



# An integral approach to the study of bromalites. Late Quaternary and neo-taphonomic case studies from arid South America

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## ABSTRACT

Bromalites are fossil traces of organisms, consisting of material from their digestive system, including coprolites, regurgitalites, consumulites, pabulites and digestilites (Hunt, 1992; Hunt and Lucas, 2021). As such, they inform about the interactions between bromalite-producing organisms and others, as well as between them and the environment generally, at a relatively fine temporal and spatial resolution. Yet, bromalites have often been dismissed in paleontological and, especially, archaeological research. This work discusses the relevance of bromalites as sources of paleoecological and even cultural information, and the importance of integrating multiple lines of evidence and different scales of analysis in the taphonomic study of bromalites. To do so, it reviews the different proxies that can be analysed, and illustrates this integral approach with examples of late Quaternary and modern contexts from an ongoing project in arid South America. It intends to show the potential of such a multiproxy and multiscale approach in order to elicit as much information as possible from these palaeobiological reservoirs.

## 1. Introduction

Bromalites are fossil traces of organisms, consisting of material from their digestive system, such as faeces and regurgitated pellets (Hunt, 1992). They include coprolites or palaeofaeces,<sup>1</sup> regurgitalites, consumulites, pabulites and digestilites (Hunt and Lucas, 2021). As byproducts of vertebrate digestion, they inform about the organisms themselves even if their remains are not present. In addition, as they contain remains and traces of other organisms and of the physical medium, they inform about the interactions between bromalite-genic organisms and others, as well as between them and the environment generally, at a relatively fine temporal and spatial resolution. Thus, they constitute a taphonomic mode (*sensu* Behrensmeyer, 1988) and, as Behrensmeyer and Hook (1992) pointed out over three decades ago, they deserve more attention and systematic study, part of which has been achieved in recent years.

Fossil scats, pellets and other bromalites are in fact a valuable source of taphonomic and palaeobiological information, which is sometimes

only preserved in this way (Andrews, 1990; Hunt, 1992; Lyman, 1994; Fernández-López, 2000; Gifford-Gonzalez, 2018, among others). This information is mainly taphonomic in nature in the broadest possible sense, as it informs both about the formation of the fossil record –both paleontological and archaeological– in terms of biases and about the palaeoecological context within which it was generated and modified to its current state. That is, it is relevant to both the negative and positive contributions of taphonomy (*sensu* Behrensmeyer and Kidwel, 1985) –such as biases in the fossil record and paleoecological information, respectively–. Furthermore, bromalites provide information about interactions between humans and other animals that is relevant to archaeological inquiry.

The aim of this work is to discuss the relevance of integrating multiple lines of evidence and different scales of analysis in the taphonomic study of bromalites, to review the different proxies that can be analysed, and to illustrate this integral approach with examples of late Quaternary and modern contexts from an ongoing research program in arid South America, specifically NW and central Argentina. The examples include

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<sup>1</sup> Palaeofaeces is a term often applied to these remains in archaeological studies, and is sometimes used to refer to those which are not fully mineralized (see, for instance, Borry et al., 2020; Shillito et al., 2020, among others).

the analysis of fossil carnivore and herbivore palaeofaeces and raptor regurgitated pellets, as well as neo-taphonomic studies of mammalian carnivore scats and raptor pellet-derived bones. These case studies have been published and presented before separately, and they are cited so as to exemplify the general approach advocated here and being applied in our research program. By considering them all together here, I intend to show the potential of such an integral approach.

## 2. A multiproxy approach to the study of bromalites

The multiproxy methodological approach advocated here aims at integrating bromalites and their contents, along with contextual information at different scales. This approach is recommended both for the analysis of fossil assemblages and for neo-taphonomic or actualistic studies, addressed at constructing frames of reference to help interpret taphonomic and paleobiologic information from the fossil record.

By integrating different lines of evidence, we can identify the taxonomic identity of the bromalite producers, which are sometimes not represented otherwise, as well as the identity of bromalite inclusions. These inclusions may remain into the bromalites, or else become isolated when their matrix disintegrates, and even so have properties that allow recognizing their bromalite origin.

As Shillito et al. (2020) put it, coprolites can be regarded as self-contained multiproxy “packages” of information. This can be extended to bromalites generally. The analytical approach favoured here allows accounting for these particular ichnofossils, both in fossil accumulations consisting mainly of bromalites and their byproducts, and in other paleontological and archaeological contexts where they are “intrusive” or “diluted” –that is, a minor component as compared to those contributed by other agents or processes (e.g., Mondini, 2005a)–. The multiproxy approach, especially when it is multi-scale, also allows supporting broader, palaeoecological inferences –including diet, home range, zoonoses, palaeoenvironment, among others–, as well as human-animal interactions and even cultural practices.

In this section, while I will be referring mainly to bromalites, all variables are meant to apply to their modern counterparts as well (carnivore scats, herbivore dung, raptor pellets, among others), which are the subject of neo-taphonomic studies. The case studies mentioned to illustrate the variables refer to both.

### 2.1. Bromalite properties

Properties of the bromalites themselves –such as size, shape, colour and odour– serve as a basis for identifying their zoological origin (Jouy-Avantin et al., 2003; Chame, 2003; Hunt and Lucas, 2012; Taglioretti et al., 2014; Sanz et al., 2016; Shillito et al., 2020, among others). Visible inclusions –indicating what the bromalite-genic actor has ingested– may also help. Yet, some studies have shown morphological variables to be ambiguous, and molecular identification through DNA, biliary acids or other methods may prove necessary (e.g., Lon-singer et al., 2015). Bromalite characterization is also intended to examine its integrity and taphonomic history (Reinhard et al., 2019), so variables such as fragmentation and weathering are relevant.

In order to accomplish this type of analysis, a robust comparative collection is necessary, including a wide array of actors, intra-specific variation, different environments in which the faeces, pellets and other digestive byproducts are produced, and different preservation conditions (see Andrews, 1990). It is sometimes difficult to convey the importance of these collections to institutions (see Denys et al., 2023), but this is a task we should not give up, especially in the context of climate change and extinctions we are currently facing.

By way of example, two case studies from the South-Central Andes can be cited. One is that of two puma (*Puma concolor*) palaeofaeces from Peñas de las Trampas 1.1 paleontological/archaeological site in Antofagasta de la Sierra, in the Argentinian Puna, dated to the final Pleistocene (>16,500 cal BP) (Petrih et al., 2019). The other one is that of

some goat (*Capra hircus*) faecal pellets from Los Viscos archaeological site in the nearby high-altitude El Bolsón valley, associated to occupations dated to the early Hispanic-Indigenous contact time (c. 400 cal AP) (Petrih et al., 2021). In both cases, faeces producers were preliminary determined by external properties and inclusions, and then checked with ancient DNA. In neither case had these species been identified otherwise at the sites, and their identification has important implications. In the case of the puma scats, this confirmed the presence of the largest modern-day carnivore at a time when humans would have been hardly entering these Andean highlands. And in that of the goat faeces, the study suggested the early presence of Eurasian livestock in an area not yet dominated by the Spanish at the time.

### 2.2. Faunal contents

In bromalites of carnivorous and omnivorous animals –including humans (Shillito et al., 2020 and references therein)–, several faunal remains can be found that have survived ingestion and passage through the digestive tract. They include both hard tissues and some others, and are informative of a number of properties of the organisms and their prey, the relationships between them and humans, and the environment generally.

#### 2.2.1. Skeletal remains

Bones and teeth are usually the main faunal remains included and preserved in bromalites. The relative abundance of certain anatomical parts of microvertebrate prey and their breakage and digestion patterns are key to identifying the zoological origin of these bromalites, as has been shown by Andrews and Fernández-Jalvo (e.g., Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo et al., 2016) and subsequently several other authors, like Montalvo and Fernández in South America (e.g., Fernández et al., 2017; Montalvo and Fernández, 2019; Montalvo et al., 2020).

We have used the approach just described to characterize the Achala fox (*Lycalopex culpaeus smithersi*), an endemic subspecies of the *Lycalopex* South American fox restricted to the Achala highlands of central Argentina, for the first time (Coll et al., 2021). Based on microvertebrate skeletal contents of modern scats, we found it to best fit the category of extreme modification (category 5 as defined by Andrews, 1990), and to display types and proportions of taphonomic attributes similar to other South American mammalian predators. We have also used the analytical approach mentioned above to identify the origin of microvertebrate skeletal remains on the surface of Los Viscos archaeological site as corresponding to the American barn owl *Tyto furcata* (Mondini et al., 2020).

While microvertebrates are the most common vertebrate prey remains to be found in bromalites, some contain skeletal remains of larger animals, even with no microvertebrates at all. In the case of meso- and mega-vertebrates, bones are usually highly fragmented and few are identifiable, if any at all. This requires rather different methodological approaches, which emphasize digestion modifications over anatomical patterning, while allowing to characterize these assemblages in a uniform way (Fisher, 1981; Mondini, 2003, 2012; Esteban-Nadal et al., 2010; Mallye et al., 2012; Campmas et al., 2018; Ballejo et al., 2022, among others).

In the case of the Pleistocene puma scats introduced above, which only contained remains of larger vertebrates with heavy digestive attrition, only two specimens could be determined, and they were identified as immature camelid bones (Mondini, 2019). This helps understand terminal Pleistocene environments and the role of top predators, as well as the context of the human peopling of the region, as it informs of the predatory community in which the earliest hunter-gatherer groups inserted, and of the potential food niche overlap of puma and human populations, the staple prey of whom were precisely camelids (Muñoz and Mondini, 2007 and bibliography therein).

While these patterns of small and larger vertebrates are very useful,

sometimes the bromalite skeletal remains are not identifiable, and more general patterns –such as bone size and modifications regardless of their identity– become important (Andrews, 1990; Stallibrass, 1990; Schmitt and Juell, 1994; Schmitt and Lupo, 1995; Sanz et al., 2016, among others). Although seldom recognized, taxon-free and element-free patterns of bromalite-derived bone accumulations and digestion modifications are in fact taphonomically informative.

In the puma case, digestive attrition in all of the bones contained in one of the scats and in most of the bones in the other one was found to be of a heavy to extreme degree (*sensu* Campmas et al., 2018) (Mondini, 2019), in agreement with previous information on these felids (see Mondini, 2017; Montalvo and Fernández, 2019 for a synthesis). This pattern is informative on these taphonomic agents even when only two out of 58 bone specimens could be identified and, in turn, it sheds light on the probably puma scatological origin of some corroded bone specimens found at Peñas de las Trampas 1.1 site.

This approach was also applied to modern scatological assemblages generated in multiple locations of Andean NW Argentina by small predators, namely foxes, where most skeletal elements corresponded to microvertebrates but only few were identifiable due to high comminution (Mondini, 2000, 2003, Mondini, 2004, 2005b, 2012). By assessing variables like the magnitude of bone accumulations and bone modifications, fragmentation and identifiability, together with contextual information, we were able to characterize these assemblages commonly accumulated in rockshelters, to establish patterned regional variation in different ecological areas, to assess significant differences with non-ingested skeletal assemblages, and to build robust frames of reference to compare to archaeological assemblages containing microvertebrate bones and teeth.

### 2.2.2. Phanera

Other faunal contents also contribute to the determination of the taxa ingested and of those who deposited the bromalites. Phanera like nails, claws, feathers and hair are resistant to digestion due to their keratin content, and are thus likely to survive the digestive system (Larkin et al., 2000; Loveras et al., 2008; Esteban-Nadal et al., 2010; Sanz et al., 2016, among others). Besides, when surrounding bone, they help preserve it throughout the digestive tract, thus playing an important taphonomic role (Andrews and Evans, 1983; Montalvo et al., 2012, among others).

Hair helped identify both the prey and the predator –who may ingest its own hair while grooming– both in the case of the modern carnivore scats from NW Argentina, where *Lycalopex culpaeus* and *Oncifelis geoffroyi* were identified (Mondini et al., 2006), and in that of the carnivores in the Achala plateau in central Argentina, where *L. culpaeus smithersi* and *Puma concolor* were determined (Pia, 2011, 2013; Pia et al., 2003), besides rodents in both of the studies. The differential preservation of bones surrounded by skin and hair was evident in digested microvertebrate anatomical segments found in the actualistic studies carried out both in NW Argentina (Mondini, 2003, 2012) and in central Argentina (Coll et al., 2021).

### 2.2.3. Parasites

Ecto- and endo-parasites are also commonly present in bromalites, both deriving from prey and from the producing animals (Reinhard, 1990; Guerra et al., 2003; Reinhard and Bryant, Jr. 2008; Beltrame et al., 2011; Fugassa et al., 2018; Chin, 2021; Cañal and Beltrame, 2022, among others). They can help identify both, as well as support biogeographical, zoonotic, and palaeoenvironmental inferences.

In the puma scats, *Toxascaris leonina* was identified among other parasites (Petrih et al., 2019). This demonstrates the presence of this nematode parasite in South America since at least the final Pleistocene, presumably before human arrival. This has implications for the common belief that its presence in modern New World wild carnivores is only due to contact with domestic carnivores. The large number of *T. leonina* eggs and their larval state in the puma coprolites suggest a high infective

capacity, implying zoonotic risk for other potential hosts, including humans.

In the early introduced got faeces presented above, a highly infectious parasite, *Fasciola hepatica*, was found among other parasites (Petrih et al., 2021) Yet, it was not found in contemporary or earlier camelid faeces at the site. This supports the hypothesis that this parasite entered the region along with Eurasian livestock, which is important to understanding the origins of a disease that has contributed to the displacement of traditional camelid pastoralism to higher altitudes and is increasingly common.

### 2.2.4. Other faunal contents

Other faunal inclusions are also found in bromalites, including fish scales, degraded soft tissues and invertebrates –such as arthropods, which tend to preserve better than others due to the chitin in their exoskeleton– (Reynolds and Aebischer, 1991; Hunt et al., 2012; Shillito et al., 2020, and references therein). Their presence and relative amount are indicative of the diet of different bromalite-producing organisms, as well as of environmental conditions.

Bromalites also contain microfossils. Faunal spherulites originate in the digesting organism or may otherwise be included in the ingested prey viscera (e.g., Canti, 1998). They help identify not just the producing taxa but also cultural practices such as past animal enclosures. In our study area in NW Argentina, Alejandra Korstanje (2005; Korstanje et al., 2014, 2021) has been able to identify the use of manure for fertilizing agricultural fields through the significant presence of camelid spherulites.

### 2.3. Plant contents

Plant macro- and micro-remains may also survive partial or complete ingestion and the passage through the digestive tract. They are informative about diet, home range, environment, anthropic disturbance and cultural practices, among other issues. Indirectly, they inform about the zoological origin of the bromalites themselves as well, like in the case of domestic animals fed with domestic plants. Even carnivores eat plants, so their remains are found in a range of bromalite producers.

#### 2.3.1. Plant macro-remains

Hard plant parts like pits, stones and seeds may survive passage through the digestive tract, and cellulose may help preserve some other parts as well, which can be identified via histology (León-Lobos and Kalin-Arroyo, 1994; Castro et al., 1994; Martínez Tosto et al., 2016; Mosca Torres et al., 2022, among others). Taphonomic studies on the effect of digestive acids on these remains, though, are rare (O'Meara, 2014).

By way of example, plant macro-remains containing well-preserved cellulose have been found in the Andean carnivore scats from modern dens (Mondini and Rodríguez, 2006). They belong mostly to grasses, overlapping with plants commonly transported by humans into rockshelters, and helped characterize carnivore diet in these arid environments. As to digestive damage on these plant remains, low levels were observed, which might be related to the relative resistance of the structures of these grasses and also partly to the dominance of small carnivores in the regional predatory community.

#### 2.3.2. Plant microfossils

Micro-plant remains such as pollen, silicophytoliths, starch, among many others, derived from ingested plants or indirectly carried by the prey ingested, are usually found in bromalites as well (Fernández-Jalvo et al., 1999; Carrión et al., 2004; Wood and Wilmshurst, 2013; Haas et al., 2013; Gil-Romera et al., 2014; Velázquez et al., 2021, among others). They are also informative of the different aspects mentioned above (Korstanje et al., 2014).

The early goat faecal pellets introduced above contained pollen of different types including one of either *Chenopodium quinoa* or

*Amaranthus* sp. (Petriugh et al., 2021). Both taxa have been recorded in the area at pre-Hispanic times, and stopped being grown there in historical times (Maloberti et al., 2016), which is in agreement with the age attributed to these pellets. Pollen also helped identify which camelid faeces might correspond to wild species (*Lama guanicoe* and/or *Vicugna*) and which to the domestic llama (*L. glama*) at this site (Petriugh et al., 2021).

#### 2.4. Chemical and molecular composition of bromalites and their contents

Chemical and molecular studies such as those of bile acids, lipids, ancient proteomics and aDNA also allow identifying both the bromalites and their contents, and are thus crucial to help tackle ambiguity in this regard (e.g., Bull et al., 1999; Shillito et al., 2011; Karpinski et al., 2017; Hagan et al., 2020; Borry et al., 2020).

In the case of the goat faecal pellets, aDNA allowed confirming that they belong to *Capra hircus*, and this is now the earliest molecular record of the species in the region (Petriugh et al., 2021). And in the case of the puma scats, this is the oldest molecular determination of a coprolite in South America and one of the oldest worldwide (Petriugh et al., 2019). Although this felid's presence in Pleistocene South America was recently demonstrated based on skeletal morphological characters (Chimento and Dondas, 2018; Prevosti and Forasiepi, 2018), this is the oldest molecular record of the species, in spite of the absence of its remains. Finally, parasite identity was also confirmed via ancient DNA, and in the case of *Toxascaris leonina*, this is the world's oldest DNA obtained for a parasite, providing a new maximum age for the recovery of ancient DNA of this origin (Petriugh et al., 2019).

Direct radiocarbon dating is another crucial analysis, when possible, as it provides taxon-dates to both the bromalite producer and the organisms ingested. As bromalites and their contents can migrate once entering the lithosphere, the association of these findings and the strata including them should be demonstrated in each case.

For that reason, we radiocarbon-dated the puma scats from Peña de las Trampas 1.1. site to 16,573–17,002 cal BP, and found them to be much younger than the stratum containing them –IV layer: 23,195–23,913 cal BP– (Petriugh et al., 2019). This could be explained by the fact that this rockshelter was used as a denning place by mega-herbivores, thus producing intensive trampling (Martínez, 2014).

There are several other molecular and chemical analyses that can be performed to bromalites, like stable isotope analyses, which are informative of diet, environment and place of origin, although the possibility of measuring the microorganisms that rapidly colonize faeces and raptor pellets after deposition renders these analyses rather problematic (Reinhard and Bryant, 1992; Yang et al., 2022).

#### 2.5. Other lines of evidence

Plenty of other studies can be performed on bromalites, the importance of which should be established case by case. They include the analysis of preserved soft tissues, diatoms, fungi, invertebrates such as arthropods, mineral contents, ancestral gut microbiomes, among others (see Sanz et al., 2016; Shillito et al., 2020; Yang et al., 2022, and bibliography therein). Thin-cut micromorphology can also help determine bromalite-producers and their contents (e.g., Shahack-Gross, 2011; Sanz et al., 2016; Shillito et al., 2020; Hunt and Lucas, 2021).

When they are not fully mineralized, bromalite supply of remains to sediments once the matrix disintegrates should also be assessed, including the chances of incorporation of inclusions and molecules to sediments, the survival potential of the different skeletal elements and plants ingested and the chances of identifying them as bromalite-genic, among others (Mondini, 2000, 2003, 2012; Shillito et al., 2020). In these cases, disentangling equifinality is crucial, as other processes may mimic digestion (e.g., Fernández-Jalvo et al., 2014).

#### 2.6. Multiproxy protocols

Just like in any other fossil remain or trace, each bromalite has its own taphonomic history and should be analysed under this light. While several multiproxy protocols for the study of bromalites are available in the literature (e.g., Reynolds and Aebischer, 1991; Coil et al., 2003; Shahack-Gross, 2011; Korstanje, 2014; Korstanje et al., 2014; Wood and Wilmshurst, 2016; Velázquez et al., 2019, 2021; Fuks and Dunseth, 2021; Tolar et al., 2021, among others), they are usually specific to some particular proxies and scales of analysis, while here we attempt to provide a broader, more integral perspective. Using consistent protocols in fossil and modern samples is also important (Coll et al., 2022).

Analytical protocols generally tend to favour some lines of evidence over others, which may even be destroyed in the process. Thus, they should aim at maximizing the amount of information to be obtained with a limited amount of material for all necessary proxies, and at processing the samples in the proper order, while taking into account the research questions to help decide what to prioritize.

### 3. Context and scales of analysis

Spatial scales beyond the bromalite unit are also advocated, as contextual information both at the site and at the regional level are crucial for fully understanding these remains and their implications for palaeobiology and archaeology (e.g., Borrero and Martín, 1996). A multi-scale approach contributes to a better understanding of bromalite taphonomy. It should consider the different scales ranging from the properties of each bromalite and its inclusions, to those of the bromalite or the inclusions assemblage, the context of deposition –be it surface or stratigraphic-, the locus or site, the region and even the macroregion, or else larger stratigraphic units across space. Each scale allows eliciting different, complementary information. The broader ones also help identify biases in the fossil record and in taphonomic research as well (see, for instance, Hunt and Lucas, 2021; Mondini, 2017; Lyman, 2018).

Besides, bromalites are part of a larger system of food consumption and recycling of ingested and non-ingested remains, including residual assemblages at kill and scavenging sites and source-areas in the case of herbivorous animals, as well as transported assemblages and leftover accumulations (Binford, 1981; Montalvo et al., 2016; Hunt and Lucas, 2021, among others). These assemblages should be regarded as a *continuum* in order to better understand the ecology of past (and modern) animals and their environments (Mondini, 2003). Taking into account the monitoring perspective (*sensu* Thomas and Mayer, 1983), that is, the behavioural context producing an accumulation and its spatial expression, is key to understanding each case in the broader picture.

Time scale is also crucial. In the case of fossil assemblages, considering the long term and potential changes through time can be very informative (e.g., Behrensmeyer et al., 1992). In actualistic studies, being sensitive to seasonal and inter-annual variations is also important (e.g., Andrews and Fernández-Jalvo, 2018).

This integral approach aims at avoiding taking singular cases as typical without an analysis of its position in the general scene. While characterizing the bromalites and contents produced by each taxon is critical, it is also important to survey the variability of specific actors under different ecological conditions, so as to avoid the risk of an essentialist assumption that one or a few cases can be extrapolated to a whole taxon. This also helps eliciting richer paleoecological information out of fossil accumulations.

By way of example, on studying the modern carnivore dens from NW Argentina, we inferred a dual taphonomic pattern concerning small and large vertebrate accumulations in rockshelters, partly related to their entry as scatological or transported remains, respectively (Mondini, 2003, 2004). Yet, they ended up in the same accumulation, as is common in denning contexts. Also, by taking a wide macroregional approach, we found that a light consumption of bones by pumas, commonly attributed to the species, is not that light under some specific



ecological conditions (Mondini, 2017).

#### 4. Conclusions

Bromalites are important sources of paleoecological and even cultural information. This work has discussed their relevance and shown the advantages of integrating multiple lines of evidence and different scales of analysis in the taphonomic study of bromalites. To do so, it has reviewed the different proxies that can be analysed, and illustrated this integral approach with examples of late Quaternary and modern contexts from an ongoing project in arid South America. This way, it has shown the potential of such a multiproxy and multiscale approach in order to elicit as much information as possible from these unique palaeobiological reservoirs.

Finally, I would like to renew the plea made over the last 35 years by Andrews (1990), Behrensmeier and Hook (1992), Hunt et al. (2012), Myhrvold (2012) and many others, to continue studying bromalites, as they are still overlooked to some extent as compared to other traces and remains (see, for instance, Zipfel et al., 2023). In archaeology, in particular, they have often been dismissed and regarded as not significant. Yet, the so-called natural agents are not merely ‘background noise’ to try and eliminate in order to make inferences about the human past (see Gifford-Gonzalez, 2018). Instead, they provide us with important palaeobiological information about what the world was like in the past. Bromalites have a significant contribution to make in this regard.

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#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

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#### References

- Andrews, P., 1990. Owls, Caves and Fossils: Predation, Preservation and Accumulation of Small Mammal Bones in Caves, with an Analysis of the Pleistocene Cave Faunas from Westbury-sub-Mendip. Natural History Museum Publications, London, UK.
- Andrews, P., Evans, E.N., 1983. Small mammal bone accumulations produced by mammalian carnivores. *Paleobiology* 9 (3), 289–307.
- Andrews, P., Fernández-Jalvo, Y., 2018. Seasonal variation in prey composition and digestion in small mammal predator assemblages. *Int. J. Osteoarchaeol.* 28 (3), 318–331.
- Ballejo, F., Hadler, P., Cherem, J.J., Bueno, L., Machado, J.S., Matarrese, A.B., Fernández, F.J., 2022. The first fossil record of a bone assemblage accumulated by New World vultures (Gruta do Presépio, Holocene, southern Brazil). *Boreas* 51, 517–697.
- Behrensmeier, A.K., 1988. Vertebrate preservation in fluvial channels. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63 (1–3), 183–199.
- Behrensmeier, A.K., Hook, R.W., 1992. Paleoenvironmental contexts and taphonomic modes. In: Behrensmeier, A.K., DiMichele, W.A., Hook, R.W., Damuth, J.D., Potts, R., Sues, H.D., Wing, S.L. (Eds.), *Terrestrial Ecosystems through Time*. University of Chicago Press, Chicago, pp. 15–136.
- Behrensmeier, A.K., Kidwell, S.M., 1985. Taphonomy’s contributions to paleobiology. *Paleobiology* 11 (1), 105–119.
- Behrensmeier, A.K., DiMichele, W.A., Hook, R.W., Damuth, J.D., Potts, R., Sues, H.D., Wing, S.L. (Eds.), 1992. *Terrestrial Ecosystems through Time*. University of Chicago Press, Chicago.
- Beltrame, M.O., Fugassa, M.H., Sardella, N.H., Civalero, M.T., Aschero, C., 2011. Raptor pellets as zooarchaeological material for paleoparasitological studies in Patagonia. *J. Archaeol. Sci.* 38 (7), 1511–1515.
- Binford, L.R., 1981. *Bones: Ancient Men and Modern Myths*. Academic Press, New York.
- Borrero, L.A., Martín, F.M., 1996. *Tafonomía de carnívoros: un enfoque regional*. In: Gómez Otero, J. (Ed.), *Arqueología. Sólo Patagonia*. CENPAT (CONICET), Puerto Madryn, pp. 189–206.
- Borry, M., Cordova, B., Perri, A., Wibowo, M., Honap, T., Ko, J., et al., 2020. CoproID predicts the source of coprolites and paleofeces using microbiome composition and host DNA content. *PeerJ* 8, e9001.
- Bull, L.D., Simpson, I.A., van Bergen, P.F., Evershed, R.P., 1999. Muck ‘n’ molecules: organic geochemical methods for detecting ancient manuring. *Antiquity* 73 (279), 86–96.
- Campmas, E., Stoetzel, E., Denys, C., 2018. African carnivores as taphonomic agents: contribution of modern coprogenic sample analysis to their identification. *Int. J. Osteoarchaeol.* 28 (3), 237–263.
- Canal, V., Beltrame, M.O., 2022. Gastrointestinal parasite diversity of South American camelids (*Artiodactyla: Camelidae*): first review throughout the native range of distribution. *Int. J. Parasitol.: Parasites and Wildlife* 19, 222–242.
- Canti, M.C., 1998. The micromorphological identification of faecal spherulites from archaeological and modern materials. *Journal of Archeological Sciences* 25, 435–444.
- Carrión, J.S., Yll, R., Riquelme, J.A., González, P., 2004. Perspectivas del análisis polínico de coprolitos y otros depósitos biogénicos útiles en la inferencia paleoambiental. In: *Miscelánea en homenaje a Emiliano Aguirre: Paleontología*, vol. II. Museo Arqueológico Regional, Alcalá de Henares, pp. 128–139. Colección Zona Arqueológica N° 4.
- Castro, S.A., Silva, S.I., Meserve, P.L., Gutiérrez, J.R., Contreras, L.C., Jaksic, F.M., 1994. Frugivoría y dispersión de semillas de pimiento (*Schinus molle*) por el zorro culpeo (*Pseudalopex culpaeus*) en el Parque Nacional Fray Jorge (IV Región, Chile). *Rev. Chil. Hist. Nat.* 67, 169–176.
- Chame, M., 2003. *Terrestrial Mammal Feces: a Morphometric Summary and Description*. Memórias do Instituto Oswaldo Cruz 98, 71–94.
- Chimento, N.R., Dondas, A., 2018. First record of *Puma concolor* (Mammalia, Felidae) in the early-middle Pleistocene of South America. *J. Mamm. Evol.* 25, 381–389.
- Chin, K., 2021. Gastrointestinal parasites of ancient nonhuman vertebrates: evidence from coprolites and other materials. In: De Baets, K., Huntley, J.W. (Eds.), *The Evolution and Fossil Record of Parasitism: Coevolution and Paleoparasitological Techniques*. Springer, Cham, pp. 359–375.
- Coil, J., Korstanje, M.A., Archer, S., Hastorf, C.A., 2003. Laboratory goals and considerations for multiple microfossil extraction in archaeology. *J. Archaeol. Sci.* 30 (8), 991–1008.
- Coll, D.G., Montalvo, C.I., Fernández, F.J., Pia, M.V., Mondini, M., 2021. Actualistic taphonomic study of the rodents digested by the Achala culpeo fox (*Lycalopex culpaeus smithersi*) in the highlands of central Argentina. *Boreas* 50, 1146–1160.
- Coll, D.G., Moreano, C., Neveu Collado, C., Arias, M.F., Agliano, F., Pia, M.V., Mondini, M., 2022. Modelos de referencia a partir de muestras actuales y su importancia para la interpretación multiproxy de bromatolitos del valle de El Bolsón, Catamarca, Argentina. *Rev. Mus. La Plata* 7, 116R. Suplemento Resúmenes, 6° Congreso Nacional de Zooloarquología Argentina.
- Denys, C., Stoetzel, E., Linchamps, P., Fernández-Jalvo, Y., Andrews, P., 2023. Importance and role of neotaphonomic collections: the example of microvertebrate and experimental collection management. *Hist. Biol.* <https://doi.org/10.1080/08912963.2023.2223230>.
- Esteban-Nadal, M., Cáceres, I., Fosse, P., 2010. Characterization of a current coprogenic sample originated by *Canis lupus* as a tool for identifying a taphonomic agent. *J. Archaeol. Sci.* 37 (12), 2959–2970.
- Fernández, F.J., Montalvo, C.I., Fernández-Jalvo, Y., Andrews, P., López, J.M., 2017. A re-evaluation of the taphonomic methodology for the study of small mammal fossil assemblages of South America. *Quat. Sci. Rev.* 155, 37–49.
- Fernández-Jalvo, Y., Andrews, P., 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *J. Archaeol. Sci.* 19 (4), 407–428.

- Fernández-Jalvo, Y., Scott, L., Denys, C., 1999. Taphonomy of pollen associated with predation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 149, 271–282.
- Fernández-Jalvo, Y., Andrews, P., Sevilla, P., Requejo, V., 2014. Digestion versus abrasion features in rodent bones. *Lethaia* 47 (3), 323–336.
- Fernández-Jalvo, Y., Andrews, P., Denys, C., Sesé, C., Stöetzel, E., Marin-Monfort, D., Pesquero, D., 2016. Taphonomy for taxonomists: implications of predation in small mammal studies. *Quat. Sci. Rev.* 139, 138–157.
- Fernández-López, S.R., 2000. *Temas de Tafonomía*. Departamento de Paleontología, Universidad Complutense de Madrid.
- Fisher, D.C., 1981. Crocodylian scatology, microvertebrate concentrations, and enamelless teeth. *Paleobiology* 7 (2), 262–275.
- Fugassa, M.H., Petrih, R.S., Fernández, P.M., Catalayud, M.C., Belleli, C., 2018. Fox parasites in pre-Columbian times: evidence from the past to understand the current helminth assemblages. *Acta Trop.* 185, 380–384.
- Fuks, D., Dunseth, Z.C., 2021. Dung in the dumps: what we can learn from multi-proxy studies of archaeological dung pellets. *Veg. Hist. Archaeobotany* 30 (1), 137–153.
- Gifford-Gonzalez, D., 2018. *An Introduction to Zooarchaeology*. Springer, Cham.
- Gil-Romera, G., Neumann, F.H., Scott, L., Sevilla-Callejo, M., Fernández-Jalvo, Y., 2014. Pollen taphonomy from hyaena scats and coprolites: preservation and quantitative differences. *J. Archaeol. Sci.* 46, 89–95.
- Guerra, R.M.S.N.C., Gazeta, G.S., Amorim, M., Duarte, A.N., Serra-Freire, N.M., 2003. Ecological analysis of acari recovered from coprolites from archaeological site of northeast Brazil. *Memórias do Inst. Oswaldo Cruz* 98, 181–190.
- Haas, J., Creamer, W., Mesiam, L.H., Goldstein, D., Reinhard, K., Rodríguez, C.V., 2013. Evidence for maize (*Zea mays*) in the late archaic (3000–1800 B.C.) in the Norte Chico region of Peru. *Proc. Natl. Acad. Sci. USA* 110 (13), 4945–4949.
- Hagan, R., Hofman, C., Hübner, A., Reinhard, K., Schnorr, S., Lewis Jr., C., et al., 2020. Comparison of extraction methods for recovering ancient microbial DNA from paleofeces. *Am. J. Phys. Anthropol.* 171, 275–284.
- Hunt, A.P., 1992. Late Pennsylvanian coprolites from the Kinney Brick Quarry, central New Mexico, with notes on the classification and utility of coprolites. *New Mexico Bureau of Mines and Mineral Resources Bulletin* 138, 221–229.
- Hunt, A.P., Lucas, S.G., 2012. Classification of vertebrate coprolites and related trace fossils. *New Mexico Museum of Natural History and Science Bulletin* 57, 137–146.
- Hunt, A.P., Lucas, S.G., 2021. The ichnology of vertebrate consumption: dentalites, gastroliths and bromalites. *New Mexico Museum of Natural History and Science Bulletin* 87, 1–215.
- Hunt, A.P., Milan, J., Lucas, S.G., Spielmann, J.A., 2012. Vertebrate coprolites. *New Mexico Museum of Natural History & Science Bulletin* 57, 1–387.
- Jouy-Avantin, F., Debenath, A., Moigne, A.M., Moné, H., 2003. A standardized method for the description and the study of coprolites. *J. Archaeol. Sci.* 30 (3), 367–372.
- Karpinski, E., Mead, J., Poinar, H., 2017. Molecular identification of paleofeces from Bechan Cave, southeastern Utah, USA. *Quat. Int.* 443, 140–146.
- Korstanje, M.A., 2005. *La organización del trabajo en torno a la producción de alimentos en sociedades agro-pastoriles formativas (Pcia. de Catamarca, Rep. Argentina)*. Unpublished PhD Thesis, Universidad Nacional de Tucumán.
- Korstanje, M.A., 2014. Multiple microfossil extraction in environmental archaeology. In: Smith, C. (Ed.), *Encyclopedia of Global Archaeology*. Springer, New York, pp. 5082–5090.
- Korstanje, M.A., Cuenya, P., Maloberti, M., 2014. El análisis múltiple de microfósiles como herramienta para estudiar paisajes agrícolas y prácticas campesinas: una síntesis metodológica. *Avances y desafíos metodológicos*. In: Belmar, C., Lema, V. (Eds.), *Arqueobotánica: miradas consensuadas y diálogos compartidos desde Sudamérica*. Universidad SEK, Santiago de Chile, pp. 252–275.
- Korstanje, A., Velázquez, N., Petrih, R., Burry, S., Mondini, M., 2021. Las heces de herbívoros en el registro arqueológico como reservorios de información paleobiológica y cultural. El caso del Valle de El Bolsón, Catamarca, en el Holoceno Tardío. In: VIII Congreso Nacional de Arqueometría. Libro de Resúmenes. Instituto de Datación y Arqueometría, Palpalá, pp. 53–54.
- Larkin, N.R., Alexander, J., Lewis, M.D., 2000. Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater Bed, Norfolk, UK. *J. Archaeol. Sci.* 27 (1), 19–31.
- León-Lobos, P.M., Kalin-Arroyo, M.T., 1994. Germinación de semillas de *Lithrea caustica* H. et A. (Anacardiaceae) dispersadas por *Pseudaloxep* sp. en el matorral de Chile Central. *Rev. Chil. Hist. Nat.* 67, 59–64.
- Lloveras, L., Moreno-García, M., Nadal, J., 2008. Taphonomic analysis of leporid remains obtained from modern Iberian lynx (*Lynx pardinus*) scats. *J. Archaeol. Sci.* 35 (1), 1–13.
- Lonsinger, R.C., Gese, E.M., Waits, L.P., 2015. Evaluating the reliability of field identification and morphometric classifications for carnivore scats confirmed with genetic analysis. *Wildl. Soc. Bull.* 39 (3), 593–602.
- Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge.
- Lyman, R.L., 2018. Actualistic neotaphonomic research on bone modifying animal species: an analysis of the literature. *Palaios* 33 (12), 542–554.
- Maloberti, M., Korstanje, M.A., Quesada, M., 2016. Historizando la producción de quinua en el Valle de El Bolsón (Departamento Belén, Provincia de Catamarca). *Mundo de Antes* 10, 117–141.
- Martínez, J.G., 2014. Contribution to the knowledge of natural history and archaeology of hunter-gatherers of Antofagasta de las Sierras (Argentine South Puna): the case of Peñas de las Trampas 1.1. In: Pintar, E. (Ed.), *Hunter-gatherers from a High-Elevation. Desert People of the Salt Puna* (Northwest Argentina). Archeopress, Oxford, pp. 71–93.
- Martínez Tosto, A.C., Burry, L.S., Arriaga, M.O., Civalero, M.T., 2016. Archaeobotanical study of Patagonian Holocene coprolites, indicators of diet, cultural practices and space use. *J. Archaeol. Sci.: Report* 10, 204–211.
- Mallye, J.B., Costamagno, S., Boudadi-Maligne, M., Prucca, A., Lauroulandie, V., Thiébaud, C., Mourre, V., 2012. Dhole (*Cuon alpinus*) as a bone accumulator and new taphonomic agent? The case of Noisetier Cave (French Pyrenees). *Journal of Taphonomy* 10 (3–4), 317–347.
- Mondini, M., 2000. *Tafonomía de abrigos rocosos de la Puna. Formación de conjuntos escatológicos por zorros y sus implicaciones arqueológicas*. *Archeofauna, International Journal of Archaeozoology* 9, 151–164.
- Mondini, M., 2003. *Formación del registro arqueofaunístico en abrigos rocosos de la Puna argentina. Tafonomía de carnívoros*. Universidad de Buenos Aires. Unpublished PhD Thesis.
- Mondini, M., 2004. Accumulation of small and large vertebrates by carnivores in Andean South America. In: Brugal, J.-P., Desse, J. (Eds.), *Petits Animaux et Sociétés Humaines. Du Complément Alimentaire aux Ressources Utilitaires*. Éditions APDCA, Antibes, pp. 513–517.
- Mondini, M., 2005a. Magnitude of faunal accumulations by carnivores and humans in the South American Andes. In: O'Connor, T. (Ed.), *Biosphere to Lithosphere: New Studies in Vertebrate Taphonomy*. Oxbow Books, Oxford, pp. 16–24.
- Mondini, M., 2005b. Use of rockshelters by carnivores in the Puna. Implications for hunter-gatherer archaeology. Before Farming, the Archaeology and Anthropology of Hunter-Gatherers [online version] 2005/2 article 3/[print version] 2005/2:158–182.
- Mondini, M., 2012. *Tafonomía de carnívoros en los Andes Centro-Sur. Madrugueras actuales y sus implicaciones para el registro arqueofaunístico*. In: Acosta, A., Loponte, D., Mucciolo, L. (Eds.), *Temas de Arqueología. Estudios Tafonómicos y Zoológicos (II). Asociación Amigos del Instituto Nacional de Antropología y Pensamiento Latinoamericano*, Buenos Aires, pp. 67–105.
- Mondini, M., 2017. Four decades of actualistic carnivore taphonomy in the Southern Neotropics: a state of the art. *Journal of Taphonomy* 15 (1–3), 123–137.
- Mondini, M., 2019. In: Acción de carnívoros en el Pleistoceno Final de la Puna Austral: el caso de Peñas de las Trampas 1.1, Antofagasta de La Sierra, Catamarca, Argentina. Universidad Nacional de Córdoba, Córdoba, pp. 158–159.
- Mondini, M., Rodríguez, M.F., 2006. Taphonomic analysis of plant remains contained in carnivore scats in Andean South America. *Journal of Taphonomy* 4 (4), 221–233.
- Mondini, M., Perovic, P.G., Rodríguez, M.F., 2006. Integrated taphonomic analysis of macrorremains in carnivore scats. In: *International Council for Archaeozoology, 10th Conference. Abstracts*. Instituto Nacional de Antropología e Historia, México D.F., pp. 129–130.
- Mondini, M., Moreano, C., Montalvo, C.I., Madozzo-Jaén, C., Arias, P., Ortiz y M.F., 2020. Decoding the microvertebrate record in Alero Los Viscos (Catamarca, Argentina): a taphonomic investigation of the surface bone assemblage. In: López-García, J.M., et al. (Eds.), *Abstracts Book: 3rd Meeting of the ICAZ Microvertebrate Working Group*. Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Tarragona, pp. 42–43.
- Montalvo, C.I., Fernández, F.J., 2019. Review of the actualistic taphonomy of small mammals ingested by South American predators. Its importance in the interpretation of the fossil record. *Publicación Electrónica de la Asociación Paleontológica Argentina* 19, 18–46.
- Montalvo, C.I., Bisceglia, S., Kin, M.S., Sosa, R.A., 2012. Taphonomic analysis of rodent bone accumulations produced by Geoffroy's cat (*Leopardus geoffroyi*, Carnivora, Felidae) in Central Argentina. *J. Archaeol. Sci.* 39 (7), 1933–1941.
- Montalvo, C.I., Tomassini, R.L., Sostillo, R., 2016. Leftover prey remains: a new taphonomic mode from the Late Miocene Cerro Azul Formation of central Argentina. *Lethaia* 49 (2), 219–230.
- Montalvo, C.I., Fernández, F.J., Tomassini, R.L., Mignino, J., Kin, M.S., Santillán, M.A., 2020. Spatial and temporal taphonomic study of bone accumulation of the burrowing owl (*Athene cucularia*) in central Argentina. *Journal of Archaeological Science Reports* 30, 102197.
- Mosca Torres, M.E., de Porras, M.E., Aschero, C.A., 2022. Early-to-Middle Holocene environmental reconstruction in the southern Puna (26° S, Argentina) from camelid coprolite records. *J. S. Am. Earth Sci.* 116, 103805.
- Muñoz, S., Mondini, M., 2007. Humans in South American faunal communities. Interactions with prey and predators in the Southern Cone. *Cour. Forschungsinstitut Senckenberg* 259, 205–211.
- Myhrvoll, N.P., 2012. A call to search for fossilised gastric pellets. *Hist. Biol.: An International Journal of Paleobiology* 24 (5), 505–517.
- O'Meara, D.P., 2014. Ruminating on the past. A history of digestive Taphonomy in experimental archaeology. In: Flores, J.R., Paardekooper, R. (Eds.), *Experiments Past: Histories of Experimental Archaeology*. Sidestone Press, Leiden, pp. 131–146.
- Petrih, R.S., Martínez, J.G., Mondini, M., Fugassa, M.H., 2019. Ancient parasitic DNA reveals *Toxascaris leonina* presence in final Pleistocene of South America. *Parasitology* 146, 1284–1288.
- Petrih, R.S., Velázquez, N.J., Fugassa, M.H., Burry, L.S., Mondini, M., Korstanje, M.A., 2021. Herbivore coprolites from the SouthSouth-Central Andes. A multiproxy study at los Viscos archaeological site, Catamarca, Argentina. *J. Archaeol. Sci.: Report* 38, 103063.
- Pia, M.V., 2011. Influencia conjunta de la vegetación, asentamientos humanos, caminos y actividades ganaderas sobre la ocurrencia y dieta de los carnívoros tope de Achala (Córdoba, Argentina). Unpublished Biological Cs. Thesis, Universidad Nacional de Córdoba.
- Pia, M.V., 2013. Trophic interactions between puma and endemic culpeo fox after livestock removal in the high mountains of central Argentina. *Mammalia* 77 (3), 273–283.
- Pia, M.V., López, M.S., Novaro, A.J., 2003. Effects of livestock on the feeding ecology of endemic culpeo foxes (*Pseudaloxep culpaus smithersi*) in central Argentina. *Rev. Chil. Hist. Nat.* 76, 313–321.

- Prevosti, F.J., Forasiepi, A.M., 2018. Evolution of South American Mammalian Predators during the Cenozoic: Paleobiogeographic and Paleoenvironmental Contingencies. Springer, Cham.
- Reinhard, K.J., 1990. Archaeoparasitology in North America. *Am. J. Phys. Anthropol.* 82 (2), 145–163.
- Reinhard, K.J., Bryant Jr., V.M., 1992. Coprolite analysis: a biological perspective on archaeology. In: Schiffer, M.B. (Ed.), *Archaeological Method and Theory*, 4. The University of Arizona Press, Tucson, pp. 245–288.
- Reinhard, K.J., Bryant Jr., V.M., 2008. Pathoecology and the future of coprolite studies in bioarchaeology. In: Stodder, A.L.W. (Ed.), *Reanalysis and Reinterpretation in Southwestern Bioarchaeology*. Arizona State University, Tempe, pp. 199–216.
- Reinhard, K.J., Camacho, M., Geyer, B., Hayek, S., Horn, C., Otterson, K., Russ, J., 2019. Imaging coprolite taphonomy and preservation. *Archaeological and Anthropological Sciences* 11, 6017–6035.
- Reynolds, J.C., Aebischer, N.J., 1991. Comparison and quantification of carnivore diet by fecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mamm. Rev.* 21, 97–122.
- Sanz, M., Daura, J., Égüez, N., Brugal, J.-P., 2016. Not only hyenids: a multi-scale analysis of Upper Pleistocene carnivore coprolites in Cova del Coll Verdaguer (NE Iberian Peninsula). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 443, 249–262.
- Schmitt, D.N., Juell, K.E., 1994. Toward the identification of coyote scatological faunal accumulations in archaeological contexts. *J. Archaeol. Sci.* 21, 249–262.
- Schmitt, D.N., Lupo, K.D., 1995. On mammalian taphonomy, taxonomic diversity, and measuring subsistence data in zooarchaeology. *Am. Antiq.* 60, 496–514.
- Shahack-Gross, R., 2011. Herbivorous livestock dung: formation, taphonomy, methods for identification, and archaeological significance. *J. Archaeol. Sci.* 38 (2), 205–218.
- Shillito, L.M., Blong, J.C., Green, E.J., van Asperen, E.N., 2020. The what, how and why of archaeological coprolite analysis. *Earth Sci. Rev.* 207, 103196.
- Shillito, L.M., Bull, I.D., Matthews, W., Almond, M.J., Williams, J.M., Evershed, R.P., 2011. Biomolecular and micromorphological analysis of suspected faecal deposits at Neolithic Çatalhöyük, Turkey. *J. Archaeol. Sci.* 38 (8), 1869–1877.
- Stallibrass, S., 1990. Canid damage to animal bones: two current lines of research. In: Robinson, D.E. (Ed.), *Experimentation and Reconstruction in Environmental Archaeology*. Oxbow Books, Oxford, pp. 151–165.
- Taglioretti, V., Sardella, N.H., Fugassa, M.H., 2014. Morphometric analysis of modern faeces as a tool to identify artiodactyls' coprolites. *Quat. Int.* 352, 64–67.
- Thomas, D.H., Mayer, D., 1983. Behavioral faunal analysis of selected horizons. In: Thomas, D.H. (Ed.), *The Archaeology of Monitor Valley 2: Gatecliff Shelter*. American Museum of Natural History, New York, pp. 353–391.
- Tolar, T., Galik, A., Le Bailly, M., Dufour, B., Caf, N., Toškan, B., Bužan, E., Zver, L., Janžeković, F., Velušček, A., 2021. Multi-proxy analysis of waterlogged preserved Late Neolithic canine excrements. *Veg. Hist. Archaeobotany* 30, 107–118.
- Velázquez, N.J., Petrih, R.S., Benvenuto, M.L., Martínez Tosto, C., Camiolo, I., Palacio, P.I., Fugassa, M.H., Valenzuela, L.O., Burry, L.S., 2019. Diseño y evaluación de un protocolo de extracción múltiple de restos vegetales, silicofitolitos, polen, parásitos, isótopos estables y ADN de heces de *Lama guanicoe*. *Anales de Arqueología y Etnología* 74 (2), 127–145.
- Velázquez, N.J., Martínez Tosto, A.C., Benvenuto, M.L., Fernández, N., Civalero, M.T., Burry, L.S., 2021. Multiproxy analysis of omnivore and herbivore coprolites: inferences on Mid-Holocene dietary habits in Argentine Patagonia. *Quat. Int.* 601 (10), 130–142.
- Wood, J.R., Wilmshurst, J.M., 2013. Pollen analysis of coprolites reveals dietary details of heavy-footed moa (*Pachyornis elephantopus*) and coastal moa (*Euryapteryx curtus*) from Central Otago. *N. Z. J. Ecol.* 37, 151–155.
- Wood, J.R., Wilmshurst, J.M., 2016. A protocol for subsampling late Quaternary coprolites for multi-proxy analysis. *Quat. Sci. Rev.* 138, 1–5.
- Yang, L., Zhang, X., Zhao, X., Xiang, H., 2022. The technological advance and application of coprolite analysis. *Frontiers in Ecology and Evolution* 9, 797370.
- Zipfel, B., Montgomery, C., Neumann, F.H., Scott, L., Choiniere, J., Hancox, J.P., 2023. Overlooked or unimportant? An overview of the coprolite collections at the University of the Witwatersrand, Johannesburg, South Africa. *Curator* 66 (1), 149–164.