



Artículo

TAPHONOMIC ANALYSIS OF RODENT BONES FROM *Lontra longicaudis* (MUSTELIDAE, CARNIVORA) SCATS IN FLUVIAL ENVIRONMENTS

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ABSTRACT. The Neotropical otter (*Lontra longicaudis*, Mustelidae, Carnivora) is defined as a generalist carnivore. Although it is a fish-crustacean feeder, rodents are commonly found in its diet, though less frequently. In order to learn about the effects that this predator produces on its prey's bones, we conducted taphonomic analysis of bone remains from scats collected in a riparian habitat of Santa Fe, Argentina. The results were compared with data of other carnivore mammals and such comparison confirmed that *L. longicaudis* produced severe destruction of bones. The evaluation of the degree of digestion showed a high number of bone remains and teeth with heavy and extreme modifications. This allows the inclusion of *L. longicaudis* in the category of extreme modifier of its prey's bones. This taphonomic study shows that *L. longicaudis* is an active accumulator of rodent remains, when this type of prey is available in the environment. The data presented in this paper provide criteria to identify the activity of this predator produced in archaeological and paleontological sites linked to fluvial environments.

RESUMEN. Análisis tafonómico de huesos de roedores en heces de *Lontra longicaudis* (Mustelidae, Carnivora) en ambientes riparios. El lobo de río *Lontra longicaudis* (Mustelidae, Carnivora) se define como un carnívoro generalista. Si bien se alimenta principalmente de peces y crustáceos, los roedores constituyen parte de su dieta, aunque en proporciones menores. Con la finalidad de evaluar los efectos que este depredador provoca en los huesos de sus presas, se analizaron tafonómicamente restos óseos de roedores recuperados de heces colectadas en un hábitat ribereño en la provincia de Santa Fe, Argentina. Los resultados fueron comparados con datos obtenidos de muestras de otros mamíferos carnívoros y confirman que *L. longicaudis* produce una destrucción muy marcada de los huesos. La evaluación de los grados de digestión indica un número alto de restos óseos y dientes con modificaciones fuertes y extremas. Por lo expuesto, se incluye a este depredador en la categoría extrema de modificación de los huesos de sus presas. El estudio tafonómico muestra que *L. longicaudis* es un activo acumulador de restos de roedores cuando estos tipos de presa están disponibles en el ambiente. Los datos que se presentan proporcionan criterios para identificar la posible acción de este depredador en yacimientos arqueológicos y paleontológicos vinculados a ambientes fluviales.

Key words: Actualistic taphonomy. Bone modifications. Carnivora. Rodent prey. *Lontra longicaudis*.

Palabras clave: Carnívora. *Lontra longicaudis*. Modificaciones óseas. Roedores presa. Tafonomía.

INTRODUCTION

Several archaeological and paleontological localities linked to fluvial environments in Argentina (e.g., Parana River basin) are rich in small mammals remains (Tonni et al., 1985; Santiago, 2004; Acosta and Pafundi, 2005; Teta et al., 2004, 2005, 2013; Sartori, 2010; Bonomo et al., 2010, 2011a, 2011b; Politis et al., 2011; Sartori and Colasurdo 2011; Sartori and Pérez Jimeno, 2012; Acosta et al., 2010; Acosta and Loponte, 2013). The formation of these assemblages is the result of a series of different taphonomic processes. Hence, taphonomic evaluation is important to document the processes and agents that may have allowed the preservation of such record. Diurnal and nocturnal raptors and carnivore mammals are the most common agents that produce small-mammal assemblages (Fernández-Jalvo, 1995; Matthews et al., 2006; Gómez, 2007; Gómez and Kauffman, 2007; Montalvo et al., 2008, 2012; Stoetzel et al., 2011). However, the appropriate interpretation of fossil or archaeological accumulations depends on having a detailed knowledge of the modern accumulations produced by different types of predators, including humans. The distinction of predation as a way of accumulating is mainly based on digestion damage, degree of breakage and anatomical representation (Dodson and Wexlar, 1979; Andrews, 1990; Fernández-Jalvo and Andrews, 1992). Andrews (1990) and Fernández-Jalvo and Andrews (1992) have established a systematic methodology to recognize the predator according to the features found on the small mammal bones related to the predator's way of ingestion and digestion.

In this regard, carnivore mammals are one of the groups that can accumulate small mammal remains in latrines, burrows, territorial demarcation areas and feeding areas (Andrews and Evans, 1983; Andrews, 1990; Mondini, 2000, 2003).

The Neotropical otter *Lontra longicaudis* (Mustelidae, Carnivora) is a semi-aquatic mammal (Larivière, 1999). It is the only *Lontra* species with a rhinarium variable in shape (Davis, 1978); the body mass of adults ranges from 5 to 15 kg (Harris, 1968), but it is generally

less than 12 kg (Bertonatti and Parera, 1994; Larivière and Jennings, 2009). This species is the most widely distributed of the three South American species of *Lontra*, occurring from central to southeastern Argentina and Uruguay (Chehebar, 1990; Emmons and Feer, 1997; Barquez et al., 2006; Larivière and Jennings, 2009; Vezzosi et al., 2014), and from sea level to an altitude of 3885 m (Castro-Revelo and Zapata-Río, 2001; Ribeiro and Miotto, 2010). It is generally solitary except during the breeding season (Emmons and Feer, 1997; Eisenberg and Redford, 1999; Larivière, 1999; Perini et al., 2009). Habitat requirements include a wide variety of tropical and temperate freshwater ecosystems with ample riparian vegetation and abundant potential den sites (Bertonatti and Parera, 1994; Soldateli and Blacher, 1996; Gori et al., 2003).

In Argentina, their spatial distribution and diet have been studied in the provinces of Misiones, Corrientes and Salta (Parera, 1993, 1996 a, 1996b; Gil, 1998; Gori et al., 2003). Detailed information about food habits and diet defined the Neotropical otter as a generalist (Wozencraft, 1993; Spínola and Vaughan, 1995; Macías Sánchez and Aranda, 1999), even opportunistic carnivore (Gallo-Reynoso et al., 2008; Bastazini et al., 2009; Perini et al., 2009). Fish and crustacean have been reported as the main food items of its diet, followed by insects, mollusks, amphibians, reptiles, birds and mammals (Macías-Sánchez and Aranda, 1999; Colares and Waldemarin, 2000; Carvalho-Junior et al., 2010; Vezzosi et al., 2014). Fruit remains and vegetal fragments were recorded in the feces; this consumption could be due to the high availability of these resources and to the easiness to catch them, regardless of the other more frequent items in its diet (Quadros and Monteiro-Filho, 2000; Quintela et al., 2012). Medium size mammal remains occurred in several samples, but small mammals (mainly rodents) are commonly found in the Neotropical otter diet, although at low frequencies (Quintela et al., 2012 and references therein).

Neotropical otter resting sites are generally close to water and may be built among tree roots in river banks (Quadros and Monteiro-

Filho, 2002; Vezzosi et al., 2014). These forest riparian environments play an important role in the formation of shelters, holts, couches, hovers, dens and sprainting sites (Quadros and Monteiro-Filho, 2002; Kasper et al., 2008). But the Neotropical otter seems to prefer solid, dry and high platforms (e.g., root systems, rocks and planks under a bridge) for sprainting in open environments with dense vegetation (Alarcon and Simões-Lopes, 2003; Gori et al., 2003). However, when these surfaces are not available, they accumulate their feces on the humid and frequently flooded surface. This activity would favor the incorporation of bone material into the archaeological or paleontological record.

The primary goal of this work is to analyze the digestive modifications produced by the Neotropical otter on the bones of its small mammal prey, which are unknown. Although these otters consume vertebrates other than mammals, we are interested in the modifications occurred on rodent bones, in order to compare these changes with those produced by other predators from the Neotropical region. Diagnostic features can be used to evaluate their role as contributor of bone accumulations in archaeological and paleontological assemblages.

MATERIALS AND METHODS

A sample of 320 feces was recovered from a riparian habitat along the banks of arroyo Potrero at 31°30'52" S, 60°29'51" W; a stream located 35 km from the city of Santa Fe, Argentina (Fig. 1). This area was characterized as a multiple use environment (Vezzosi et al., 2014). The stream is part of the floodplain of

the Leyes river that flows across the Paraná alluvial valley, and it is nearly perpendicular to the main direction of the Paraná river (Iriondo et al., 2007). The feces were cleaned following the methodology described by Kasper et al. (2008). The resulting prey items of Neotropical otter, composed of different hard (bones) and soft (skin and hair) tissue, were previously used for dietary studies (see Vezzosi et al., 2014). Only rodent bones were taphonomically evaluated, because rodents are the prey most frequently recorded and analyzed in taphonomic studies of small prey of carnivorous mammals. In this regard, there is taphonomic assessment data obtained from accumulations produced by other terrestrial carnivores using the same methodology. This proves they constitute valid references for comparisons. For the osteological identifications, we used the reference collections of the Museo Provincial de Ciencias Naturales "Florentino Ameghino" (Santa Fe, Argentina) and the osteological collections of Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina).

The minimum number of specimens (NISP), minimum number of individuals (MNI) and minimum number of skeletal elements (MNE) were calculated following Badgley (1986). MNI of rodents was calculated using the lower incisors, both in situ and isolated, using only the portion of tooth containing the tip.

The taphonomic analysis followed the methodology proposed by Andrews (1990) and Fernández-Jalvo and Andrews (1992), which includes an assessment of:

1. The relative abundance of rodent skeletal elements considering the representation of each one in the context of the MNI, $[MNE_i/(E_i \times MNI)] \times 100$, where the MNE_i is the minimum number of particular skeletal elements in the sample and E_i is the expected number of that skeletal element in an individual.

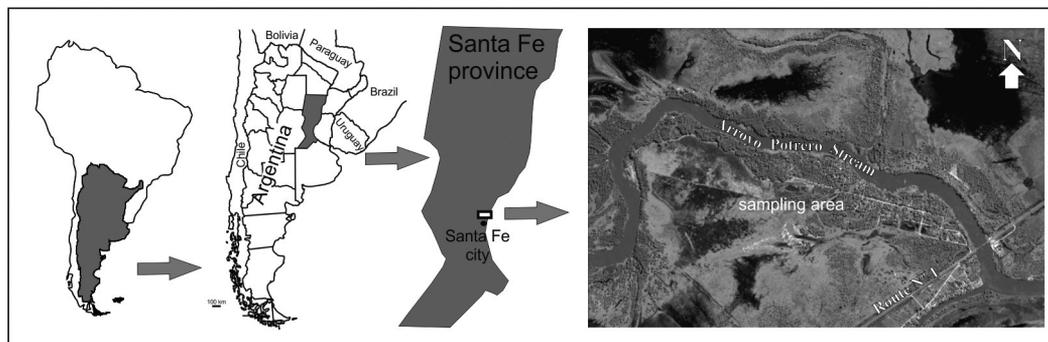


Fig. 1. Geographic location of the sampling area in Santa Fe province, Argentina.

2. The proportion of the different rodent bones in the sample has been calculated by means of three different indexes (see Andrews, 1990): (a) postcranial remains vs. cranial remains, calculated by comparing the number of humeri plus femora to the number of mandibles plus maxillae $(f+h)/(md+mx)$; (b) the abundance of five postcranial elements (humerus, radius, ulna, femur and tibia) compared to the abundance of mandibles, maxillae and isolated molars (pc/c) , and (c) the loss of distal limb elements, as shown by an index comparing the number of tibiae and radii with the number of femora and humeri in the sample $(t+u)/(f+h)$.

3. The degree of breakage considering the complete remains separately from the different parts of long bones (proximal and distal epiphyses, and diaphyses) was also calculated. The mean percentages of fragmentation of cranial and postcranial elements (number of broken bones out of total number of bones; Souttou et al., 2012) were evaluated. In order to compare these data with those available from other Neotropical mammals, these percentages were only evaluated on maxillae, mandibles, femora, humeri, tibiae, and ulnae.

4. The degree of digestive corrosion produced on teeth (incisors and molars), proximal fragments of femora, and distal parts of humeri was studied.

RESULTS AND DISCUSSION

Diet composition

The Neotropical otter would be best defined as a generalist, even opportunistic, carnivore that includes crustaceans, fish and, in lower proportion, small mammals and insects among its prey (Vezzosi et al., 2014). Small rodents represent the most common mammalian items found in the majority of the investigations concerning the feeding habits of the Neotropical otter (e.g. Helder and Andrade, 1997; Pardini, 1998; Larivière, 1999; Alarcon and Simões-Lopes, 2004; Kasper et al., 2004a, 2004b, 2008; Quintela et al., 2008, 2012; Vezzosi et al., 2014). Nevertheless, some larger mammals have also been mentioned as potential prey in the diet of this species: armadillos (Cingulata, Dasypodidae), coypu *Myocastor coypus* (Rodentia, Myocastoridae), capybara *Hydrochoerus hydrochaeris* (Rodentia, Hydrochoeridae), white eared opossum *Didelphis albiventris* (Didelphimorphia, Didelphidae) and Andean hog-nosed skunk *Conepatus chinga* (Carnivora, Mephitidae) (Co-

lares and Waldemarin, 2000; Quintela and Gatti, 2009; Quintela et al., 2008, 2012). However, none of these studies mentioned what type of bone remains allowed the identification of the species listed above, except Quintela and Gatti (2009) that reported the presence of osteoderms of armadillos in the feces analyzed.

In Corrientes (Argentina), Neotropical otters mainly feed on fish (mostly Cichlidae, Characidae, Synbranchidae, Loricariidae and Erythrinidae), but also on crustaceans and molluscs, as in other areas (Pardini, 1998; Kasper et al., 2008; Quintela et al., 2008; Chemes et al., 2010). Vertebrates other than fish were observed in the summer diet composition (Gori et al., 2003). However, in lotic environments, mammals were consumed during winter and spring (Vezzosi et al., 2014). Smaller prey items were consumed in the water, making several swallowing head movements on the surface, but larger ones were grabbed with the claws and taken ashore (Parera, 1993).

In agreement with other Neotropical otter diet studies (see Vezzosi et al., 2014), fish (Osteichthyes) was the most common prey in the sample, but other vertebrates such as crustaceans and insects were also very frequent in the feces. Mammals were represented by two families of rodents, Cricetidae: marsh rats *Holochilus* sp., colilargo *Oligoryzomys flavescens* and Caviidae: cuis *Cavia aperea*. Cricetidae represent 17% and Caviidae 11% of prey items in the total sample (see Vezzosi et al., 2014). Cricetid bones were mentioned in zooarchaeological literature of neighbor regions in the sampling area, but their presence is generally attributed to incidental introduction, not to the predator being an accumulator (e.g. Santiago, 2004; Acosta and Pafundi, 2005). Furthermore, *Cavia aperea* has been considered to be an additional biological and nutritional resource in the diet of the prehispanic societies that lived in the wetland of the lower Parana basin during the late Holocene (Acosta and Loponte, 2013).

Anatomical representation

The total sample yielded 2381 rodent bone remains. This number includes all the indeterminate bone fragments (686; 28.81%). From the total NISP (1695), a MNE of 1461 skeletal

elements was calculated. **Fig. 2** shows the percentage of each skeletal element recovered according to the MNE.

Among the remains analyzed in the sample, more than 70% were anatomically identified. This proportion is high compared with other Neotropical carnivore mammals, e.g., 56% in *Puma concolor* (Puma) sample, and only 25% in *Conepatus chinga* (Andean hog-nosed skunk) sample (Montalvo et al., 2007, 2008). A high number of metapodials, vertebrae, isolated incisors and molars was recovered. Other skeletal elements did not exceed 5% of frequency in the total sample. The great number of vertebrae and metapodials may be related to their abundance within the skeleton of each individual, whereas the number of isolated teeth may be directly related to the breakage of cranial elements (maxillae and mandibles) and the consequent loss of teeth from their alveoli. Scapulae, radii, ribs, calcanei and astragali had a very low frequency in the sample. Mondini (2000) recorded a low representation of vertebrae of carnivore scats (mainly from small-sized canids) in the sample, attributing this to the loss through chewing. The same interpretation could explain the low representation of vertebrae in the Neotropical otter sample.

The frequency of skeletal elements is similar to what has been described for the samples from the Felidae *P. concolor* and Geoffroy's cats *Leopardus geoffroyi* (Montalvo et al., 2007, 2012). The frequency of incisors is higher in the Neotropical otter sample (**Fig. 3**). The frequency of these teeth is high among the most common elements found in fossil or zooarchaeological assemblages, because they

are relatively resistant to post-depositional modifications (Matthews, 2006).

A relative abundance of identified skeletal elements was calculated, considering an MNI of 46 individuals (**Table 1**).

The average relative abundance of rodent bones was 32.34%; only mandibles, maxillae, femora and isolated incisors exceeded 50%. Similar averages were obtained in samples from the Mustelidae *Martes martes* (Pine marten; 35.80%, Andrews, 1990) and *C. chinga* (36.73%, Montalvo et al., 2008). However, the average obtained was intermediate between values reported for the Viverridae *Genetta genetta* (Genet; 27.28%, Andrews, 1990) and the felids *P. concolor* (22.11%, Montalvo et al., 2007) and *L. geoffroyi* (41.66%, Montalvo et al., 2012).

When these data were compared with available skeletal representations from other carnivore mammals that lived in the same sampling area (Pautasso, 2008) with a similar average of relative abundance (*P. concolor* and *L. geoffroyi*; Montalvo et al., 2007, 2012), an analogous distribution of skeletal elements with a good preservation of mandibles, maxillae, humeri, femora, tibiae and incisors was observed (**Fig. 3**). In these cases, the representation of the relative abundance of skeletal elements could not be used to make an adequate distinction between different predators (Andrews, 1990; Matthews, 2006).

Conepatus chinga occurs in sympatry with the Neotropical otter in some freshwater environments of the Paraná river valley (Canesini et al., 2008, Pautasso, 2008). While the average of relative abundance between samples of *C. chinga* and Neotropical otter

is similar, the distribution of skeletal elements shows clear differences, mainly in cranial elements (**Fig. 4**). These differences might be due

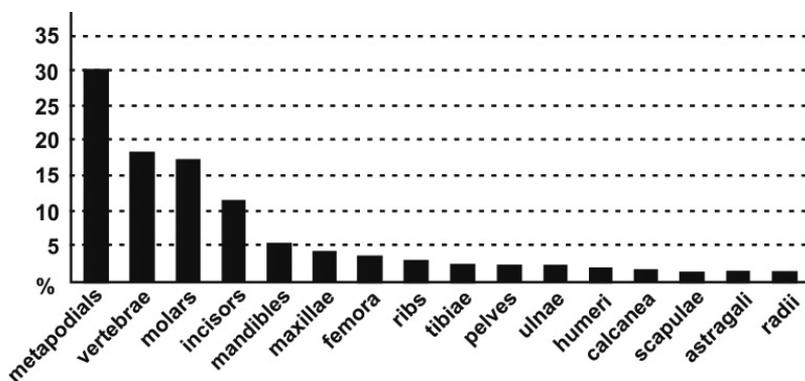


Fig. 2. Percentage of different rodent skeletal elements (MNE=1461).

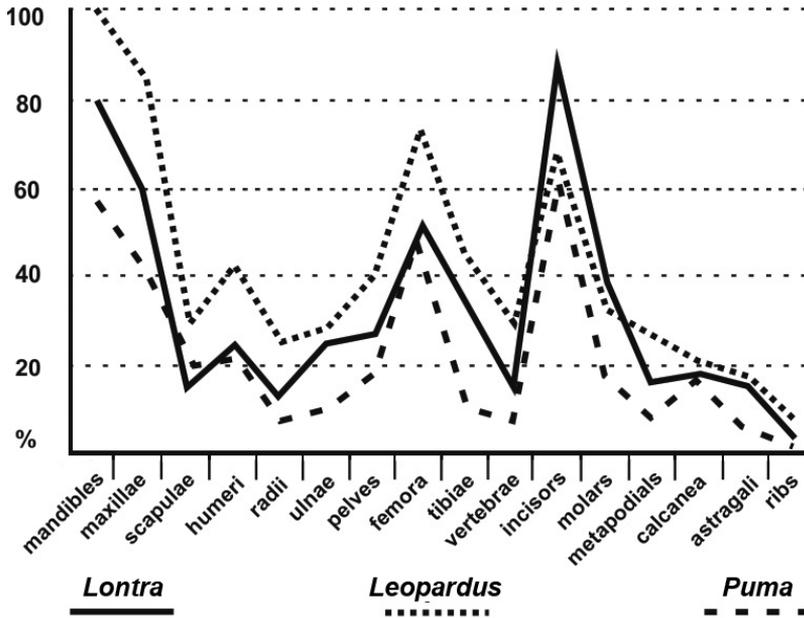


Fig. 3. Relative abundance of rodent skeletal elements identified in the *Lontra longicaudis* sample compared with data from *Puma concolor* and *Leopardus geoffroyi*.

to the high degree of breakage and destruction of skeletal elements evaluated for the *C. chinga* sample, together with the high number of non-identifiable small fragments and bone splinters recovered from their scats (Montalvo et al., 2008). These dif-

ferences may help distinguishing between the samples of both predators.

On the other hand, these results had some similarities with the samples of *M. martes* and *G. genetta* (Andrews, 1990), making it difficult to differentiate the predator based on anatomical representation (Fig. 5). In the latter cases, the differences found in the anatomical representation could be related to characteristics of predators and prey. Moreover, the environmental variables that are constantly fluctuating in the Neotropical otter's home range (Pardini, 1998; Kasper et al., 2008; Vezzosi et al., 2014) could be another factor which determines the availability and proportions of the different types of ingested prey and the consequent preservation of different skeletal elements in the environments. Although rodent preys and other micromammals were reported earlier in the Neotropical otter's diet in the literature, their presence in the diet composition has been considered occasional or even rare (Kasper et al., 2008, Quintela et al., 2008, Chemes et al., 2010). The results presented here show that these prey were fully eaten, and although the bones may have been destroyed, all the skeletal elements of their prey are represented in the studied sample.

Table 1

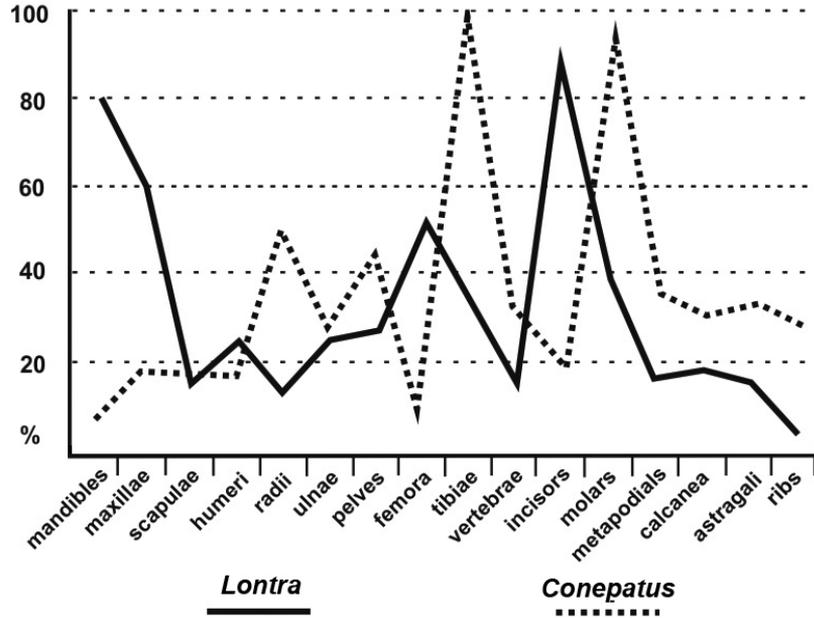
Relative abundance of identified rodent skeletal elements in the *Lontra longicaudis* sample.

	MNE	% Rel. Ab.
mandibles	74	80.43
maxillae	54	58.70
scapulae	14	15.22
humeri	22	23.91
radii	12	13.04
ulnae	23	25.00
pelvis	24	26.09
femora	46	50.00
tibiae	30	32.61
vertebrae	259	15.64
incisors	157	85.33
molars	243	37.73
metapodials	435	16.89
calcanea	16	17.39
astragali	14	15.22
ribs	38	4.28

Fig. 4. Relative abundance of rodent skeletal elements identified in the sample of *Lontra longicaudis* compared with data from *Conepatus chinga*.

We used several indexes in order to analyze the relationship between cranial and postcranial elements (Table 2).

The low values of the indexes pc/c and f+h/mb+mx give an idea of the degree of preservation of the cranial elements, as both show differences with the postcranial elements. However, a better preservation of cranial elements was recorded in samples of *P. concolor* (Montalvo et al., 2007). Andrews (1990) studied carnivore mammals and observed that, in general, there is a bias



in the proportion of cranial with respect to postcranial rodent prey elements. The lack of postcranial elements as a characteristic of the sample can be associated to the differential destruction produced by chewing. Nevertheless, it should be mentioned, as it will be discussed later,

that the preserved cranial remains are all broken, indicating that the chewing process has markedly affected them (Andrews, 1990). The result obtained for the index $t+r/f+h$ shows an important loss of distal elements with respect to proximal

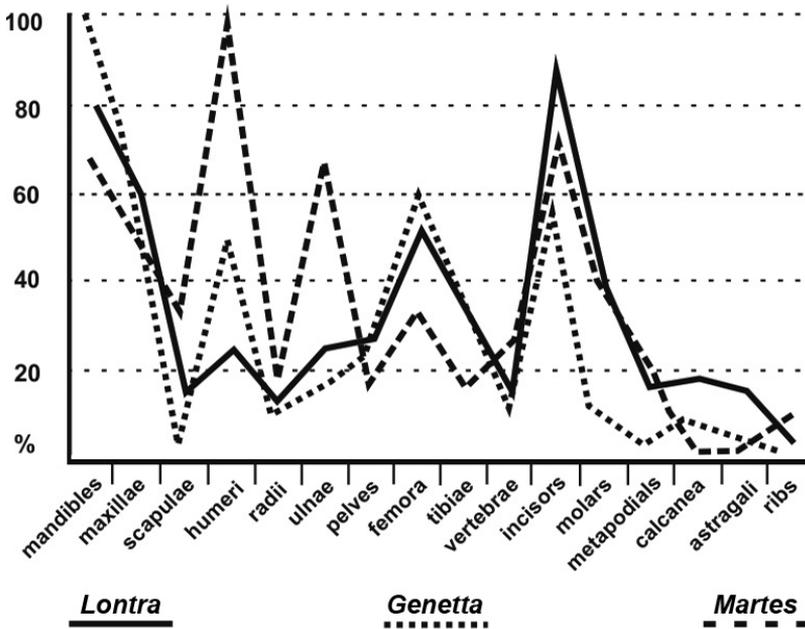


Fig. 5. Relative abundance of rodent skeletal elements identified in the sample of *Lontra longicaudis* compared with data from *Martes martes* and *Genetta genetta*.

Table 2

Indexes (see text) calculated for the *Lontra longicaudis* sample.

	Ratio
pc/c*8/5	53.13
(f+h)/(md+mx)	35.85
(t+r)/(f+h)	77.94

ones. This result is similar to that given by Andrews (1990) for mammalian predators.

Breakage and mechanical bone modifications

The degree of breakage was high in all the rodent skeletal elements in the total sample (MNE = 1461). Whole skulls, mandibles or maxillae were not found but portions of maxillae and mandibles with teeth in the alveoli. However, 72% of maxillae had a single tooth or were edentulous. The most frequent mandibular remains were those with one or two molars or were edentulous (65%). Only nine maxillae and nine mandibles of Cricetidae had all molars in situ. Incisors and molars had the highest breakage rate (more than 90%).

Only in young individual remains of *Cavia aperea*, mandibles and maxillae were best preserved. The loss of teeth, both from mandibles and maxillae, was frequent. These features of the caviid remains allow the differentiation of the Neotropical otter sample from others found in archaeological contexts in the lower area of the Paraná river wetland where the complete-

ness of different anatomical elements is high (Acosta and Pafundi, 2005).

Among the postcranial elements, whole humeri were recovered. However, proximal femora, tibiae and ulnae, and distal humeri were the most frequent remains (Table 3).

As regards broken long bones, when the fracture types were analyzed there was a clear predominance of spiral and stepped fractures (sensu Marshall, 1989), related to chewing processes (Fig. 6, a-b). Break edges generally occurred with rounding and polishing (Fig. 6, a-c). The high percentage of indeterminable bone fragments could also be related to the destruction during chewing, but only two bone fragments had perforations that were interpreted as tooth marks. These marks are scarce, likely because breakage is more frequent than marking. Among the cranial and postcranial elements evaluated for the degree of breakage, whole elements were only preserved among humeri and mandibles (Table 4). The evaluation of the percentage of fragmentation allowed comparing this sample with others of similar relative abundance (*P. concolor*, *C. chinga* and *L. geoffroyi*). In every case, maxillae were broken. The Neotropical otter broke more skeletal remains than *P. concolor* and *L. geoffroyi*, but still retained whole skeletal elements. On the other hand, *C. chinga* broke all bones (Fig. 7). The Neotropical otter produced extensive destruction of remains, generating an assemblage mainly formed by broken bones; this allows placing this predator in the category of maximum modification of the bones of rodent preys.

Table 3

Breakage of postcranial elements in the *Lontra longicaudis* sample.

	Femur		Humerus		Tibia		Ulna	
	MNE	%	MNE	%	MNE	%	MNE	%
Complete	0	0	4	18.18	0	0	0	0
Proximal	23	71.74	4	18.18	15	50	23	100
Distal	13	28.26	14	63.64	10	33.33	0	0
Shaft	0	0	0	0	5	16.67	0	0

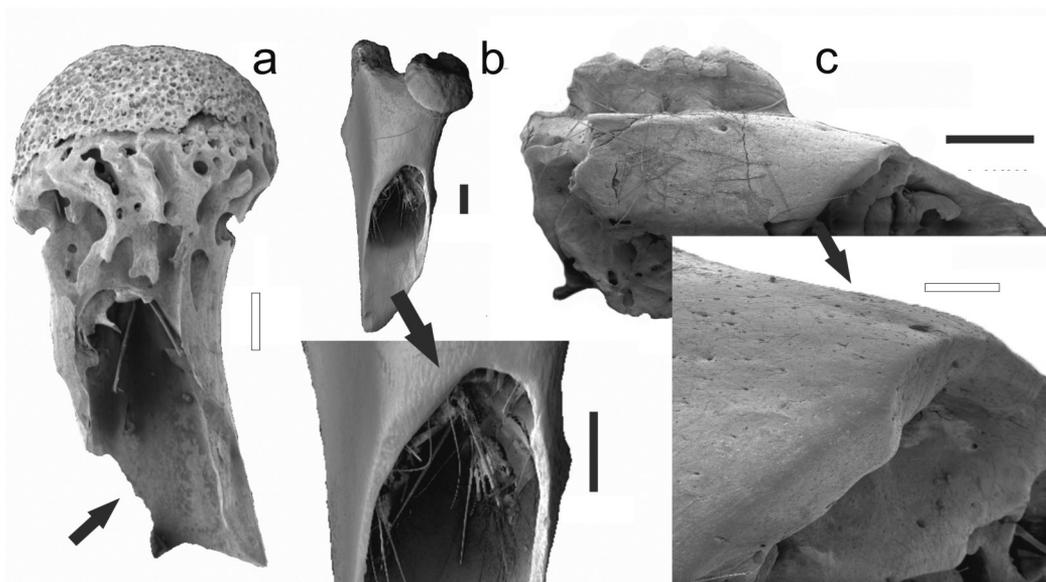


Fig. 6. Scanning electron microscope pictures showing broken bones with spiral fractures. a) Proximal femur; b) proximal femur and enlargement of break area with rounding and polishing; c) portion of maxilla with M3 and enlargement of break area with rounding and polishing. White scale bar: 200 μ ; black scale bar: 1mm.

Table 4

Number and percentage of fragmentation of cranial and postcranial elements in the *Lontra longicaudis* sample (TNB: total number of bones; NBB: number of broken bones; PF: percentage of fragmentation = number of broken bones out of the total number of bones).

	TNB	NBB	PF
femora	46	46	100
humeri	22	18	81.82
tibiae	30	30	100
ulnae	23	23	100
maxillae	54	54	100
mandibles	74	65	87.84

Digestion

All remains showed modifications by digestion. Some of them were minimal, but in 61.97% of the analyzed elements evidence of digestion was strong or extreme (**Table 5**, **Fig. 8**). Teeth were severely affected by heavy and extreme modifications, changing both the

enamel and dentine (**Fig. 8 b-i**). Caviid molars were intensely affected by digestion and were mainly evaluated as extremely modified (**Fig. 8 b-d**). Several specimens, mainly from cricetid rodents, exhibited fine cracks on the dentine of the tooth crown (**Fig. 8 a, f**). As regards other specimens, the enamel tended to separate from the dentine at the enamel/dentine junction with the root (**Fig. 8 a**). It is clear that the Neotropical otter affected a larger proportion of incisors with heavy and extreme evidences of digestion than other small and middle-sized terrestrial carnivores (Mondini, 2000, 2003; Mattews, 2006; Montalvo et al., 2008; 2012).

This sample is dominated by cricetid rodents. The digestion categories recognized by Andrews (1990), when applied to cricetids, differed in degree from those for Caviidae, as was described by Demirel et al. (2011) for Muridae and Arvicolidae. In this sample it was observed that while molars of Caviidae were moderately digested, cricetid teeth only showed early stages of digestion. Differences could be related with the size and tooth morphology of prey species. Considering this evaluation, the

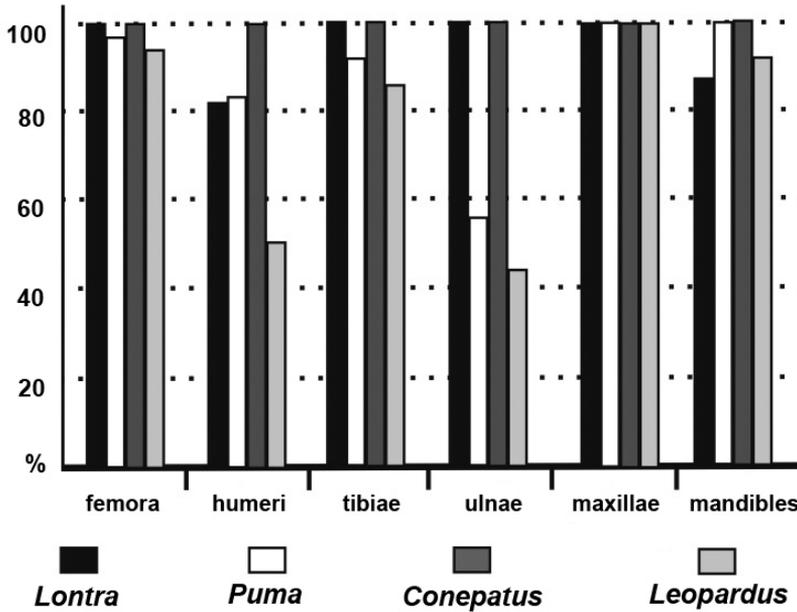


Fig. 7. Percentage of fragmentation (PF) of rodent cranial and postcranial elements in *Lontra longicaudis* sample compared with data from *P. concolor*, *C. chinga* and *L. geoffroyi*.

Neotropical otter produced extreme modifications in rodent molars by digestion.

The proximal femora showed extreme modifications in a very high percentage of remains. In the case of the proximal humeri, the most common class was that with heavy modification (Fig. 8 k, l).

The evaluation of the percentage of remains with digestive modification allowed the comparison of this sample with others of similar relative abundance (*P. concolor* and *L. geoffroyi*) (Fig. 9). These predators showed a higher per-

centage of remains with light and moderate modifications whereas Neotropical otters produced more remains with heavy modification.

On the other hand, all the recovered remains from *C. chinga* sample had a heavy

digestive action, and the percentages of skeletal elements with heavy to extreme modifications were high (Montalvo et al., 2008).

Final remarks

In the Neotropical otter sample, the main modifications of the rodent bones are due to the breakage produced by the mechanical action of teeth before or during ingestion. This process is correlated with high values of fragmentation to facilitate the action of digestive enzymes. Using the methodology proposed by Andrews (1990),

Table 5

Evaluation of percentages of digestion in rodent postcranial elements (proximal femur and distal humerus) and teeth (incisors and molars) in the *Lontra longicaudis* sample, following the criteria of Andrews (1990).

	% light	% moderate	% heavy	% extreme
Femur	23.53	14.71	23.53	38.24
Humerus	21.05	21.05	42.11	15.79
Incisor in situ	0.65	26.80	39.87	32.68
Isolated incisor	17.86	25.00	32.14	25.00
Molar in situ	12.96	32.72	33.95	20.37
Isolated molar	25.51	13.17	26.34	34.98

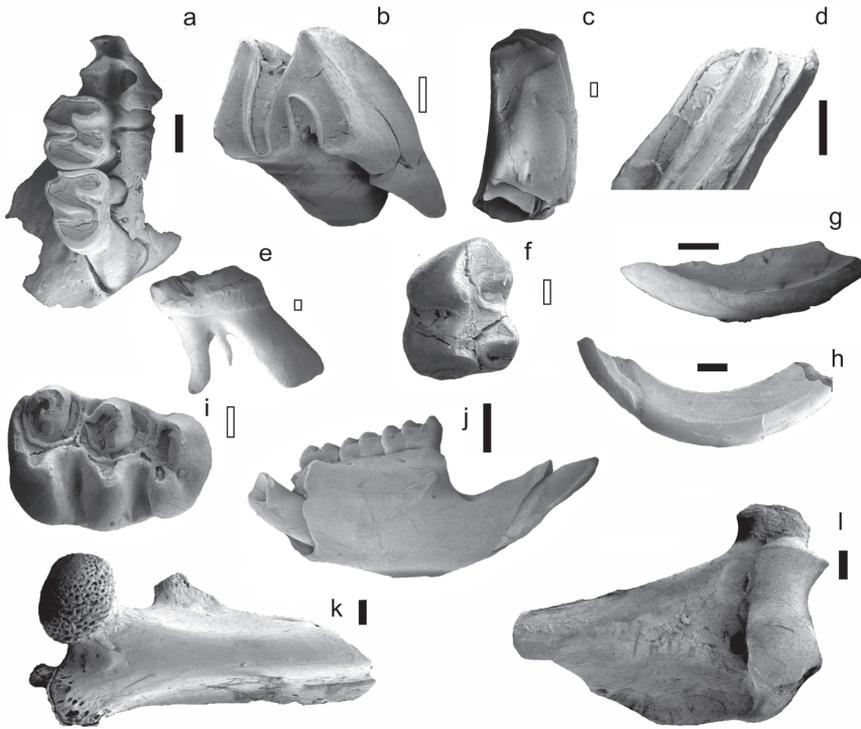


Fig. 8. Scanning electron microscope pictures showing digestion traces on rodent bones, following the criteria of Andrews (1990). a) Cricetidae mandible with molars with moderate digestion; b) isolated Caviidae molar with light digestion; c) isolated Caviidae molar with heavy digestion; d) isolated Caviidae molar with extreme digestion; e) isolated Cricetidae molar with moderate digestion; f) isolated Cricetidae molar with heavy digestion; g) and h) isolated incisors with moderate digestion; i) isolated Cricetidae molar with moderate digestion; j) Cricetidae mandible showing molars with light digestion and incisor with moderate digestion; k) proximal femur with heavy digestion; l) distal humerus with light digestion. White scale bar: 200 μ ; black scale bar: 1mm.

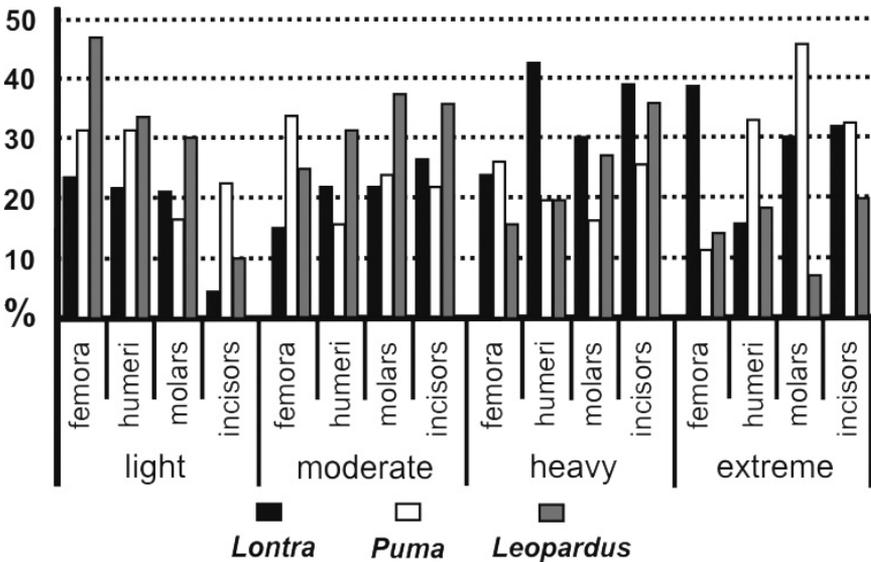


Fig. 9. Percentage of remains with digestive modification recovered from *Lontra longicaudis* sample compared with data from *P. concolor* and *L. geoffroyi*.

these results allow assigning the Neotropical otter to the extreme modification category with respect to rodent remains recovered in all scats (Table 6). Based on a small sample, Andrews (1990) located the otters among the predators that affect bones with extreme modifications. This analysis also indicates that the modifications produced by this species include variables from categories 3, 4 and 5; category 3 (moderate) is the least frequent, though. Variables from category 5 (extreme) are in agreement with the high degree of breakage that occurs during chewing (Andrews, 1990).

CONCLUSIONS

The terrestrial and semiaquatic carnivore mammals produce significant damage on prey bones both during chewing and through the digestive tract (Andrews, 1990). The degree of breakage in the Neotropical otter sample was very high in the case of rodent cranial and postcranial elements. However, it was possible to identify several species of Cricetidae and Caviidae. The skeletal elements were also anatomically assessed, given that many of

them were well preserved. A high number of vertebrae, metapodials, incisors and isolated molars were assessed in the sample, whereas scapulae, radii, ribs, calcanei and astragali had very low frequencies. The relative abundance was also calculated and the best represented skeletal elements were mandibles, maxillae, femora and isolated incisors (more than 50% of representativeness). The results obtained from the Neotropical otter were similar to those from the terrestrial felids *Puma* and *Leopardus*, also showing a better representation of cranial elements (mainly isolated teeth) and proximal elements of the limbs. The evaluation of the degree of digestion showed a high number of remains with heavy and extreme modifications. These results allow the location of the Neotropical otter in the extreme modification category, in line with Andrews (1990).

While fish were the most frequent prey in this sample (Vezzosi et al., 2014), rodent (Cricetidae and Caviidae) remains were also abundant. This taphonomic study is the first one to investigate rodent remains from feces of *Lontra longicaudis*, and it shows that this predator is an active rodent remains accumula-

Table 6

Categorization of *Lontra longicaudis* according to the analyzed variables following the criteria of Andrews (1990).

	Category 1	Category 2	Category 3	Category 4	Category 5
Relative abundance (pc/c)				■	■
Distal elements loss		■			
Breakage of postcrania					■
Breakage of skull					■
Loss of zygomatic processes					■
Maxillary tooth loss				■	
Breakage of mandibles					■
Mandibular tooth loss				■	
Loss of isolated teeth				■	
Breakage of teeth					■
Digestion of molars				■	
Digestion of incisors				■	
Digestion of postcrania				■	

tor when this type of prey is available in the environment. Furthermore, this study contributes to the understanding of the presence of rodents in archaeological and paleontological accumulations in fluvial areas and freshwater environments. Nevertheless, it is essential to continue the investigation on the taphonomic signature (in other vertebrate prey, mainly in fish) produced by the Neotropical otter before data can be extrapolated to create models to interpret vertebrate remains in archaeological and paleontological assemblages related to fluvial environments.

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