Martín-Perea, David M.; Domingo, Maria S.; Cantero, Enrique; [et al.]. «Recurring taphonomic processes in the carnivoran-dominated Late Miocene assemblages of Batallones-3, Madrid Basin, Spain». Lethaia, (September 2021). DOI 10.1111/let.12445

# Recurring taphonomic processes in the carnivoran-dominated assemblages of Batallones-3 (Late Miocene, Madrid Basin, Spain)

David M. Martín-Perea[a, b, c]*, M. Soledad Domingo[d], Enrique Cantero[a], Lloyd A. Courtenay[e], Alberto Valenciano[f], Lucía R. Sualdea[b], Juan Abella[g, h], Jorge Morales[a]

[a] Palaeobiology Department, National Natural Sciences Museum – CSIC, Madrid, Spain

[b] Geodynamics, Stratigraphy and Palaeontology Department, Faculty of Geology, Complutense University of Madrid, Madrid, Spain

[c] Institute of Evolution in Africa – IDEA, Madrid, Spain

[d] Sciences, Social Sciences and Mathematics Education Department, Faculty of Education, Complutense University of Madrid, Madrid, Spain

[e] Department of Cartographic and Land Engineering, Higher Polytechnic School of Avila, University of Salamanca, Avila, Spain

[f] Earth Sciences Department, Paleontology Area and Environmental Sciences Research Institute (IUCA), Zaragoza University, Zaragoza, Spain

[g] Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Spain

[h] Biodiversity National Institute (INABIO), Quito, Ecuador

*Corresponding author: davidmam@ucm.es

## Abstract

Carnivoran-dominated fossil sites are scarce in the fossil record but provide precious information on the diversity and ecology of past carnivoran guilds. The Cerro de los Batallones sites host the oldest carnivoran-dominated assemblages, with the highest carnivoran abundances observed in the fossil record. Batallones-3 (Late Miocene, Madrid Basin, Spain) hosts three discrete, carnivoran-dominated fossiliferous levels deposited in a 15 m diameter, 4 m high pseudokarstic cavity with 1 m high talus cone located beneath the mouth of the cavity on the roof. Levels I, II and III are multitaxic multidominant assemblages, with the sabretooth cats *Promegantereon ogygia* and *Machairodus aphanistus* and the ursid *Indarctos arctoides* being the most abundant species. These carnivoran-dominated assemblages are autochthonous and show diagenetically fractured but well-preserved remains (complete, little to no weathering or abrasion). Root marks and manganese oxide precipitation are common and more abundant in Level III, due to modern pedogenic processes. There are also a few allochthonous, badly preserved (weathered and abraded) herbivore remains that were washed into the cavity. The taphonomic homogeneity of all three levels suggest recurring taphonomic and geologic processes throughout the accumulation of infill in the cave. The trap-like nature of the cave, unbroken, and largely unweathered carnivoran bones suggest these predators intentionally jumped into the cave but were unable to escape.

**Keywords:** Taphonomy, Mammals, Carnivoran, Vallesian, Pseudokarst

## Introduction

Carnivore fossil remains commonly outnumber herbivore remains in mammalian fossil sites, with carnivorans usually represented by less than 10% of the total Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI; Klein & Cruz-Uribe 1984). This amount of carnivores in fossil sites is a result of the position of this group of animals at the top of the trophic pyramid in living communities, where they constitute a small portion of the ecosystem biomass, with herbivore to carnivore ratios estimated at 50:1 in modern ecosystems (Eisenberg 1981; Stock & Harris 1992; Farlow 1993).

For this reason, there are few known carnivoran-dominated fossil sites, most of them Pleistocene or Holocene in age. The best examples are the Pleistocene localities of Rancho La Brea (Stock 1972; Marcus & Berger 1984; Stock & Harris 1992; Binder *et al.* 2002; Feranec *et al.* 2009), Talara (Lindsey & Seymour 2015), La Carolina (Hoffstetter 1952), Sima de los Huesos (Arsuaga *et al*. 1997; García *et al*. 1997), Moonshine Cave (White *et al*. 1984) and Middle Butte Cave (White *et al*. 1984). At Rancho La Brea, Talara and La Carolina, it is proposed that herbivores trapped in asphalt attracted carnivores, which also became trapped. Similar taphonomic histories are inferred for the other carnivoran-dominated localities, although in caves. In these cases, either karstic caves (Sima de los Huesos) or Lava Blisters (Moonshine Cave and Middle Butte) acted as natural traps, where carnivores entered the cave to feed on entrapped herbivores but became trapped themselves (Arsuaga *et al*. 1997; García *et al*. 1997; White *et al*. 1984).

Not all fossil sites interpreted as the result of natural trapping host carnivoran-dominated assemblages. Natural Trap Cave (Gilbert 1978; Martin & Gilbert 1978; Chomko & Gilbert 1987; Wang & Martin 1993), Rantis Cave (Marder *et al*. 2011) and Trinchera-Galería (García & Arsuaga 1998) in the Pleistocene, and Cupcake Cave shaft (Lord *et al*. 2016), McEachern's Deathtrap Cave (Kos 2003) and Shield Trap Cave (Oliver 1986; Oliver *et al*. 1986) in the Holocene are all examples of naturally trapped, herbivore-dominated assemblages in karstic caves. The differences between these herbivore-dominated and carnivore-dominated sites are attributed to different entrance modes, with animals being trapped after active entrance in carnivoran-dominated assemblages and due to accidental entrance in herbivore-dominated assemblages (White *et al*. 1984).

Since the discovery of the Cerro de los Batallones (Batallones Butte) sites in 1991, two carnivoran-dominated sites, Batallones-1 and Batallones-3, have provided precious information on the diversity of carnivorans in the past. These sites are unique for numerous reasons: 1) dating back to the Miocene, these sites host the oldest known carnivoran-dominated assemblages, 2) both assemblages host the highest carnivoran abundances observed in the fossil record, 3) the excellent nature of preservation and skeletal completeness of the remains allows the description of new or poorly-known species, and 4) the peculiar, piping pseudokarst nature of the cavities constitutes a new geological setting for fossil assemblages. These sites constitute an exceptional archive that expands our knowledge of the diversity and ecology of these ancient carnivoran guilds and the taphonomic history of these uncommon fossil localities.

## The Cerro de los Batallones complex

The Cerro de los Batallones complex is located 30km south of Madrid (Spain, Figure 1A), and 1 km east of Valdemoro (Figure 1B) and belongs to the municipality of Torrejón de Velasco. The paleontological complex is comprised of nine sites, which host rich and diverse faunal assemblages (Morales 2017) including a wide array of carnivorans, such as sabretooth cats (Antón *et al*. 2004; Salesa *et al*. 2006, 2008, 2010; Monescillo *et al*. 2014; Siliceo *et al*. 2014; Antón *et al*. 2020), other felids (Salesa *et al*. 2012), amphicyonids (Peigné *et al*. 2008; Siliceo *et al*. 2015; Morales *et al*. 2017; Siliceo *et al*. 2017, 2020; Morales *et al*. 2021), ailurids (Peigné *et al*. 2005; Antón *et al*. 2006; Salesa *et al*. 2006; Salesa *et al.* 2017), ailuropod ursids (Abella *et al*. 2012, 2013, 2015; Abella & Valenciano 2017), hyaenids (Fraile 2016, 2017), mustelids and mephitids (Valenciano *et al*. 2015; Valenciano 2017; Valenciano *et al*. 2020; Valenciano & Govender 2020), herbivorous mammals, including proboscideans (Alberdi *et al*. 2017), perissodactyls (Romano *et al*. 2017; Sanisidro & Cantalapiedra 2017; Domingo *et al*. 2018), and artiodactyls (Sánchez *et al*. 2009; Sánchez *et al*.

2011; Pickford 2015; Ríos *et al*. 2017; Ríos & Morales 2019). These sites have also yielded a rich assemblage of small mammals, including rodents, insectivores and lagomorphs (López-Antoñanzas *et al*. 2010; 2014; Álvarez-Sierra *et al*. 2017; Medina-Chavarrías *et al*. 2019).

Based on their faunal association, the Cerro de los Batallones sites are inferred to have a late Vallesian age (ca. 9.1 Ma; early Late Miocene; Domingo *et al*. 2007; Morales *et al*. 2008; López-Antoñanzas *et al*. 2010; Gómez Cano *et al*. 2011). However, the rodent fauna indicates the sites differ in age, with Batallones-10 being the oldest, followed by Batallones-1, with Batallones-3 being the youngest site in the Cerro de los Batallones complex (López-Antoñanzas *et al*. 2010). In any event, given that López-Antoñanzas *et al*. (2010) placed all the Batallones localities either in the local subzone J2 (dated 9.71-9.48 Ma) or J3 (9.34-9.05 Ma), the age difference between the oldest and youngest of these localities is at most of 0.3 Myr.

The Cerro de los Batallones sites are vertical, hourglass-shaped cavities (Figure 1C) formed in the Late Miocene due to soil piping pseudokarstic processes (Pozo *et al*. 2004; Calvo *et al*. 2013) in a woodland palaeoenvironment with patches of wooded grassland (Domingo *et al*. 2013b, 2016). In most of these caves, the basal strata are dominated by carnivoran remains which formed when the cavities were natural traps (Domingo *et al*. 2011, 2012, 2013a) whereas the upper strata host more typical herbivore-dominated assemblages, probably formed around ponds that corresponded to the upper part of the cavities as they were filled with sediment. However, at Batallones-3, located in the slope of the Batallones butte, only one stratum is preserved, and it contains the carnivoran-dominated assemblage. It is not known whether an upper stratum existed and if it did, it could have been lost to erosion..

. The cavity has a diameter of ~15 metres with an 8-metre-wide, ~1-metre-high debris cone below the vertical entrance. The debris cone is composed of collapsed cavity blocks embedded in a detritic matrix, which hosts plant remains and abundant freshwater fauna (gastropods, river crabs, amphibians and some beaver remains). These materials are inferred to come from the upper part of the hourglass-shaped cavity, which in this case would have acted as a small pond or a permanent water body before roof collapse (Abella *et al*. 2017).

Recent studies have confirmed the existence of discrete fossiliferous levels in both the upper (at Batallones-10) and lower parts (at Batallones-3) of the cavities (Martín-Perea *et al*. 2020). Three discrete fossiliferous levels were found in the lower part of the hourglass structure at Batallones-3 (Figure 2).

The identification of discrete fossiliferous levels makes it necessary to analyse each of them independently to better characterise the taphonomic history of the site which, in turn, will allow more accurate future palaeoecological and palaeoenvironmental inferences of such similar assemblages. In this work, a detailed taphonomic and comparative study is carried out for each of the levels present at Batallones-3 to understand the biostratinomic and diagenetic processes of this carnivoran-dominated assemblage and to assess whether or not these different assemblages differ in their taphonomy.

## Materials and Methods

Batallones-3 has undergone numerous excavations, including a campaign in  2001 and continuous annual interventions from 2005 through 2017, ranging in duration from three weeks to six weeks. Standard fossil vertebrate excavation protocols were followed Eberth *et al*. 2007). The extraction of fossils was documented on-site, including taxonomic features, element identification, mapping of bones (x, y and z coordinates) and the trend and plunge of elongated bones. Unidentified bone fragments and splinters smaller than 4 cm were not mapped.

Artificial intelligent systems (AI) were used to identify discrete fossiliferous levels within Batallones-3. AI methods followed Martín-Perea *et al*. (2020) and consisted of: (1) unsupervised Machine Learning for density-based clustering, (2) expert-in-the-loop Collaborative Intelligence Learning for the integration of geological data and (3) supervised learning for fine-tuning of fossiliferous level models. Once the levels had been identified across several sections of the site, supervised Random Forest (RF) and Support Vector Machines (SVM) models were used to classify remaining fossils into their corresponding fossiliferous levels. These algorithms were trained using a traditional machine learning approach, employing k-fold cross-validation (k = 10), a 70:30% train:test split, and random searches for hyperparameter optimization. An 80% probability threshold was established for each prediction to determine whether a fossil should be classed as indeterminable (<80%) or not (>80%). In cases where SVM and RF disagree on a class label, the model with the greatest confidence in their prediction was used for the final classification.

Each fossil was then provided with a final class probability. Overall confidence for the final classified site was established and calculated using robust statistical metrics, reporting the median confidence as well as a +/- margin of error using non-symmetric inter-quartile ranges marking 68.3% of overall variability (Höhle & Höhle 2009). Finally, agreement between the two machine learning algorithms was determined measuring for inter-rater reliability through the calculation of Cohen's Kappa (k) coefficient (Cohen 1960).

Trend and plunge of elongated fossils in each level were plotted on equal area (Schmidt) stereographic projections with inverse area smoothing. A stereographic projection was plotted for each of 8 theoretical 2 $m^2$ grids around the debris cone for each fossil level. A detailed spatial analysis was carried out using R software (Spatstat library; Baddeley *et al.* 2015) to represent fossil densities per taxon per level.

A taphonomical analysis was carried out for each of the identified discrete fossiliferous levels. Number of Identified Specimens (NISP) and Minimum Number of Elements (MNE) were calculated following Lyman (1994). To calculate MNE, age, side and the superposition of anatomical markers have been taken into account. Since NISP may differentially exaggerate sample sizes across taxa (Lyman 2008), Minimum Number of Individuals (MNI) was also calculated. Relative Abundance (Ri) of particular skeletal elements for the dominant taxa (*Machairodus aphanistus*, *Promegantereon ogygia* and *Indarctos arctoides*) were calculated with the formula by Andrews (1990):

$$\mathrm{Ri} = \frac{\mathrm{MNEi}}{\mathrm{MNI\ x\ Ei}} \mathrm{x}\ 100$$

where Ri is the relative abundance of element i, MNEi is the minimum number of element I in the sample, MNI is the minimum number of individuals of the taxon, and Ei is the number of times that element i appears in a complete skeleton. In order to determine whether or not there were significant bias in the skeletal representation of different taxa, Kolmogorov-Smirnov tests were performed comparing the observed skeletal representation to the expected skeletal representation according to the MNI estimated for each taxon.

Age at death of carnivoran individuals was calculated based the eruption and replacement of teeth, degree of wear of occlusal surfaces and bone epiphysiary fusion. These were grouped into juveniles, prime adults and old individuals, following Stiner (1990).

A systematic examination of bone surface modifications was carried out with an 8X-15X hand lens following Blumenschine (1995). Given the taphonomic homogeneity of the assemblage and the large number of remains, 10% of the elements in level were randomly selected for taphonomic evaluation (479 for Level I, 405 for Level II, 171 for Level III). Although unidentified bone fragments with an elongated axis smaller than 4 cm and splinters were not mapped, a random sample of 1004 of these remains was also taphonomically analysed.

Breakage analyses followed the criteria of Villa & Mahieu (1991) and Lyman (1994). Perpendicular and smooth (dry) fractures often occur in recrystallized or permineralized bones due to diagenetic processes, whereas spiral, irregular and saw-toothed (green) fractures mainly occur in fresh, collagen-rich bones, usually produced by carnivoran or anthropic activity and trampling (Lyman 1994). Bone completeness was analysed following Pesquero *et al*. (2013) using the following categories: complete, almost complete (bones only missing a chip), more than one-half complete, and one-half complete or less.

Weathering was estimated according to Behrensmeyer's (1978) scale from 0 (not weathered, exposed for less than one year before burial) to Stage 5 (extremely weathered, exposed for 15-30 years before burial). Note that other authors, such as Lyman & Fox (1989) have warned that direct correlations between weathering stages and time should be considered with caution as other taphonomic factors (microenvironment, skeletal element, taxon, agents of exposure and burial) might produce deviations.

Abrasion is indicative of the erosion caused to the remains by means of friction with sedimentary particles. Stages proposed by Alcalá (1994) were used to analyse abrasion: intact bone (Stage 1), rounded bone (Stage 2) and polished and smoothed bone (Stage 3).

Other surface modifications such as corrosion, digestion, root markings, presence of manganese oxide, trampling, rodent marks and carnivore marks were also recorded, following Fisher (1995) and Fernández-Jalvo & Andrews (2016). Diagnostic criteria defined by Blumenschine (1988, 1995) were used to identify carnivore marks.

Statistical analyses (chi-square tests) were carried out to compare the three discrete fossiliferous levels at Batallones-3. Additionally, these were also compared to the Batallones-1 assemblage. In order to avoid type I errors, we set our significance level at $p = 0.01$. In the Supporting Information, we provide the adjusted residuals of those analyses that were statistically significant in order to shed light on the specific variables that contribute more strongly to the observed differences (values outside the two-sigma interval [-1.96, 1.96).

## Results

### *Batallones-3 discrete fossiliferous levels*

The three discrete fossiliferous levels previously described at Batallones-3 (Martín-Perea *et al*. 2020) could be observed throughout the site (Figure 2). Out of the 18,922 fossil remains recovered from the excavations, 16,178 had complete coordinate data (x, y and z values). A total of 10,553 fossil remains were classified with over 80% confidence into one of the three fossil levels: 4794 into Level I, 4048 into Level II and 1711 into Level III.

Both machine learning algorithms agreed on 89.2% of classifications, with RF generally considered the most confident. Overall probability of level association revealed models where 99.6 +/- [0.004, 0.006] % confident of the final classifications for the Batallones-3 site levels I, II and III. Furthermore, calculations reveal models have a 75-1% likelihood of agreement according to Cohen's k. This implies substantial agreement between models, thus supporting the use of both RF and SVM for the systematic analyses of this site.

*Assemblage data*

A total of 16 large-mammal species have been identified at Batallones-3, out of which 12 are carnivoran species (Table 1). The felids *Promegantereon ogygia* (NISP = 956, 20.13%) and *Machairodus aphanistus* (NISP = 752, 15.83%) as well as the ursid *Indarctos arctoides* (NISP = 918, 19.33%) dominate the Level I assemblage (Table 1). Similarly, Level II is dominated by *Promegantereon ogygia* (NISP = 1117, 27.67%), *Machairodus aphanistus* (NISP = 844, 20.91%) and *Indarctos arctoides* (NISP = 517, 12.81%; Table 1). The same is true for the Level III assemblage, which is multidominant but with *Machairodus aphanistus* remains (NISP = 537, 31.44%) being more abundant than *Promegantereon ogygia* (NISP = 110, 6.44%) and *Indarctos arctoides* (NISP = 149, 8.72%; Table 1). The remaining carnivores are represented in notably lower proportions. The statistical test points to a significant difference in the carnivoran composition between Level I and Level III (Table 2), with *Machairodus aphanistus* (more abundant in Level III than in Level I) and *Protictitherium crassum* (more abundant in Level I than in Level III) having more weight in this comparison (see Supplementary Information).

Table 3 shows the skeletal element proportions in Batallones-3 levels. Vertebrae constitute the most abundant skeletal element of Level I (15.05%), Level II (15.52%)

and Level III (18.09%) assemblages. Moderately abundant elements (over 2% of the assemblage) include incisors, ribs, femurs, metapodials, phalanges, sesamoids, carpal and tarsal bones. A total of 461 (9.62%) remains were anatomically unidentifiable in Level I, 210 (5.17%) in Level II and 91 (5.33%) in Level III (Table 3).

Skeletal completeness percentages for *Machairodus* aphanistus, *Promegantereon* ogygia and *Indarctos arctoides* are high in Levels I and II (Figures 3A-F), but decrease in Level III (Figures 3G-I). Even though vertebrae constitute the most abundant elements for the total sample (Table 3), vertebrae and ribs are underrepresented for any taxon in any level (Figure 3).

### *Spatial data*

Batallones-3 has an excavated area of 160 m$^2$. Bedrock floor has been reached throughout the site, while the lowermost cave walls are also observable (Figure 2). The uppermost section of the cave was lost due to erosion on slopes along the northwest side of the cave(Figure 2). The three fossiliferous levels dip away from the centre to the walls of the cave and rest disconformably over a debris cone of collapsed cave fragments (Figures 2B, 2C).

Trend and plunge data were represented on several stereographic projections per level per 16 m$^2$ grids around the debris cone (Figure 4). Stereographic projections indicate bones generally dipping very gently (sub-horizontal) towards the northwest or towards the wall of the cave.

Fossil densities were visualized per level per species in plan view (X-Y plain) using the “spatstat” R package. The number of clusters per level closely resembles the MNI for each species in that given level, as exemplified for *Indarctos arctoides* remains in Levels I, II and III (Figure 5).

*Bone modification data*

Breakage, along with root etching, is the most pervasive taphonomic alteration in all Batallones-3 fossiliferous levels (Figure 6). Although some bones are fractured, with bones presenting more than 3 fractures making up 37.5% of the Level I assemblage, 43.1% of Level II and 43.8% of Level III (Figures 6A, B and C), the majority of remains are complete: 84.4% complete bones in Level I, 76.4% in Level II and 53.4% in Level III (Figures 6D, E and F). These fractures appear in different angles, types (Figure 6G, H and I) and most have smooth fracture plane surfaces: 63.4% of fractures in Level I, 58.0%in Level II and 67.9% of fractures in Level III (Figures 6J, K and L). In general, there is homogeneity among Batallones-3 levels when the fracture categories are statistically compared. Nevertheless, as for bone completeness, there are significant statistical differences between Level I and Level III, and between Level II and Level III (Table 2). In Level III, bones that are less than one half complete are significantly more abundant than in Level I and Level II, where complete bones are more abundant (Figure 6; Supporting Information).

Unweathered bones (Stage 0) dominate in all Batallones-3 levels (Table 4). Weathering Stage 1 is only observed in 0.6% of Level III fossil remains, whereas for unidentified bones with no assigned level it is slightly higher (2.5%). Only three unidentified remains (0.3 %) showed Weathering Stage 2. No bones displayed Weathering Stages 3 or higher. Abrasion follows a similar pattern with a predominance of Abrasion Stage 1 (intact, non-abraded bone; Table 4). Abrasion Stage 2 only affects 5.3% of the remains in Level III and 7.7% in unidentified remains whereas Stage 3 is only observed in a few unidentified remains with no assigned level (0.4%). There are no statistically significant differences between levels for weathering or abrasion (Table 2).

Root marks are common throughout Batallones-3 levels: 43.8% of remains are root marked in Level I, 59.7% in Level II and 64.4% in Level III (Table 4). Trampling was only observed in 1.6% of the unidentifiable remains, none of which were assigned to a level. There is no evidence of rodent or carnivore marks or digestion alteration in any Batallones-3 levels.

The vast majority of analysed remains exhibited manganese oxide precipitations: 73.5% in Level I, 84.7% in Level II and 91.8% in Level III. Manganese oxides are common along fractures and widespread on bone surfaces.

## Discussion

Using traditional methods, which often make it difficult to recognize discrete horizons, a taphonomy study would have been conducted on the entire deposit, obfuscating potential differences through the time averaged assemblage. This problem was minimized using AI, which identified three discrete fossil levels at Batallones-3 and assigned 65% of the fossil remains into these levels. This enabled a more accurate understanding of the environmental history of the site.

The carnivoran guilds in all three Batallones-3 levels, which includes 12 species, is the most diverse of the Cerro de los Batallones complex. Moreover, carnivoran species dominate the assemblage, which, as has previously been stated, is uncommon in the fossil record. Our taxonomic study of the Batallones-3 fossil material provides unprecedented information on such rare carnivoran-dominated assemblages. The similarities between the three levels indicate (1) all were subject to the same taphonomic conditions and (2) indicates taphonomic conditions did not skew assemblage data.

Batallones-3 Levels I, II and III comprise multitaxic and multidominant assemblages, dominated by the sabretooth felids *Promegantereon ogygia* and *Machairodus aphanistus* and the ursid *Indarctos arctoides* (Table 1). Statistical analyses of the MNI of the carnivoran species composition of the three levels reveal that Levels I and II exhibit a similar carnivoran composition, which differ from Level III (Table 2; Supporting Information).

In Levels I and II, which are deeper and therefore older, *Promegantereon ogygia* is more abundant than the other sabretooth felid, *Machairodus aphanistus*, which in turn becomes the dominant carnivoran taxon in the youngest level, Level III. Other trends in the carnivoran guild involve a decrease in the hyaenid *Protictitherium crassum* and the mustelid *Eomellivora piveteaui* and a slight increase in the two amphicyonid species. The ursid *Indarctos arctoides* does not show a clear trend: its MNI decreases from Level I to Level II, the increases in Level III.

When comparing Batallones-3 with Batallones-1 in terms of carnivoran faunal composition, statistically significant differences emerge related to the presence/absence of some of the carnivoran species, as revealed by the values of the adjusted residuals of the chi-square analysis (Supporting Information). These differences were previously discussed by Domingo *et al.* (2016) and mainly pertain to the presence of the ailurid *Simocyon batalleri* at Batallones-1 and its absence at Batallones-3, and the presence of the ursid *Indarctos arctoides* and the mustelid *Eomellivora piveteaui* at Batallones-3 and its absence from Batallones-1. Evaluation of the residuals also reveals differences in the abundance of *Magericyon anceps*, which is greater at Batallones-1 than in any Batallones-3 levels. Apart from the aforementioned absences of taxa, the adjusted residuals also show that the frequencies of *Promegantereon ogygia* (higher at Batallones-1), and *Thaumastocyon* sp. (greater at Batallones-3 Level III), play an important role in the statistically significant differences between Batallones-3 Level III and Batallones-1 (Supporting Information).

As indicated by Domingo *et al.* (2016), these species abundance differences could represent biological trends, such as diversity turnover or changes in population densities in the Madrid Basin over time. The accumulation of the Batallones-1 and Batallones-3 assemblages was asynchronous; they were deposited in the following order, from oldest to youngest: Batallones-1, Batallones-3 Level I, Batallones-3 Level II and Batallones-3 Level III (López-Antoñanzas *et al.* 2010), and our analyses indicate that *Machairodus aphanistus*, *Indarctos arctoides* and *Thaumastocyon* sp. became more abundant through time, whereas the abundance of individuals of *Promegantereon ogygia*, *Protictitherium crassum* and *Simocyon batalleri* decreased. Further light will be shed on these trends in future studies, which will consider not only Batallones-1 and Batallones-3, but other Cerro de los Batallones localitiesonce they are excavated and studied. Furthermore, the identification of discrete fossiliferous levels (following Martín-Perea *et al.* 2020) within the other Cerro de los Batallones localities will provide more information on faunal compositional changes.

The low percentages of anatomically unidentified remains in Batallones-3 (9.62% in Level I, 5.17% in Level II and 5.33% in Level III) are indicative of the good state of preservation of these fossils. Although the remains are fractured (Figures 6A, B and C), many of them are complete (Figures 6D, E and F) and well preserved (Figure 7). Interestingly, there are statistically significant differences of bone completeness in the Batallones-3 levels, between Level I and Level III and between Level II and Level III (Table 2; Supporting Information). The bones are most complete in Levels I and II, whereas in Level III 30.7% of the bones are one-half or less complete. Level III, the highest level, was very close to the current surface and damage may be related to rooting and slope erosion. The fractures at Batallones-3 are mostly perpendicular in long bones (Figures 6G, H and I) and smooth (63.4% in Level I, 58.0% in Level II and 67.9% in Level III; Figures 6J, K and L), which is indicative of diagenetic breakage (Figure 7, Figure 8B). The bone completeness at all three Batallones-3 levels significantly differ from that at Batallones-1 (Table 2). This difference, on comparing Batallones-3 Level I and Level II with Batallones-1, is due to the higher abundance of complete bones, together with a lower abundance of almost complete bones at Batallones-3 compared to Batallones-1 (Supporting Information). In any case, the bones present a high degree of integrity, as complete and almost complete bones are prevalent. Nevertheless, when comparing Batallones-3 Level III with Batallones-1, the primary difference is the abundance of bones which are one-half or less complete at Batallones-3 Level III in comparison with Batallones-1.

Although the most abundant skeletal elements are vertebrae (15.05% in Level I, 15.52% in Level II and 18.09% in Level III), all other skeletal elements are represented (Table 3). The very low representation of vertebrae and ribs for all taxa (Figure 3) could be due to the difficulty in assigning these to a particular species, given the lack of diagnostic characters. Nonetheless, the percentages of skeletal completeness for *Machairodus* aphanistus, *Promegantereon* ogygia and *Indarctos arctoides* are generally high (Figure 3), and Kolmogorov-Smirnov tests indicate that there is no significant anatomical bias relative to complete skeletons (Table 5). These results suggest individuals were complete in the thanatocoenosis and taphocoenosis.

Furthermore, the fossil remains are found in monotaxic clusters, which when represented per level, show approximately the same number of clusters as of MNI (Figure 5). This appears to indicate that the remains have undergone little, if any, biostratinomic or fossildiagenetic displacement. Conversely, the trend data for elongate remains show that although they were not significantly displaced, they were slightly reoriented (Figure 4). This partial and slight reorientation likely took place during the episodic sedimentary infilling of the cavity, since the mean trend and plunges of the fossil remains coincide with the inferred entry of alluvial sediments presenting a north-western direction, following the slope dip of the Batallones butte rim (Figure 1).

Given the stable humidity and temperature levels in caves, as well as the lack of direct sunlight, bones can remain unburied long periods of time without undergoing heavy weathering (Wang & Martin 1993). For this reason, estimates of time before burial according to weathering stages (Behrensmeyer 1978) are not applicable in this scenario. Most of the bones at Batallones-3 are unweathered (Weathering Stage 0), which is accounted for by the protective environment of the chamber. From a statistical viewpoint, the three levels are similar in terms of weathering (Table 2). The same is true when compared to Batallones-1, where unweathered bones were also prevalent (Domingo *et al.* 2013a). Abrasion data imply that most of the bones were not significantly impacted by sedimentary particles or by each other in any of the Batallones-3 assemblages, a circumstance also observed at Batallones-1 (Tables 2 and 4). The prevalence of unabraded bones, alongside the monotaxic clusters, along with the associated and articulated complete or partial skeletons (Figure 8), reinforces the interpretation of an autochthonous taphocoenosis (Fernández-López 1990), maintaining its *in situ* properties.

Bones displaying trampling, higher degrees of weathering or abrasion are very scarce (Table 4), corresponding either to unidentified remains or to herbivore mammal species (Figures 7F and G). These elements, which in most cases are not classified into any discrete fossiliferous level, likely correspond to allochthonous taphocoenoses, transported and deposited along with sediment into the cavity. In the case of the herbivore remains, this allochthony appears to be reinforced by the almost total lack of remains.

Plant roots constitute common biological agents that can biochemically damage bone (Sarjeant 1975; Behrensmeyer 1978; Mikulás 1999, 2001; Fernández-Jalvo *et al*. 2002; Tjelldén *et al*. 2016; Paes-Neto *et al*. 2018). These types of alterations are well known in both archaeological and palaeontological contexts (e.g. Mikulás 2001; Fernández-Jalvo & Andrews 2016). Root marks are common at Batallones-3 on the surface of teeth (Figure 7B) and bones (Figure 7C). Root marks are present in 43.8% of the remains from Level I, 59.7% from Level II and 64.4% from Level III (Table 4). This increasing prevalence of root marks towards the shallow level of Batallones-3 is evidenced by the statistical analysis: Level III shows a significant higher abundance of root-marked bones than Level I (Table 2; Supporting Information); and Level II shows a statistically marginal greater abundance ($p = 0.02$) of root-marked bones than Level I. This points to a progressive increase in root-marking in the shallower assemblage of Batallones-3. Although it is difficult to assess when these modifications took place, the most plausible scenario is that these are present-day root marks, mainly the result of artificial pine tree reforestation in the area sometime between 1994 and 2000 (damage to the bones by modern roots was observed throughout the Batallones-3 excavations), and to a lesser extent, of the effect of natural shrubs on the butte slopes before and during this period. The three levels from Batallones-3 show significantly higher abundances of bones with root marks than Batallones-1 (Table 2; Supporting Information). As they are located on the butte slope, modern soil comes into contact with the Batallones-3 fossiliferous deposits, whereas Batallones-1 is located towards the centre of the butte and, therefore, too deep to be subjected to present-day edaphic processes, including plant root activity.

Significant differences in the percentages of remains with manganese oxide coatings appear to be associated with the abundance of root marked specimens, as they follow the same trend (Tables 2 and 4). It has been suggested that biological processes and soil humification expedite precipitation of manganese oxides on fossil remains (e.g. Shahack-Gross *et al.* 1997; Marín-Arroyo *et al.* 2008). Statistically significant differences are observed between all three Batallones-3 levels and Batallones-1 in terms of the presence of bones presenting manganese oxides, which are much more abundant at Batallones-3. Once again, this might be because the Batallones-1 fossil bones are better protected from pedogenic processes, due to their deeper position in the butte.

There are no carnivore-marked bones at Batallones-3. The pervasiveness of root marks could be affecting other taphonomic modifications or even hindering correct taxonomical or anatomical identification. Such could be the case for carnivore marks, which might be obscured by root etching. Nonetheless, and given that at Batallones-1, the other carnivoran-dominated assemblage from Cerro de los Batallones, carnivore marks are practically non-existent (0.30%), we believe that there are few tooth marks on the bones at Batallones-3, and that this is not an artefact of other superimposed taphonomic processes. Although it might seem puzzling that a carnivoran-dominated site displays such a low number of tooth-marked bones, different hypotheses can account for this. For example, taphonomic analyses performed on felid-consumed carcasses conclude that very few marks are left (Domínguez-Rodrigo & Barba 2006; Domínguez-Rodrigo *et al*. 2007; Gidna *et al*. 2014; Parkinson *et al*. 2015; Organista *et al*. 2016), which could explain the extremely low percentages of carnivore marks in the Cerro de los Batallones sites, where sabre-toothed cats are the dominant carnivoran species. In their study of the Batallones-1 assemblage, Domingo *et al.* (2013a) also suggested that the low incidence of carnivore marks could be the result of a low level of exploitation of carcasses because there was abundant supply of meat or because carnivorans died quickly after entrapment (from exhaustion, hypothermia, illness, toxic gases, poisoning from drinking water or injuries after entrance). Also, it is possible that carnivores were searching for water during droughts, as opposed to just food.

Finally, trampling marks are very scarce at Batallones-3. Again, root marks might have obscured evidence in this sense. However, trampling is also extremely scarce at Batallones-1, which suggests trapped carnivorans did not move a lot inside the chamber (due to the above mentioned conditions - exhaustion, injuries or illness).

Given the inference that the carnivoran-dominated assemblages in Levels I, II and III at Batallones-3 are autochthonous, with a few scattered allochthonous remains, there are only two likely scenarios for the formation of these deposits: these were created either by denning activities or by the cavity acting as a natural trap. As for the hypothesis that Batallones-3 acted as a den for carnivoran species, from a taxonomical point of view, prey species (generally, herbivores) dominate bone assemblages in these scenarios. Carnivoran MNI's in den assemblages (from 6% to 53%; Brain 1981; Wang & Martin 1993; Marean & Ehrhardt 1995; Pokines & Kerbis Peterhans 2007) differ greatly from the overwhelming majority of carnivoran remains in all Batallones-3 levels.

The geomorphology of the cavity in Batallones-3, exhibiting a vertical hourglass shape, is inferred to only have one entrance in the middle of the cave roof, directly >3 metres above the debris cone (Calvo *et al*. 2013; Martín-Perea *et al*. 2017). This opening likely presented difficult entry and hindered exit. The absence of tooth marks or spiral fractured bones resulting from consumption, supports the hypothesis that the assemblages were not produced as a consequence of denning activities.

Ursids, such as *Ursus deningeri* and *Ursus spelaeus*, are one of the most common dwellers of Pleistocene and Holocene caves, which usually result in fossil assemblages abundant in carnivoran (mainly ursid) remains. Since these assemblages are frequently found alongside human remains or artefacts, archaeologists have paid special attention to this interaction. Study of data on ursid mortality is of particular interest with regard to the taphonomic history of cave-bear assemblages (Webb 1988; Gargett 1996; Stiner *et al*. 1996; García *et al*. 1997; Wolverton 2001, 2006) and to establishing whether it more closely resembles a hibernation death assemblage (Stiner *et al*. 1996; Stiner 1998) or a natural trap (Wolverton 2001, 2006).

Although Ailuropodinae ursids are not known to hibernate, *Indarctos arctoides* mortality profiles (Figure 9) more closely resemble ursid prime-dominated natural-trap assemblages (García *et al*. 1997; Wolverton 2001, 2006), compared to living-structure assemblages resulting from natural hibernation deaths (Stiner 1998; Wolverton 2006). Claw marks, which can be interpreted as resulting from the action of trapped live animals, have been documented alongside ursid assemblages (Bednarik 1994, 2004). These marks are normally found in karstic cavities with hard limestone bedrock walls. In turn, the peculiar pseudokarstic formation of the Cerro de los Batallones cavities, carved into a sepiolite-rich marl bedrock (Pozo *et al*. 2004; Calvo *et al*. 2013), would preclude the formation of these claw markings.

Faunal concentrations in natural traps in caves can be either accidentally produced by falling (passive accumulation) or intentional through purposefully entering these cavities (active accumulation, Lyman 1994). Accidental passive accumulations are unselective, both taxonomically and ontogenetically, and will result in a diverse, unbiased assemblage (Wang & Martin 1993). This is clearly not the case for any of the Batallones-3 fossiliferous levels, which are dominated by prime adult carnivorans, presenting very few herbivore remains (Table 1, Figure 9). Consequently, a recurring, intentional entrance of carnivores into the cavity is the most likely scenario (Figure 10). Since most of the herbivore remains are allochthonous, it is safe to assume carnivores were not lured into the cavity in order to scavenge herbivore remains, but rather were searching for water. The absence of carnivore marks on the carnivoran remains suggests these were not scavenged either.

Furthermore, as for the moment of death of the trapped animals, it is difficult to infer whether these died as a consequence of the fall or *a posteriori* for other reasons. Although the absence of trampling could suggest otherwise, the geomorphology of the cave, with the opening inferred to be >3 meters above the ground, would not entail a mortal fall. The absence of fragmented bones which would suggest falling-related injuries, reinforces this idea. Other causes of death such as exhaustion or hypothermia, as explained above, appear to constitute more logical options. Moreover, it seems counterintuitive that carnivores would risk their lives intentionally to access the cavity. The vertical distance between the cave opening and the cave floor would appear less high due to the presence of the 1-metre-high debris cone beneath the cave entrance, which would facilitate entry. However, once the carnivores intentionally entered the cavity, they would be unable to escape due to the inward-slanting cave walls and the insurmountable >3-meter-high cave opening.

The presence of the giant tortoise *Titanochelon bolivari* (Pérez-García & Vlachos 2014) in all three levels is not surprising given this testudinid is exceptionally frequent in continental facies in the Madrid Basin. It is uncertain, however, whether the remains of this testudinid at Batallones-3 are autochthonous or allochthonous. On one hand, giant tortoises could have actively and intentionally entered the cavity attracted to water, looking for a place to breed or to bathe in mud in order to regulate body temperature, as observed in extant giant tortoises (Walton *et al.* 2019). Although it seems implausible that tortoises jumped into the cave, the phreatic level might have risen intermittently, sufficing to partially fill the cavity, granting easy access to the tortoises but difficult subsequent egress. These animals, unable to exit the partially filled cavity, would have died of exhaustion. Well preserved (unabraded, unweathered) remains, some of these articulated or associated, and the presence of these throughout all three fossiliferous levels, makes this scenario feasible. It cannot, however, be ruled out that the *Titanochelon* remains might be allochthonous, deriving from the older, freshwater assemblage before the cave opening was formed (Figure 10A).

The few taphonomic differences between the Batallones-3 levels, and also between Batallones-3 and Batallones-1, are related to *post-mortem*, pedogenic alterations, which are possibly modern, such as root markings, manganese oxide precipitation and a slightly lower bone completeness in Level III. The homogeneity of taphonomic properties between levels and even between Batallones-1 and Batallones-3 (Table 2) suggests recurring taphonomic and geologic processes throughout the infill process of the cave, which implied the successive intentional entry of carnivorans and their subsequent entrapment (Figure 10). Given that almost one third of the carnivoran species known for this time period (~9.8 to 8.8 Ma) are exclusively from the Cerro de los Batallones sites, there is a vital need for future palaeoecological and palaeoenvironmental studies of each of the Batallones-3 levels. The present study ensures that these studies can be conducted without risk of differential taphonomic histories skewing the assemblage data.

## Conclusions

The Batallones-3 site (Madrid Basin, Spain) hosts an unusual fossil assemblage, both because of its location in a pseudokarstic cavity and its carnivoran-dominated composition. Artificial intelligence systems enabled us to identify three fossiliferous levels embedded within the massive Batallones-3 deposit.

Batallones-3 Levels I and II are multitaxic multidominant assemblages containing two sabretooth cats, *Promegantereon ogygia* and *Machairodus aphanistus,* and an ursid, *Indarctos arctoides,* which is the most abundant species. On the other hand, Batallones-3 Level III is also a multitaxic multidominant assemblage, although it is primarily dominated by *Machairodus aphanistus*. Prime adults dominate all three assemblages. Statistically significant differences in the carnivoran faunal composition may be a function of faunal changes in the populations of carnivoran species throughout the accumulation of these assemblages.

These carnivoran-dominated assemblages are autochthonous, with diagenetically fractured but well preserved remains (complete, little to no weathering or abrasion), presenting abundant root marks and manganese oxide precipitation, with a very small amount of allochthonous, badly preserved (weathered and abraded) herbivore remains. Statistical analyses reveal homogeneity in most of the taphonomic variables of the assemblages. A trend can be seen, however, which is associated with the higher prevalence of pedogenic and erosional slope processes (more root marks, manganese oxide precipitates and bone incompleteness) in the shallower Batallones-3 Level III.

We propose that all three levels were mainly formed by the active entrance of carnivorans into the cavity. These were likely attracted by water and subsequently became trapped. Many of the taphonomic characteristics of Batallones-3, including the prevalence of carnivorans, coincide with those observed in the previously studied neighbouring Batallones-1 site. Indeed, both sites present a similar formation scenario. Future palaeoecological and palaeoenvironmental studies can therefore be conducted in each level with the assurance that differential taphonomic histories have not biased the assemblage data; this would provide a better understanding of the diversity and ecology of these important Late Miocene carnivoran faunas.

## Acknowledgements

We thank everyone involved in the excavation campaigns carried out at Batallones-3. Excavations carried out in the Cerro de los Batallones are funded by the Dirección General de Patrimonio Cultural (Comunidad de Madrid). David M. Martín-Perea was funded by an FPI Predoctoral grant BES-2016-079460 from the Spanish Government associated with Projects CGL2015-6833-P and PGC2018-094122-B-100. Alberto Valenciano was funded by a "Juan de la Cierva Formación" program (FJC2018-036669-I) from the Spanish Ministry of Science, Innovation and Universities and by the Aragon Government (E33_17R). Juan Abella was funded by the Generalitat de Catalunya (CERCA Programme and Beatriu de Pinós) contract 2017-BP-00223 from AGAUR. This study is also a contribution of Projects PGC2018-094122-B100 (AEI/FEDER, UE), CGL2016-76431-P (AEI/FEDER, UE) and the research groups CSIC-64-1538 and CAM-UCM-910607. The authors declare no conflict of interest. The authors thank Antonio Rodríguez-Hidalgo, an anonymous reviewer and Associate Editor Brooks Britt, whose helpful suggestions greatly improved this manuscript.

## References

Abella, J., Alba, D.M., Robles, J.M., Valenciano, A., Rotgers, C., Carmona, R., Montoya, P. & Morales., J. 2012: *Kretzoiarctos* gen. nov. the oldest member of the giant panda clade. *PLoS ONE 7*, e48985.

Abella, J., Valenciano, A., Pérez-Ramos, A., Montoya, P. & Morales, J. 2013: On the Socio-Sexual Behaviour of the Extinct Ursid *Indarctos arctoides*: An approach based on its baculum size and morphology. *PLoS ONE 8,* e73711.

Abella, J., Pérez-Ramos, A., Valenciano, A., Alba, D.M., Ercoli, M.D., Hontecillas, D., Montoya, P. & Morales, J. 2015: Tracing the origin of the panda's thumb. *The Science of Nature 102,* 1-13.

Abella, J. & Valenciano, A. 2017: *Indarctos arctoides*: Los ancestros de los grandes osos panda. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 302-316. Museo Arqueológico Regional, Madrid, Spain.

Abella, J., Valenciano, A., Martín-Perea, D.M., Montoya, P. & Morales, J. 2017: Batallones-3 un paraíso de diversidad en carnívoros. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 278-296. Museo Arqueológico Regional, Madrid, Spain.

Alberdi, M.T., de la Iglesia, A., Montoya, P. & Morales, J. 2017: La ciénaga de los mastodontes. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 395-410. Museo Arqueológico Regional, Madrid, Spain.

Alcalá, L. 1994: Macromamíferos Neógenos de la Fosa de Alfambra-Teruel. *Instituto de Estudios Turolenses 554*.

Álvarez-Sierra, M.A., García-Paredes, I., Gómez Cano, A.R., Hernández-Ballarín, V., van den Hoek Ostende, L.W., López-Antoñanzas, R., López-Guerrero, P., Oliver, A. & Peláez-Campomanes, P. 2017: Los micromamíferos del Cerro de los Batallones. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos* *del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 516-529. Museo Arqueológico Regional, Madrid, Spain.

Andrews, P. 1990: *Owls, caves and fossils*. Chicago, The University of Chicago Press.

Antón, M., Salesa, M.J., Morales, J. & Turner, A. 2004: First known complete skulls of the scimitar-toothed cat *Machairodus aphanistus* (Felidae, Carnivora) from the Spanish late Miocene site of Batallones-1. *Journal of Vertebrate Paleontology 24*, 957-969.

Antón, M., Salesa, M.J., Pastor, J.F., Peigné, S. & Morales, J. 2006: Implications of the functional anatomy of the hand and forearm of *Ailurus fulgens* (Carnivora, Ailuridae) for the evolution of the "false-thumb" in pandas. *Journal of Anatomy 209*, 757-764.

Antón, M., Siliceo, G., Pastor, J.F., Morales, J. & Salesa, M.J. 2020: The early evolution of the sabre-toothed felid killing bite: the significance of the cervical morphology of *Machairodus aphanistus* (Carnivora: Felidae: Machairodontinae). *Zoological Journal of the Linnean Society 188*, 319-342.

Arsuaga, J.L., Martínez, I., Gracia, A., Carretero, J.M., Lorenzo, C., García, N. & Ortega, A.I. 1997: Sima de los Huesos (Sierra de Atapuerca, Spain): The site. *Journal of Human Evolution 33,* 109-127.

Baddeley, A., Rubak, E. & Turner, R. 2015: *Spatial Point Patterns: Methodology and applications with R*. Chapman and Hall/CRC Press.

Bednarik, R.G. 1994: Wall markings of the cave bear. *Studies in Speleology 9*, 51-70.

Bednarik, R.G. 2004: Rock markings of humans and other animals. *Rock art research 21*, 57-84.

Behrensmeyer, A.K. 1978: Taphonomic and ecologic information from bone weathering. *Paleobiology 4*, 140-158.

Binder, W.J., Thompson, E.N. & van Valkenburgh, B. 2002: Temporal variation in tooth fracture among Rancho La Brea dire wolves. *Journal of Vertebrate Paleontology 22*, 423-428.

Blumenschine, R.J. 1988: An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *Journal of Archaeological Science 15*, 483-502.

Blumenschine, R.J. 1995: Percussion marks, tooth marks and the experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *Journal of Human Evolution 29*, 21-51.

Calvo, J.P., Pozo, M., Silva, P.G. & Morales, J. 2013: Pattern of sedimentary infilling of fossil mammal traps formed in pseudokarst at Cerro de los Batallones, Madrid Basin, central Spain. *Sedimentology 60*, 1681-1708.

Chomko, S. & Gilbert, B.M. 1987: The late Pleistocene/Holocene Faunal Record in the Northern Bighorn Mountains, Wyoming. *In* Graham, R.W., Semken, H.A. & Graham, M.A. (eds.), *Late Quaternary Mammalian Biogeography and Environments of the Great Plains and Prairies*, 21-35. Illinois State Museum, Springfield.

Cohen, J. 1960: A coefficient of agreement for nominal scales. *Educational and Psychological Measurement 20*, 37-46.

Domingo, M.S., Alberdi, M.T. & Azanza, B. 2007: A new quantitative biochronological ordination for the Upper Neogene mammalian localities of Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology 255*, 361-376.

Domingo, M.S., Domingo, L., Sánchez, I.R., Alberdi, M.T., Azanza, B. & Morales, J. 2011: New insights on the taphonomy of the exceptional mammalian fossil sites of Cerro de los Batallones (Late Miocene, Spain) based on rare earth element geochemistry. *Palaios 26*, 55-65.

Domingo, M.S., Alberdi, M.T., Azanza, B. & Morales, J. 2012: Mortality patterns and skeletal physical condition of the carnivorans from the Miocene assemblage of Batallones-1 (Madrid Basin, Spain). *Neues Jahrbuch fur Geologie und Palaeontologie-Abhandlungen 265*, 131-145.

Domingo, M.S., Alberdi, M.T., Azanza, B., Silva, P.G. & Morales, J. 2013a: Origin of an assemblage massively dominated by carnivorans from the Miocene of Spain. *PLOS ONE 8*, e63046.

Domingo, M.S., Domingo, L., Badgley, C., Sanisidro, O. & Morales, J. 2013b: Resource partitioning among top predators in a Miocene food web. *Proceedings of the Royal SocietyB: Biological Sciences 280*, 20122138.

Domingo, M.S., Domingo, L., Abella, J., Valenciano, A., Badgley, C. & Morales, J. 2016: Feeding ecology and habitat preferences of top predators from two Miocene carnivore-rich assemblages. *Paleobiology 42*, 489-507.

Domingo, M.S., Cantero, E., García-Real, I., Chamorro Sancho, M.J., Martín-Perea, D.M., Alberdi, M.T. & Morales, J. 2018: First radiological study of a complete dental ontogeny sequence of an extinct equid: implications for equidae life history and taphonomy. *Scientific reports 8*, 1-11.

Domínguez-Rodrigo, M. & Barba, R. 2006: New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivore-hominid-carnivore hypothesis falsified. *Journal of Human Evolution 50*, 170-194.

Domínguez-Rodrigo, M., Egeland, C.P. & Pickering, T.R. 2007: Equifinality in carnivore tooth marks and the extended concept of archaeological palimpsests: implications for models of passive scavenging in early hominids. *Breathing life into fossils: taphonomic studies in honor of CK (Bob) Brain*, 255-267.

Eberth, D.A., Rogers, R.R. & Fiorillo, A.R. 2007. A practical approach to the study of bonebeds. *In* Rogers, R.R., Eberth, D.A. & Fiorillo, A.R. (eds.), *Bonebeds: Genesis, analysis and paleobiological significance*, 265-331. Chicago: The University of Chicago Press.

Eisenberg, J. 1981: *The Mammalian Radiation*. Chicago, The University of Chicago Press.

Farlow, J.O. 1993: On the rareness of big, fierce animals: speculations about the body sizes, population densities, and geographic ranges of predatory mammals and large carnivorous dinosaurs. *American Journal of Science 293*, 167-199.

Feranec, R.S., Hadly, E.A. & Paytan, A. 2009. Stable isotopes reveal seasonal competition for resources between late Pleistocene bison (Bison) and horse (Equus) from Rancho La Brea, southern California. *Palaeogeography, Palaeoclimatology, Palaeoecology 271*, 153-160.

Fernández-Jalvo, Y., Sánchez-Chillón, B., Andrews, P. & Alcalá-Martínez, L. 2002: Morphological taphonomic transformations of fossil bones in continental environments, and repercussions on their chemical composition. *Archaeometry 44*, 353-361.

Fernández-Jalvo, Y. & Andrews, P. 2016: *Atlas of taphonomic identifications: 1001+ Images of Fossil and Recent Mammal Bone Modification*. Springer, London.

Fernández-López, S. 1990: El significado de la autoctonía/aloctonía tafonómica. *Reunión de Tafonomía y Fosilización*, 115-124.

Fisher, J.W. 1995: Bone surface modifications in zooarchaeology. *Journal of Archaeological Method and Theory 2*, 7-68.

Fraile, S. 2016: *Estudio de Protictitherium crassum del Cerro de los Batallones (Torrejón de Velasco, Madrid): aportación a la filogenia y evolución de la familia hyaenidae*. PhD Thesis, Complutense University of Madrid, Spain.

Fraile, S. 2017: *Protictitherium crassum*, la pequeña hiena de 9 millones de años del Cerro de los Batallones. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 224-234. Museo Arqueológico Regional, Madrid, Spain.

García, N., Arsuaga, J.L. & Torres, T. 1997: The carnivore remains from the Sime de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain). *Journal of Human Evolution 33*, 155-174.

García, N. & Arsuaga, J.L. 1998: The carnivore remains from the hominid-bearing Trinchera-Galería, Sierra de Atapuerca, Middle Pleistocene site (Spain). *Geobios 31*, 659-674.

Gidna, A.O., Kisui, B., Mabulla, A., Musiba, C. & Domínguez-Rodrigo, M. 2014: An ecological neo-taphonomic study of carcass consumption by lions in Tarangire National Park (Tanzania) and its relevance for human evolutionary biology. *Quaternary International 322*, 167-180.

Gilbert, B.M. 1978: Natural Trap Cave. *Wyoming Wildlife 42*, 10-13.

Gómez-Cano, A.R., Hernández Fernández, M. & Álvarez-Sierra, M.A. 2011: Biogeographic provincialism in rodent faunas from the Iberoccitanian Region (southwestern Europe) generates severe diachrony within the Mammalian Neogene (MN) biochronologic scale during the Late Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology 307*, 193-204.

Hoffstetter, R. 1952: Les Mammifères Pléistocènes de la République de l'Équateur. *Mémoires de la Société Géologique de France 66*, 1-391.

Höhle, J. & Höhle, M. 2009: Accuracy assessment of digital elevation models by means of robust statistical methods. *ISPRS Journal of Photogrammetry and Remote Sensing 64*, 398-406.

Klein, R.G. & Cruz-Uribe, K. 1984: *The analysis of animal bones from archaeological sites*. Chicago, The University of Chicago Press.

Kos, A.M. 2003: Characterisation of post-depositional taphonomic processes in the accumulation of mammals in a pitfall cave deposit from southeastern Australia. *Journal of Archaeological Science 30*, 781-796.

López-Antoñanzas, R., Peláez-Campomanes, P., Álvarez-Sierra, M.A. & García-Paredes, I. 2010: New species of *Hispanomys* (Rodentia, Cricetodontinae) from the Upper Miocene of Batallones (Madrid, Spain). *Zoological Journal of the Linnean Society 160*, 725-747.

López-Antoñanzas, R., Peláez-Campomanes, P. & Álvarez-Sierra, A. 2014: New species of *Rotundomys* (Cricetinae) from the Late Miocene of Spain and its bearing on the phylogeny of *Cricetulodon* and *Rotundomys*. *PLoS ONE 9*, e112704.

Lord, T.C., Thorp, J.A. & Wilson, P. 2016: A wild boar dominated ungulate assemblage from an early Holocene natural pit fall trap: Cave shaft sediments in northwest England associated with the 9.3 ka BP cold event. *The Holocene 26*, 147-153.

Lyman, R.L. & Fox, G.L. 1989: A critical evaluation of bone weathering as an indication of bone assemblage formation. *Journal of Archaeological Science 16*, 293-317.

Lyman, R.L. 1994: *Vertebrate Taphonomy*. Cambridge University Press.

Lyman, R.L. 2008: *Quantitative Paleozoology*. Cambridge University Press.

Lyndsey, E.L. & Seymour, K.L. 2015: "Tar pits" of the western Neotropics: paleoecology, taphonomy, and mammalian biogeography. *Natural History Museum of Los Angeles County Science Series 42*, 111-123.

Marcus, L.F. & Berger, R. 1984: The significance of radiocarbon dates for Rancho La Brea. *In* Martin, P.S. & Klein, R.G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, 159-188. University of Chicago Press, Chicago.

Marder, O., Yeshurun, R., Lupu, R., Bar-Oz, G., Belmaker, M., Porat, N., Ron, H. & Frumkin, A. 2011: Mammal remains at Rantis Cave, Israel, and Middle-Late Pleistocene human subsistence and ecology in the Southern Levant. *Journal of Quaternary Science 26*, 769-780.

Marean, C.W. & Ehrhardt, C.L. 1995: Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth's den. *Journal of Human Evolution 29*, 515-547.

Marín-Arroyo, A.B., Landete Ruiz, M.D., Vidal Bernabeu, G., Seva Román, R., González Morales, M.R. & Straus, L.G. 2008: Archaeological implications of human-derived manganese coatings: a study of blackened bones in El Mirón Cave, Cantabrian Spain. *Journal of Archaeological Science 35,* 801-813.

Martin, L.D. & Gilbert, B.M. 1978: Excavations at Natural Trap Cave. *Transactions of the Nebraska Academy of Sciences 6*, 107-116.

Martín-Perea, D.M., Aldama, J., Domingo, M.S., Valenciano, A., Abella, J. & Morales, J. 2017: 3D reconstruction of the carnivoran-dominated assemblage of Batallones-3 (Late Miocene, Madrid Basin, Spain). *Insight into Paleoart 1*, 59-63.

Martín-Perea, D.M., Courtenay, L.A., Domingo, M.S. & Morales, J. 2020: Application of artificially intelligent systems for the identification of discrete fossiliferous levels. *PeerJ 8*, e8767.

Medina-Chevarrías, V., Oliver, A., López-Guerrero, P., Peláez-Campomanes, P. & Álvarez-Sierra, M.A. 2019: New insights on *Hispanomys moralesi* (Rodentia, Mammalia) and its use as biostratigraphical indicator. *Journal of Iberian Geology 45*, 641-654.

Mikulás, R. 1999: Notes on the concept of plant trace fossils related to plant-generated sedimentary structures. *Vestník Ceského Geologického Ústavu 74*, 39-42.

Mikulás, R. 2001: Modern and fossil traces in terrestrial lithic substrates. *Ichnos 8*, 177-184.

Monescillo, M.F.G., Salesa, M.J., Antón, M., Siliceo, G. & Morales, J. 2014: *Machairodus aphanistus* (Felidae, Machairodontinae, Homotherini) from the late Miocene (Vallesian, MN10) site of Batallones-3 (Torrejón de Velasco, Madrid, Spain). *Journal of Vertebrate Paleontology 34*, 699-709.

Morales, J., Pozo, M., Silva, P.G., Domingo, M.S., López-Antoñanzas, R., Álvarez-Sierra, M.A., Antón, M., Martín Escorza, C., Quiralte, V., Salesa, M.J., Sánchez, I.M., Azanza, B., Calvo, J.P., Carrasco, P., García-Paredes, I., Knoll, F., Hernández-Fernández, M., van den Hoek Ostende, L., Merino, L., van der Meulen, A.J., Montoya, P., Peigné, S., Peláez-Campomanes, P., Sánchez-Marco, A., Turner, A., Abella, J., Alcalde, G.M., Andrés, M., DeMiguel, D., Cantalapiedra, J.L., Fraile, S., García Yelo, B.A., Gómez Cano, A.R., López Guerrero, P., Oliver Pérez, A. & Siliceo, G. 2008: El sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid: estado actual y perspectivas. *Palaeontologica Nova 8*, 41-117.

Morales, J. 2017: Vertebrados miocenos de los yacimientos del Cerro de los Batallones. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 36-40. Museo Arqueológico Regional, Madrid, Spain.

Morales, J., Abella, J. & Valenciano, A. 2017. *Thaumastocyon*: los extraños Amphicyonidae de Batallones-3. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 338-351. Museo Arqueológico Regional, Madrid, Spain.

Morales, J., Abella, J., Sanisidro, O., Valenviaco, A. 2021. Ammitocyon kainos gen. et sp. nov., a chimerical amphicyonid (Mammalia, Carnivora) from the late Miocene carnivore traps of Cerro de los Batallones (Madrid, Spain). *Journal of Systematic Palaeontology 20,* 1-23.

Oliver, J.S. 1986: *The taphonomy and paleoecology of Shield Trap Cave (24CB91), Carbon County, Montana*. PhD dissertation, University of Maine.

Oliver, J.S., Bonnichsen, R. & Sorg, M.H. 1989: *Analogues and site context: bone damages from Shield Trap Cave (24CB91), Carbon County, Montana, USA*. University of Maine Center for the Study of First Americans.

Organista, E., Pernas-Hernández, M., Gidna, A., Yravedra, J. & Domínguez-Rodrigo, M. 2016: An experimental lion-to-hammerstone model and its relevance to understand hominin-carnivore interactions in the archeological record. *Journal of Archaeological Science 66*, 69-77.

Paes-Neto, V.D., Francischini, H., Martinelli, A.G., Marinho, T.S., Ribeiro, L.C.B., Soares, M.B. & Schultz, C.L. 2018: Bioerosion traces on titanosaurian sauropod bones from the Upper Cretaceous Marília Formation of Brazil. *Alcheringa 42*, 415-426.

Parkinson, J.A., Plummer, T. & Hartstone-Rose, A. 2015: Characterizing felid tooth marking and gross bone damage patterns using GIS image analysis: An experimental feeding study with large felids. *Journal of Human Evolution 80*, 114-134.

Peigné, S., Salesa, M.J., Antón, M. & Morales, J. 2005: Ailurid carnivoran mammal *Simocyon* from the late Miocene of Spain and the systematics of the genus. *Acta Paleontologica Polonica 50*, 219-238.

Peigné, S., Salesa, M.J., Antón, M. & Morales, J. 2008: A new Amphicyonine (Carnivora: Amphicyonidae) from the upper Miocene of Batallones-1, Madrid, Spain. *Palaeontology 51*, 943-965.

Pérez-García, A. & Vlachos, E. 2014: New generic proposal for the European Neogene large testudinids (Cryptodira) and the first phylogenetic hypothesis for the medium and large representatives of the European Cenozoic record. *Zoological Journal of the Linnean Society 172*, 653-719.

Pesquero, M.D., Alcalá, L. & Fernández-Jalvo, Y. 2013: Taphonomy of the reference Miocene vertebrate site of Cerro de la Garita, Spain. *Lethaia 46*, 378-398.

Pickford, M. 2015: Late Miocene Suidae from Eurasia: the *Hippopotamodon* and *Microstonyx* problem revisited. *Münchner Geowissenschaftliche Abhandlungen 42*, 1-124.

Pokines, J.T. & Kerbis Peterhans, J.C. 2007: Spotted hyena (*Crocuta crocuta*) den use and taphonomy in the Masai Mara National Reserve. *Journal of Archaeological Science 34*, 1914-1931.

Pozo, M., Calvo, J.P., Silva, P.G., Morales, J., Peláez-Campomanes, P. & Nieto, M. 2004: Geología del sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid. *Geogaceta 35*, 143-146.

Ríos, M., Sánchez, I.M. & Morales, J. 2017: A new giraffid (Mammalia, Ruminantia, Pecora) from the late Miocene of Spain, and the evolution of the sivathere-samothere lineage. *PLoS ONE 12*, e0185378.

Ríos, M. & Morales, J. 2019. A new skull of *Decennatherium rex* Ríos, Sánchez and Morales, 2017 from Batallones-4 (upper Vallesian, MN10, Madrid, Spain). *Palaeontologia Electronica*, 22.2.pvc_1.

Romano, C.O., Pesquero, M.D. & Alberdi, M.T. 2017: *Hipparion*: los caballos de Batallones. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 426-440. Museo Arqueológico Regional, Madrid, Spain.

Salesa, M.J., Antón, M., Peigné, S. & Morales, J. 2006: Evidence of a false thumb in a fossil carnivore clarifies the evolution of pandas. *Proceedings of the National Academy of Science 103*, 379-382.

Salesa, M.J., Antón, M., Peigné, S. & Morales, J. 2008: Functional anatomy and biomechanics of the postcranial skeleton of *Simocyon batalleri* (Viret, 1929) (Carnivora, Ailuridae) from the Late Miocene of Spain. *Zoological Journal of the Linnean Society 152*, 593-621.

Salesa, M.J., Antón, M., Turner, A. & Morales, J. 2010: Functional anatomy of the forelimb in *Promegantereon ogygia* (Felidae, Machairodontinae, Smilodontini) from the Late Miocene of Spain and the origins of the sabre-toothed felid model. *Journal of Anatomy 216*, 381-396.

Salesa, M.J., Antón, M., Morales, J. & Peigné, S. 2012: Systematics and phylogeny of the small felines (Carnivora, Felidae) from the late Miocene of Europe: a new species of Felinae from the Vallesian of Batallones (MN10, Madrid, Spain). *Journal of Systematic Palaeontology 10*, 87-102.

Salesa, M.J., Antón, M., Siliceo, G. & Peigné, S. 2017: Los otros félidos de Batallones. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 322-336. Museo Arqueológico Regional, Madrid, Spain.

Sánchez, I.M., Domingo, M.S. & Morales, J. 2009: New data on the Moschidae (Mammalia, Ruminantia) from the upper Miocene of Spain (MN10-MN11). *Journal of Vertebrate Paleontology 29*, 567-575.

Sánchez, I.M., Quiralte, V. & Morales, J. 2011: Presence of the bovid *Austroportax* in the upper Miocene fossil site of Batallones-1 (MN10, Madrid Basin, Madrid). *Estudios Geológicos 67*, 637-642.

Sanisidro, O. & Cantalapiedra, J. 2017: Los rinocerontes del Cerro de los Batallones. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 410-421. Museo Arqueológico Regional, Madrid, Spain.

Sarjeant, W.A.S. 1975: Plant trace fossils. *In* Frey, R.W. (ed.), *The study of trace fossils: a synthesis of principles, problems and procedures in ichnology*, 163-179. Springer-Verlag, New York.

Shahack-Gross, R., Bar-Yosef, O. & Weiner, S. 1997. Black-coloured bones in Hayonim Cave, Israel: differentiating between burning and oxide staining. *Journal of Archaeological Science 24, 439-446.*

Siliceo, G., Salesa, M.J., Antón, M., Monescillo, M.F.G. & Morales, J. 2014: *Promegantereon ogygia* (Felidae, Machairodontinae, Smilodontini) from the Vallesian (late Miocene, MN10) of Spain: morphological and functional differences in two noncontemporary populations. *Journal of Vertebrate Paleontology 34*, 407-418.

Siliceo, G., Salesa, M.J., Antón, M., Pastor, J.F. & Morales, J. 2015: Comparative Anatomy of the Shoulder Region in the late Miocene Amphicyonid *Magericyon anceps* (Carnivora): Functional and Paleoecological Inferences. *Journal of Mammalian Evolution 22*, 243-258.

Siliceo, G., Salesa, M.J., Antón, M., Peigné, S. & Morales, J. 2017: Functional anatomy of the cervical región in the late Miocene amphicyonid *Magericyon anceps* (Carnivora, Amphicyonidae): implications for its feeding behavior. *Palaeontology 60*, 329-347.

Siliceo, G., Antón, M., Morales, J. & Salesa, M.J. 2020: Built for Strength: Functional Insights from the Thoracolumbar and Sacrocaudal Regions of the Late Miocene Amphicyonid *Magericyon anceps* (Carnivora, Amphicyonidae) from Batallones-1 (Madrid, Spain). *Journal of Mammalian Evolution 27*, 497-518.

Stiner, M.C. 1990: The use of mortality patterns in archaeological studies of hominin predatory adaptations. *Journal of Anthropological Archaeology 9*, 305-351.

Stiner, M.C., Arsebük, G. & Howell, F.C. 1996: Cave bears and Paleolithic artifacts in Yarimburgaz Cave, Turkey: dissecting a palimpsest. *Geoarchaeology 11*, 279-327.

Stiner, M.C. 1998: Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *Journal of Human Evolution 34*, 303-326.

Stock, C. 1972: Rancho La Brea: a record of Pleistocene life in California. *Natural History Museum of Los Angeles County Science Series 20*, 1-81.

Stock, C. & Harris, J.M. 1992: Rancho la Brea: A record of Pleistocene life in California. *Natural History Museum of Los Angeles County Science Series 37*, 1-113.

Tjelldén, A.K.E., Kristiansen, S.M., Matthiesen, H. & Pedersen, O. 2016: Impact of roots and rhizomes on wetland archaeology: a review. Conservation and Management of Archaeological Sites 17, 370-391.

Valenciano, A., Abella, J., Sanisidro, O., Hartstone-Rose, A., Alvarez-Sierra, M.A. & Morales, J. 2015: Complete description of the skull and mandible of the giant mustelid *Eomellivora piveteaui* Ozansoy, 1965 (Mammalia, Carnivora, Mustelidae) from

Batallones (MN10), late Miocene (Madrid, Spain). *Journal of Vertebrate Paleontology 35*, e934570.

Valenciano, A. 2017: Mofetas, martas, tejones y rateles gigantes del Cerro de los Batallones. *In* Morales, J. (ed.), *La Colina de los Tigres Dientes de Sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*, 322-336. Museo Arqueológico Regional, Madrid, Spain.

Valenciano, A. & Govender, R. 2020: New fossils of *Mellivora benfieldi* (Mammalia, Carnivora, Mustelidae) from Langebaanweg 'E' Quarry (South Africa, early Pliocene): re-evaluation of the African Neogene mellivorines. *Journal of Vertebrate Paleontology,* e1817754.

Valenciano, A., Pérez-Ramos, A., Abella, J. & Morales, J. 2020: A new hypercarnivorous mustelid (Mammalia, Carnivora, Mustelidae) from Batallones, late Miocene (MN10), Torrejón de Velasco, Madrid, Spain). *Geodiversitas 42*, 103-121.

Villa, P. & Mahieu, E. 1991: Breakage patterns of human long bones. *Journal of Human Evolution 21*, 27-48.

Walton, R., Baxter, R., Bunbury, N., Hansen, D., Fleischer-Dogley, F., Greenwood, S. & Shaepman-Strub, G. 2019: In the land of giants: habitat use and selection of the Aldabra giant tortoise on Aldabra Atoll. *Biodiversity and Conservation 28*, 3183-3198.

Wang, X. & Martin, L.D. 1993: Natural trap cave. *National Geography Research Explorer 9*, 422-435.

White, J.A., McDonald, H.G., Anderson, E., Soiset, J.M. 1984: Lava blisters as carnivore traps. *Special Publication Carnegie Museum of Natural History, Carnegie Museum of Natural History 8*, 241-256.

Wolverton, S. 2001: Caves, ursids and artifacts: a natural-trap hypothesis. *Journal of Ethnobiology 21*, 55-72.

Wolverton, S. 2006: Natural-trap ursid mortality and the Kurtén Response. *Journal of Human Evolution 50*, 540-551.

**Table 1.** Number of Identified Specimens (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) of the large taxa in Batallones-3 levels. Mortality patterns of individuals is given in brackets (young/prime adult/old).

| | | **Level I** | | | | | **Level II** | | | | | **Level III** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Family/Order** | **NISP** | **%NISP** | **MNE** | **MNI** | **%MNI** | **NISP** | **%NISP** | **MNE** | **MNI** | **%MNI** | **NISP** | **%NISP** | **MNE** | **MNI** | **%MNI** |
| *Machairodus aphanistus* | Felidae/Carnivora | 752 | 15.83 | 730 | 7 (0/7/0) | 15.56 | 844 | 20.91 | 824 | 8 (1/7/0) | 20.51 | 537 | 31.44 | 530 | 7 (1/6/0) | 41.18 |
| *Promegantereon ogygia* | Felidae/Carnivora | 956 | 20.13 | 913 | 10 (1/9/0) | 22.22 | 1117 | 27.67 | 1042 | 12 (1/11/0) | 30.77 | 110 | 6.44 | 101 | 3 (0/3/0) | 17.65 |
| *Leptofelis vallesiensis* | Felidae/Carnivora | 4 | 0.08 | 4 | 1 (0/1/0) | 2.22 | 1 | 0.02 | 1 | 1 (0/1/0) | 2.56 | 0 | 0.00 | 0 | 0 (0/0/0) | 0.00 |
| Felidae indet. | Felidae/Carnivora | 29 | 0.40 | - | - | - | 27 | 0.59 | - | - | - | 5 | 0.23 | - | - | - |
| *Indarctos arctoides* | Ursidae/Carnivora | 918 | 19.33 | 782 | 9 (3/6/0) | 20.00 | 517 | 12.81 | 434 | 6 (2/4/0) | 15.38 | 149 | 8.72 | 136 | 3 (0/3/0) | 17.65 |
| *Magericyon anceps* | Amphicyonidae/Carnivora | 12 | 0.25 | 12 | 1 (0/1/0) | 2.22 | 32 | 0.79 | 30 | 1 (0/1/0) | 2.56 | 50 | 2.93 | 50 | 1 (0/1/0) | 5.88 |
| *Ammitocyon kainos* | Amphicyonidae/Carnivora | 14 | 0.29 | 14 | 1 (0/1/0) | 2.22 | 14 | 0.35 | 14 | 1 (0/1/0) | 2.56 | 56 | 3.28 | 56 | 1 (0/1/0) | 5.88 |
| Amphicyonidae indet. | Amphicyonidae/Carnivora | 2 | 0.04 | - | - | - | 7 | 0.17 | - | - | - | 90 | 5.27 | - | - | - |
| *Protictitherium crassum* | Hyaenidae/Carnivora | 110 | 2.32 | 110 | 6 (0/6/0) | 13.33 | 105 | 2.60 | 102 | 3 (0/3/0) | 7.69 | 13 | 0.76 | 12 | 1 (0/1/0) | 5.88 |
| *Eomellivora piveteaui* | Mustelidae/Carnivora | 85 | 1.79 | 85 | 4 (0/4/0) | 8.89 | 109 | 2.70 | 109 | 3 (0/3/0) | 7.69 | 2 | 0.12 | 2 | 1 (0/1/0) | 5.88 |
| aff. *Adroverictis* sp. | Mustelidae/Carnivora | 8 | 0.17 | 8 | 1 (0/1/0) | 2.22 | 1 | 0.02 | 1 | 1 (0/1/0) | 2.56 | 0 | 0.00 | 0 | 0 (0/0/0) | 0.00 |
| *Circamustela peignei* | Mustelidae/Carnivora | 5 | 0.11 | 5 | 1 (0/1/0) | 2.22 | 1 | 0.02 | 1 | 1 (0/1/0) | 2.56 | 0 | 0.00 | 0 | 0 (0/0/0) | 0.00 |
| Mustelidae indet. | Mustelidae/Carnivora | 65 | 1.37 | - | - | - | 65 | 1.61 | - | - | - | 9 | 0.53 | - | - | - |
| Mephitidae nov. gen. et sp. | Mephitidae/Carnivora | 3 | 0.06 | 2 | 1 (0/1/0) | 2.22 | 0 | 0.00 | 0 | 0 (0/0/0) | 0.00 | 0 | 0.00 | 0 | 0 (0/0/0) | 0.00 |
| *Promephitis* nov. sp. | Mephitidae/Carnivora | 19 | 0.40 | - | - | - | 4 | 0.10 | - | - | - | 2 | 0.12 | - | - | - |
| Carnivora indet. | Carnivora | 85 | 1.79 | - | - | - | 18 | 0.45 | - | - | - | 3 | 0.18 | - | - | - |
| | **Total Carnivora** | **3067** | **64.36** | **2665** | **42 (4/38/0)** | **93.33** | **2862** | **70.82** | **2558** | **37 (4/33/0)** | **94.87** | **1026** | **60.01** | **887** | **17 (1/16/0)** | **100** |
| *Hipparion* cf. *matthewi* | Equidae/Perissodactyla | 3 | 0.06 | 3 | 1 (0/1/0) | 2.22 | 4 | 0.10 | 4 | 1 (0/1/0) | 2.56 | 0 | 0.00 | 0 | 0 | 0.00 |
| Rhinocerotidae indet. | Rhinocerotidae/Perissodactyla | 0 | 0.00 | - | - | - | 1 | 0.02 | - | - | - | 0 | 0.00 | - | - | - |
| | **Total Perissodactyla** | **3** | **0.063** | **3** | **1 (0/1/0)** | **2.22** | **5** | **0.12** | **4** | **1 (0/1/0)** | **2.56** | **0** | **0.00** | **0** | **0** | **0.00** |
| *Hippopotamodon major* | Suidae/Artiodactyla | 2 | 0.04 | 2 | 1 (0/1/0) | 2.22 | 1 | 0.02 | 1 | 1 (0/1/0) | 2.56 | 0 | 0.00 | 0 | 0 | 0.00 |
| *Austroportax* sp. | Bovidae/Artiodactyla | 3 | 0.06 | 3 | 1 (0/1/0) | 2.22 | 0 | 0.00 | 0 | 0 | 0.00 | 0 | 0.00 | 0 | 0 | 0.00 |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bovidae indet. | Bovidae/Artiodactyla | 3 | 0.06 | - | - | - | 0 | 0.00 | - | - | - | 1 | 0.06 | - | - | - |
| | **Total Artiodactyla** | **8** | **0.168** | **5** | **2 (0/2/0)** | **4.44** | **1** | **0.02** | **1** | **1 (0/1/0)** | **2.56** | **1** | **0.06** | **0** | **0** | **0.00** |
| Herbivore indet. | | 10 | 0.21 | - | - | - | 0 | 0.00 | - | - | - | 0 | 0.00 | - | - | - |
| Aves indet. | | 178 | 3.75 | - | - | - | 185 | 4.58 | - | - | - | 44 | 2.58 | - | - | - |
| Testudines indet. | Testudines | 103 | 2.17 | - | - | - | 44 | 1.09 | - | - | - | 67 | 3.92 | - | - | - |
| *Varanus marathoniensis* | Varanidae/Squamata | 40 | 0.84 | - | - | - | 3 | 0.07 | - | - | - | 0 | 0.00 | - | - | - |
| Reptilia indet. | | 4 | 0.08 | - | - | - | 3 | 0.07 | - | - | - | 0 | 0.00 | - | - | - |
| Indetermined | | 1337 | 28.15 | - | - | - | 934 | 23.14 | - | - | - | 570 | 33.37 | - | - | - |
| | **Total** | **4750** | **100** | **2683** | **45** | **100** | **4037** | **100** | **2566** | **39** | **100** | **1708** | **100** | **888** | **17** | **100** |

**Table 2.** Chi-square tests to compare the three fossiliferous levels of Batallones-3 and Batallones-1. Above the diagonal are the p-values. Below diagonal is the chi-square statistic. Significant differences when p<0.01.

| | | **Batallones-3** | | | |
|---|---|---|---|---|---|
| | | **Level I** | **Level II** | **Level III** | **Batallones-1** |
| **%NISP Carnivora - Artiodactyla - Perissodactyla** | Batallones-3 Level I | - | 1.00 | 1.00 | 1.00 |
| | Batallones-3 Level II | 0.00 | - | 1.00 | 1.00 |
| | Batallones-3 Level III | 0.00 | 0.00 | - | 1.00 |
| | Batallones-1 | 0.00 | 0.00 | 0.00 | - |
| **%MNI Carnivoran species** | Batallones-3 Level I | - | 0.52 | *< 0.01* | *< 0. 01* |
| | Batallones-3 Level II | 5.19 | - | 0. 02 | 0. 06 |
| | Batallones-3 Level III | 20.98 | 15.25 | - | *< 0. 01* |
| | Batallones-1 | 53.31 | 45.27 | 49.67 | - |
| **%NISP Number of fractures** | Batallones-3 Level I | - | 0.63 | 0.16 | *< 0. 01* |
| | Batallones-3 Level II | 1.86 | - | 0.80 | *< 0. 01* |
| | Batallones-3 Level III | 5.19 | 0.93 | - | *< 0. 01* |
| | Batallones-1 | 22.11 | 30.86 | 36.81 | - |
| **%NISP Fracture angle** | Batallones-3 Level I | - | 0.013 | 0.12 | *< 0. 01* |
| | Batallones-3 Level II | 16.10 | - | *< 0. 01* | 0.03 |
| | Batallones-3 Level III | 7.35 | 22.47 | - | *< 0. 01* |
| | Batallones-1 | 33.24 | 13.77 | 44.59 | - |
| **%NISP Fracture surface** | Batallones-3 Level I | - | 0.60 | 0.10 | *< 0. 01* |
| | Batallones-3 Level II | 1.03 | - | 0.09 | *< 0. 01* |
| | Batallones-3 Level III | 4.64 | 4.75 | - | *< 0. 01* |
| | Batallones-1 | 29.73 | 32.30 | 45.70 | - |
| **%NISP Bone completeness** | Batallones-3 Level I | - | 0.15 | *< 0. 01* | *< 0. 01* |
| | Batallones-3 Level II | 5.40 | - | *< 0. 01* | *< 0. 01* |
| | Batallones-3 Level III | 25.50 | 20.40 | - | *< 0. 01* |
| | Batallones-1 | 26.88 | 12.52 | 38.23 | - |
| **%NISP Weathering** | Batallones-3 Level I | - | 1.00 | 1.00 | 1.00 |
| | Batallones-3 Level II | 0.00 | - | 1.00 | 1.00 |
| | Batallones-3 Level III | 0.00 | 0.00 | - | 1.00 |
| | Batallones-1 | 0.00 | 0.00 | 0.00 | - |
| **%NISP Abrasion** | Batallones-3 Level I | - | 0.31 | 0.02 | 1.00 |
| | Batallones-3 Level II | 1.01 | - | 0.09 | 0.31 |
| | Batallones-3 Level III | 5.18 | 2.75 | - | 0.02 |
| | Batallones-1 | 0.00 | 1.01 | 5.13 | - |
| **%NISP Trampling** | Batallones-3 Level I | - | 1.00 | 1.00 | 1.00 |
| | Batallones-3 Level II | 0.00 | - | 1.00 | 1.00 |
| | Batallones-3 Level III | 0.00 | 0.00 | - | 1.00 |
| | Batallones-1 | 0.00 | 0.00 | 0.00 | - |
| **%NISP Root marks** | Batallones-3 Level I | - | 0.02 | *< 0. 01* | *< 0. 01* |
| | Batallones-3 Level II | 5.18 | - | 0.46 | *< 0. 01* |
| | Batallones-3 Level III | 8.97 | 0.54 | - | *< 0. 01* |

| | | | | | |
|---|---|---|---|---|---|
| | Batallones-1 | 54.93 | 84.04 | 94.57 | - |
| **%NISP Manganese oxides** | Batallones-3 Level I | - | 0.05 | *< 0. 01* | *< 0. 01* |
| | Batallones-3 Level II | 3.72 | - | 0.46 | *< 0. 01* |
| | Batallones-3 Level III | 11.51 | 2.41 | - | *< 0. 01* |
| | Batallones-1 | 44.63 | 68.81 | 88.27 | - |
| **%NISP Carnivore marks** | Batallones-3 Level I | - | 1.00 | 1.00 | 1.00 |
| | Batallones-3 Level II | 0.00 | - | 1.00 | 1.00 |
| | Batallones-3 Level III | 0.00 | 0.00 | - | 1.00 |
| | Batallones-1 | 0.00 | 0.00 | 0.00 | - |

**Table 3.** Skeletal element frequencies for Batallones-3 levels expressed as Number of Identified Specimens (NISP) and percentages.

| | **Level I** | | **Level II** | | **Level III** | |
|---|---|---|---|---|---|---|
| | **NISP** | **%** | **NISP** | **%** | **NISP** | **%** |
| Horn | 2 | 0.04 | 0 | 0.00 | 0 | 0.00 |
| Skull | 52 | 1.08 | 35 | 0.86 | 22 | 1.29 |
| Mandible | 55 | 1.15 | 43 | 1.06 | 11 | 0.64 |
| Molar | 23 | 0.48 | 16 | 0.39 | 3 | 0.18 |
| Premolar | 46 | 0.96 | 45 | 1.11 | 8 | 0.47 |
| Canine | 34 | 0.71 | 57 | 1.40 | 15 | 0.88 |
| Incisor | 118 | 2.46 | 116 | 2.86 | 30 | 1.76 |
| Indet. Tooth | 15 | 0.31 | 6 | 0.15 | 2 | 0.12 |
| Hyoid | 10 | 0.21 | 3 | 0.07 | 8 | 0.47 |
| Atlas | 19 | 0.40 | 16 | 0.39 | 3 | 0.18 |
| Axis | 22 | 0.46 | 14 | 0.34 | 9 | 0.53 |
| Vertebra | 721 | 15.04 | 630 | 15.52 | 309 | 18.09 |
| Sternebra | 39 | 0.81 | 34 | 0.84 | 23 | 1.35 |
| Rib | 367 | 7.66 | 262 | 6.45 | 134 | 7.85 |
| Clavicle | 9 | 0.19 | 14 | 0.34 | 2 | 0.12 |
| Scapula | 41 | 0.86 | 35 | 0.86 | 21 | 1.23 |
| Pelvis | 69 | 1.44 | 43 | 1.06 | 11 | 0.64 |
| Baculus | 5 | 0.10 | 1 | 0.02 | 5 | 0.29 |
| Humerus | 21 | 0.44 | 57 | 1.40 | 30 | 1.76 |
| Radius | 72 | 1.50 | 55 | 1.36 | 19 | 1.11 |
| Ulna | 78 | 1.63 | 54 | 1.33 | 28 | 1.64 |
| Femur | 78 | 1.63 | 84 | 2.07 | 30 | 1.76 |
| Tibia | 84 | 1.75 | 70 | 1.72 | 18 | 1.05 |
| Fibula | 23 | 0.48 | 44 | 1.08 | 10 | 0.59 |
| Patella | 47 | 0.98 | 48 | 1.18 | 10 | 0.59 |
| Carpal/Tarsal | 415 | 8.66 | 356 | 8.77 | 148 | 8.67 |
| Astragalus | 53 | 1.11 | 51 | 1.26 | 18 | 1.05 |
| Calcaneus | 60 | 1.25 | 60 | 1.48 | 17 | 1.00 |
| Indet. Metapodial | 0 | 0.00 | 85 | 2.09 | 36 | 2.11 |
| Metacarpal | 167 | 3.48 | 150 | 3.70 | 59 | 3.45 |
| Metatarsal | 184 | 3.84 | 141 | 3.47 | 47 | 2.75 |
| 1st Phalanx | 374 | 7.80 | 287 | 7.07 | 126 | 7.38 |
| 2nd Phalanx | 296 | 6.17 | 255 | 6.28 | 98 | 5.74 |
| 3rd Phalanx | 247 | 5.15 | 230 | 5.67 | 94 | 5.50 |
| Indet. Phalanx | 107 | 2.23 | 111 | 2.73 | 52 | 3.04 |
| Sesamoid | 340 | 7.09 | 321 | 7.91 | 145 | 8.49 |
| Turtle shell | 40 | 0.83 | 20 | 0.49 | 16 | 0.94 |
| Indetermined | 461 | 9.62 | 210 | 5.17 | 91 | 5.33 |
| **TOTAL** | **4794** | | **4048** | | **1711** | |

**Table 4.** Other surface bone modifications per level. Indet. = Unidentifiable remains with no assigned fossiliferous level.

| | Level I | | Level II | | Level III | | Indet. | |
|---|---|---|---|---|---|---|---|---|
| | **NISP** | **%** | **NISP** | **%** | **NISP** | **%** | **NISP** | **%** |
| **Weathering** | | | | | | | | |
| Stage 0 | 479 | 100.0 | 405 | 100.0 | 170 | 99.4 | 976 | 97.2 |
| Stage 1 | 0 | 0.0 | 0 | 0.0 | 1 | 0.6 | 25 | 2.5 |
| Stage 2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 3 | 0.3 |
| **Abrasion** | | | | | | | | |
| Stage 1 | 479 | 100.0 | 399 | 98.5 | 162 | 94.7 | 923 | 91.9 |
| Stage 2 | 0 | 0.0 | 6 | 1.5 | 9 | 5.3 | 77 | 7.7 |
| Stage 3 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 4 | 0.4 |
| **Root marks** | 210 | 43.8 | 242 | 59.7 | 110 | 64.4 | 618 | 61.6 |
| **Trampling** | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 16 | 1.6 |
| **Manganese oxides** | 352 | 73.5 | 343 | 84.7 | 157 | 91.8 | 598 | 59.6 |

**Table 5.** Skeletal completeness for Batallones-3 Levels I, II and III most abundant carnivorans. Teeth, vertebrae, ribs, and sesamoids were removed for the estimation of the percentage of skeletal completeness. Kolmogorov-Smirnov test compares the MNE and the expected number of elements for the MNI per taxa, per level. p > 0.01 = not significantly different. p < 0.01 = significantly different.

| | | **Kolmogorov-Smirnov Test** | |
|---|---|---|---|
| | **% Skeletal completeness** | **D** | **p** |
| **Level I** | | | |
| *Machairodus aphanistus* | 71.29 | 0.50 | 0.039 |
| *Promegantereon ogygia* | 71.17 | 0.43 | 0.111 |
| *Indarctos arctoides* | 70.15 | 0.36 | 0.267 |
| **Level II** | | | |
| *Machairodus aphanistus* | 75.20 | 0.57 | 0.012 |
| *Promegantereon ogygia* | 72.69 | 0.43 | 0.111 |
| *Indarctos arctoides* | 62.07 | 0.50 | 0.039 |
| **Level III** | | | |
| *Machairodus aphanistus* | 55.09 | 0.57 | 0.012 |
| *Promegantereon ogygia* | 45.62 | 0.50 | 0.039 |
| *Indarctos arctoides* | 33.67 | 0.64 | 0.029 |

## Figure legends

**Figure 1.** A. Map of the Iberian Peninsula showing the location of Madrid and Valdemoro. B. Location of Batallones-1 and Batallones-3 sites, west of Valdemoro. C. Theoretical hourglass shaped cavity, with an upper herbivore-dominated assemblage and a lower, carnivoran-dominated assemblage. Modified from Pozo *et al.* (2004) and Domingo *et al.* (2013a).

**Figure 2.** Spatial distribution of Batallones-3 fossil remains. A. Plan view (X-Y coordinate plane). B. X-Z cross section (left), showing the fine-tuned discrete fossiliferous level models. C. X-Z cross section (right), showing the fine-tuned discrete fossiliferous level models.

**Figure 3.** Skeletal element proportions expressed as Relative Abundance (Ri) in Batallones-3. A, D and G. *Machairodus aphanistus* skeletal element proportions in Batallones-3 Levels I, II and III, respectively. B, E and H. *Promegatereon ogygia* skeletal element proportions in Batallones-3 Levels I, II and III, respectively. C, F and I. *Indarctos arctoides* skeletal element proportions in Batallones-3 Levels I, II and III, respectively. Mand = mandible, Vert = vertebra, Scap = scapula, Pel = pelvis, Hum = humerus, Rad = radius, Uln = ulna, Fem = femur, Tib = tibia, Pat = patella, Carp/Tars = carpal/tarsal, Mtc/Mtt = metacarpal/metatarsal, Phal = phalanx, Sesa = sesamoid.

**Figure 4.** Stereographic projections of the elongated axis of remains. Mean trend and plunge represented by plus sign. A. Level I stereographic projections. B. Level II stereographic projections. C. Level III stereographic projections. Cold colours: lower density of remains. Warm colours: higher density of remains.

**Figure 5.** *Indarctos arctoides* fossil densities for Batallones-3 levels. Density values represent the number of points per square unit (cm), per quadrat. A. Level I *Indarctos arctoides* fossil densities. B. Level II *Indarctos arctoides* fossil densities. C. Level III *Indarctos arctoides* fossil densities. The MNI of *Indarctos arctoides* per level is provided in the lower right corner.

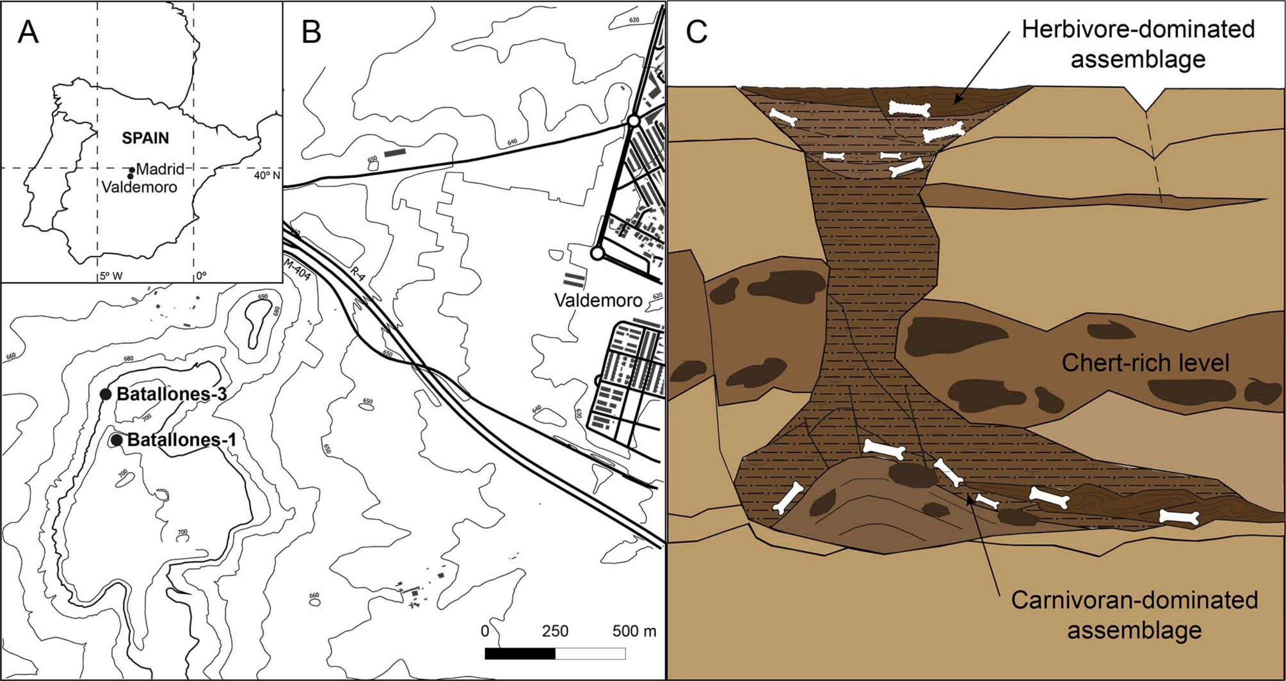
**Figure 6.** Bone breakage at Batallones-3. A, B and C. Number of fractures. D, E and F. Degree of bone completeness. G, H, and I. Fracture type/angle. J, K and L. Fracture surface. A, D, G and J. Level I remains. B, E, H and K. Level II remains. C, F, I and L. Level III remains.

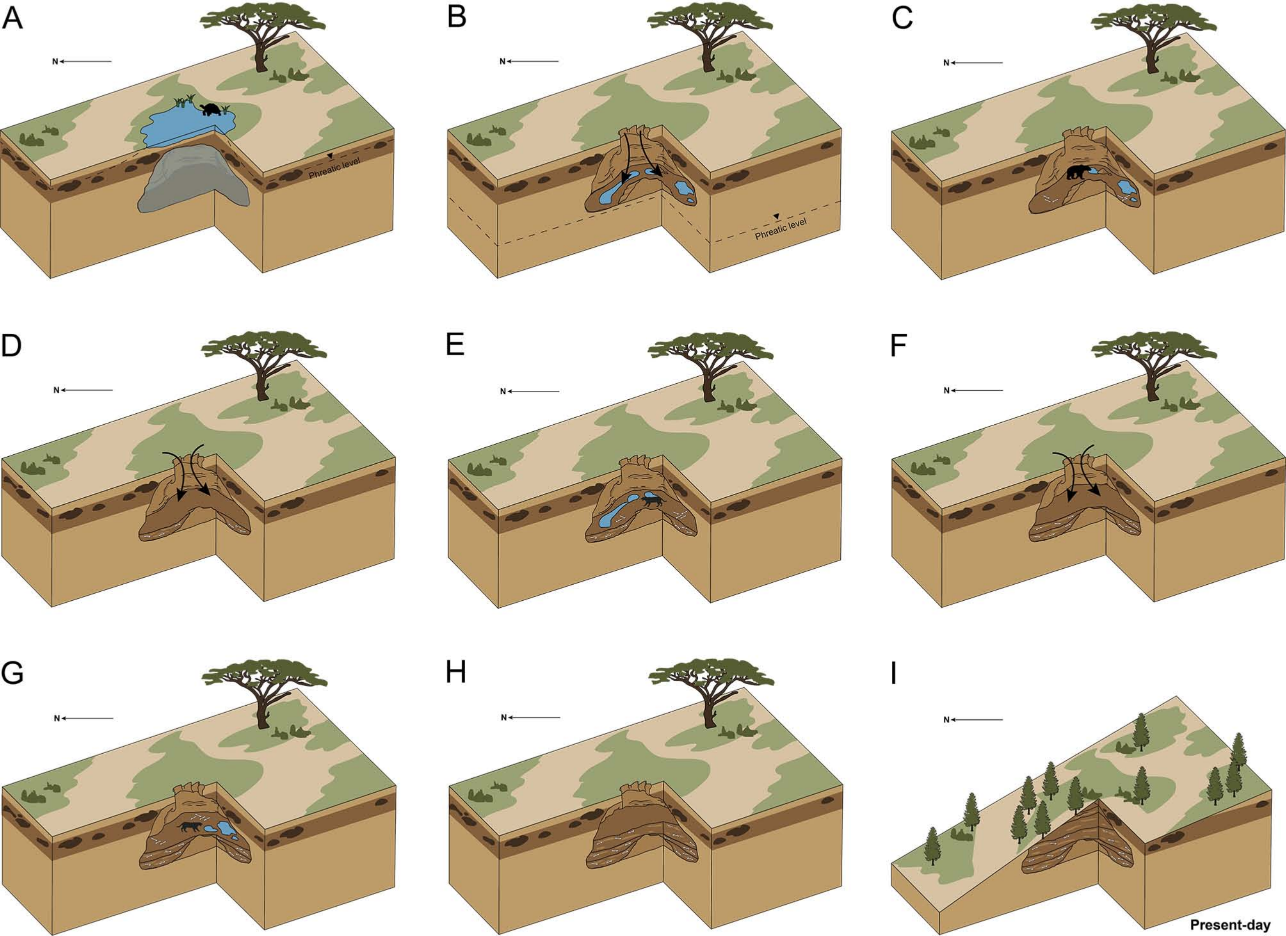
**Figure 7.** A. Common Batallones-3 taphonomic modifications. Ailuropodine bear *Indarctos arctoides* skull BAT-3’15-1000 (Level I), displaying typical Batallones-3 taphonomical modifications on autochthonous remains. Fractures are due to fossildiagenetic breakage. Note that, despite the high frequency of fractures, the skull is complete. B. Detail of the root-marked upper carnassial (P4). C. Detail of root marks on the mandible. D and E. Sabretooth felid *Promegantereon ogygia* right femur BAT-3’09-1236 (Level III) with perpendicular fossildiagenetic fractures with smooth fracture surfaces. F and G. Allochthonous herbivore remains in the Batallones-3 assemblage. F. *Hipparion* inferior molar BAT-3’12-1695 (Undetermined level). G. *Hipparion* incisors with mandible fragments BAT-3’11-1716 and BAT-3’11-1717 (Level I).

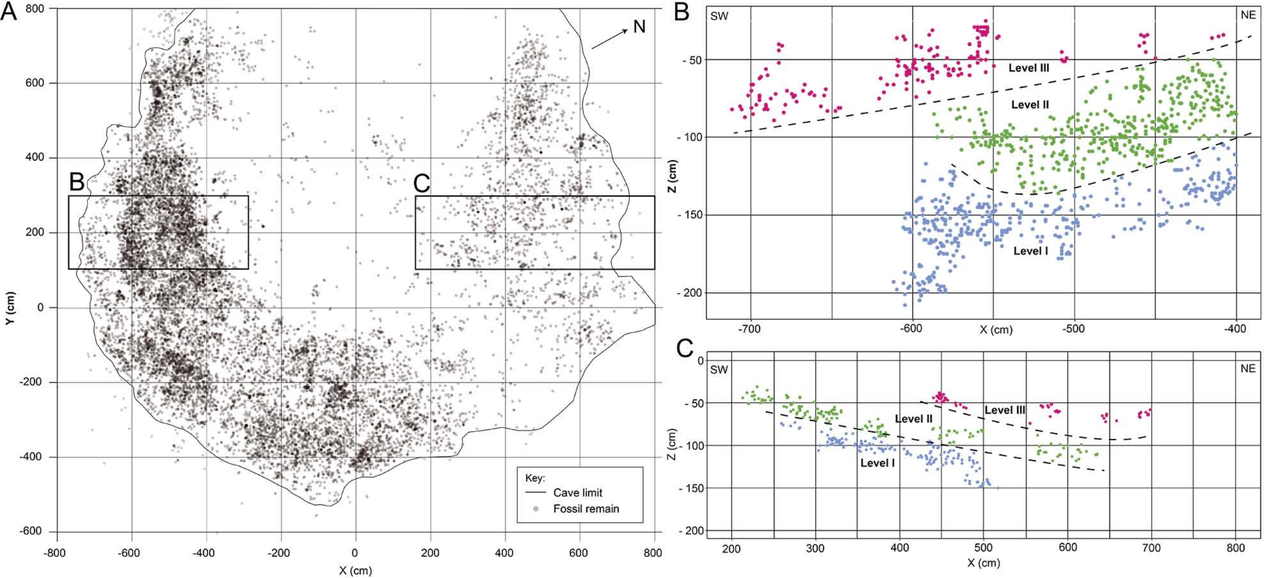
**Figure 8.** Batallones-3 associated and articulated remains. A. *Machairodus aphanistus* articulated carpals, metacarpals, and phalanges. B. Associated *Magericyon anceps* radius, ulna, tibia, femur, and vertebrae. Note diagenetic fractures affecting both bones and surrounding matrix.

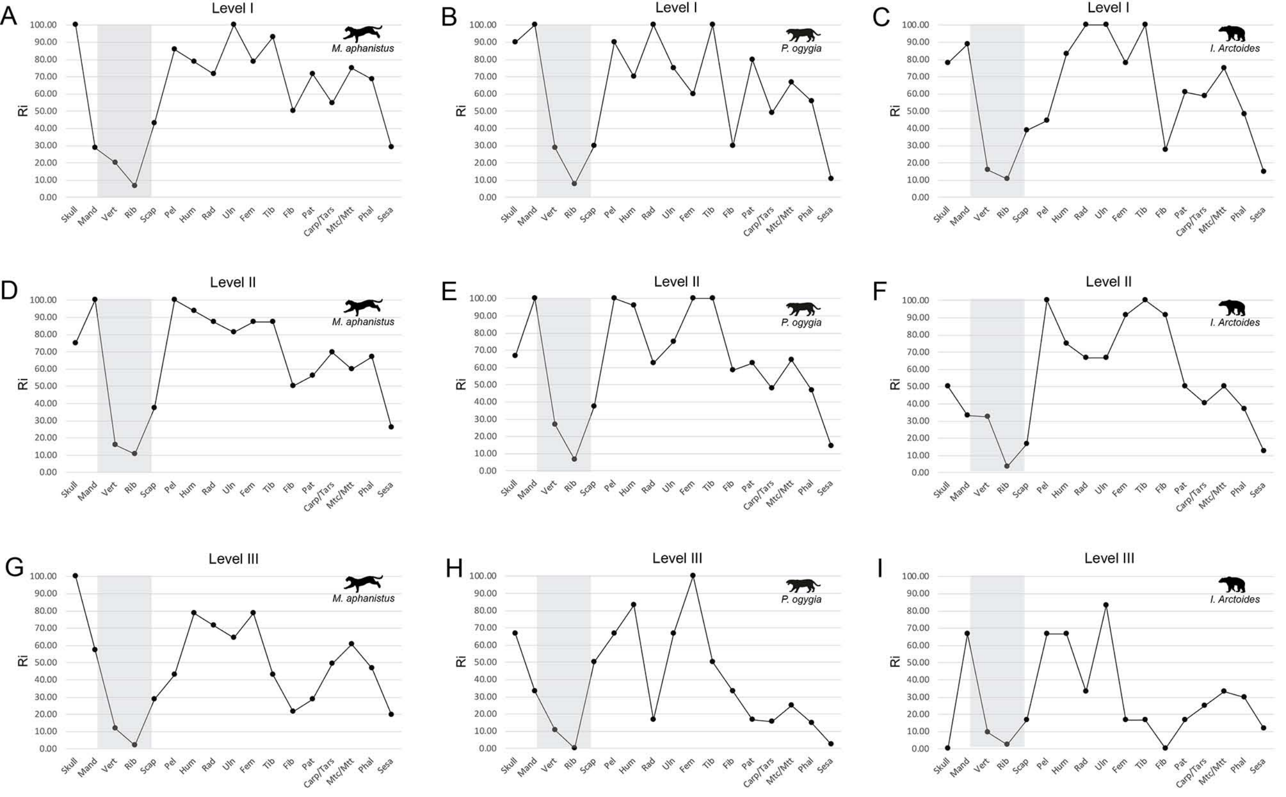
**Figure 9.** Mortality patterns for *Indarctos arctoides* individuals for each level, compared to other ursid-abundant assemblages. YC = Yarimburgaz Cave, a hibernation death assemblage (Stiner *et al.* 1996; Stiner 1998). LC = Lawson Cave and JC = Jerry Long Cave (Wolverton 2006), two natural trap bear assemblages.

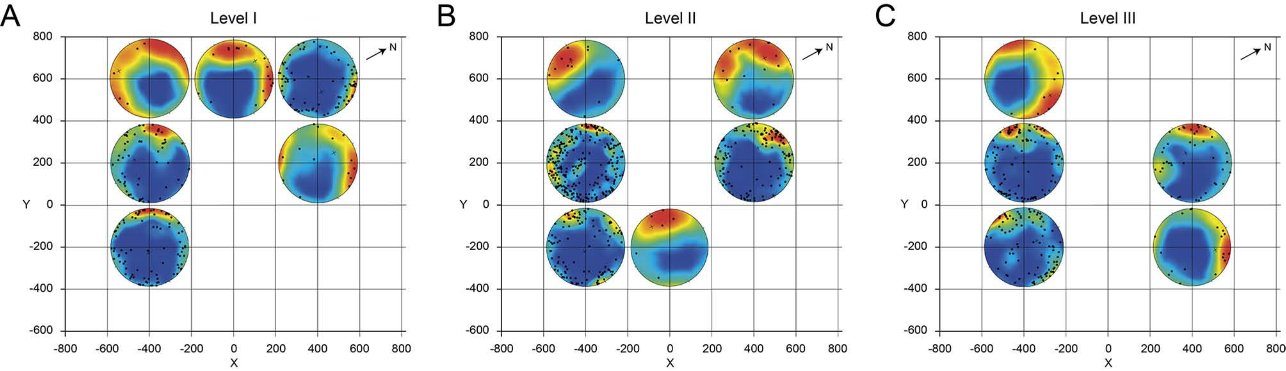
**Figure 10.** Taphonomic history of the Batallones-3 assemblage. A. Permanent water body before cavity roof collapse. B. Descent of phreatic level, roof collapse and debris cone formation. C, E and G. Natural trapping of carnivores (autochthonous assemblages). D, F and H. Alluvial sediment and allochthonous remains input. C. Batallones-3 Level I. E. Batallones-3 Level II. G. Batallones-3 Level III. I. Present day slope erosion, pine replantation. Due to slope erosion, it is uncertain if an upper herbivore-dominated assemblage was ever formed after step H.

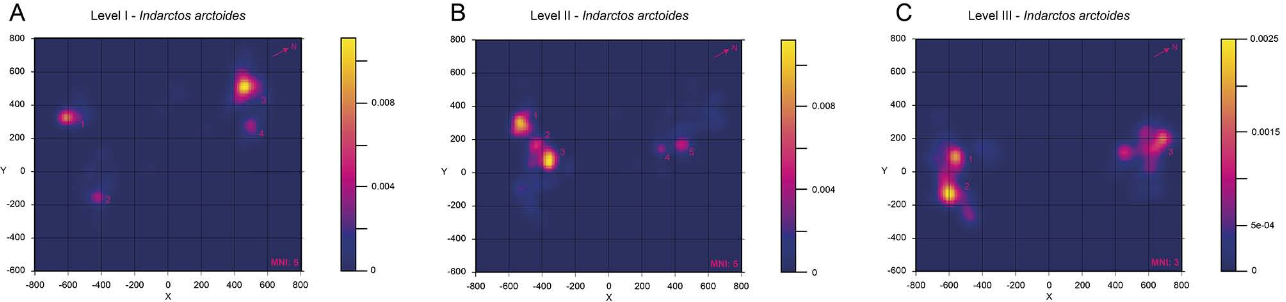

A
SPAIN
Madrid
Valdemoro
40º N
5º W
0º
B
620
640
650
M-404
R-4
Valdemoro
690
680
660
Batallones-3
700
Batallones-1
650
630
660
0
250
500 m
C
Herbivore-dominated assemblage
Chert-rich level
Carnivoran-dominated assemblage

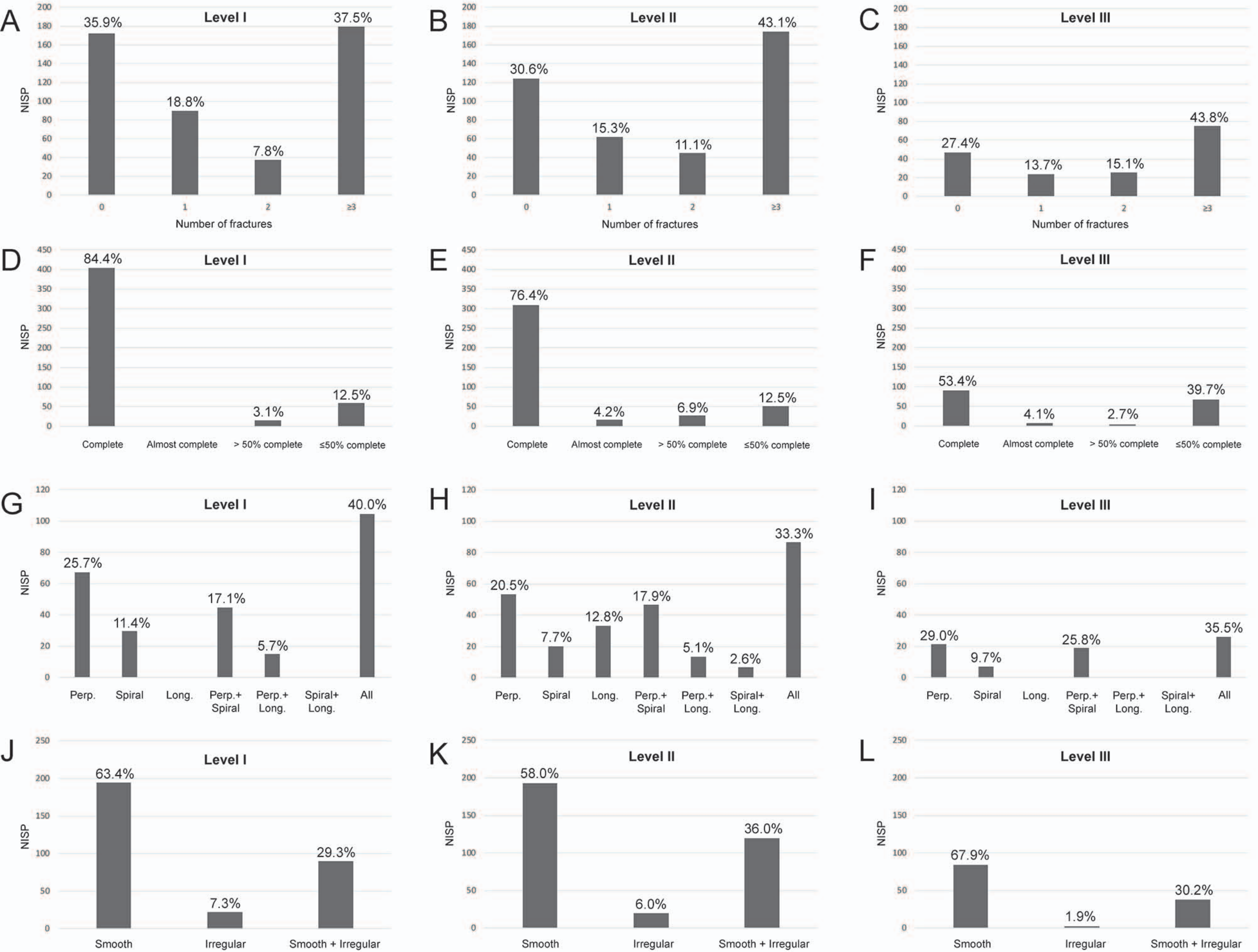

A
N
Phreatic level
B
N
Phreatic level
C
N
D
N
E
N
F
N
G
N
H
N
I
N
Present-day

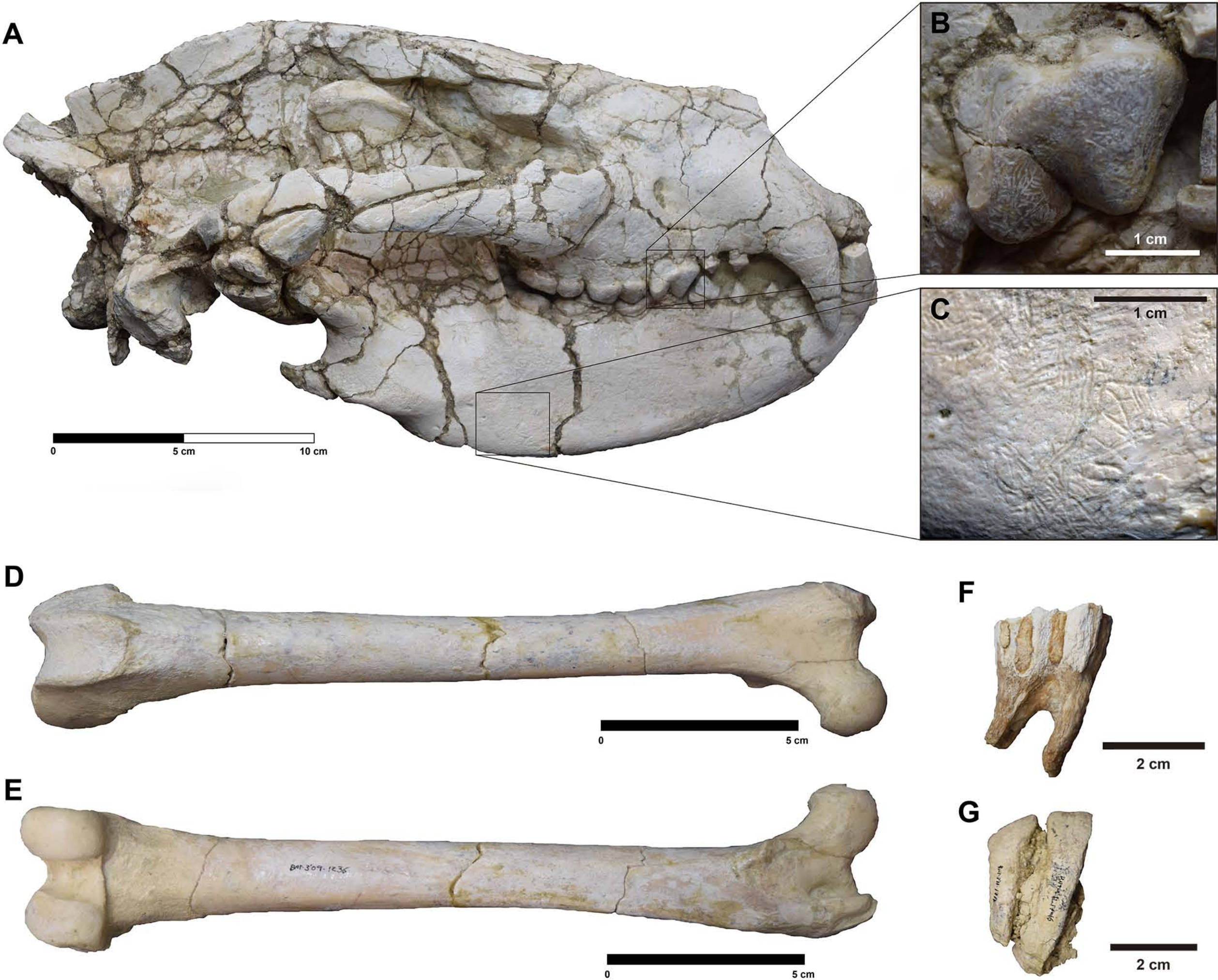

A
N
B
C
Key:
Cave limit
Fossil remain
Y (cm)
X (cm)
800
600
400
200
0
-200
-400
-600
-800
-600
-400
-200
0
200
400
600
800
B
SW
NE
Level III
Level II
Level I
Z (cm)
- 50
- 100
- 150
- 200
-700
-600
-500
-400
X (cm)
C
SW
NE
Level III
Level II
Level I
Z (cm)
0
- 50
- 100
- 150
- 200
200
300
400
500
600
700
800
X (cm)

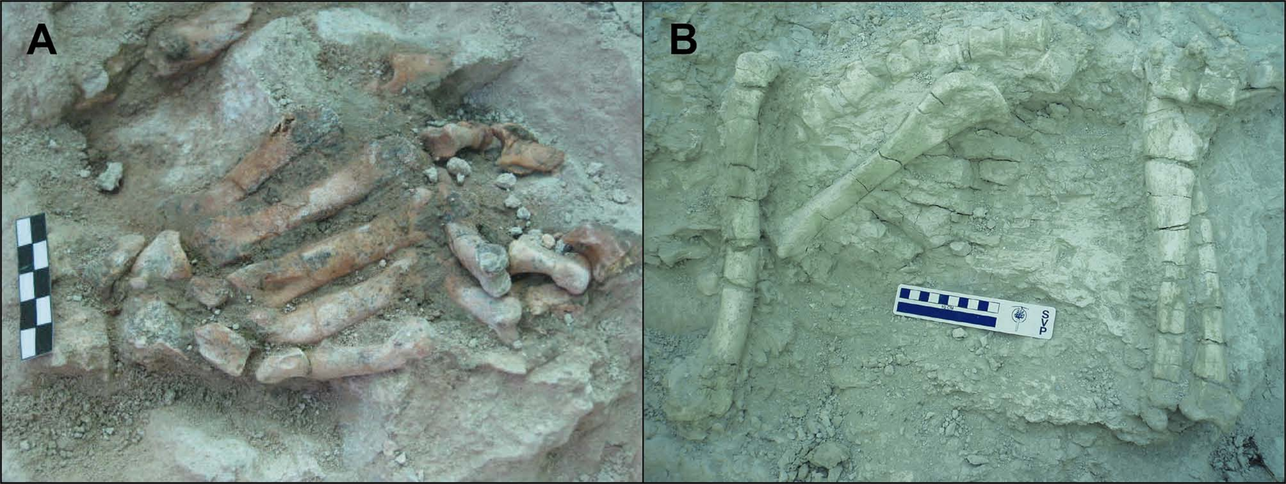

A
B
C
D
E
F
G
H
I
Level I
Level II
Level III
M. aphanistus
P. ogygia
I. Arctoides
Ri
0.00
10.00
20.00
30.00
40.00
50.00
60.00
70.00
80.00
90.00
100.00
Skull
Mand
Vert
Rib
Scap
Pel
Hum
Rad
Uln
Fem
Tib
Fib
Pat
Carp/Tars
Mtc/Mtt
Phal
Sesa

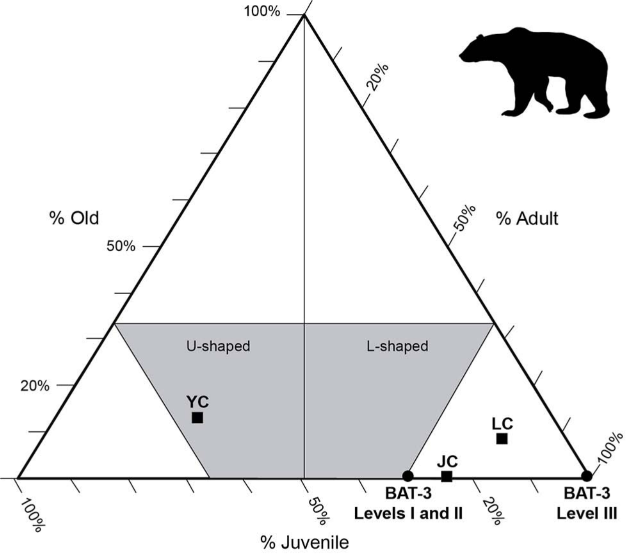

A
Level I
B
Level II
C
Level III
N
800
600
400
200
0
-200
-400
-600
Y
-800
-600
-400
-200
0
200
400
600
800
X


A
Level I - *Indarctos arctoides*
N
1
2
3
4
MNI: 5
0.008
0.004
0
B
Level II - *Indarctos arctoides*
N
1
2
3
4
5
MNI: 5
0.008
0.004
0
C
Level III - *Indarctos arctoides*
N
1
2
3
MNI: 3
0.0025
0.0015
5e-04
0
800
600
400
200
0
-200
-400
-600
Y
-800
-600
-400
-200
0
200
400
600
800
X


A
Level I
NISP
35.9%
18.8%
7.8%
37.5%
0
1
2
≥3
Number of fractures
B
Level II
30.6%
15.3%
11.1%
43.1%
C
Level III
27.4%
13.7%
15.1%
43.8%
D
Level I
84.4%
3.1%
12.5%
Complete
Almost complete
> 50% complete
≤50% complete
E
Level II
76.4%
4.2%
6.9%
12.5%
F
Level III
53.4%
4.1%
2.7%
39.7%
G
Level I
25.7%
11.4%
17.1%
5.7%
40.0%
Perp.
Spiral
Long.
Perp.+ Spiral
Perp.+ Long.
Spiral+ Long.
All
H
Level II
20.5%
7.7%
12.8%
17.9%
5.1%
2.6%
33.3%
I
Level III
29.0%
9.7%
25.8%
35.5%
J
Level I
63.4%
7.3%
29.3%
Smooth
Irregular
Smooth + Irregular
K
Level II
58.0%
6.0%
36.0%
L
Level III
67.9%
1.9%
30.2%


A
0
5 cm
10 cm
B
1 cm
C
1 cm
D
0
5 cm
E
BAT-3'09-1236
0
5 cm
F
2 cm
G
2 cm


A
B
10 CM
SVP


100%
20%
50%
100%
% Old
50%
20%
% Adult
U-shaped
L-shaped
YC
LC
JC
100%
50%
20%
% Juvenile
BAT-3
Levels I and II
BAT-3
Level III