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Taphonomy and paleoecology of mammals preserved in swampy deposits (Formosa Province, Argentina): new light on a key environmental context for the evolution of Quaternary vertebrates in Southern South America

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ABSTRACT

Quaternary continental deposits of South America are characterized by the abundance and diversity of vertebrate remains preserved in different environmental contexts. However, the studies focused on interpreting the origin of the assemblages are scarce. The taphonomic features of the mammal specimens from the Río Bermejo Formation, Formosa Province (Argentina), are analyzed. The bearing levels belong to the Upper Pleistocene-lower Holocene, and were interpreted as swampy deposits that filled channels of the ancient Bermejo River, an environmental context little evaluated from the taphonomic point of view. The assemblage includes Xenarthra, Notoungulata, Carnivora, Artiodactyla and Proboscidea. The evidence suggests that the assemblage is composed by specimens preserved in the place of death or close to it, with short time of subaerial exposure and little or no transport. After burial, the specimens were also affected by diverse processes directly related to the swamp deposits where they were buried. In this case, the taphonomic evidence, along with the sedimentary characteristics of the bearing levels allowed the recognition of the channel-fill mode for this assemblage. Also, this study provides new information for an area that was very important in the evolution of vertebrates in Northeastern Argentina since the Late Pleistocene.

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Introduction

Studies of Quaternary vertebrates from the Northwest, Chaco and Mesopotamian regions of Argentina have increased largely in the last 15 years, although their knowledge is far from that of other areas, e.g. Pampean region (Carlini et al. 2008; Zurita et al. 2009). Even though the fossils recorded in different environmental contexts of these regions, and others of South America, are very diverse and abundant, taphonomic studies allowing the interpretation of the origin of the assemblages, as well as the mode in which the remains were modified, are still scarce (e.g. Pomi 2009; Tomassini et al. 2010; Araújo-Junior et al. 2012, 2013; Fariña et al. 2013; Araújo-Júnior 2015; Méndez et al. 2016; Tomassini et al. 2015; Montalvo et al. 2017; Tomassini et al. 2017).

Isolated mammal remains have been reported from several localities of the Chaco region (Tonni and Scillato-Yané 1997; Alcaraz and Zurita 2004). However, most of them come from deposits of the Río Bermejo Formation exposed at the margins of the Bermejo River, particularly in the localities of Villa Escolar, Lucio V. Mansilla and El Colorado, Formosa Province (Figure 1; see Prevosti et al. 2005; Zurita et al. 2009; Bogan et al. 2012; Zurita et al. 2014). The fossiliferous levels of this unit have been assigned to the Upper Pleistocene-lower Holocene and

interpreted as swampy deposits that filled channels of the ancient Bermejo River (Iriondo 2010).

In this paper, the number of mammal taxa known for the Río Bermejo Formation (see Zurita et al. 2014) is increased, adding as well, a few remains of Osteichthyes (Bogan et al. 2012). The abundance of specimens and the taxonomic diversity, always with precise geographic and stratigraphic data, allowed a preliminary taphonomic study of the assemblage. All the studied specimens were recovered from the same stratigraphic levels, cropping out at different localities along 100 km of the left margin of the Bermejo River (Figure 1(B) and (C)).

These mammal specimens are here described and their taphonomic features are analyzed. The processes that affected the specimens before and after burial, as well as their possible taphonomic histories are interpreted on the basis of the obtained data. The taphonomic features, along with the sedimentological characteristics of the bearing levels suggested the assignment of the assemblage to a particular taphonomic mode. This study provides new information about the preservation of bones in swampy deposits, an environmental context little studied from a taphonomic point of view; which, in turn, was very important for the evolution of the vertebrates from Northeastern Argentina since the Late Pleistocene.

Geographic and geologic background

The Chaco plain comprises 840,000 km², including Paraguay, Bolivia, and part of Northern Argentina. From an environmental viewpoint, this plain is characterized by tropical semiarid to tropical humid climate with the development of woods, savannahs and large swamps (Iriondo 2010). It is composed of three systems: Western Chaco, Eastern Chaco (the study area of this contribution), and the Paraná-Paraguay belt. The Eastern Chaco of Argentina (East of the Chaco and Formosa provinces, Northwest of the Corrientes Province, and North of the Santa Fe Province; Figure 1(A)) includes the distal sectors of the megafans of large rivers (e.g. Bermejo, Pilcomayo, Salado), in which permanent and temporary swamps are crossed by ancient fluvial channels (Iriondo 1984, 2010; Orfeo and Iriondo 2012). These environments encompass an approximate area of 125,000 km². The largest swamps are 100–200 km long, and 3–10 km wide, generally less than 1 m deep (Iriondo 2010).

The megafan of the Bermejo River is located in distal sites of the Chaco foreland basin. The back-bulge of this basin is characterized by numerous small and shallow paleo-channels, which are filled with very fine grained sandy or silty muds that represent

swampy deposits accumulated during the Quaternary (Mc Glue et al. 2016). The relief in the area is smooth, with very low slopes and development of surface runoff (Iriondo 2010). This context is ecologically very significant due to the high diversity of birds, mammals, amphibians and reptiles, which is in turn characterized by the seasonal variability of biodiversity (Benzaquén et al. 2013).

Iriondo (2010) defined the Río Bermejo Formation 25 km south of the locality Las Lomitas (Figure 1(B)), where the outcrops reach near 2 m thick and can be divided into four levels (Figure 2(A) and (B)). The Level 1, at the lower portion, includes a yellowish loam, formed by 41% silt, 35% clay/colloids and 23% very fine sand, with root traces. The Level 2 is composed of dark-gray clayey silts with very fine sand as accessory fraction, with numerous vertical root traces 2–3 mm in cross section and molds of leaves. The Level 3 is formed by dark-gray clayey sands and clayey silts with very fine sand as accessory fraction, and abundant organic matter. The Level 4 is represented by grayish green and reddish silty clays with manganese nodules and molds of leaves. Iriondo (2010) stated that all these levels represent swampy deposits that filled paleo-channels of the ancient Bermejo River.

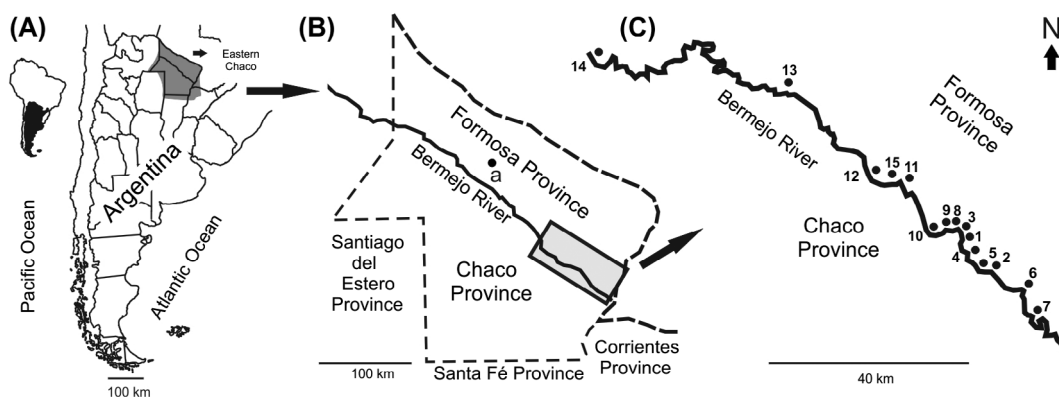


Figure 1. Map of the fossiliferous localities included in this study. (A) Area covered by the Eastern Chaco in Argentina. (B) Location of the prospected area on the Bermejo River, Formosa Province; (a) Las Lomitas locality (type locality of the Río Bermejo Formation). (C) Distribution of the sites: (1) Villa Escolar; (2) Lucio V. Mansilla; (3) Galo Cué; (4) Marca Luna; (5) Desaguadero de Ayala; (6) El Bananal; (7) Estancia 'Sol de Mayo' ('Hertelendi'); (8) Estancia 'El Bermejito'; (9) Estancia 'Tres de Mayo'; (10) Estancia 'El Progreso'; (11) Estancia 'Don Felipe'; (12) Estancia 'Don Pérez'; (13) Estancia 'La Josefina'; (14) El Colorado; (15) km 100 Navegación del Río Bermejo (N.R.B.).



Figure 2. Deposits of the Río Bermejo Formation. (A) View of the left bank of the Bermejo River, showing outcrops of this unit; (B) Detail of the Río Bermejo Formation deposits cropping out at Villa Escolar (locality 1, Figure 1(C)).

Note: The two bearing levels of the studied specimens are located in the lower-middle section of the sequence.

The studied mammal specimens were recovered from deposits of the Río Bermejo Formation cropping out at the left margin of the Bermejo River, along near 100 km, between the localities El Colorado (26°18' S, 59°22' W) and Estancia 'Sol de Mayo' ('Hertelendi') (26°45' S, 58°32' W), Formosa province, Argentina (localities 14 and 7 respectively, Figure 1(C)). Most of the specimens come from Level 2 and only a few were recorded in the transition between levels 1 and 2; taking into account the lithological homogeneity between these two levels, we consider that all fossils come from a single fossiliferous deposit.

One radiocarbon dating, performed on bivalves recovered from Level 2, near Villa Escolar locality, yielded 9570 ± 90 years BP (Zurita et al. 2014). Optically Stimulated Luminescence (OSL) dating were also performed near Villa Escolar locality; one of them, in Level 1, yielded 92200 ± 9650 years BP while another one, in Level 2, associated with one of the specimens studied in this work (*Neosclerocalyptus* sp.), yielded 84000 ± 8820 years BP. Although differences between these two types of dating have to be solved, the deposits of the Río Bermejo Formation and the included fauna can be assigned to the Upper Pleistocene-lower Holocene (Zurita et al. 2009; 2014).

Materials and methods

All the materials are housed in the paleontological collection of the Museo Provincial de Ciencias Naturales de Villa Escolar (Formosa Province, Argentina), under the acronym PVE-F. Fish remains were not included in the taphonomic analysis.

The taxa represented in the assemblage were grouped according to their estimated body mass (EBM): megamammals (>1000 kg), large mammals (100–1000 kg), middle mammals (10–100 kg), small mammals (1–10 kg) and micromammals (<1 kg) (modified from Araújo-Júnior and Porpino 2011). The taxonomic and anatomic representation was determined on the basis of the following indexes (sensu Badgley 1986): NISP (number of identified specimens per taxon), MNE (minimum number of elements) and MNI (minimum number of individuals; determined on the most abundant element per taxon in each studied locality).

The hydrodynamic sorting, on the basis of the susceptibility of the different skeletal elements to be transported by water flows, was determined using two methodologies. The FTI (Fluvial Transport Index) proposed by Frison and Todd (1986) was used for mammals with EBM >200 kg; FTI >75 (high susceptibility), FTI 50–75 (intermediate susceptibility) and FTI <50 (low susceptibility). According to Araújo-Júnior et al. (2012), this is the best index to assess assemblages of large-sized Quaternary mammals of South America. The Voorhies groups (Voorhies 1969) were used for mammals with EBM <200 kg; Group I (high susceptibility), Group II (intermediate susceptibility), and Group III (low susceptibility). Groups I/II and II/III are transitional between the main groups.

The following taphonomic features were analyzed:

- (1) Degree of articulation, considering articulated specimens, disarticulated but associated specimens, and disarticulated and isolated specimens (Behrensmeier 1991).
- (2) Degree of breakage, considering complete or incomplete specimens.
- (3) Types of fracture, evaluated on long limbs bones (femur, tibia, radius, ulna) and ribs, considering the classification proposed by Gifford-González (1989): spiral, produced in fresh bones; longitudinal, produced mainly in dry bones; and transverse, produced once the bones lost its organic components. The texture of the fracture surface was described as smooth or stepped (Gifford-González 1989).
- (4) Degree of weathering, considering unaltered specimens, specimens with loss of surface bone material, and specimens with deep loss of bone material (Alcalá 1994).
- (5) Degree of abrasion, considering unaltered specimens, specimens with rounding, and specimens with polishing (Alcalá 1994).
- (6) Degree of staining, considering the presence of specimens with dark spots in the outer surface. The color of the specimens and spots was determined using the Munsell table (Munsell 2000).
- (7) Degree of corrosion, considering the presence of specimens with degradation of the bone material, with or without color change.
- (8) Degree of encrustation, considering the presence of specimens with calcareous concretions.
- (9) Degree of post-burial deformation, considering the presence of specimens with changes in their original shape.
- (10) Degree of bioerosion, considering specimens with evidences that suggest the activity of other organisms (e.g. trampling marks, teeth marks, digestive corrosion).

Taphonomic analysis

Taxonomic and anatomic representation

Numerous mammal specimens of Xenarthra, Notoungulata, Carnivora, Artiodactyla and Proboscidea were recovered in the studied localities (Table 1). At Lucio V. Mansilla (locality 2, Figure 1(C)), six disarticulated but associated vertebrae of Osteichthyes assigned to cf. *Synbranchus marmoratus* Bloch 1795 (Synbranchidae) were also recorded (see Bogan et al. 2012); however, considering the low number of specimens recovered, they were not included in this taphonomic study.

The NISP of this assemblage is 669, the MNE 530, and the MNI 138 (Table 2). The MNE varied from 1 to 93 among different localities, whereas MNI varied from 1 to 37 (Table 1). The assemblage includes a large diversity of herbivorous and carnivorous mammals (Table 2). A high predominance, both in number of specimens and individuals, of Cingulata xenarthrans (glyptodonts, dasypodids, and pampatheres), particularly *Pampatherium* Ameghino, 1891, *Neosclerocalyptus* Paula Couto, 1957 and *Glyptodon* Owen 1838; was determined. To a lesser extent, artiodactyls were also abundant (Table 2). Thus, this assemblage can be considered as multitaxic and multidominant. Most taxa are extinct, only *Lama guanicoe* Muller, 1776, *Panthera onca* Linnaeus 1758; *Procyon cancrivorus* Cuvier 1798 and *Chaetophractus* have living representatives. Noteworthy, *P. onca*, *P. cancrivorus* and both species of *Chaetophractus*

Table 1. Values of MNE and MNI in the fossiliferous localities studied for the different groups of mammals represented in the assemblage.

Taxa	Localities (MNE/MNI)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Xenarthra	21/8	49/19	5/2	–	11/2	64/4	2/2	25/5	23/4	90/10	7/5	25/6	–	14/5	82/22
Notoungulata	1/1	4/3	–	–	–	–	–	–	1/1	–	–	–	–	–	–
Artiodactyla	15/2	21/14	6/2	–	–	–	–	–	6/1	–	9/3	–	11/3	2/2	5/2
Carnivora	3/1	–	1/1	–	–	–	–	–	–	–	1/1	–	–	6/1	–
Proboscidea	1/1	–	–	1/1	–	–	–	–	–	–	–	–	–	–	6/1
Mammalia indet.	10/1	1/1	–	–	–	–	–	–	–	–	1/1	–	–	–	–
Total MNE/MNI	51/14	75/37	12/5	1/1	11/2	64/4	2/2	25/5	30/6	90/10	18/10	25/6	11/3	22/8	93/25

Note: See Figure 1 for the numbers assigned to each locality.

Table 2. Values of minimum number of elements (MNE), minimum number of individuals (MNI) and estimated body mass (EBM) obtained for the different mammal taxa recorded in the assemblage.

Taxa			MNE	MNI	EBM (kg)
Cingulata	Pampatheriidae	<i>Pampatherium typum</i>	59	7	~95
		<i>Pampatherium</i> sp.	96	9	–
		<i>Holmesina paulacoutoi</i>	21	5	~200
		Pampatheriidae indet.	23	4	–
	Glyptodontidae	<i>Neosclerocalyptus</i> cf. <i>N. paskoensis</i>	1	1	~300
		<i>Neosclerocalyptus</i> sp.	94	28	–
		<i>Glyptodon</i> sp.	35	14	~850–2000
		Glyptodontidae indet.	56	17	–
	Dasypodidae	<i>Propaopus</i> sp.	18	4	~50
		<i>Chaetophractus</i> sp.	2	1	~1.5
Dasypodidae indet.		2	1	–	
Tardigrada	Mylodontidae	<i>Scelidotherium leptcephalum</i>	9	1	~800–1000
		Mylodontidae indet.	1	1	–
Artiodactyla	Megatheriidae	<i>Megatherium</i> sp.	1	1	~4600–6000
		Cervidae	1	1	~50
	Camelidae	<i>Morenelaphus lujanensis</i>	10	3	–
		<i>Morenelaphus</i> sp.	2	2	–
		Cervidae indet.	2	2	–
		<i>Lama guanicoe</i>	3	3	~100
		<i>Lama</i> sp.	1	1	–
		<i>Hemiauchenia paradoxa</i>	7	2	~190
		<i>Hemiauchenia</i> sp.	5	1	–
		Camelidae indet.	7	2	–
Artiodactyla indet.	39	13	–		
Notoungulata	Toxodontidae	<i>Toxodon</i> sp.	6	5	~1100–1600
Carnivora	Felidae	<i>Panthera onca</i>	3	1	~95–135
	Canidae	<i>Procyon</i> cf. <i>P. troglodytes</i>	6	1	~15–25
	Procyonidae	<i>Procyon cancrivorus</i>	1	1	~3–8
	Carnivora indet.	1	1	–	
Proboscidea	Gomphotheriidae	Gomphotheriidae indet.	8	3	~5000–7600
Mammalia indet.			12	3	–
Total			530	138	

Note: The values of EBM are based on Fariña et al. (1998, 2013), Prevosti and Vizcaíno (2006) and Vizcaíno et al. (2011).

Fitzinger 1871 (*C. villosus* Desmarest 1804 and *C. vellersus* Gray 1865) inhabit today the Eastern Chaco region.

The recorded taxa displayed a wide range of estimated body masses (Table 2), from dasypodids like *Chaetophractus* (~1.5 kg) up to Gomphotheriidae indet. (~5000–7600 kg). There was a high predominance, both in amount of specimens and individuals, of megamammal (>1000 kg) and large mammals (100–1000 kg), mainly represented by Tardigrada and Cingulata xenarthrans. To a lesser extent, several medium mammals (10–100 kg) were recovered, mostly Camelidae and Cervidae artiodactyls. Small mammals (1–10 kg) were very scarce and micromammals (<1 kg) were absent.

The most frequent skeletal elements were isolated osteoderms of cingulate carapaces, including Glyptodontidae, Pampatheriidae and Dasypodidae (MNE = 335), although several carapace fragments with articulated osteoderms were also found (MNE = 29). Isolated teeth, vertebrae, ribs and phalanges

also showed high MNE values, whereas the remaining elements were scarce (Figure 3). Cranial elements represent 38.32% of the sample, axial skeleton and girdles 23.35%, and appendicular skeleton 38.33%.

All the groups of Frison and Todd (1986) -here considered for mammals with EBM >200 kg- and Voorhies (1969) -here considered for mammals with EBM <200 kg- were recorded. Skulls and phalanges, not included in the study of Frison and Todd (1986), were considered as elements with low/intermediate susceptibility and high susceptibility respectively (see Voorhies 1969; Korth 1979). Isolated teeth, not included in the studies of Frison and Todd (1986) and Voorhies (1969), were considered as elements with low/intermediate susceptibility (see Behrensmeyer 1975; Korth 1979). So far, there is no information available concerning the susceptibility of cingulate osteoderms, which are the most abundant specimens of this assemblage (but see Discussion), neither of antlers of cervids.

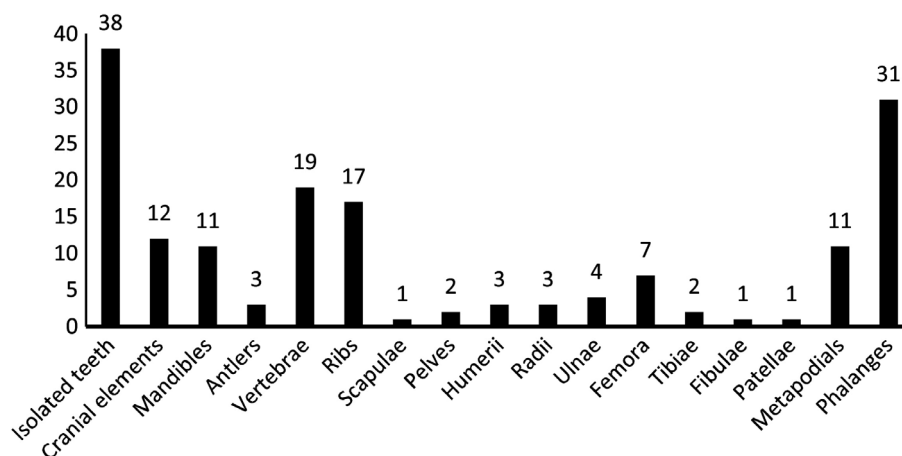


Figure 3. Minimum number of elements (MNE) determined in the assemblage; except for isolated osteoderms and fragments of carapaces.

Degree of articulation

Disarticulated but associated specimens were the most abundant (57%), represented by vertebrae, osteoderms (Figure 4(A)), ribs, and long limb bones; in addition, several palates and mandibles retained the teeth within the alveoli (Figure 4(B)). In some cases, the specimens of a single individual lost their original anatomical position and were regrouped without apparent order (Figure 4(C)). Disarticulated and isolated specimens (37%) were represented by osteoderms, teeth (Figure 4(D)) and antlers (Figure 4(E)). Articulated specimens were very scarce (6%), including fragments of dorsal carapaces with several osteoderms (Figure 4(F)) and caudal tubes with vertebrae inside; noteworthy, they were in turn associated with others elements assigned to the same individual.

Breakage

Complete specimens represent 54% of the sample, including mainly phalanges, skulls, and mandibles. Fragments of cingulate carapaces were mostly incomplete, and among isolated osteoderms, only 43% were complete. Most isolated teeth, ribs and vertebrae were incomplete. All incomplete limb long bones and ribs displayed transverse fractures with stepped surfaces. Most specimens showed significant surface cracking; in some cases, the cracks were filled with clays that present similar composition to the host deposits.

Degree of weathering

A very high percentage of specimens were unaltered (61%). About 26% of the specimens, mainly shaft of long bones, ribs and skulls, showed loss of surface bone material; in these cases, slight splitting parallel to the main axis of the bone and patterns of mosaic surface flaking were identified (Figure 5(A) and (B)). Around 13% of the specimens, mainly vertebrae and distal end of long bones, showed loss of deep bone material; in these cases, portions of the spongy tissue were exposed (Figure 5(C)).

Degree of abrasion

Most specimens were unaltered (87%). Only 13% of the specimens displayed slight rounding on the edges, mainly isolated

osteoderms and, to a lesser extent, ribs and distal ends of long bones (Figure 5(D)).

Degrees of post-burial deformation, staining and encrustation

Materials preserved in general their original shape, except for six specimens with evidence of deformation. Five of them are skulls of *Hemiauchenia* sp. Gervais and Ameghino, 1880 (PVE-F38 and PVE-F104), *Procyon cf. P. troglodytes* Giebel, 1855 (PVE-F45), *P. onca* (PVE-F130) and *Pampatherium* sp. (PVE-F37); the remaining one is a vertebra of *Toxodon* sp. Owen, 1837 (PVE-F116). The specimens PVE-F38 (Figure 5(E)), PVE-F104, PVE-F45 (Figure 5(F)), and PVE-F130 show lateral compression, affecting the region of nasals, premaxillae and maxillae. In addition, dentaries (PVE-F104), zygomatic arch (PVE-F45), and frontals (PVE-F130) were also modified. PVE-F37 is laterally compressed and shows modifications of the *foramen magnum* and both zygomatic arches. In PVE-F116, the lateral compression modified the neural arch and produced a slight inclination of the dorsal spine (Figure 5(E)). All these specimens had numerous cracks with different orientation (Figure 5(B), (E) and (F)), most of them filled with clays that present similar composition to the host deposits.

The 7% of the specimens showed calcareous concretions on the outer surface, in some cases as very thin coatings and in others as hollow cylinders, 0.5 mm in diameter, identified as rhizoliths (Figure 5(G)). The assemblage is rather homogeneous in the color of specimens, with a high predominance (NISP = 631) of very light gray (Hue 10 YR 8/2); followed by other colors, light brownish gray (Hue 5 YR 8/1), brownish gray (Hue 5 YR 4/1), and pale yellowish orange (Hue 10 YR 8/6). The 90.43% of the specimens showed dark spots, generally with dendritic habit, covering areas varied in size, attributed to staining by with manganese oxides (Figure 5(H)).

Degree of bioerosion

Behrensmeyer (1988) mentioned that marks associated to processes of trampling and predator/scavenger activity are common in this type of preservational context. Although we do not reject

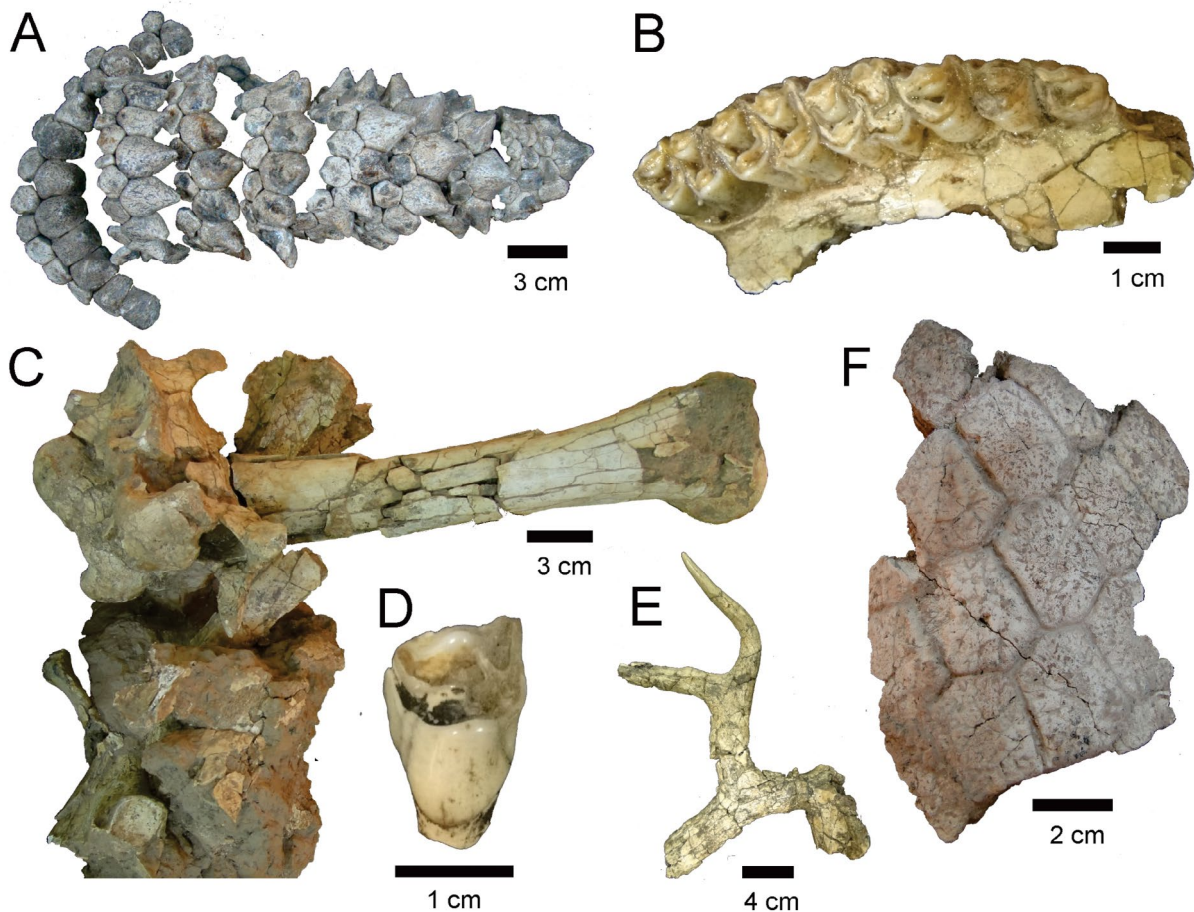


Figure 4. Degree of articulation. (A) PVE-F85, disarticulated but associated osteoderms of *Glyptodon* sp.; (B) PVE-F26, palate of cf. *Morenelaphus* retained the teeth within the alveoli; (C) PVE-F4, postcranial elements of Camelidae indet. without their original anatomical position; (D) PVE-F139, isolated molar of Artiodactyla indet.; (E) PVE-F117, isolated antler of cf. *Morenelaphus* sp.; (F) PVE-F12, articulated dorsal carapace of Glyptodontidae indet.

this possibility, at the moment there was no evidence of these processes in the assemblage.

Discussion

Taphonomic history

The Eastern Chaco region (Northeastern Argentina) is characterized by numerous paleo-channels associated with the ancient Bermejo River, on which wide wetland systems are developed (Benzaquén et al. 2013). This particular environmental context, which has currently a high diversity of vertebrates, began to form in the Late Pleistocene. Iriondo (2010) stated that, during the Quaternary, swamps were key areas for the evolution of plants and animals, as well as refuges of particular ecosystems. Bearing this in mind, the analysis of the faunal assemblage recovered in the Río Bermejo Formation turns out very interesting in several aspects: (1) it was found in levels interpreted as swampy deposits filling paleo-channels of the ancient Bermejo River; (2) it comprises a large amount of specimens and individuals of diverse herbivorous and carnivore mammal taxa; (3) it corresponds to the Late Pleistocene-early Holocene, the interval when swamps began their development acquiring the current design in the area; and (4) it includes taxa that became extinct at the end of

the Pleistocene and beginning of the Holocene, together with others (*P. onca*, *P. cancrivorus*, *Chaetophractus*) that currently inhabit the area.

The 15 sites studied here, located along 100 km of the left margin of the Bermejo River, supplied numerous specimens (MNE = 530) of many individuals (MNI = 138). The number of specimens and individuals varied markedly among localities. Taking into account that all fossils were recovered from the same stratigraphic level and that the modern swamps in the area have large extensions (100–200 km long, 3–10 km wide; see Iriondo 2010), the specimens of the different localities were considered as members of a single assemblage.

Most identified taxa (e.g. *S. leptoccephalum* Owen, 1840; *H. paradoxa* Gervais and Ameghino, 1880; *Toxodon* sp., *Glyptodon* sp., *Megatherium* sp. Cuvier, 1796) belong to the typical 'Pampean' fauna and suggest open environments, arid to semiarid and cold, with development of wide grasslands. Only *H. paulacoutoi* Cartelle and Bohórquez, 1985 and *P. cancrivorus* have an inter-tropical origin, reflecting warm and humid conditions (Zurita et al. 2014; and references therein). In this context, it is possible to consider that the representatives of the assemblage had different requirements and, therefore, reflect variations in the composition of the biocenosis according to the environmental

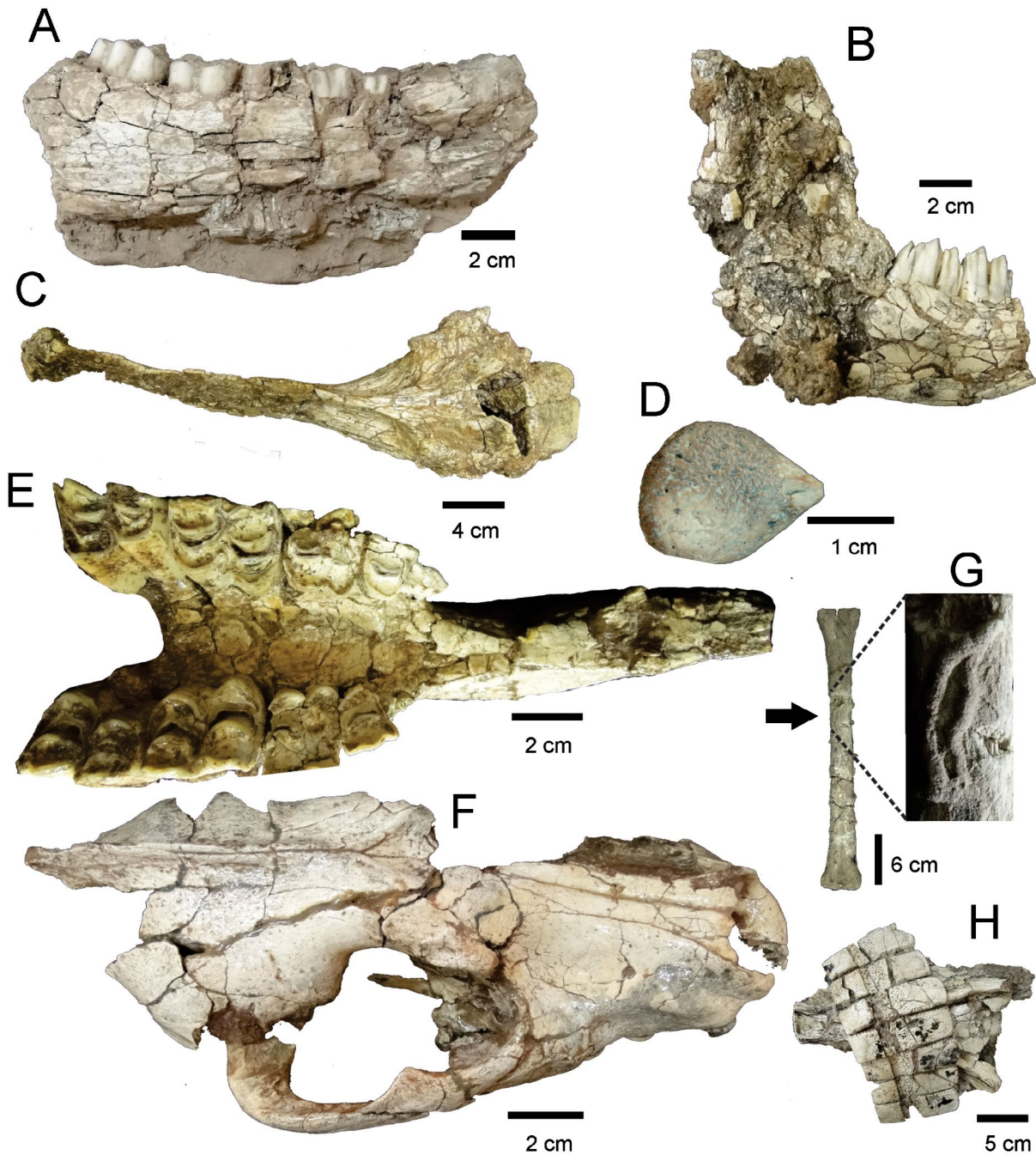


Figure 5. Weathering. (A) PVE-F43, mandible of *Artiodactyla* indet. showing slight splitting; (B) PVE-F57, mandible of *Cervidae* indet. showing slight splitting and mosaic surface flaking; (C) PVE-F116, vertebra of *Toxodon* sp. showing exposition of spongy tissue on the dorsal spine and post burial deformation. Abrasion. (D) PVF-F11 isolated osteoderm of *Glyptodon* sp. with rounding. Post-burial deformation. (E) PVE-F 38, skull of *Hemiauchenia* sp. in ventral view; (F) PVE-F45, skull of *Protocyon* cf. *P. troglodytes* in dorsal view. Encrustation. (G) PVE-F21, metapodial of cf. *Morenelaphus* sp. showing rhizoliths in the outer surface (arrow and enlargement). Staining. (H) PVE-F27, fragment of dorsal carapace of *Pampatherium* sp., showing dark spots attributed to impregnation with manganese oxides.

and climatic changes that occurred in the region during the represented interval.

Cingulates, especially *Pampatherium*, *Neosclerocalyptus* and *Glyptodon*, showed the highest values of MNE and MNI; this predominance was also recorded in other Quaternary deposits of the Northeast of Argentina, particularly in the Toropí/Yupoí Formation, Corrientes Province (Francia et al. 2015). This aspect could be related to the abundance of osteoderms in

the carapaces of the diverse representatives of this group, which greatly increases its preservation potential.

Most specimens belong to large skeletal elements of megamammals (>1000 kg) and large mammals (100–1000 kg). No micromammals have been so far recorded and small mammals are scarce. Behrensmeier (1988) stated that microfauna may be preserved in channel-fill deposits; at the moment, only the record of fish remains confirms this proposal. This situation

poses an unsolved equifinality: (1) large bones of animals with high estimated body mass are more resistant to destructive taphonomic processes and having higher preservation potential than small bones of small mammals and micromammals (see Behrensmeyer et al. 1979; Behrensmeyer 1991); (2) small bones corresponding to animals with high estimated body mass are present but scarce, even more if they are considered in the context of each individual. This low representation could be associated with the development of diverse biostratinomic processes (e.g. weathering, trampling, predators/scavengers activity, transport by water flows) (see Palmquist et al. 1992); however, no evidence supporting this proposal was recorded in the assemblage.

Cingulate osteoderms were the predominant skeletal elements of the assemblage, in accordance with their abundance in the carapaces of the represented taxa. It was estimated that ~800 osteoderms form the carapace of Dasypodidae (Montalvo et al. 2016; Brambilla and Ibarra 2017), and ~2000 that of Glyptodontidae (Gillette and Ray 1981). Isolated teeth, phalanges, vertebrae and ribs, which are among the most abundant elements of the mammal carcass (see Moore 1994), were also numerous.

Skeletal elements of all the groups proposed by Frison and Todd (1986) and Voorhies (1969) here used for analyze mammals with EBM >200 kg and EBM <200 kg respectively, were recorded, suggesting low degree of hydrodynamic sorting for the original thanatocoenosis. These results are in agreement with the low energy interpreted for the swamps that constituted the environmental context where the bones were accumulated.

There are currently no experimental studies to assess the susceptibility of osteoderms to be mobilized by water flows. Noteworthy, some of the studied localities yielded a high number of osteoderms of diverse cingulate taxa. For example, in locality 15 (km 100 Navigation of the Bermejo River (NRB)), 82 osteoderms of 13 individuals were recovered, which implies a high loss of osteoderms considering the high number of these elements present in each carapace (see above). In this regard, it was suggested that, because osteoderms have abundant spongy bone tissue and low structural density (Hoffstetter 1958), they could be easily transported (see Araújo-Júnior et al. 2013).

Disarticulated but associated specimens were the most abundant. In these cases, the time of exposure of the carcass would have been enough for the separation of the different bones, but without undergoing a significant mobilization and dispersion. The associated specimens that were regrouped, without apparent anatomical arrangement, correspond to portions of the carcass of single individuals. The few articulated specimens suggest that some portions of the carcass were buried rapidly with connective tissues still present. The predominance of these two stages is consistent with the low energy interpreted for the environmental context in which the bones were accumulated. Disarticulated and isolated specimens suggest that, in some cases, the time of exposure was more prolonged. Taking into account that there is no evidence indicating trampling or activity of predators/scavengers, it is possible to consider that probably the vegetation and the wet conditions of the swamps and/or the development of low energy water flows favored the disarticulation and the spatial rearrangement of some specimens (see Coe 1980; Badiola et al. 2009).

Complete specimens are the most abundant in the assemblage; this suggests that, in general, the time of exposure of the bones to destructive taphonomic processes was short. Among incomplete specimens, only transverse fractures with stepped surfaces were identified, which are related to post-burial processes, once the bones have lost their organic components and are mineralized (Shipman 1981; Gifford-González 1989). In this case, these fractures are probably related to the lithostatic load of the overlying deposits. The intense cracking observed on the outer surface of many specimens was also attributed to this process. The absence of fractures commonly associated with the pre-burial stage (e.g. spiral, longitudinal) supports the proposal suggesting that the permanence of the bones on the surface, exposed to destructive processes (e.g. trampling, predator/scavenger activity), was short.

Most specimens showed no signs of weathering. Among those affected, the modifications were usually very slight. It is noteworthy the lack of weathering marks on cingulate osteoderms, particularly because this element has a very thin outer layer of compact bone tissue (Hoffstetter 1958) susceptible to be rapidly affected. These characteristics suggest: (1) a relatively short time of permanence of the bones on surface exposed to atmospheric agents (see Andrews 1990); (2) the abundant vegetation present in the swamps protected the bones from the atmospheric agents (see Coe 1980; Shipman 1981).

Specimens with no abrasion were predominant. Among those affected (mainly isolated osteoderms), modifications were very slight. Osteoderms would be more susceptible than other elements to be altered by this process because the presence of a very thin outer layer of compact bone tissue. On this basis, it is possible to suggest that the time span of exposure to the abrasive conditions of the sedimentary particles mobilized by water flows would have been short or the intensity was low; this proposal is consistent with the low energy interpreted for the type of environmental context where the bones were accumulated.

Some specimens showed clear modifications of their original shape (e.g. compression), interpreted as the result of deformation processes occurred during the early fossil-diagenesis, probably due to lithostatic load of the overlying sediments. In this context, before replacement with new minerals is completed, the bones exhibit ductile behavior and respond with some plasticity to the external stresses, so that their shape can be adapted to lower tension states (Fernández-López 2000; Arbour and Currie 2012). In turn, commonly during this stage, deformation is accompanied by breakage and cracking, as observed in the studied specimens.

Different attributes linked with the characteristics of the host deposits were recorded. Precipitation of manganese oxides reflects alkaline and oxidizing conditions of the preservation environment during dry periods (López-González et al. 2006; Marín Arroyo et al. 2008; Tomassini et al. 2014). In this regard, Iriondo (2010) mentioned the presence of manganese nodules in the fossiliferous levels considered here. Calcareous encrustation suggest alkaline conditions of the preservation environment during dry periods (Lyman 1994; Fernández-López 2000); particularly rizoliths indicate that, at least for a time, bones were buried near the surface, probably in horizons A or B of the soil where roots develop (Klappa 1980; Montalvo 2004). Identification of

clays with similar composition to the host levels inside the transverse fractures and cracks associated with plastic deformation suggests that the filling occurred during post-burial stages.

Taphonomic mode

Fluvial environments are usually highly fossiliferous contexts (Behrensmeyer and Hook 1992). In particular, river systems with development of many abandoned channels often contain, especially in the filling deposits, very complete assemblages from an ecologic standpoint, including both aquatic and terrestrial vertebrates (Wing 1984; Behrensmeyer 1988). Modern swamps of Eastern Chaco (Figure 6), developed in the paleo-channels of the ancient Bermejo River, are characterized by very prolific ecosystems. Permanent or semi-permanent water bodies, with abundant and varied associated vegetation, attract animals that go to drink and feed, especially during times when these resources are scarce in the alluvial plains (Adámoli et al. 2008; Iriondo 2010). Bearing this in mind, and in addition to the characteristics of the recovered assemblage (e.g. abundance of specimens and individuals, high taxonomic diversity), it is inferred that during

the Quaternary this type of environmental context would have also been key for the development and evolution of faunal communities of the region.

The assemblage of the Río Bermejo Formation includes specimens of herbivorous and carnivorous mammals that, during the Late Pleistocene-early Holocene, inhabited the swamps formed in the abandoned channels of the Bermejo River, or in the surrounding areas. The recorded taphonomic characteristics (e.g. low degree of bioclastic sorting, predominance of articulated/associated specimens, high percentage of complete specimens, absence of pre-burial fractures, low percentage of specimens with signs of weathering and abrasion) suggest that, in general, the bones were preserved in the place of death or close to it [*in situ* preserved specimens and peripheral specimens respectively, according to the classification proposed by Araújo-Junior (2016)], with short time of exposure and little or no transport. It is also interpreted that bones were buried gradually. No evidences of reworking were recorded.

Taphonomic studies related to the preservation of vertebrates in swampy deposits are very scarce. Even so, the features recorded in the assemblage of Río Bermejo Formation coincide,



Figure 6. View of a modern swamp linked to the Bermejo River in Formosa Province.

Table 3. Comparison of the taphonomic characteristics described by Behrensmeyer (1988) for the channel-fill mode with those observed in the assemblage of the Río Bermejo Formation.

Characteristics	Channel-fill mode (Behrensmeyer 1988)	Río Bermejo Formation
Lithology	Mudstones, silts, clays, fine sands, nodule conglomerates	Clay, silt and fine sand. No coarse sediments were recorded
Type of vertebrates	Aquatic and terrestrial	Aquatic and terrestrial
Body sizes	A wide range usually present, including microfauna	Mainly megamammals and large mammals. Micromammals were absent (fish remains were recovered)
Bioclastic sorting	Size-sorting in coarser sediments; variable to poor sorting otherwise	Low; all the groups proposed by Frison and Todd (1986) and Voorhies (1969) were represented.
Articulation/association	Variable; more frequent in finer sediments	Predominance of disarticulated but associated specimens. Articulated specimens were scarce
Breakage	Variable; more complete in finer sediments	Predominance of complete specimens
Weathering	–	Predominance of unaltered specimens. Affected specimens showed different degree of weathering (most of them slight).
Abrasion	Edges fresh to rounded, usually fresh in mudstones	Marked predominance of unaltered specimens. The few affected specimens show slight rounding on the edges.

in general, with the observations performed in similar environmental contexts (e.g. Behrensmeyer and Hook 1992; Badiola et al. 2009; and references therein).

Behrensmeyer (1988) defined taphonomic modes as recurrent patterns of preservation of the organic remains in a specific sedimentary context, and with characteristic taphonomic features. For fluvial channel deposits, this author proposed channel-lag and channel-fill taphonomic modes; channel-lag assemblages originate under the influence of sustained active flow, whereas channel-fill assemblages occur after the channel is abandoned. Based on the available sedimentological and taphonomic information (Table 3), the assemblage of the Río Bermejo Formation can be assigned to the channel-fill taphonomic mode. In this taphonomic mode the temporal resolution ranges between 10^2 and 10^4 years and the spatial resolution is local, including autochthonous and parautochthonous specimens (Behrensmeyer and Hook 1992); the evidences recorded in the studied assemblage are consistent with these interpretations.

Conclusions

The assemblage recovered from the swampy deposits of the Río Bermejo Formation (Upper Pleistocene-lower Holocene) includes specimens of diverse mammal groups and fishes. These specimens, preserved in the place of death of the organisms or very near, were affected along their taphonomic history by diverse processes occurred before and after the burial. Based on the sedimentological and taphonomic characteristics, the assemblage can be assigned to the channel-fill mode. The evidences obtained suggest that the swamps developed during the Quaternary in the Eastern Chaco (Argentina) would have been favorable contexts for the preservation of vertebrate bones.

The interpretation of the mechanisms that favored the formation of this type of assemblages, developed in a spatially restricted area (with autochthonous and parautochthonous specimens) and during a short interval, is essential for the study of ecologic, biologic, biogeographic issues, among others, of the recorded paleocommunities. In this sense, it is considered that, such as today, since the Late Pleistocene swamps were very valuable areas from the faunal point of view, hosting numerous and diverse vertebrates. The evidence suggests that the biocenosis that inhabited the swamps associated to the ancient Bermejo River was composed of taxa currently extinct together with others with living representatives, some of them still inhabiting the area.

In South America, numerous assemblages of Quaternary vertebrates preserved in diverse environmental contexts have been documented; however, taphonomic studies are scarce. This paper provides new information on the preservation characteristics in a particular environmental context -swampy deposits developed in abandoned channels-, and can be a reference framework for the study of other major river systems of the southern part of the continent (e.g. Pilcomayo, Salado, Paraná), in which sedimentary sequences and faunal assemblages are similar to those of the Bermejo River.

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