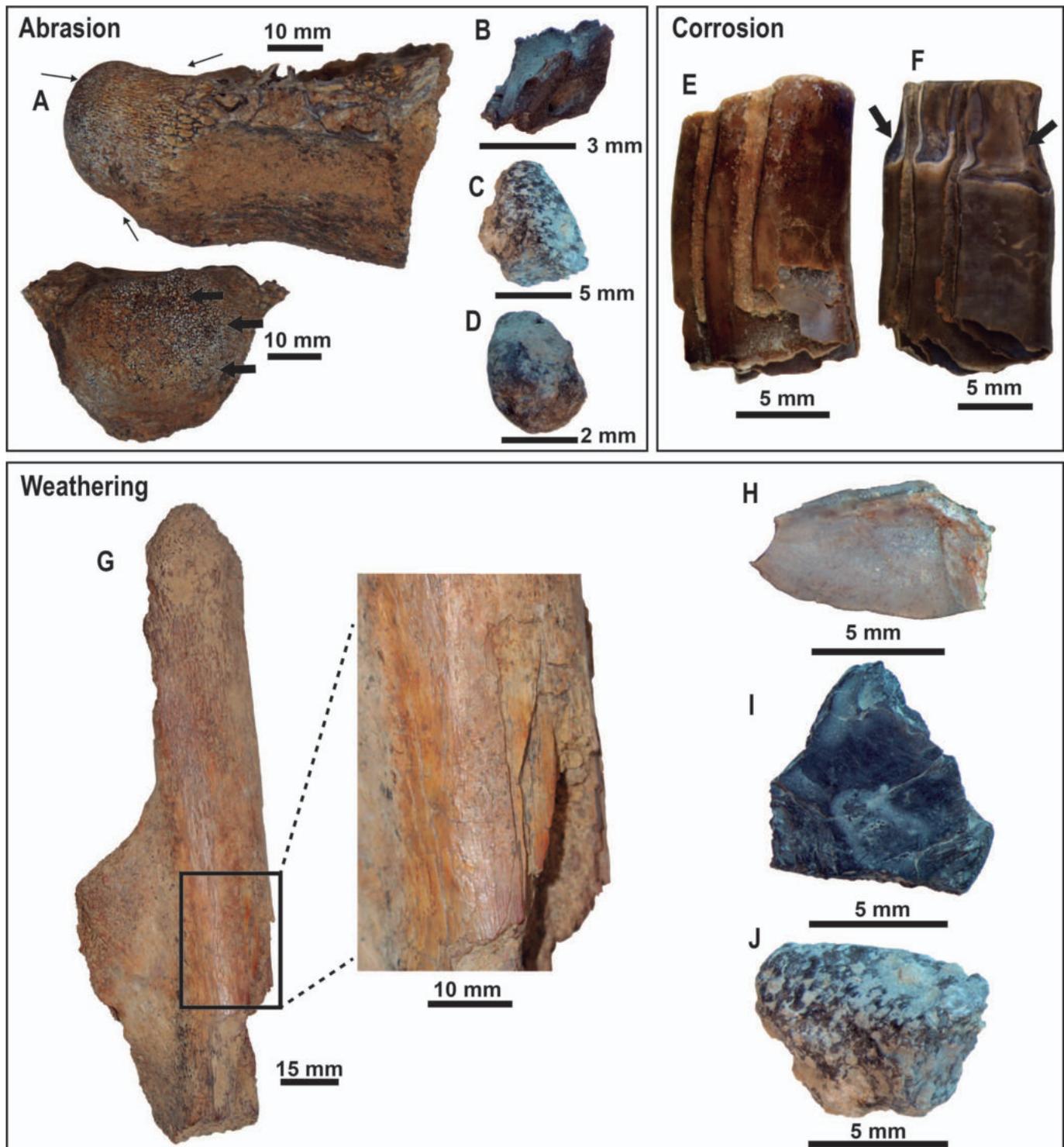


FIG. 3.—Examples of taphonomic modifications on vertebrate specimens recovered from Niterói and Talismã localities. **A)** Arrows indicate rounding and exposure of spongy bone in a crocodylian vertebra. **B)** Small vertebrate fragment showing absence of abrasion. **C)** Medium stage of abrasion. **D)** High stage of abrasion. **E)** Rodent tooth showing the absence of corrosion. **F)** Rodent tooth showing the presence of corrosion, as indicated by arrows. **G)** Bone exhibiting desiccation cracks. **H)** Small vertebrate fragment showing the absence of weathering. **I)** Low stage of weathering. **J)** High stage of weathering.

TABLE 2.—Taphonomic characteristics of vertebrate fossils from Niterói and Talismã sites. Abbreviations: NISP = number of identifiable specimens, SW = screen-washing.

Site	Niterói			Talismã		
	SW	Excavation	Total	SW	Excavation	Total
Number of specimens (N)	3,676	113	3,789	49,109	794	49,903
Number of identifiable specimens (NISP)	1,039	56	1,095	32,335	486	32,821
% identifiable specimens	28.3%	49.5%	28.9%	65.8%	61.2%	65.8%
Density N/kg (SW)		245.1 specimens/kg			2728.3 specimens/kg	
Density NISP/kg (SW)		69.3 NISP/kg			1796.4 NISP/kg	
Bone articulation and association	100% disarticulated and disassociated			100% disarticulated and disassociated		
Mean long axis (excavation)		49.4 mm			40.0 mm	
% Total Fragmentation (complete)	2.7%	27.5%	3.4%	1.9%	9.6%	2.2%
Abrasion						
Stage 0	90.1%	87.0%	90.0%	93.5%	96.0%	93.7%
Stage 1	6.4%	13.0%	6.6%	5.6%	3.9%	5.5%
Stage 2	2.5%	0%	2.4%	0.8%	0.1%	0.7%
Stage 3	1.0%	0%	1.0%	0.1%	0%	0.1%
Weathering						
Stage 0	91.8%	94.3%	91.9%	98.2%	99.5%	98.3%
Stage 1	5.4%	5.7%	5.4%	1.3%	0.3%	1.2%
Stage 2	1.5%	0%	1.5%	0.2%	0.1%	0.2%
Stage 3	1.3%	0%	1.2%	0.3%	0%	0.3%
Shape						
Tabular	71.8%	35.9%	71.0%	91.7%	53.2%	91.1%
Elongate	16.0%	27.0%	16.2%	6.1%	32.7%	6.5%
Equidimensional	9.2%	9.0%	9.2%	1.2%	7.2%	1.3%
Conical	3.0%	28.1%	3.6%	1.0%	6.8%	1.1%

The samples collected through screen-washing are mostly tabular (71.8% in Niterói; 91.7% in Talismã) in both sites (Table 2). However, the distributions are more distinct considering the quarried samples, in which the tabular elements are still the most abundant, but less predominant (35.9% in Niterói; 53.2% in Talismã).

There is no consensus on how to interpret the predominance of tabular specimens in the assemblage. Some studies suggest that they can indicate lower energy conditions in the depositional environments because they are presumably more susceptible to transportation (e.g., Wilson 2008; Calede 2016 [but see Boaz and Behrensmeyer 1976]; Dominguez-Rodrigo et al. 2018). Alternatively, smaller tabular elements, as those recovered preferentially by screen-washing, could be overrepresented because they are more quickly buried, increasing their chances of preservation (Moore and Norman 2009).

Hydraulic Equivalency

Most specimens recovered from Niterói (89.8%) and Talismã (96.6%) are 1–5mm long. The specimens collected via excavation are larger and reach a maximum length of 153 mm in Niterói and 254 mm in Talismã. Based on the equivalency analysis of Behrensmeyer (1975, p. 496), the diameters of specimens collected in both sites are hydraulic equivalent to quartz grains larger than 0.3 mm in diameter, and in minor proportions, to granules and pebble sized grains. This contrasts with the size of the matrix grains of both deposits which are mud dominated. This disparity between the hydraulic equivalency of specimens and the rock matrix suggests that the bioclasts and sediments were not transported together in the same system for long distances. The skeletal remains from both fossil accumulations were most likely not transported far from the site of death and were deposited in a low energy environment. Therefore, both localities are classified as autochthonous to parautochthonous fossil assemblages.

Voorhies Groups

Both groups with the least (VG II) and most transportable (VG I) elements of crocodylians are represented in the fossil assemblages of Niterói and Talismã. The intermediate group (VGI/II) elements were identified only in Talismã (Table 3). Although the most transportable skeletal elements (VG I) are dominant in both assemblages, the survival of specific bones in the VG II is higher, as predicted from the MNI of 1 individual in Niterói and 3 individuals in Talismã. Ribs, vertebrae, and osteoderms, which are part of the VG I, have low survival percentages in Talismã (16.6%, 20.6% and 18.6%, respectively) and the last two also have low survival percentages in Niterói (11.1% and 0.5%, respectively). The highest survival rates for skeletal remains are found for bones in the VG II, for example, femurs (83.3%), jaws (66.6%) and tibiae (50%) in Talismã, and calcaneum (50%) and jaw bones (33.3%) in Niterói.

Weathering

Most specimens (91.9%, Niterói; 98.3%, Talismã) do not exhibit weathering marks (Stage 0; Table 2, Figs. 3H, 6C). Only 5.4% of specimens in Niterói and 1.2% in Talismã display superficial cracking indicative of the earliest stage of weathering (Stage 1; Fig. 3G, 3I). Deeper fracturing and loss of bone surface, which characterize moderate (Stage 2) and higher (Stage 3) weathering, were recognized in 2.8% of specimens in Niterói and 0.4% specimens in Talismã (Fig. 3J). Only a small proportion of the specimens exhibited weathering marks that could suggest that they suffered subaerial exposure before the burial. However, because the skeletal elements were buried in aquatic settings, it is difficult to completely rule out the possibility that at least part of these weathering marks were produced under subaqueous conditions (Eberth et al. 2007b).

The weathering profiles show that most skeletal elements were not exposed subaerially for a long period in both localities, although the weathering stage distributions are statistically different (Online Supple-

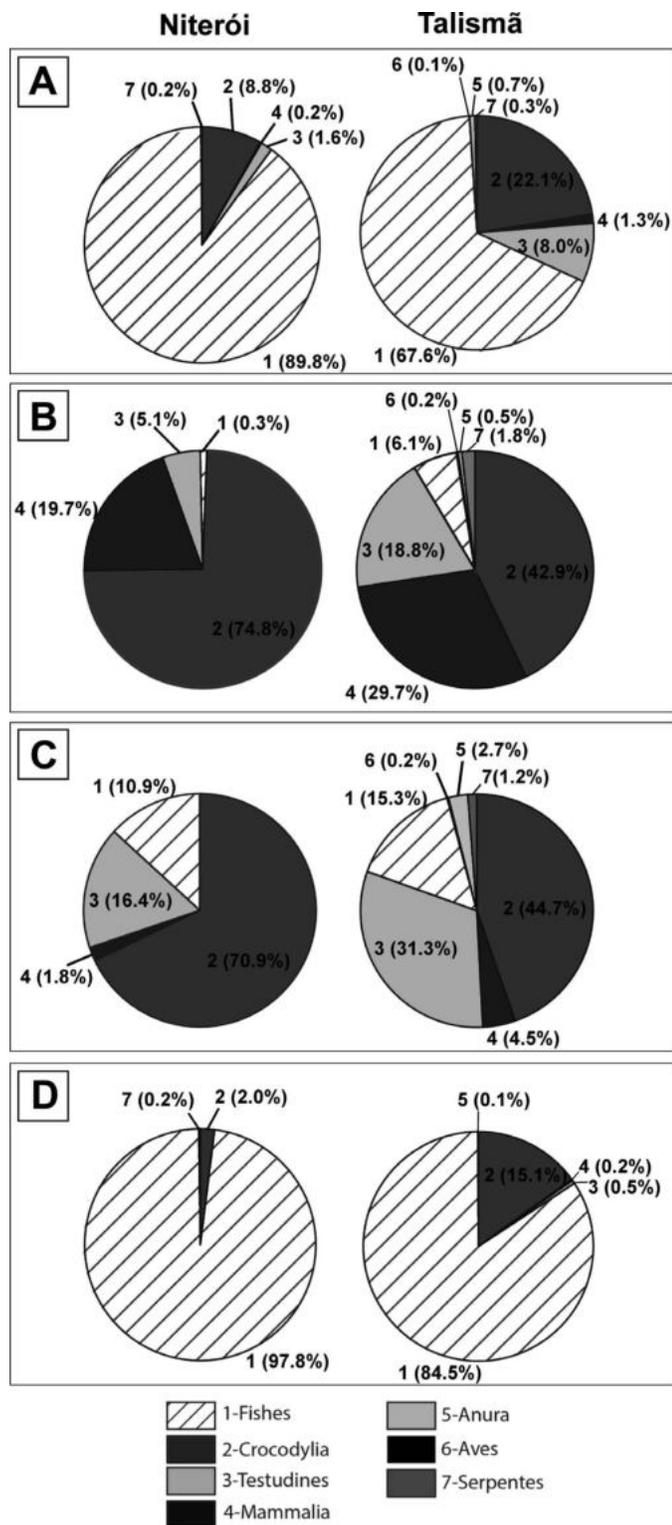


FIG. 4.—Relative abundances of Niterói and Talismã vertebrates. The percentages of identified specimens for each major vertebrate group are shown for different samples. **A)** Excavated and sieved specimens collected in the 2015–2016 field season. **B)** Previously collected specimens housed in the paleontology collection of the Federal University of Acre. **C)** Specimens collected in the 2015–2016 field season only by excavation. **D)** Specimens collected in the 2015–2016 field season only by screen-washing.

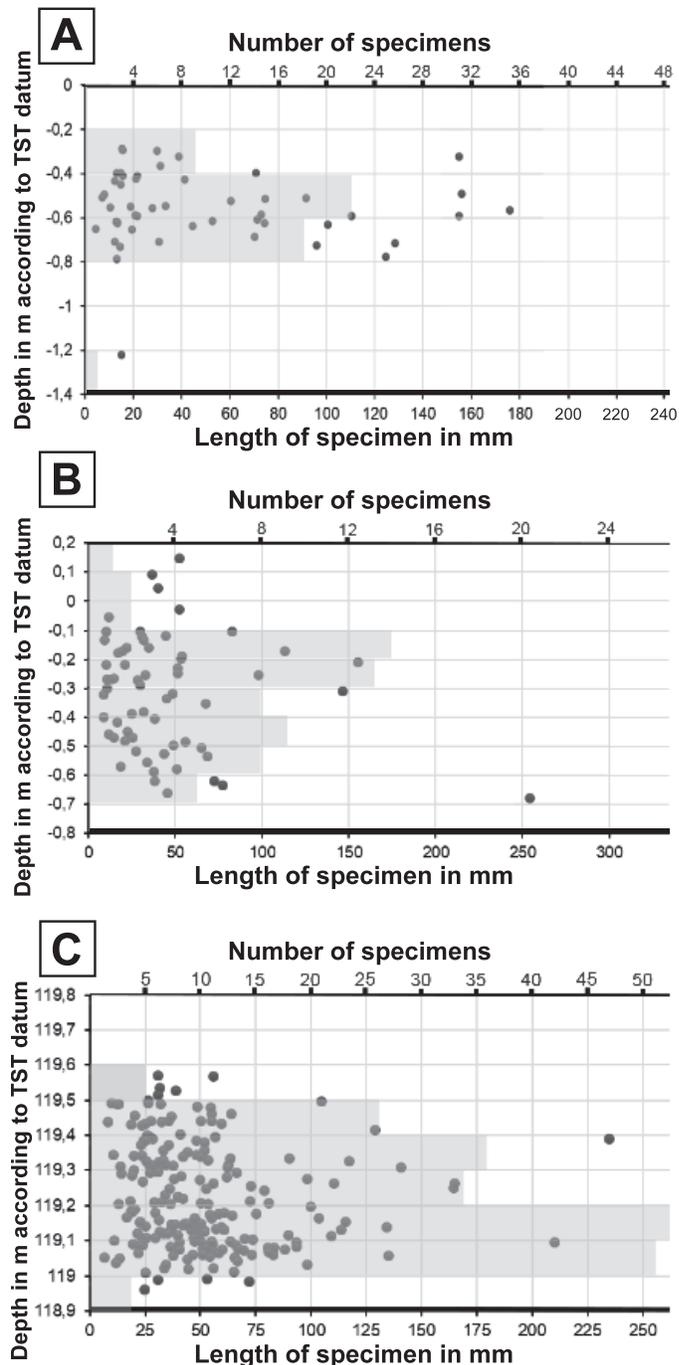


FIG. 5.—Vertical distribution of specimens versus specimen size. **A)** Niterói site. **B, C)** Two different quarry squares at Talismã. The shaded squares correspond to the number of specimens, while the dots correspond to the length of specimens.

mental File Table S4). The adjusted residuals show that the numbers of specimens modified by weathering are significantly overrepresented at Niterói (Online Supplemental File Table S4).

Weathering stage distributions are very similar when excavated and sieved collections are compared with unweathered elements dominating in both sites (Table 2). However, while the moderate and high levels of weathering are absent in the excavated samples, except for the moderate level in Talismã (0.1% of the specimens), they are represented in the sieved samples from Niterói and Talismã. The complications in recognizing

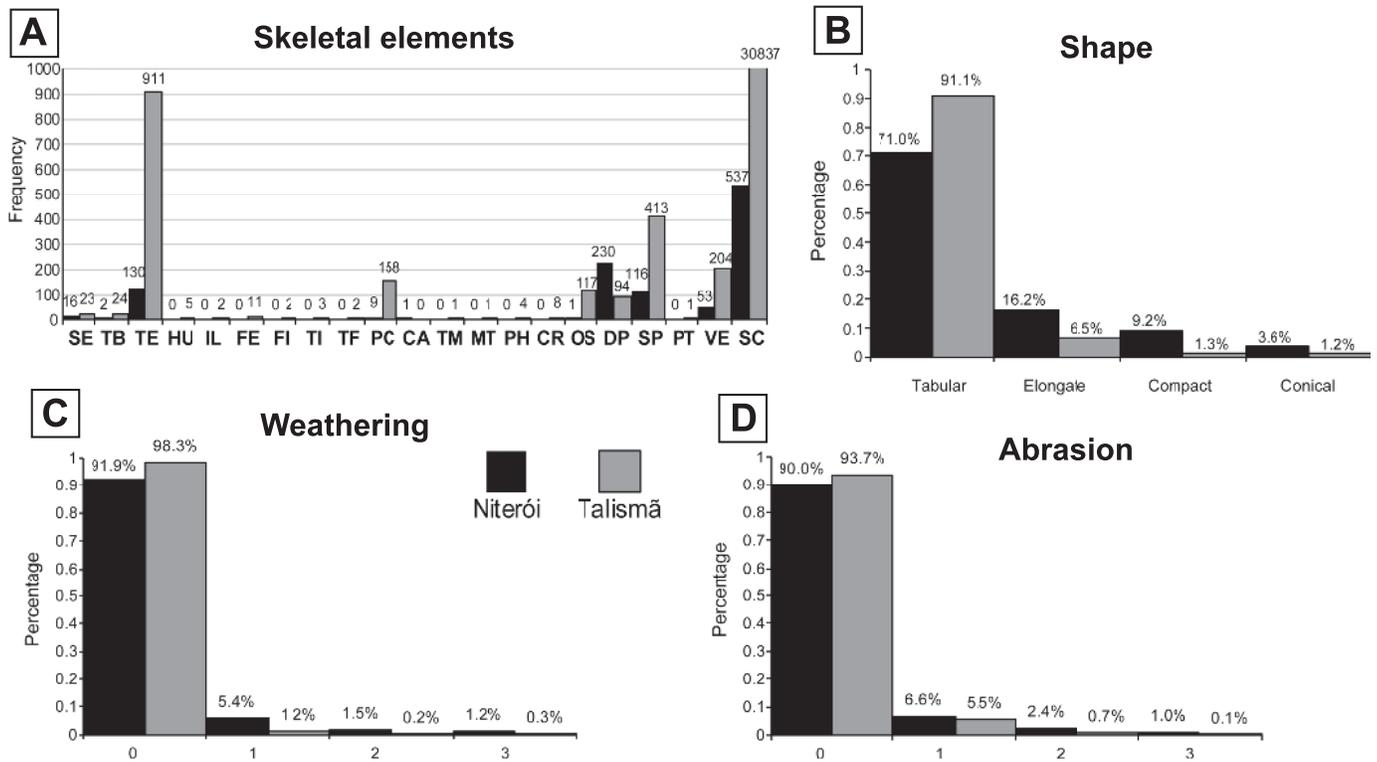


FIG. 6.—Taphonomic signatures of Niterói and Talismã assemblages based on specimens recovered by excavation and screen-washing. **A**) Abundance of skeletal elements. Abbreviations: SE = skull elements; TB = tooth-bearing elements; TE = teeth; HU = humeri; IL = ilia; FE = femora; FI = fibulae; TI = tibiae; TF = tibiofibula; PC = plastron/carapace fragments; CA = calcanei; TM = tarsometatarsi; MT = metatarsi; PH = phalanges; CR = cervical ribs; OS = osteoderms; DP = dermal plates; SP = spines; PT = pterygiophores; VE = vertebrae; SC = scales. **B**) Elements representativeness according to the four shape classes. **C**) Frequency of specimens in the four stages of weathering. **D**) Frequency of specimens in the four stages of abrasion.

weathering stages in small bioclasts could partially explain the presence of higher levels of weathering in these specimens. Small bioclasts have severely reduced surface areas which makes the distinction between weathering marks and marks produced by other taphonomic processes more difficult.

Abrasion

Most fossils recovered from the two localities exhibited no evidence of abrasion (90.0%, Niterói; 93.7%, Talismã; Table 2, Figs. 3B, 6D). Low (Stage 1), moderate (Stage 2), and high (Stage 3) abrasion comprise respectively, 6.6%, 2.4%, and 1.0%, of specimens from Niterói, with values relatively lower in Talismã, where they correspond to 5.5%, 0.7%, and 0.1% of specimens (Fig. 3A, 3C, 3D). Although graphically similar, the distribution of abrasion profiles in the two sites are significantly different (Online Supplemental File Table S4). The adjusted residuals indicate that the proportions of specimens affected by abrasion are overrepresented at Niterói and underrepresented in the Talismã material (Online Supplemental File Table S4).

The high number of unabraded specimens at both sites suggest that most skeletal elements were minimally or not transported, but the relation between the distance of transport and rounding is not so straightforward. For instance, skeletal elements can be transported long distances showing no signs of abrasion (Argast et al. 1987; Aslan and Behrensmeyer 1996; Van Orden and Behrensmeyer 2010).

Variations in the levels of abrasion according to the collecting methods occur in both assemblages but are relatively low. Most bioclasts are not abraded and indicate the same taphonomic history of minimal or absent transportation. However, the moderate and high levels of abrasion are

usually represented by the smaller bioclasts recovered by screen-washing (Table 2). The frequent association of smaller weathered elements with abrasion marks suggest that elements exposed to subaerial conditions in other regions could have been introduced to the fossiliferous deposits through transportation facilitated by their smaller size (e.g., Dodson 1973; Korth 1979) indicating a minor allochthonous contribution to the deposits.

Other Taphonomic Characteristics

Only very few specimens show signs of corrosion in the two localities. Three fish teeth from Niterói and four mammal teeth from Talismã display loss of dental tissue, the latter with both enamel and dentine affected (Fig. 3). Potential tooth marks or bioerosion traces have not been identified. Trample marks, recognized as sets of parallel striations on bone surfaces, were not observed in any specimen.

DISCUSSION

Depositional Environment

The sedimentological context of Niterói and Talismã indicate the same depositional environment of shallow and quiet waters. The fossiliferous massive mudstones of both localities, which are green-grayish, suggest deposition under low energy and reducing conditions, in a lacustrine/swampy environment (Maia et al. 1977; Behrensmeyer and Hook 1992; Latruesse et al. 2007). The abundant carbonaceous debris is another piece of evidence of the reducing conditions (Behrensmeyer and Hook 1992). At Niterói, the presence of palynomorphs produced by plants associated with aquatic habitats (e.g., the fern spore *Azolla* and the angiosperm pollen

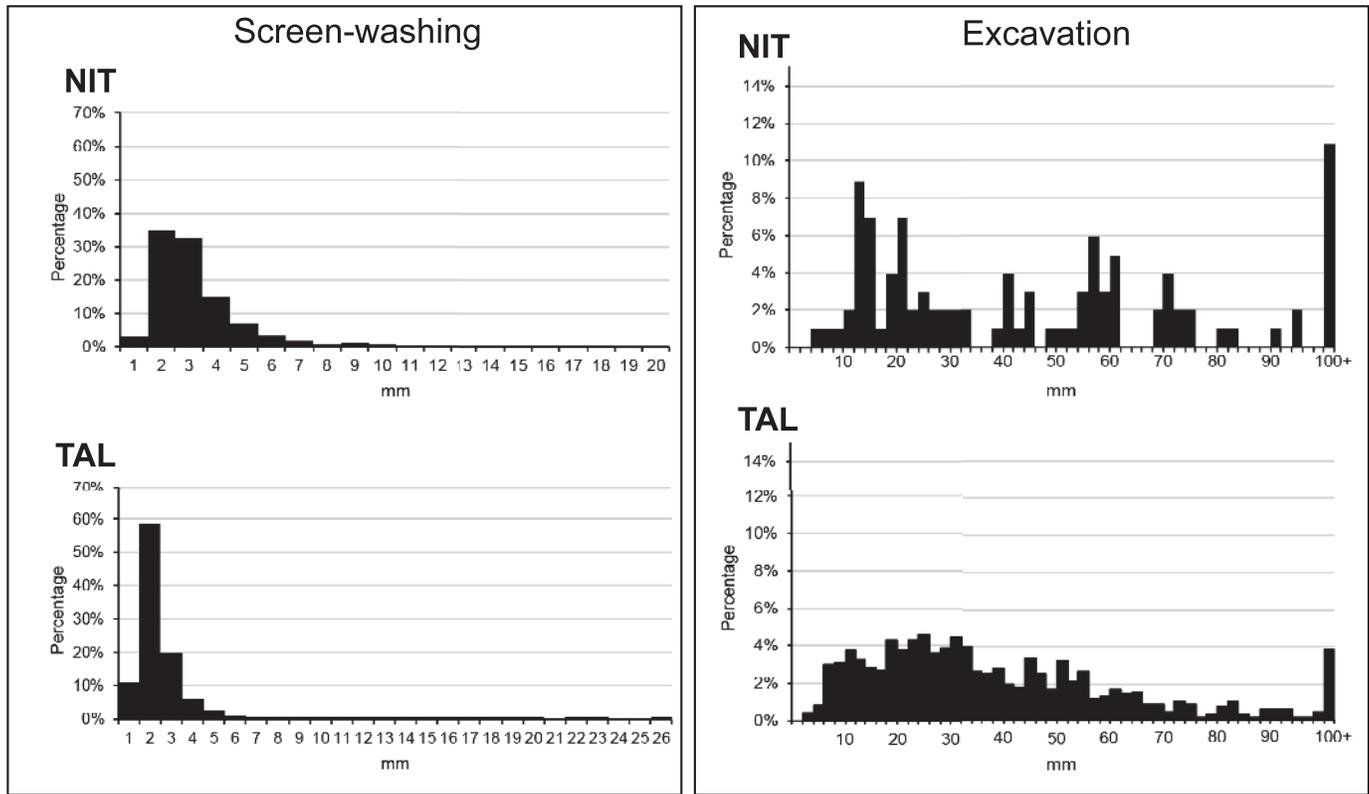


FIG. 7.—Size distributions of bioclasts recovered by screen-washing and excavation in Niterói (NIT) and Talismã (TAL).

TABLE 3.—Survival of skeletal elements of an average crocodylian skeleton predicted from MNI versus actual frequency at Niterói and Talismã.

Elements	Expected in one individual	Niterói (MNI = 1)			Talismã (MNI = 3)		
		Number found	Predicted number	Recovered	Number found	Predicted number	Recovered
Group I							
Ribs (cervical)	16	0	16	0%	8	48	16.6%
Vertebrae ¹	~63	7	~63	11.1%	39	~189	20.6%
Osteoderms ²	~206	1	~206	0.5%	115	~618	18.6%
Group I and II							
Phalanges	58	0	58	0%	4	174	2.3%
Ulnae	2	0	2	0%	0	6	0%
Scapulae	2	0	2	0%	0	6	0%
Group II							
Femurs	2	0	2	0%	5	6	83.3%
Tibiae	2	0	2	0%	3	6	50%
Fibulae	2	0	2	0%	2	6	33.3%
Humeri	2	0	2	0%	1	6	16.60%
Metapodia	20	0	20	0%	1	60	1.60%
Calcanea	2	1	2	50%	0	6	0%
Jaws	6	2	6	33.3%	12	18	66.60%
Skull bones ³	33	3	33	9%	2	99	2%

¹ Number of vertebrae for *Melanosuchus* (Vieira et al. 2016), but this number can vary between 56 and 66 in Crocodylia.

² Number of osteoderms for “Jacare” (*Caiman* or *Melanosuchus*; Huxley 1859). Note that the number of osteoderms in extant crocodylian species is highly variable, because of the different number of rows and scutes per row in the body (English 2018); and also, some species have osteoderms in the ventral and appendicular regions (Seidel 1979; Hill 2010), that potentially increases the number of osteoderms.

³ Number of cranial elements excluding premaxillae and maxillae elements.

Corsinipollenites oculusnoctis) also supports deposition in an aquatic environment, where lacustrine and swampy settings prevailed (Latrubesse et al. 2007).

The more specific depositional environment is harder to determine. The absence of channel sandstones underlying the fossil deposits makes the hypothesis of deposition in abandoned channels very unlikely. Additionally, the lack of mudcracks and syndepositional evaporites, besides the common presence of plant debris, argue against deposition in ephemeral lakes (Behrensmeier and Hook 1992). The absence of root casts could favor the attribution of lacustrine instead of swampy conditions to both bonebeds (e.g., Ullman et al. 2017), however, it is difficult to exclude the possibility that the casts were not preserved because of bioturbation or hydraulic disturbance of the sediments.

The vertebrate fauna recovered in both assemblages can occur in a variety of habitats. The aquatic fauna composed of potamotrigonids, characids, serrasalmids, and siluriforms fishes currently inhabit many fluvio-lacustrine environments, such as rivers, lakes and floodplains. The semi-aquatic fauna, which includes turtles, *Eunectes* snakes, and frogs, can also be found in all these kinds of environments (e.g., Strimple 1993; Souza 2009). Perhaps the most interesting fossil is the lungfish *Lepidosiren*, which can be found today living in a wide array of freshwater environments, but prefers the stagnant waters of lakes and swamps, often under low oxygen and seasonal drying conditions (Lundberg et al. 2010; Almeida-Val et al. 2010).

Taphonomic Interpretation

The fossiliferous horizons of Niterói and Talismã do not show evidence that the bones and teeth were primarily accumulated by biogenic agents. Such assemblages typically present a limited number of taxa with similar body sizes that result from the selective feeding behavior of the predators (Pratt 1989; Khajuria and Prasad 1998). This contrasts with the high taxonomic diversity and different sizes and habits of the vertebrates found in both sites. Moreover, skeletal remains exhibit rare indications of digestion by predators. Only a few teeth display loss of dental material that could be attributed to gastric corrosion, whereas no teeth marks were found in any of the bones from both localities. Even so, the skeletal evidence and the presence of coprolites indicate a small biogenic contribution to the assemblages.

It is also very unlikely that the bioclasts accumulated predominantly by fluvial/hydraulic events. The fine-grained sediments in combination with the low degrees of abrasion, the great disparity between the hydraulic equivalences of most bioclasts, and the dominance of Voorhies Group I elements (most transportable) indicate low energy conditions during deposition and limited transportation of bioclasts before burial. Furthermore, from a theoretical standpoint, it is hard to explain the origin of local concentrations of thousands of specimens only due to the hydraulic action. Elements of different sizes and taxonomic groups introduced to the hydraulic flow from distinct areas and times would tend to disperse over time and not concentrate (Rogers and Kidwell 2007; Rogers and Brady 2010).

Taphonomic and sedimentological data from Niterói and Talismã suggest that the concentration of bioclasts were predominantly attritional in aquatic environments, i.e., were formed by the accumulation of skeletal remains derived from the local community over long periods of time, under low sedimentation and weak hydraulic energy. Therefore, the thanatocoenoses of both deposits are inferred to be autochthonous to parautochthonous because they consist of the remains of organisms that lived in the environment recorded by the sedimentary layer (Behrensmeier and Hook 1992). The attraction of terrestrial animals to the aquatic environments for water consumption and feeding can explain their occurrences in Niterói and Talismã. As the terrestrial, semi-aquatic and aquatic animals perished because of predation, diseases, senescence, and

other natural causes, they gradually contributed to the thanatocoenosis with their skeletal remains (Rogers and Kidwell 2007; Rogers and Brady 2010). A portion of these deaths could have been the result of environmental stresses caused by the climate seasonality and variations in the water levels (Latrubesse et al. 2007, 2010). However, features of Niterói and Talismã assemblages are not congruent with this scenario, especially because of the absence of both sedimentological (mud cracks, caliche, and evaporites) and taphonomic (mono/paucispecific assemblage, vertical grading of specimens in some contexts) characteristics related to drought in the fossiliferous beds (e.g., Shipman 1975).

Low sedimentation rates promoted the attritional accumulation of bioclasts, which in turn probably exposed the skeletal remains to biostratinomical processes for long periods of time. This is consistent with the high degrees of disarticulation, dissociation and skeletal fragmentation observed in both localities (Table 2). Moreover, most specimens comprise elements that are both resistant to destructive agents and abundant in the skeleton, such as scales, dermal plates, teeth, vertebrae, and osteoderms (Fig. 6A). Disarticulation, dissociation and skeletal fragmentation could be enhanced by the occurrence of bioturbation (Behrensmeier 1991), but direct evidence of this process was not found in the studied deposits. The presence of coprolites and skeletal corrosion in some elements suggest at least a minimal influence of predators and/or scavengers disturbing the carcasses in the aquatic environment. The absence of weathering marks in most fossils in the two localities indicate a limited or no subaerial exposition of the skeletal remains (Fig. 6C), which is consistent with the inferred aquatic depositional conditions. The aquatic environment probably prevented drastic temperature and humidity variations, delaying the organic degradation of bones and teeth associated with the appearance of weathering cracks (Behrensmeier 1978).

The autochthony of both assemblages is suggested by the combination of the following features: (1) the fine-grained sediments; (2) low levels of abrasion; (3) lack of hydraulic equivalence between skeletal remains and the host matrix; (4) abundance of VG I bones; (5) presence of the least and most transportable elements (VG I and VG II); (6) size and shape heterogeneity; (7) absence of vertical grading; and (8) high concentration of fossils. The few elements showing signs of abrasion and weathering may have been introduced to the deposits by low energy currents and are considered a small allochthonous addition to the assemblages. These low energy currents could have locally reworked and disturbed the skeletal remains, contributing to their disarticulation, dissociation, and fragmentation. This is also suggested by the higher survival of the least transportable elements (VG II), even though VG I elements are more abundant. While water flows might have played a role in the size sorting of bioclasts (Fig. 7), the higher abundance of small specimens is likely better explained by intensive fragmentation caused by biostratinomical and post-depositional processes (e.g., sieving), but also a higher abundance of small vertebrates in the local community.

Because attritional accumulations result from the gradual buildup of skeletal remains derived from non-contemporaneous generations of organisms, they exhibit a certain degree of time-averaging (Rogers and Kidwell 2007). For instance, the temporal resolution of fossiliferous accumulations deposited in lacustrine attritional conditions is estimated to vary between 10^0 to 10^3 years (Behrensmeier and Hook 1992; Rogers 1993).

Taphonomic Comparisons

The Niterói and Talismã bonebeds represent two of a limited number of attritional accumulations in lentic environments that have been taphonomically analyzed. Although the high variability of the taphonomic features within assemblages was considered a signature of this type of bone concentration (e.g., channel-fill mode) (Behrensmeier 1988), many of the studied deposits are relatively uniform regarding their taphonomic

characterization (Online Supplemental File Table S2). Skeletal elements are usually isolated and incomplete, whereas most bone surfaces are unabraded and unweathered (Online Supplemental File Table S2). Variations in the preservation of the attritional assemblages are not surprising considering how the taphonomic histories can be affected by different sedimentation rates, hydraulic influence, local diversity, and diagenetic conditions (e.g., Behrensmeyer 1988; Rogers and Kidwell 2007). For instance, in both bonebeds documented in this study and in others from the Early Cretaceous of Spain (Buscalioni et al. 2008) and the Late Cretaceous of USA (Rogers and Brady 2010), the degree of disarticulation and fragmentation is relatively higher, probably related to lower sedimentation rates and consequent prolonged exposure. In contrast, other assemblages were more rapidly buried and less affected by biostratigraphic processes, such as those from the Quaternary (Méndez et al. 2017) and early Miocene of Argentina (Montalvo et al. 2019). The wide spectrum of preservational patterns within and across attritional assemblages highlights the importance of detailed taphonomic investigations in each assemblage to assess particular taphonomic biases that might affect paleoenvironmental and paleoecological inferences.

The vertebrate fossils of Niterói and Talismã were preserved under similar sedimentological and taphonomic conditions. In both sites, the bone representation comprises elements that are numerous in the vertebrate skeleton and resistant to the destructive agents. Moreover, there is a predominance of unabraded and unweathered elements, and size and shape distributions (at least in relation to the screen-washing samples) are graphically similar. But, the distributions of shape, abrasion, and weathering when compared statistically are significantly different, indicating “strict” non-isotaphonomic conditions (Online Supplemental File Table S4). The presence of mudclasts and slightly higher levels of abrasion and weathering in Niterói, for instance, could be associated to a greater influence of hydraulic flows during the genesis of the assemblage in relation to Talismã (Potter et al. 2005; Latrubesse et al. 2010; Li et al. 2017).

The evaluation of isotaphonomy and application of the concept to paleoecological and paleoenvironmental reconstructions is still lacking for most vertebrate deposits, although some progress has been made (Brinkman et al. 2004; Rogers and Brady 2010; Peterson et al. 2011, 2017; Cullen and Evans 2016; Cullen et al. 2016; Rogers et al. 2017). Likewise, further taphonomic studies of other vertebrate localities from the Acre Basin (e.g., Cozzuol 2006) and also localities with likely similar preservational histories from Peru (e.g., Antoine et al. 2016), Colombia (e.g., Czaplewski 2003) and Venezuela (e.g. Sánchez-Villagra and Aguilera 2006) will contribute to a larger understanding of the continental taphonomic modes and the comparability of faunas from the Proto-Amazonia during the Miocene.

CONCLUSIONS

The analysis of quarried and screen-washed specimens from Niterói and Talismã sites revealed a relatively diverse vertebrate fauna, including the presence of some new taxa. Aquatic forms (Osteichthyes) are the most abundant in both sites, followed by semi-aquatic (e.g., Crocodylia) and terrestrial (large rodents, xenarthrans) forms, in line with what would be expected for thanatocoenosis produced in lacustrine-swampy environments such as those inferred for Niterói and Talismã.

Sedimentological and taphonomic evidence suggests that the deposition of the studied beds of Niterói and Talismã occurred under similar conditions in shallow and quiet waters of lacustrine/swampy environments. Skeletal remains accumulated primarily by attritional mortality of the local community in a low sedimentation environment. Thus, the fossil assemblages are predominantly autochthonous to parautochthonous. The low sedimentation rates exposed the thanatocoenosis to biostratigraphic processes for a longer time, which can explain the high levels of

disarticulation, disassociation, fragmentation, and differential removal of skeletal elements. At the same time, the aquatic conditions delayed the organic degradation of bones and teeth, resulting in the low degrees of weathering. Attritional accumulations present some degree of time-averaging, which in attritional aquatic conditions is estimated in tens to thousands of years. This imposes some restrictions on paleoecological inferences for short temporal scales, but on the other hand, increases the chances of abundant and rare taxa of the biocenosis being captured by the fossil record (Martin 1999; Rogers and Brady 2010).

The results show that the collecting methods must be taken into account in the assessment of the taphonomic signatures. This was especially true when considering the variation in size, shape, and taxonomic composition of specimens recovered by quarrying and screen-washing. A combination of different collecting methods potentially prevents the introduction of significant bias in the taphonomic interpretation of the fossil assemblages and allows more robust inferences.

This study is the first detailed taphonomic analysis of vertebrate assemblages from the Solimões Formation. The findings indicate that the lacustrine/swampy environments in the western Brazilian Amazonia during the upper Miocene played an important role in supporting diverse and abundant communities of vertebrates, while providing preservational conditions conducive to the formation of vertebrate bonebeds, such as those in Niterói and Talismã. Comparisons of the studied sites with other published attritional accumulations in lentic environments show that bonebeds with remarkable variability in taphonomic features can be formed even under similar conditions. Besides presenting new information on a particular mode of preservation, the collected data can be used as a reference point to taphonomic investigations of other comparable assemblages, especially from the Miocene of South America.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: <https://www.sepm.org/supplemental-materials>.

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