



# The first fossil record of a bone assemblage accumulated by New World vultures (Gruta do Presépio, Holocene, southern Brazil)

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Here we present the first fossil record of a bone assemblage that could have been accumulated by New World vultures (Cathartidae). The bone remains were found in an archaeological rockshelter called Gruta do Presépio (GPR), located in the tropical rainforest environment of Santa Catarina State, southern Brazil, where groups of hunters and gatherers lived from the Early to Middle Holocene (9.3–4.6 cal. ka BP) until the Late Holocene (1.3 cal. ka BP). The results of taphonomic analysis of the archaeological sample are compared with actualistic taphonomic modifications produced by New World vultures. The findings of autopodials (mainly phalanges) of medium and large mammals, with a high degree of digestive corrosion but without tooth marks, could be related to the pellet deposit pattern of New World vultures. Seven mammal taxa associated with a forest environment were identified, four of which were obtained from pellets deposited by Cathartidae; these included some native taxa (Cervidae, Dasypodidae, Felidae and Tayassuidae) that are frequently consumed today by these scavenger birds. The bone and tooth remains contained in the pellets regurgitated by Cathartidae were found together with faunal remains discarded by humans that lived in GPR from the Early to the Late Holocene. This palimpsest highlights the relevance of archaeological and actualistic taphonomic studies.

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Archaeological sites frequently constitute palimpsests of cultural and natural processes (Bailey 2007; Borrero 2014). For instance, successive bone assemblages can be accumulated by humans and other predators or scavengers throughout the stratigraphy or in different parts of an archaeological site. Taphonomy is the discipline responsible for addressing these problems (Lyman 1994, 2010; Borrero 2014). In South America, several types of taphonomic research (actualistic, archaeological, palaeontological) focus on the role of carnivorous mammals and birds of prey as accumulators (e.g. Mondini 1995, 2017; Martin & Borrero 1997; Borrero *et al.* 2005, 2018; Gómez & Kaufmann 2007; Montalvo *et al.* 2007, 2008, 2012; Mondini & Muñoz 2008; Muñoz *et al.* 2008; López *et al.* 2017; Montalvo & Fernández 2019; Scheifler *et al.* 2020). However, few taphonomic contributions have come from recent samples of New World vultures of the Cathartidae family (Reeves 2009; Ballejo *et al.* 2012; Spradley *et al.* 2012; Dabbs & Martin 2013; Ballejo 2016), and there is no archaeological or palaeontological evidence in the fossil record to show them as accumulators. Conversely, several European

studies have demonstrated the active role of Old World vultures (Accipitridae) in fossil record formation (e.g. Robert & Vigne 2002a, b; Davis *et al.* 2007; Costamagno *et al.* 2008; Marín-Arroyo *et al.* 2009; Robert & Reumer 2009; Marín-Arroyo & Margalida 2012).

Cathartidae are strictly scavengers that feed on carrion of large ungulates, but they can include smaller vertebrates in their diets (Wallace & Temple 1987; Del Hoyo *et al.* 1994; DeVault *et al.* 2003; Kelly *et al.* 2007; Lambertucci 2007; Lambertucci *et al.* 2009; Ballejo & De Santis 2013; Ballejo *et al.* 2017). Although six species of Cathartidae occur in South America, only four are found in southern Brazil: the American black vulture (*Coragyps atratus*), the turkey vulture (*Cathartes aura*), the lesser yellow-headed vulture (*Cathartes burrovianus*), and the king vulture (*Sarcoramphus papa*) (Del Hoyo *et al.* 1994). Although the distribution of the Andean condor (*Vultur gryphus*) is geographically distant from southern Brazil (>1500 km to the west), there is a fossil record of this species in Lagoa Santa, Minas Gerais, dating from the Early Holocene (Alvarenga 1998). These species are large birds that occur in open areas, roosting,

foraging and living socially in large groups on cliffs, rockshelters, or trees; they feed on dead animals of any size (Del Hoyo et al. 1994; Kelly et al. 2007; Ballejo & De Santis 2013; Ballejo 2016). The distribution range of *C. atratus* stretches from southern North America to southern South America, while *C. aura* occurs in a diversity of environments from the southern border of Canada to the extreme south of Argentina, and *V. gryphus* is distributed from the Andes Mountains of Venezuela to the extreme south of Argentina and Chile (Del Hoyo et al. 1994; Lambertucci 2007; Lambertucci et al. 2009). Therefore, this species can be considered part of the Cathartidae inhabiting the eastern lowlands of Brazil during the Early Holocene. Three species of this family (*C. atratus*, *C. aura* and *V. gryphus*) have undergone actualistic studies that could be useful as modern for comparison with the fossil record (Ballejo et al. 2012) and also for forensic purposes (Reeves 2009; Spradley et al. 2012; Dabbs & Martin 2013). These scavenger birds may scatter carcass parts around the site of a dead animal, or bones may be transported in their pellets to bird nesting or roosting sites on rocky cliff ledges and in trees; these carcass parts can become mixed with the food remains of carnivorous mammals or humans (Ballejo et al. 2012; Marín-Arroyo & Margalida 2012). Therefore, identification of the accumulating agents of faunal assemblages recovered from archaeological sites is a valuable tool with which to make palaeoecological, palaeoenvironmental and palaeoeconomic interpretations (Marín-Arroyo & Margalida 2012).

We present here the first fossil record of a bone assemblage that could have been accumulated by New World vultures. The sample came from an archaeological site located in the rainforest environment of southern Brazil, where groups of hunters and gatherers also discarded animal bones consumed during the Holocene. The results of the taphonomic analysis of the archaeological samples are compared with actualistic data on taphonomic modifications produced by New World vultures.

## Material and methods

### *Archaeological site, environments and the archaeological sample studied*

The Gruta do Presépio (GPR) archaeological site is located close to the southern margin of the Itajaí do Oeste river, in Rio do Oeste municipality, Santa Catarina State, southern Brazil (latitude 27°12'31.41''S, longitude 49°46'38.97''W, altitude 442 m a.s.l., Fig. 1A–C). GPR is situated within an archaeological complex that includes three other archaeological sites: Gruta do Tigre, Fenda do Tigre and Oficina do Tigre. Rio do Oeste lies within the Atlantic Forest Biome (IBGE 2019), and its vegetation is the Tropical Rainforest of the Alto Vale do Itajaí. This forest is mainly characterized by low richness

of tropical trees and great homogeneity of the dominant species, such as *Aspidosperma olivaceum*, *Copaifera trapezifolia* and *Ocotea* spp., which present high abundance and frequency (Klein 1978). The current vegetation is represented by small fragments of this forest type in an agricultural matrix (Vibrans et al. 2012). The climate is mild mesothermal, with average temperatures of between 10 and 15 °C, and extremely humid, with no periods of drought (IBGE 1978).

GPR is a large rockshelter (35 m wide at the mouth and 17 m long) eroded out of a shale outcrop superimposed by layers of sandstone; this context is also found in Gruta do Tigre and Fenda do Tigre archaeological sites (Machado et al. 2019). Because this rockshelter was used for a long time for religious purposes, a wall was built that artificially separates the shelter into two parts: the first part, internal, extends from the far end of the rockshelter to the wall, and the second, external, extends from the wall to the drip line (Fig. 1D). The roof of the rockshelter covers both parts. Eight 1 × 1 m and one 1 m × 50 cm archaeological excavation units were dug in the internal part (area 1) of the rockshelter, and three of 1 × 1 m in the external part (area 2) (Fig. 1D). Excavation area 2 resulted in eight layers, defined according to sedimentological and cultural features. The principal cultural input was detected in layers 6 and 7. Layer 8, the deepest one, did not present lithic remains. The rock base of the shelter, composed of shale, was reached at about 113 cm. The sedimentary filling of GPR varied between silty sand and clayey sand, with the general predominance of a sandy matrix. The extracted sediments were sieved through 2–4 mm sized mesh. Archaeological remains were identified and collected, including faunal bones (fishes, frogs, lizards, birds, and small, medium and large mammals), mollusc shells (gastropods and bivalves), and lithic artifacts and charcoals (Machado et al. 2019). General information on the stratigraphy and chronology is presented in Table 1.

A total of 1215 faunal remains were obtained from three excavation units of area 2 (N17L51, N18L51 and N17L58; Fig. 1D), including the remains deposited by Cathartidae (NISP = 144). Based on the chronostratigraphical analysis, we divided this sample into the following temporal units: Early to Middle Holocene (layers 5–8) and Late Holocene (layers 1–4). Faunal remains with evidence of human exploitation recovered from all units of both excavation areas at GPR are being fully studied.

### *Comparative actualistic samples*

The actualistic information of Cathartidae for South America came from northwestern Patagonia (44°11'55.7''S, 71°05'43.1''W, Fig. 1A). The pellet samples ( $N = 619$ ) were collected in two communal roosts of *C. aura* ( $N = 96$ ) and eight communal roosts of *C. atratus* ( $N = 334$ ), which were both located in trees, and five

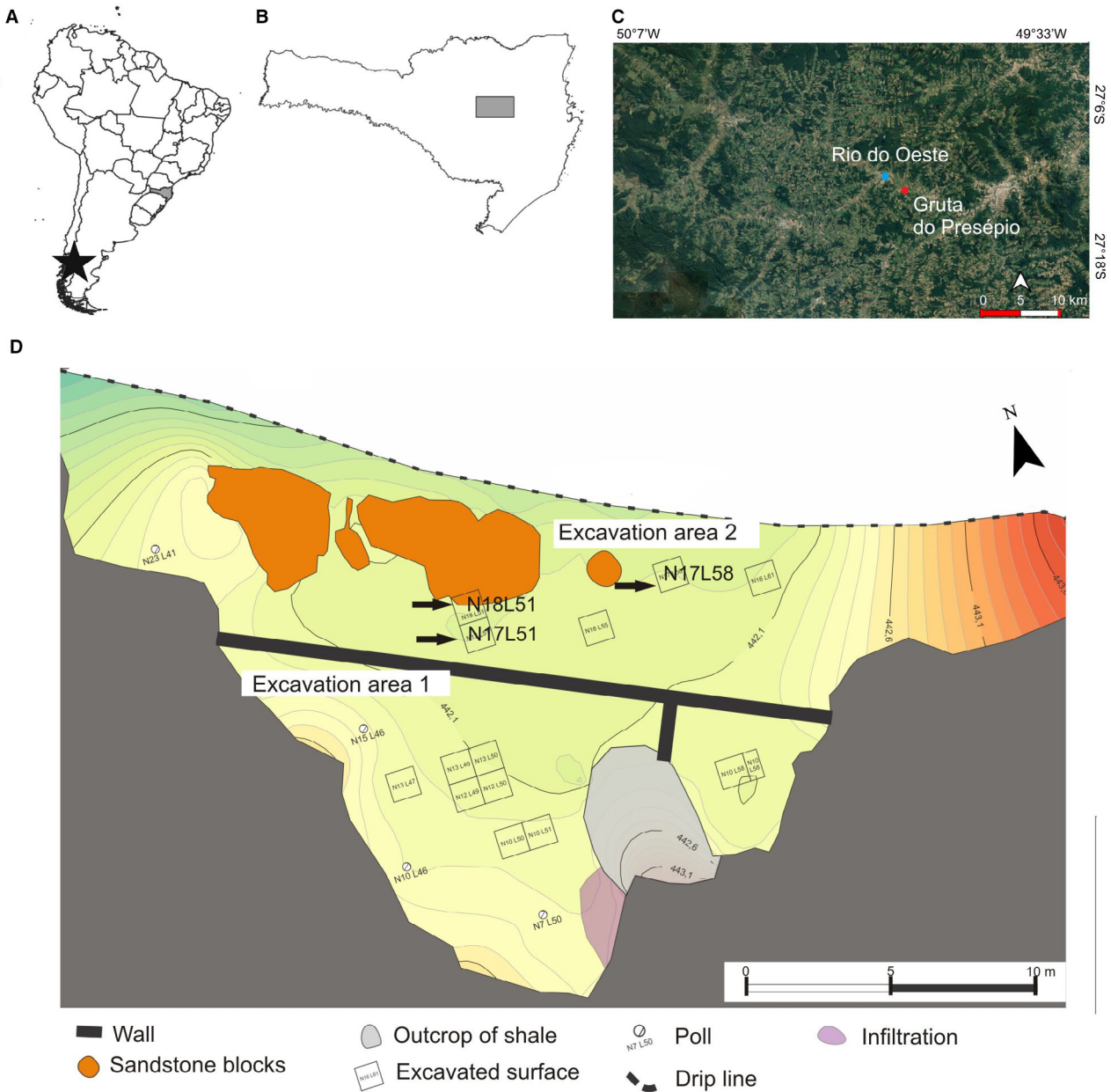


Fig. 1. A–C. Geographical location of the archaeological site Gruta do Presépio in Santa Catarina State, Brazil. The black star on the map of South America (A) indicates the location in northwestern Patagonia of the recent study samples of New World vultures. D. Plan of the site showing the location of the excavations. Black arrows indicate grids with bones accumulated by New World vultures.

communal roosts of *V. gryphus* ( $N = 189$ ) located in a rockshelter (see Table S1 for more details of the sample localities).

This area presents a cold climate with strong westerly winds and a significant west–east rainfall gradient, from 800 to 300 mm, respectively, precipitation falling mainly in the winter. The environment includes high elevations of the North Patagonian Andes (2000–2300 m a.s.l.) and low mountains (1300–1800 m a.s.l.) of the Pre-cordillera (Giacosa *et al.* 2005); it is characterized by shrubby and grassy steppe (León *et al.* 1998). Despite the climate and environment being quite

different than the GPR location, we consider that the actualistic taphonomic information of the aforementioned samples is valuable for comparison purposes, as they are well systematized and use the same taphonomic methodology as the archaeological samples (Table 2). In addition, raptor pellets have been widely used in actualistic models for comparison with the fossil records of areas with different climatic and environmental conditions, given that they usually present similar taphonomical patterns (e.g. Andrews 1990; Fernández *et al.* 2017; Fernández *et al.* 2019; Montalvo & Fernández 2019).

**Table 1.** Gruta do Presépio schematic sequence: stratigraphy and chronology. Calibration was carried out using the CALIB 8.2 program. \*The depth and layer data were collected from layers 1–6: N17L51; layer 7: N17L51/N18L51; and layer 8: N18L51.

Layers	Depth (cm*)	Sedimentary composition	Main dates ( $^{14}\text{C}$ a BP)	Calibrated age (median probability; a BP)	Temporal units
1	0–15	Silty sand			Late Holocene
2	15–20	Silty sand			
3	20–35	Silty sand			
4	35–40	Silty sand	1450±30	1311	
5	40–60	Silty sand	4150±30	4632	Early to Middle Holocene
6	60–73	Clayey sand	8330±30	9301	
7	73–98	Clayey sand			
8	98–113	Clayey sand			

### Methods

The material was cleaned with brushes and water in the Laboratório de Estudos Interdisciplinares em Arqueologia do Departamento de História da Universidade Federal de Santa Catarina (UFSC, Florianópolis, Santa Catarina, Brazil) and then identified taxonomically through comparison with recent specimens of the mammal collection of the Ecology and Zoology Department of the UFSC.

The mammals recovered were divided into three size categories: small (<5 kg; *Nasua nasua*, *Eira barbara*, *Dasyypus*, *Lepus europaeus*, *Reithrodon auritus*), medium (between 5 and 20 kg; *Lycalopex*) and large (>20 kg; *Tayassuidae*, *Cervidae*, *Tapirus terrestris*, *Puma concolor*, *Ovis aries*). The average body mass of the species represented was obtained from the Macroecological Database of Mammalian Body Mass (MOM), version 4.1 (Smith *et al.* 2003). The palaeoenvironmental interpretation is based on the use of mammals as indicators of environmental conditions: knowledge of the presence or absence of several species in conjunction with their environmental requirements enables palaeoecological inferences to be made (e.g. Andrews 1990; Tonni *et al.* 1999).

Bone and tooth remains were identified according to the following measures of taxonomic abundance and skeletal parts: NSP (total number of specimens), NISP (number of identified specimens per taxon), MNE (minimum number of elements) and MNI (minimum number of individuals) (Grayson 1984). The extent of bone fragmentation of the assemblage was measured by the ratio NSP/NISP. As NSP/NISP increases, the fragments are smaller and less identifiable (Lyman 2008).

In addition, digestive corrosion was evaluated using the classification of Ballejo (2016), which is a modified version of the original proposal made by Robert & Vigne (2002a) and Lloveras *et al.* (2014). These authors developed a categorization that enables classification of mammalian autopodial elements according to the degree of digestive corrosion: the gradient of modification due to digestive corrosion goes from light and moderate to heavy and extreme (Table 2). Finally, the digestive corrosion observed in the molars of small mammals found in the recent samples was evaluated considering four categories of predators, and based on the classification (light, moderate, heavy and extreme) proposed by Fernández *et al.* (2017).

### Results

#### *Faunistic samples from Gruta do Presépio*

Bones recovered at excavation units N17L51, N18L51 and N17L58 of GPR correspond to mammals and indeterminate splinters (Table 3). The extent of fragmentation (NSP/NISP) shows a very fragmented bone assemblage (mostly in the Early to Middle Holocene), with a high proportion of splinters and a low level of specific identification. Determination of most specimens was possible only to body-size classes (Early to Middle Holocene NISP% = 42.3; Late Holocene NISP% = 51.1). Regarding NISP values, the dasypodid *Dasyypus* sp. (armadillo) and the tayasuid (peccary) were the most represented taxa in both temporal units. In the case of *Dasyypus*, however, the relative value decreases considerably in terms of MNI since most of the elements

**Table 2.** Degrees of digestive corrosive of ingested bones and osteoderms generated by the digestive acids of scavenger birds; used by Ballejo *et al.* (2012), modified from Robert & Vigne (2002a) and Lloveras *et al.* (2008).

Category	Description
Light	Signs of 'attack' invisible to the naked eye, only recognized under stereomicroscope. Less than 25% of the bone surface is affected.
Moderate	Porosity around both articular surfaces. Bone destruction may have occurred, but is very localized.
Heavy	The entire surface of the bone is affected; bone is perforated to the marrow cavity. Advanced bone destruction affects more than 50% of the bone. Extensive rounding of edges. Possible splitting and cracking.
Extreme	Entire parts of the bone missing. Strong rounding of edges. Identification of the bone element is difficult.

Table 3. Relative abundance of taxa recovered from Gruta do Presépio for each temporal unit.

	Weight (kg)	Early–Middle Holocene			Late Holocene		
		NISP	MNE	MNI	NISP	MNE	MNI
Mammalia indet. (medium–large)		5	5	1	16	16	1
Mammalia indet. (medium–small)		28	28	2	73	71	2
Cetartiodactyla indet.		0	0	0	6	5	1
Cervidae indet.		1	1	1	3	3	1
Tayassuidae indet.	26.8	10	9	2	15	15	3
<i>Tapirus terrestris</i>	207.5	2	2	1	0	0	0
Carnivora indet.		12	8	1	1	1	1
Felidae indet.		1	1	1	0	0	0
<i>Puma concolor</i>	51.6	0	0	0	1	1	1
<i>Nasua nasua</i>	3.8	2	2	1	0	0	0
<i>Eira barbara</i>	3.9	1	1	1	2	2	1
<i>Dasypus</i> sp.	2.4	23	21	1	57	43	1
Total		85	78	12	174	157	12
Indet. (splinters)		400			556		
Total NISP		485			730		
NISP/NISP		5.71			4.19		

belonging to this species were osteoderms from the carapace, which are numerous in each individual. Few specimens were recorded for the other taxa recovered from GPR. The mustelid *Eira barbara* (tayra) was recorded in both temporal units. The tapirid *Tapirus terrestris* (lowland tapir) and the procyonid *Nasua nasua* (South American coati) were recorded only in the Early to Middle Holocene unit. The felid *Puma concolor* (puma) was identified in the Late Holocene unit.

Different taphonomic trajectories were observed in the samples studied, encompassing human exploitation and bird scavenging. The samples were affected by postdepositional processes (Table S2). We focus here on the remains deposited by New World vultures (NISP = 144), where digestive corrosion is prevalent (Table 4).

Concerning the small mammal group, the main category of digestive corrosion observed was extreme corrosion, followed by heavy and light (Fig. 2A). In the medium and large mammals all the categories were

present, although most of the bones of medium mammals showed moderate or extreme corrosion (Fig. 2A).

The few remains recovered from the Early to Middle Holocene with evidence of digestive corrosion (an osteoderm (*Dasypus*), a vertebra (small–medium mammal), autopodials (felid and small–medium mammal) and a splinter) showed porosities, rounding of edges, splitting, cracking, large holes and loss of bone tissue compatible with heavy and extreme categories of modification (Table 4). Only the vertebra was fractured. Regarding the Late Holocene, all the corrosion categories were observed in the following proportions: light (29.7%), moderate (7.8%), heavy (23.9%) and extreme (38.4%). Of all the identified digested specimens, 63.1% were broken (Table 4), and limb bones evidenced rough, angular fracture edges. The *Dasypus* osteoderms had a high degree of digestive corrosion, from those with the entire surface affected (29.7%; Fig. 3A) to others with greater damage, observed as a very thin layer of bone

Table 4. Different types of digestive corrosion in bone remains recovered from Gruta do Presépio. F% = fracture %; L = light; M = moderate; H = heavy; E = extreme.

Bone	Early–Middle Holocene						Late Holocene					
	N	F%	L	M	H	E	N	F%	L	M	H	E
Hyoid	0	0	0	0	0	0	1	100	0	0	1	0
Vertebrae	1	100	0	0	0	1	3	100	0	1	1	1
Rib	0	0	0	0	0	0	1	100	0	0	1	0
Humerus	0	0	0	0	0	0	1	100	0	0	1	0
Tibia	0	0	0	0	0	0	2	100	1	1	0	0
Basipodial	1	0	0	0	0	1	2	0	0	2	0	0
Astragalus	1	0	0	0	1	0	3	33	0	1	1	1
Calcaneus	0	0	0	0	0	0	1	0	0	0	0	1
Metapodial	0	0	0	0	0	0	2	0	0	1	1	0
Phalange	1	0	0	0	0	1	12	50	4	4	2	2
Osteoderm	1	0	0	0	1	0	37	70	0	0	11	26
Indet.	1	100	0	0	1	0	73	100	36	1	14	22
Total	6		0	0	3	3	138		41	11	33	53

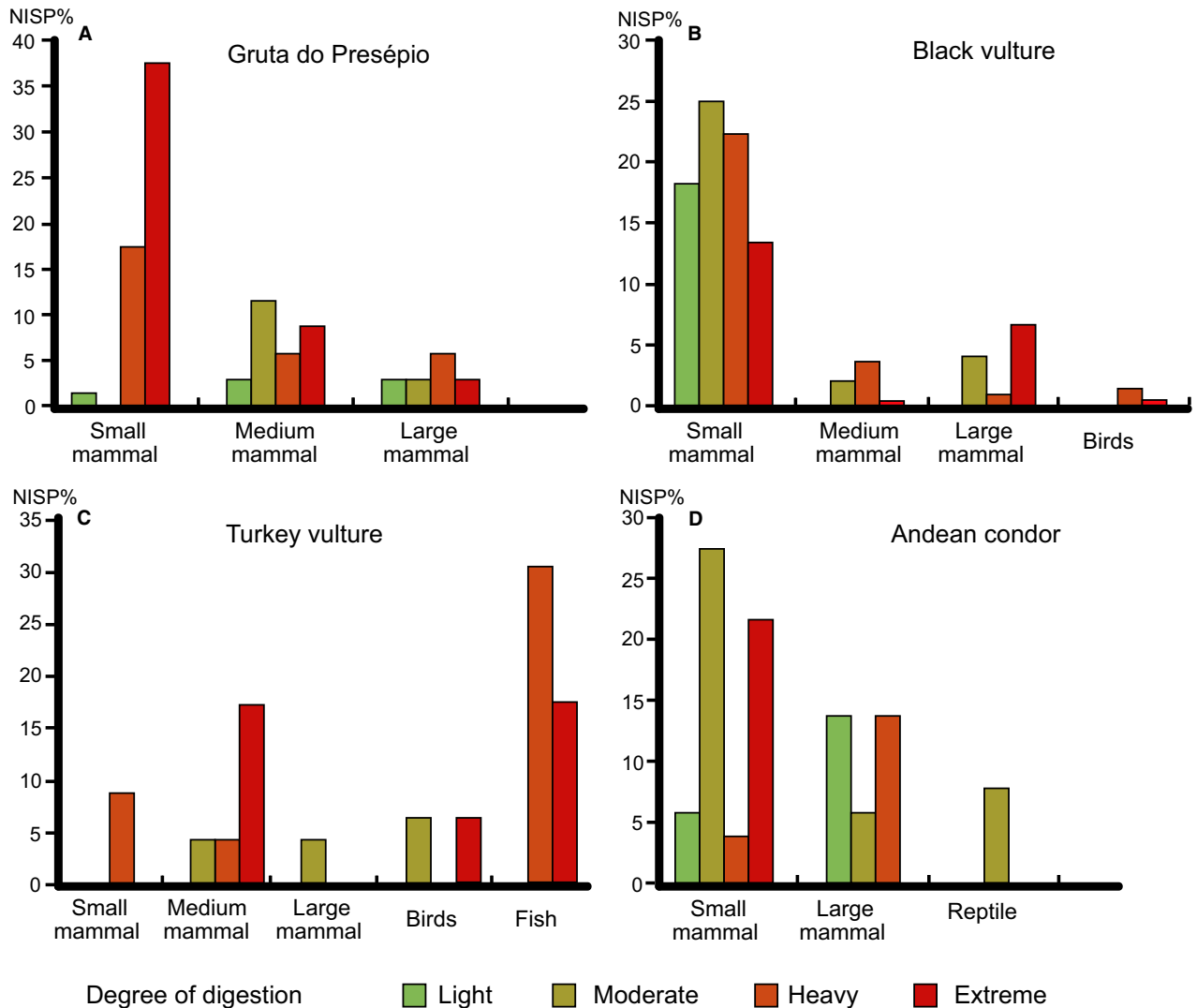


Fig. 2. Percentage degree of digestive corrosion, evaluated for archaeological and scavenger samples. A. Gruta do Presépio. B. *Coragyps atratus*. C. *Cathartes aura*. D. *Vultur gryphus*.

(70.3%; Fig. 3B). Autopodials with digestive corrosion were relatively well represented (Table 4). They mostly consisted of phalanges of cervids, tayasuids and *Dasypus*, with different degrees of digestive corrosion, from those with porosities and perforations (Fig. 3C), to metapodials of small–medium mammals and basipodials, the latter including some unidentified elements that were severely digested: astragali of tayasuids and the calcaneus of a medium mammal (Fig. 3D). In addition, three vertebrae of mammals showed digestive corrosion of a moderate to extreme degree (Fig. 3E). Two tibiae of cervids and one humerus of a medium–large mammal were lightly to heavily corroded. The entire surface of a hyoid fragment belonging to a cervid presented digestive corrosion and broken and rounded ends (Fig. 3F). Finally, several unidentified splinters were found with different degrees of digestive corrosion, mostly light (49.3%) and extreme (30.1%) (Table 4).

#### *Pellet samples of modern New World vultures*

*Coragyps atratus*. – A total of 340 bone and tooth remains in the 344 pellets were found, 43.8% of which corresponded to unidentified fragments. This moderate level of identification is also reflected in the values of the ratio NSP/NISP (Table 5). The majority of identified specimens belonged to the exotic European hare *Lepus europaeus* (NISP = 142), followed by the domestic sheep *Ovis aries* (NISP = 23) and the small cricetid rodent *Reithrodon auritus* (NISP = 8). Finally, unidentified mammals (NISP = 14) and birds (NISP = 4) were also recorded.

All the identified remains showed evidence of digestive corrosion, and 14% were fractured. Regarding the small mammal group, all the categories of digestive corrosion were represented with high frequencies, although most of the bones showed moderate or heavy corrosion

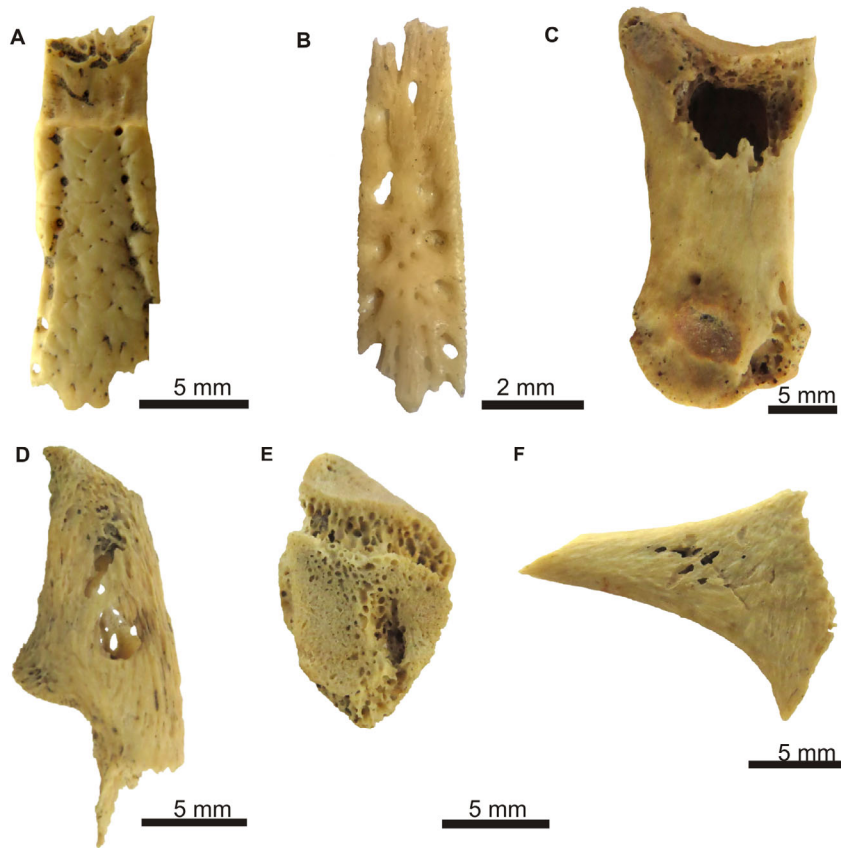


Fig. 3. Examples of bones found in Gruta do Presépio archaeological site (Late Holocene), showing modification attributed to the action of New World vultures. A. Mobile osteoderm of *Dasyypus* sp. with heavy corrosion. B. Mobile osteoderm of *Dasyypus* sp. with extreme corrosion. C. Second phalanx of Cervidae with a large hole close to the proximal articular facet. D. Calcaneus of medium mammal showing surface porosities and perforations. E. Vertebra of medium mammal showing extreme corrosion. F. Hyoid fragment of Cervidae showing heavy digestive corrosion.

(Fig. 2B). In the case of medium mammals, the heavy digestive corrosion category was the most frequent, followed by moderate and extreme. Conversely, the extreme and moderate digestive corrosion categories were higher in bones of large mammals. The few bones of birds exhibited heavy or extreme corrosion (Fig. 2B).

For *L. europaeus* the autopodials were the bones most represented (60.6%), followed by vertebrae (21.8%) and teeth (9.2%). The remaining bones (tibia, patella, radius, maxilla and mandible) were present in even lower proportions. The phalanges (NISP = 71) of this leporid showed different degrees of digestive corrosion, from elements with signs of 'attack' invisible to the naked eye (39.4%), porosity around both articular surfaces (35.2%), to specimens with no bone marrow (16.9%) or only proximal or distal parts remaining (8.5%). In addition, the vertebrae of *L. europaeus* (NISP = 31) displayed strong digestive corrosion (48.4%), followed by extreme (29%) and moderate (22.6%). In the case of *O. aries*, 73.9% of the specimens were incisors showing extreme digestive corrosion. Phalanges of this species (NISP = 5) exhibited a large hole near the proximal

articular facet or entire parts of the bones were missing (Fig. 4A, B). The isolated molars of *R. auritus* showed evidence of moderate and extreme digestive corrosion. Finally, 149 unidentified splinters showed digestive corrosion.

*Cathartes aura*. – A total of 92 bone and tooth remains were recovered from the 96 pellets found (Table 5), 50% of which were unidentified fragments (NSP/NISP = 2). Fish remains were the most represented (NISP = 22), followed by remains of *Lycalopex* sp. (NISP = 12), *L. europaeus* (NISP = 4), and *O. aries* (NISP = 2). Unidentified birds (NISP = 6) were also recorded.

All the identified remains presented evidence of digestive corrosion, and 36% were fractured. Among the small mammal group, the four remains showed heavy corrosion. Most of the bones of the medium mammals showed extreme corrosion, followed by moderate and heavy (Fig. 2C). Among medium mammals the extreme digestive corrosion category predominated, followed by moderate and heavy. The two bones belonging to large mammals presented moderate corrosion. The bones of

Table 5. Different levels of digestive corrosion observed in bone remains recovered from New World vulture pellet samples. F% = fracture %; L = light; M = moderate; H = heavy; E = extreme.

	<i>Coragyps atratus</i>						<i>Cathartes aura</i>						<i>Vultur gryphus</i>					
	NISP	F%	L	M	H	E	NISP	F%	L	M	H	E	NISP	F%	L	M	H	E
Skull	1	100	0	0	0	1	3	100	0	0	2	1	0	0	0	0	0	0
Hyoid	0	0	0	0	0	0	0	0	0	0	0	0	5	20	0	1	4	0
Maxilla	6	100	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0
Mandible	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1
Incisor	25	0	2	7	4	12	2	0	0	2	0	0	0	0	0	0	0	0
Molar	10	0	0	2	3	5	2	0	0	0	2	0	0	0	0	0	0	0
Vertebrae	33	33	0	7	16	10	23	100	0	0	14	9	14	29	0	5	1	8
Sacrum	0	0	0	0	0	0	0	0	0	0	0	0	1	9	0	0	0	1
Rib	4	0	0	1	3	0	0	0	0	0	0	0	13	85	7	3	3	0
Sternum	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Scapula	0	0	0	0	0	0	1	0	0	0	0	1	1	100	0	1	0	0
Humerus	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelvis	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Femur	1	100	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Radius	1	100	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tibia	2	100	0	0	1	1	0	0	0	0	0	0	1	100	0	0	1	0
Patella	6	0	0	2	3	1	0	0	0	0	0	0	2	0	0	1	0	1
Sesamoid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astragalus	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Calcaneus	2	0	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0
Metapodial	12	75	2	10	0	0	6	100	0	0	0	6	3	100	0	3	0	0
Phalange	80	25	30	30	13	7	7	29	0	4	1	2	10	30	3	7	0	0
Total	191	14	35	61	54	41	46	36	0	7	20	19	51	23	10	21	9	11
Indet.	149						46						52					
Total NSP	340						92						103					
NSP/NISP	1.78						2						2.02					

birds exhibited moderate and extreme corrosion, while the bones of fishes evidenced heavy and extreme corrosion (Fig. 2C).

In the case of fishes, 63.6% of vertebrae suffered strong digestive corrosion, with destruction of their haemal and neural spines. The other vertebrae displayed extreme digestive corrosion, where almost the entire bone was altered. The entire surface of the metapodials of *Lycalopex* sp. (NISP = 6) were corroded, leaving the edges of the bones markedly thinned or broken. All the phalanges of this canid (NISP = 5) presented porosities: in most cases they had perforations and the proximal or distal articular facets were missing. The calcaneus of this species showed porosity and destruction in the posterior part (Fig. 4C). In addition, the enamel of *L. europaeus* molars was reduced to small islands on the dentine, a clear indication of heavy digestion. The incisors of *O. aries* (NISP = 2) suffered moderate digestive corrosion, the enamel being removed only in parts, mainly at the edges. Finally, 46 unidentified splinters were affected by digestive corrosion.

*Vultur gryphus*. – A total of 103 bone and tooth remains were found in the 171 pellets (Table 5), 50.5% of which were undetermined fragments (NSP/NISP = 2.02). Most of the identified specimens corresponded to *L. europaeus* (NISP = 28), followed by bones of *O. aries*

(NISP = 16) and of cervids (NISP = 1). Finally, undetermined mammals (NISP = 2) and reptiles (NISP = 4) were found.

All the identified remains presented evidence of digestive corrosion, 23% being fractured. In the small mammal group all the categories of digestive corrosion were represented, although most of their bones showed moderate or extreme corrosion (Fig. 2D). In contrast, the light and heavy corrosion categories were more frequent in bones of large mammals, followed by moderate corrosion. The few bones found of reptiles displayed moderate corrosion (Fig. 2D).

The phalanges (NISP = 10) and metapodials (NISP = 3) of *L. europaeus* suffered digestive corrosion mostly on the articular surface. The vertebrae (NISP = 7) of this leporid were severely damaged and fragmented, with extreme corrosion in all cases. Mandibles (NISP = 1) of *L. europaeus* showed heavy corrosion. In addition, the ribs (NISP = 3) of this species were affected by moderate or heavy corrosion. The ribs (NISP = 10) of *O. aries* corresponded to medial fragments, with light (NISP = 7), moderate (NISP = 1) and heavy (NISP = 2) digestive corrosion (Fig. 4D). Hyoid fragments (NISP = 5) of this species were recovered with moderate (NISP = 1) and heavy (NISP = 4) digestive corrosion (Fig. 4E). A vertebra of *O. aries* was found that had its entire surface affected (Fig. 4F). Finally, 52 unidentified splinters were found.





Fig. 4. Examples of digestive bone modification found in recent samples of New World vultures. *Coragyps atratus*: A–B. First and third phalange of *Ovis aries* showing heavy corrosion. *Cathartes aura*: C. Calcaneus of *Lycalopex* sp. with moderate corrosion. *Vultur gryphus*: D. Rib fragment of *O. aries* with heavy corrosion. E. Hyoid of *O. aries* with heavy corrosion. F. Vertebra of *O. aries* with heavy corrosion.

## Discussion

### *New World vultures as accumulators in Gruta do Presépio*

The skeletal remains recovered from the New World vulture pellets analysed here were represented by a small number of elements in relation to the number of pellets; thus, very large pellet deposits of these scavenger birds are required in order to accumulate a large bone assemblage. The three actualistic samples had therefore to be combined due to their small size. Figure 5 shows the comparison of levels of digestive corrosion from the Late Holocene GPR and the average of the three modern species of Cathartidae. If all the available samples are considered together, a different pattern of digestive corrosion is observed, mostly in the categories light, moderate and extreme. The archaeological sample also shows an increasing trend towards the categories of greater bone damage (Fig. 5A). In these samples, there is a positive correlation between the values for categories in the archaeological and actualistic samples, but this is low and not significant ( $r_s = 0.2$ ;  $p = 0.92$ ). However, when small mammals are excluded from the computations this positive correlation is stronger ( $r_s = 0.4$ ;  $p = 0.75$ ), although it drops to high negative values when the small mammals are considered separately ( $r_s = -0.8$ ;  $p = 0.33$ ). The non-significant results of these correlations, coupled with the small sample size, hinders the scope of our interpretation; however, this does not preclude observation of general trends. To sum up, it is

clear that the archaeological and actualistic samples show more similar digestive corrosion patterns for medium and large mammals (Fig. 5B) than for small mammals (Fig. 5C).

The samples of the three New World vulture species have similar fragmentation index values (NSP/NISP), close to 2 (Table 5), as a consequence of the splinters found (roughly 50% of the total), which have no precise taxonomic identification. The higher fragmentation recorded in these archaeological samples (Table 3), most of which had rough, angular fracture edges, were probably increased by trampling, a common postdepositional taphonomic process in caves and rockshelters where circulation space is restricted (e.g. Andrews 1990; Lyman 1994).

In both archaeological and actualistic samples, the autopodial elements (mostly phalanges) were the most digested (Tables 4, 5). Despite phalanges not being of value nutritionally, they are common in zooarchaeological records generated by humans because they are frequently collected along with elements of higher nutritional content (i.e. entire limbs). In addition, the phalanges are often associated with skinning processes, and may be transported for later use as tools (e.g. Binford 1981; Lyman 1994; Politis *et al.* 2011). In this sense, the high levels of digestive corrosion (mainly porosities, perforation, rounding of edges and missing parts) on phalanges could provide a clue as to how to discriminate the New World vulture assemblages from those accumulated by humans (Ballejo *et al.* 2012). In addition, the congruence observed in the findings of digested hyoids of large mammals in GPR (Fig. 3F) and in *Vultur gryphus* pellet samples (Fig. 4E) may be related to ingestion of this bone by scavenger birds when they eat the tongue (e.g. Bellati & von Thungen 1990). In contrast, when humans remove the tongue of large prey they do not ingest the hyoid, leaving only cut marks from the use of tools (e.g. Kooyman *et al.* 2006: fig. 4; Merritt 2017). Unlike the findings for scavenger birds, there are no records of digestion marks in hyoids found in the scat of carnivorous mammals. Bones ingested by carnivorous mammals are affected by both digestive acids and the action of mastication. Thus, an important overall difference between the bone remains accumulated by these two agents is the high level of breakage, crenulation and holes found in bones due to the chewing action of mammals and the frequency of skeletal elements (bone remains decrease as prey size increases) in carnivore scats, suggesting that smaller prey items were swallowed without much chewing (e.g. Martin & Borrero 1997; Montalvo *et al.* 2007; Mondini 2017; Montalvo & Fernández 2019). For example, bones recovered from scats of the large felid *Puma concolor* yield fragmentary remains with light to heavy categories of digestive corrosion, crenulation and tooth marks (e.g. Martin & Borrero 1997; Borrero *et al.* 2005, 2018; Montalvo *et al.* 2007; Mondini & Muñoz 2008; Muñoz *et al.* 2008;

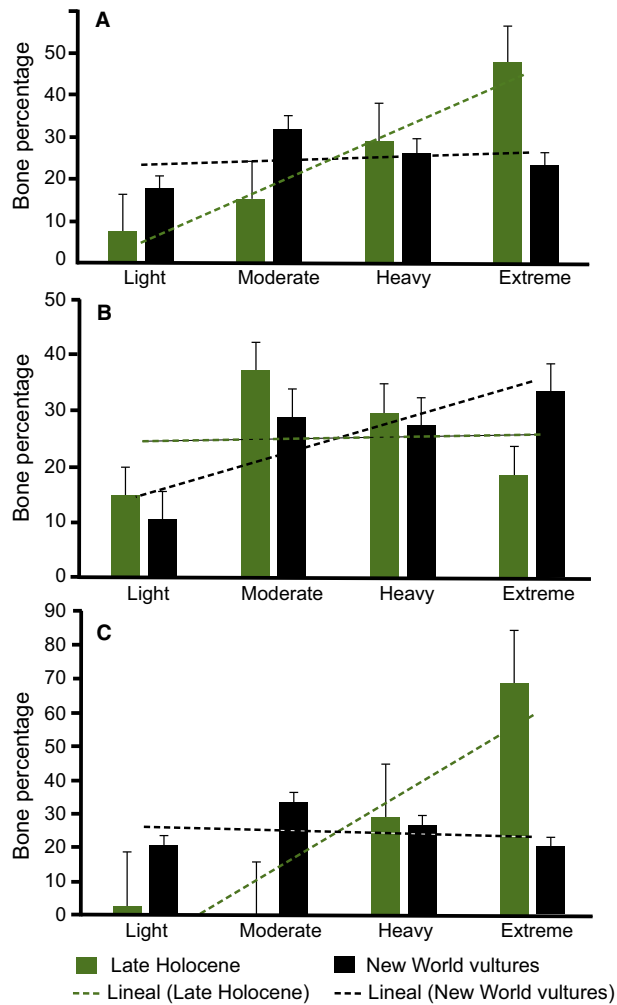


Fig. 5. Histograms showing the proportions of digestive corrosion categories of bones from the Late Holocene found in Gruta do Presépio, and the average of the three modern species of Cathartidae analysed here. A. All mammal body sizes. B. Medium and large mammals. C. Small mammals.

Mondini 2017; Montalvo & Fernández 2019). In addition, smaller carnivores such as the felid *Leopardus geoffroyi*, the mephitid *Conepatus chinga*, and canids of the genus *Lycalopex*, produce bone and tooth modifications with crenulations, tooth marks, and a high proportion of breakage and digestive corrosion, including all the categories, because their chewing crushes their prey before ingestion (e.g. Mondini 1995, 2017; Gómez & Kaufmann 2007; Montalvo *et al.* 2008, 2012; López *et al.* 2017; Montalvo & Fernández 2019; Scheifler *et al.* 2020).

Figure 6 shows comparison of the curves of MNE% (for endoskeletal elements) of the Late Holocene in GPR, the average of samples of the three modern species of Cathartidae, and samples of carnivorous mammals. Archaeological and actualistic samples are quite similar, yielding high values of phalanges and vertebrae, although the Late Holocene sample is richer in osteo-

derms than the modern samples. High levels of autopodial elements and some osteoderms were also found in previous actualistic studies of *C. atratus* pellet samples from northwestern Patagonia (Ballejo *et al.* 2012: figs 2e, 3). Otherwise, these characteristics differ from the bone assemblages made by facultative scavenger birds of the area, such as *Caracara plancus* and *Milvago chimango*. Both species can feed on the carcasses of medium and large animals but cause little damage to them; they do not usually ingest bone remains and so there are none present in their pellets (Montalvo & Fernández 2019 and references cited therein). Regarding the carnivorous mammals of South America, in central Argentina *P. concolor* scats contain abundant metapodials, vertebrae, femora, tibiae, humeri, ulnae and osteoderms mainly belonging to ungulates, carnivores, armadillos, lagomorphs and rodents (Montalvo *et al.* 2007). In southern Patagonia, this large felid accumulated a high proportion of vertebrae, ribs and autopodial elements (mainly carpals) of *O. aries* in several lairs located in a rockshelter and on its slope (Martin & Borrero 1997). In central east Argentina, *Lycalopex griseus* scats contain high levels of skulls, isolated teeth and vertebrae (Gómez & Kaufmann 2007). Furthermore, a high number of autopodials of large mammals were transported to a rockshelter by the canid *Lycalopex* in northwestern Argentina (Mondini 1995). In contrast, small felids, mainly of the genus *Leopardus*, can accumulate a high proportion of small mammal skulls and long bones (Montalvo *et al.* 2012; López *et al.* 2017; Montalvo & Fernández 2019; Scheifler *et al.* 2020).

Taphonomic analysis of the New World vulture pellet samples presented here showed some similarities with taphonomic results based on pellets of the bearded vulture (*Gypaetus barbatus*) recovered from locations in western Europe (Robert & Vigne 2002a, b; Marín-Arroyo *et al.* 2009; Marín-Arroyo & Margalida 2012). This Old World vulture generates accumulations that include bones of small (leporids), medium (carnivores) and large mammals (ungulates), with a higher number of phalanges than other elements; its digestive acids can remove the superficial layers of bone, especially in the articulations, exposing the spongy tissue. However, in contrast to the New World vultures, *G. barbatus* fractures the bones markedly before ingestion, dropping them over rocky areas, leading to breakage patterns similar to human marrow processing (Robert & Vigne 2002a, b; Marín-Arroyo *et al.* 2009; Marín-Arroyo & Margalida 2012). The Egyptian vulture (*Neophron percnopterus*), on the other hand, produces bone assemblages with few elements that show digestive corrosion (Sanchis Serra *et al.* 2013; Lloveras *et al.* 2014). This Old World vulture can transport uneaten remains to its nest, frequently located in caves and rockshelters, and causes perforations in the bones using its beak. In addition, the bone assemblages generated by *N. percnopterus* vary in anatomical representation

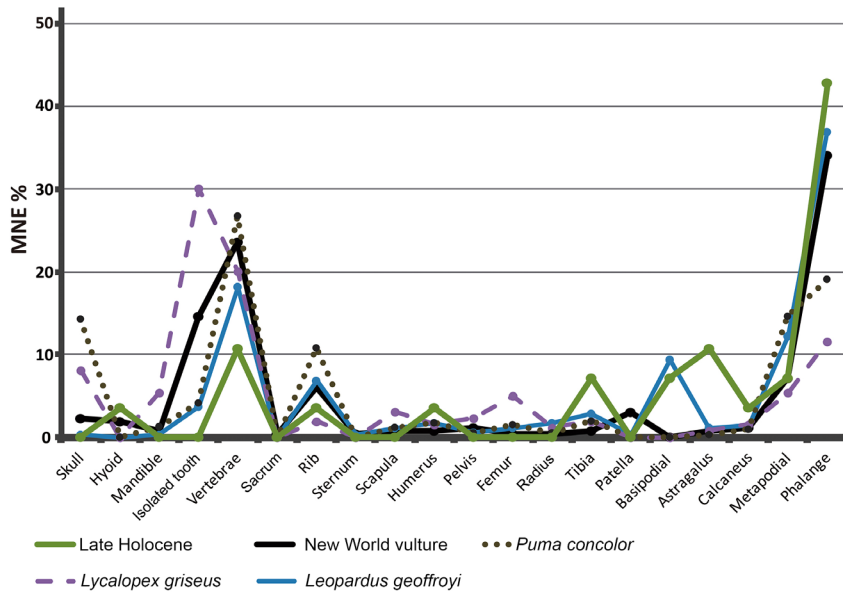


Fig. 6. Taphonomic comparison of Late Holocene endoskeletal elements from Gruta do Presépio and actualistic data of modern New World vulture, *Puma concolor* (Montalvo *et al.* 2007), *Lycalopex griseus* (Gómez & Kaufmann 2007) and *Leopardus geoffroyi* (Scheifler *et al.* 2020).

according to prey size, and show greater taxonomic diversity than assemblages accumulated by New World vultures (Lloveras *et al.* 2014).

Ballejo *et al.* (2012) proposed two taphonomic models for New World vultures as accumulators in the fossil record: (i) open-air sites, containing most skeletal parts (but no autopodials) of medium and large vertebrates, showing non-penetrating scratches and scratches of shallow penetration, notches, and some punctures in skulls, mandibles, and scapulae; and (ii) rockshelter or cave sites, containing pellets or their remains, with high relative abundance of bones of medium vertebrates that show strong digestive corrosion, and autopodials of large mammals also with strong digestive corrosion. Considering both scenarios, on bones recovered from GPR there is no evidence of notching on the edges, punctures, or scratches that could be associated with the action of vultures when they scavenge on the carcasses at the site of the animal's death (Reeves 2009; Lloveras *et al.* 2014). Therefore, the findings of autopodials (mainly phalanges) of medium and large mammals and armadillo osteoderms with a high degree of digestive corrosion but no tooth marks can be related to a pellet deposit pattern of New World vultures (Ballejo *et al.* 2012; Ballejo 2016).

To summarize, the New World vultures can contribute to archaeological site formation in different ways: by removing bone elements or fragments from the original carcass and depositing them in distant areas, or introducing elements from an external carcass into the archaeological site (Fig. 7). All this could happen on the same time scale, possibly introducing an equifinality issue if the taphonomic features of these scavenger birds are not correctly differentiated from those produced by

humans and scavengers. The bones contained in the pellets of these scavenger birds can easily become mixed in with faunal remains discarded from human food, as recorded at GPR (Fig. 7, Table S2). This archaeological palimpsest highlights the importance of taphonomic study of all the remains recovered at a site, and comparison with actualistic taphonomic models. In addition, it is also important to bear in mind that taphonomic identification of New World vultures as accumulators in archaeological sites can prevent incorrect palaeoeconomic and palaeoenvironmental interpretation (Ballejo *et al.* 2012).

#### *Palaeoecology of the New World vultures at Gruta do Presépio*

Seven mammalian taxa were identified from the excavation units N17L51, N18L51 and N17L58 of GPR, including one Dasypodidae, one Felidae, one Tayassuidae and one Cervidae; four of these taxa came from pellets deposited by New World vultures. New World vultures can roost and nest in rockshelters and feed on different types of vertebrates, mostly mammals of any size. The dietary versatility of Cathartidae members depends primarily on the availability of carrion, which is why they currently feed primarily on cattle; however, in areas where cattle are scarce, they expand their diet to include native taxa similar to those found deposited in GPR by these birds (e.g. Coleman & Fraser 1987; Kelly *et al.* 2007; Lambertucci *et al.* 2009; Ballejo & De Santis 2013; Ballejo 2016). Only the medium and large carnivorous mammals such as the felids *Panthera*, *Puma* and *Leopardus*, and the canids *Lycalopex* and *Speothos*

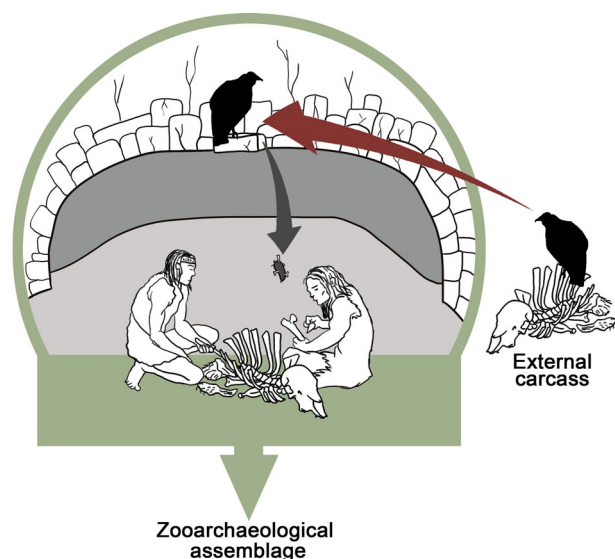


Fig. 7. Schematic model of New World vultures intervening in the zooarchaeological context by removing bone elements or fragments from a dead animal at an external site and depositing them in an archaeological site; the elements then become mixed in with faunal remains discarded from human food.

can predate on large mammals such as tayasuids and cervids (Redford & Eisenberg 1992; Wilson & Reeder 2005; Moreno *et al.* 2006). It is interesting to note that *Panthera*, *Puma* and *Lycalopex* can transport prey or bones to rockshelters or caves (e.g. Mondini 1995, 2017; Borrero *et al.* 2018).

Regarding palaeoenvironmental/climatic reconstructions, palynological studies indicated a colder climate than today in the Late Pleistocene in Santa Catarina, which was corroborated by isotopic study of stalagmites from the Botuverá cave. During the Middle to Late Holocene, forest establishment was associated with increased moisture (Behling 1998; Behling & Negrelle 2001; Cruz *et al.* 2006; Oliveira *et al.* 2012; Behling & Oliveira 2018; Val-Peón *et al.* 2019). Mammals recorded in the GPR excavation units corroborated these data, since *Tapirus terrestris*, *Nasua nasua* and *Eira barbara* occur predominantly in forest, occasionally feeding in or crossing open environments (e.g. agricultural fields, grasslands). The other taxa recorded in GPR, such as *Dasyopus*, Cervidae and Felidae, also occur in open and forested environments (Cáceres *et al.* 2007). It is possible that the absence of *N. nasua*, *T. terrestris* and Tayassuidae in the Late Holocene is related to a preservation issue in these excavation units, since these species were found in the internal part of the rockshelter (excavation area 1) and currently inhabit the study area, as does *E. barbara* (Dragoo 2009; Keys 2009).

## Conclusions

A pellet deposit pattern of New World vultures (Cathartidae) could be recognized in the sum of taphonomic

attributes observed in the faunal assemblages recovered from the Holocene period of the GPR excavation units N17L51, N18L51 and N17L58: the findings of autopodials (mostly phalanges), hyoids of medium and large mammals, and armadillo osteoderms with a high degree of digestive corrosion (mainly with porosities, perforation, rounding of edges and missing parts) but no tooth marks. In fact, this is the first fossil record of a bone assemblage accumulated by these scavenger birds. This conclusion was arrived at through comparison with actualistic taphonomy information derived from pellet samples belonging to three members of the family Cathartidae currently inhabiting northwestern Patagonia: *Coragyps atratus*, *Cathartes aura* and *Vultur gryphus*.

The New World vultures can roost and nest in rockshelters and feed on different types of vertebrates. Seven mammal taxa associated with forest environments were identified from units N17L51, N18L51 and N17L58 of GPR, including some native taxa (Cervidae, Dasypodidae, Felidae and Tayassuidae) frequently consumed today by these scavenger birds when livestock are scarce. Four of these taxa were found in pellets deposited by Cathartidae.

The bone and tooth remains contained in pellets regurgitated by these scavenger birds were found together with faunal remains discarded by humans that inhabited GPR from the Early to the Late Holocene. Palimpsests are a common feature in archaeological and palaeontological deposits and always require detailed taphonomic analysis, which is fundamental for palaeo-economic and palaeoecological interpretation.

*Author contributions.* – LB and JSM conceived, and acquired funding for the project, and with PH, JJC and ABM collected the material from GPR. FJF and FB conducted taphonomic analysis. FB conducted fieldwork and analysis of recent Cathartidae material. FB, FJF and PH prepared the figures. All authors participated in writing and revising the manuscript.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at <http://www.boreas.dk>.

*Table S1.* Taxa found in New World vulture pellet samples from northwestern Patagonia: number of identified specimens per taxon –NISP– (minimum number of individuals –MNI–). 1. Chacabuco I, Neuquén province (40°35'41.45"S, 70°58'16.81"W); 2. Chacabuco II, Neuquén province (40°37'49.99"S, 70°59'17.30"W); 3. Chaqueñita, Río Negro province (40°52'49.04"S, 70°39'35.05"W); 4. Chocón, Neuquén province (39°15'38.12"S, 68°46'42.55"W); 5. Condor-erita, Río Negro province (40°50'27.99"S, 71°2'12.06"W); 6. Dina Huapi, Río Negro province (41°04'47.15"S, 71°09'27.84"W); 7. El Condor I, Río Negro province (41°11'57.84"S, 71°03'45.15"W); 8. El Condor II, Río Negro province (41°09'16.93"S, 71°04'33.76"W); 9. Fragua Grande, Río Negro province (41°02'36.05"S, 71°00'46.93"W); 10. Isla Victoria, Neuquén province (40°58'42.15"S, 71°31'08.75"W); 11. Jones, Neuquén province (40°59'16.73"S, 71°15'47.07"W); 12. La Buitrera, Río Negro province (41°17'35.07"S, 71°08'45.06"W); 13. Las Estacas, Neuquén province (40°49'53.28"S, 71°34'04.16"W); 14. Los Coihues, Río Negro province (41°09'10.28"S, 71°24'11.87"W); 15. Pipilcura, Río Negro province (40°56'48.80"S, 70°51'46.13"W).

*Table S2.* Taphonomic modification of bones from Gruta do Presépio for each temporal unit. C = complete; F = fracture; TA = thermoalteration; CM = cut marks; NF = negative flake scars; DC = digestive corrosion; E = extreme with hole; H = heavy; M = moderate; L = light.