Taphonomy of mammalian fossil bones from the debris-flow deposits of Somosaguas-North (Middle Miocene, Madrid Basin, Spain)

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ABSTRACT

Debris-flow hosted assemblages dominated by mammalian remains are very scarce in the fossil record and few examples are reported. Herein we present a detailed taphonomic study of Somosaguas-North (Madrid Basin, Spain), a Middle Miocene mammalian-dominated site embedded in debris-flow deposits, in order to increase our knowledge of the mode of formation of fossiliferous assemblages in this depositional context. The assemblage includes 6592 large-mammal remains belonging to at least 10 different species. Fossils are found in matrix-supported, poorly-sorted coarse arkosic sandstones and fine conglomerates, which are interpreted as the result of successive debris-flow deposits. Breakage constitutes a pervasive taphonomic alteration in the bone assemblage; however, together with unidentifiable bone fragments, we also found complete to almost complete skeletal elements. Bone remains are isolated, a fact that is indicative of a time of exposure of the carcasses long enough to enable decay and complete disarticulation. There are no associations of elements belonging to the same individual, which suggests that, prior to or during debris-flow transport, bones were profusely dispersed. Based on the taphonomic evidence, we suggest that Somosaguas-North assemblage was formed by successive debris-flow transport and burial of pre-existing thanatocoenoses. Bones from those thanatocoenoses were modified by biostratinomic agents (trampling, weathering) in varying degrees depending on their time of exposure. Debris-flow transport produced further abrasion and breakage in collagen-depleted bones. Our results are congruent with an environmental context of semiarid landscapes presenting long arid periods and highly irregular hydrological seasonality. Finally, we compared the Somosaguas-North assemblage with other debris-flow hosted vertebrate assemblages. Although Somosaguas-North shares taphonomic features with some of these sites, it is not possible to define consistent and single taphonomic patterns for debris-flow assemblages, given the varied taphonomic histories of the remains prior to and during debris-flow transport.

1. Introduction

The Cenozoic Madrid Basin (Spain) (Fig. 1) contains very abundant continental fossiliferous deposits to the extent that much of our knowledge of the Spanish mammalian faunas dated in the MN5 biochronological unit (Mammal Neogene units, Mein (1975); Middle Aragonian, Middle Miocene) derives from this basin (Alberdi, 1985; Peláez-Campomanes et al., 2003; Hernández-Ballarín et al., 2011; Domingo L. et al., 2012a). Despite the richness of sites, the wealth of studies on the systematics of the faunas and the good control of the geological context, taphonomic studies of the Madrid Basin mammalian sites are very scarce (but see Domingo et al., 2013). In many cases, comprehensive taphonomic studies have been hindered by the fact that many of these localities are found within the limits of the city of Madrid and in the context of public works, and fossils therefore have to be extracted as fast as possible and there is little chance of continuing excavations once public works are completed and sites are covered up

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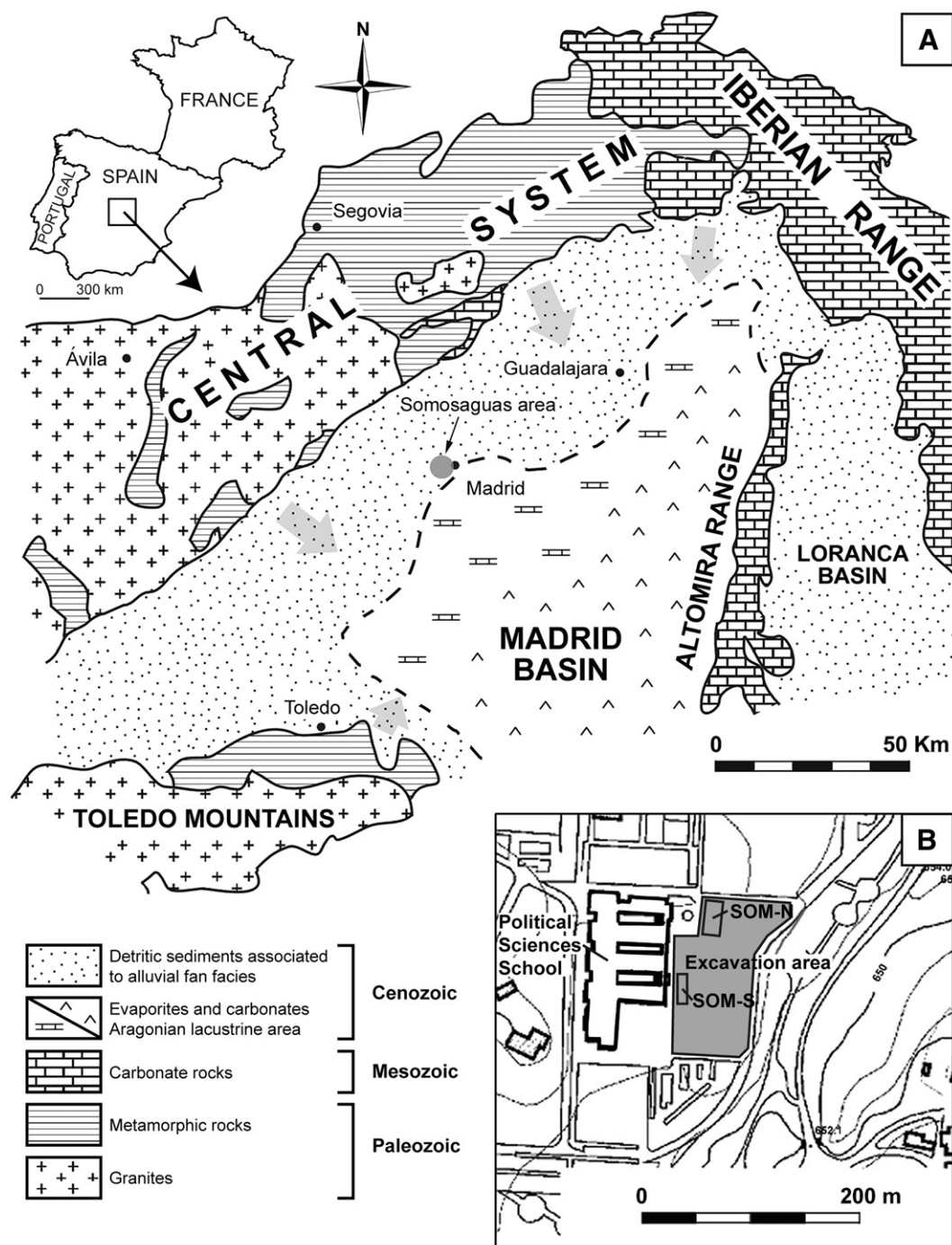
Fig. 1. Location of Somosaguas fossil sites. A. Geological map of the Madrid Basin and geographical situation of Somosaguas sites. Grey arrows indicate clastic material source areas. On the map in the upper left hand corner, the situation of the Madrid Basin in Spain is indicated. B. Excavation area of the Somosaguas fossil sites within the Somosaguas Campus of the Complutense University of Madrid. SOM-N = Somosaguas-North, SOM-S = Somosaguas-South.
(Modified from Calvo et al. (1989) and Fesharaki et al. (2007).)

(Morales, 2000; Trabada Guijarro et al., 2006). In this article, we present a detailed taphonomic study of the large-mammal assemblage of Somosaguas-North (SOM-N), a fossil locality in the Madrid Basin that lies outside the limits of the city of Madrid. SOM-N was not found in the context of public works and therefore has not been subjected to urgent excavation. This site is part of the Somosaguas paleontological complex, located on the campus of the Complutense University of Madrid in the town of Pozuelo de Alarcón (~15 km to the west of the city of Madrid). The site is excavated annually since 1998 by undergraduate and graduate students as part of a paleontological training program under the guidance of instructors and researchers from the aforementioned university (López-Martínez et al., 2000; Castilla et al., 2006; Benítez-López et al., 2009; Fesharaki et al., 2012).

The Somosaguas sites have been studied from a variety of viewpoints which include the stratigraphy, sedimentology and mineralogy of the debris-flow and mud-flow deposits that host the sites (Mínguez Gandú, 2000; Cuevas-González, 2005; Fesharaki et al., 2007, 2015; Carrasco et al., 2008; Díez-Canseco et al., 2012), as well as the systematics (Luis and Hernando, 2000; Mazo, 2000; Salesa and Morales, 2000; Salesa and Sánchez, 2000; Sánchez, 2000; van der Made and Salesa, 2004; Hernández Fernández et al., 2006; Ansón, 2013; Pérez-García, 2013; Pickford and Laurent, 2014) and the biochronology, paleoecology

and paleobiogeography of the vertebrate fauna (Cuezva and Elez, 2000; López-Martínez et al., 2000; Hernández Fernández et al., 2003, 2006; Cuevas-González, 2005; Pina et al., 2008; Domingo L. et al., 2009, 2012a, 2012b; Perales et al., 2009; Torroba et al., 2010; Hernández-Ballarín et al., 2011; García Yelo et al., 2014; Menéndez et al., 2015; Blanco and Hernández Fernández, 2016). A total of 24 mammal species has been described at the Somosaguas sites. Less abundant remains of birds, lizards and turtles have also been found (Hernández Fernández et al., 2006). Small mammal taxa (mainly rodents) enabled the sites to be dated as belonging to the local zone E (Luis and Hernando, 2000; Hernández Fernández et al., 2006; Hernández-Ballarín et al., 2011), which is included in the MN5 unit and spans the time between 14.05 and 13.75 Ma (Mein, 1975; Daams et al., 1999).

From a paleoclimatic viewpoint, the Somosaguas sites are contemporaneous with the cooling episode that took place immediately after the Middle Miocene Climatic Optimum as a consequence of the reestablishment of the ice cap in Eastern Antarctica (Flower and Kennett, 1994; Zachos et al., 2001; Lewis et al., 2008). A temperature decrease and increased aridity associated with this event have been directly detected at the Somosaguas sites by means of carbon and oxygen stable isotope analyses in mammalian tooth enamel (Domingo L. et al., 2009, 2012a) and through study of the composition of clastic sediments (Fesharaki et al., 2015). Previous studies based on the small-mammal association, herbivore assemblage, sedimentological characteristics, and the composition of the clay minerals have supported the existence of a savanna biome in the Somosaguas area, in a tropical semiarid climate with an alternation of long dry periods and short wet periods (Luis and Hernando, 2000; Hernández Fernández et al., 2003, 2006; Cuevas-González, 2005; Carrasco et al., 2008; Perales et al., 2009).

Only a few mammalian-dominated debris-flow hosted sites have been described in the fossil record (see 'Discussion' section), and to the best of our knowledge, only one Miocene debris-flow locality, Paşalar (Turkey), has been reported in the literature (Andrews and Ersoy, 1990; Andrews, 1995). In this work, we conduct a detailed taphonomic study of the debris-flow hosted Miocene site of SOM-N in order to improve our knowledge of the biostratinomic and fossildiagenetic processes the mammalian remains underwent in this depositional context. We compare our results with those obtained by Polonio and López-Martínez (2000), who performed a preliminary taphonomic analysis of the fossil material recovered at SOM-N in the first field season. After eighteen field seasons, it has become necessary to reevaluate the taphonomic circumstances that led to the formation of this assemblage. The description by Polonio and López-Martínez (2000) of the taphonomic alterations displayed by the SOM-N fossils was highly qualitative due to the shortage of information available from the first field season. The richness of the taphonomic data gathered throughout the eighteen field seasons has enabled us to provide quantitative data for characterizing the biostratinomic and fossildiagenetic features of the SOM-N assemblage.

Additionally, we have compiled information on all the vertebrate debris-flow assemblages found in the literature that provided detailed taphonomic data. Our aim is to compare the SOM-N data with these sites in order to shed more light on the similarities and differences of the taphonomic signatures displayed by bones subject to this depositional regime.

2. Geologic context

2.1. Madrid Basin

The Madrid Basin is located in central Spain (Fig. 1) and, together with the Intermediate Depression (also known as Loranca Basin), forms the Tagus Basin. The two sub-basins became independent in the Paleogene with the uplift of the Altomira Range (Alonso-Zarza et al., 2004). The Madrid Basin occupies over 10,000 km^2 and is filled by Cenozoic continental deposits that reach a maximum thickness of 3500 m. The mineralogy of these deposits reflects the composition of the mountain ranges surrounding the basin, because they constitute their source areas. To the north and west, the Central System is mainly composed of
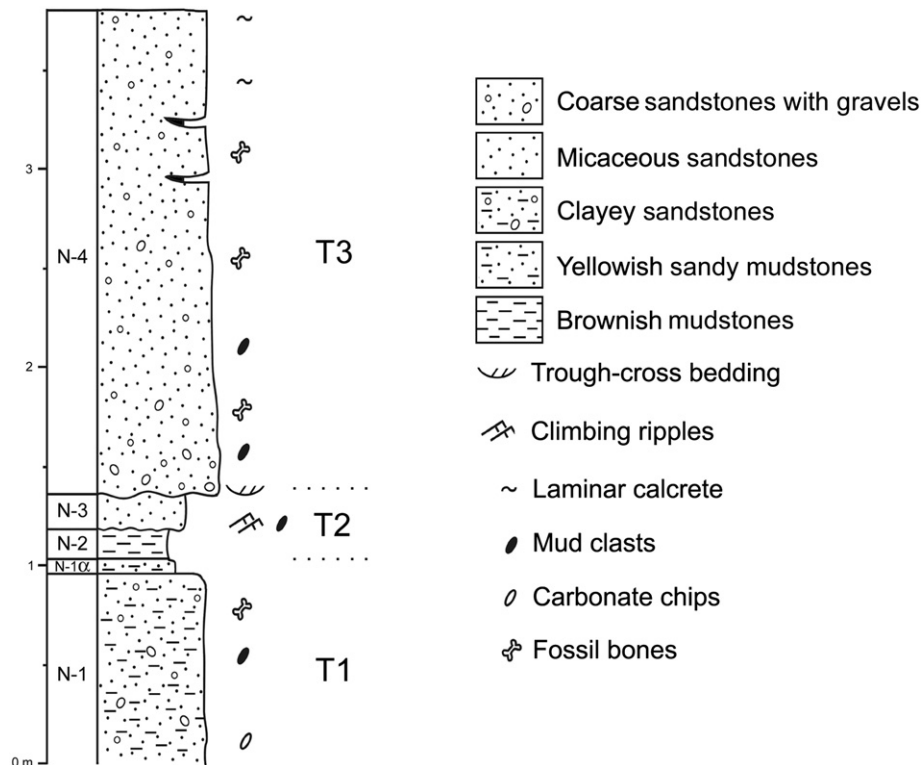

Fig. 2. Stratigraphic section of Somosaguas-North (SOM-N) showing the three units (T1, T2, T3) described in the text. (Modified from Mínguez Gandú (2000) and Fesharaki et al. (2007).)

granitic and metamorphic rocks; to the south, the Toledo Mountains are also integrated by granitic and metamorphic rocks; to the east, the Iberian and Altomira Ranges are primarily made up of sedimentary rocks (Alonso-Zarza et al., 2004) (Fig. 1).

Neogene sediments are ubiquitous in the Madrid Basin. During the early and middle Miocene, the central area of the basin was occupied by lacustrine and palustrine systems fringed by alluvial fans and fluvial distributary facies which together formed a centripetal drainage system, a sedimentary pattern typical of an endorheic geomorphological setting (Alonso-Zarza et al., 2004). During the late Miocene to the early Pliocene, the Madrid Basin became an exhorheic basin. The Madrid Basin Neogene succession therefore mainly comprises Miocene deposits, overlain by a thin and discontinuous Pliocene sequence (Alonso-Zarza et al., 2004). The Miocene sequence is divided into three units: 1) the Lower Unit (Ramblian to Lower Aragonian, ~25–19 Ma), which is composed of different types of sediments responding to the abovementioned concentric model. The central areas present lacustrine deposits mainly comprising evaporites (sulfates, carbonates and chlorides) and, towards the borders of the basin, there are gradations of detritic materials (fluvial systems and alluvial fans), 2) the Intermediate Unit (Middle Aragonian to Lower Vallesian, ~19–10 Ma), where the concentric model of the Lower Unit is repeated but the detritic deposits are more extended as a consequence of the re-activation of the Central System uplift, and 3) the Upper Unit (Upper Vallesian to Turolian, ~10–5 Ma), characterized by a change in the sedimentation pattern, as the basin no longer responds to a concentric configuration (Alonso-Zarza et al., 2004). The base of the Upper Unit is made up of terrigenous deposits accumulated by fluvial systems exhibiting a north-south direction. The upper part of this unit is made up of carbonate sediments that accumulated in a fresh-water fluviolacustrine system (Alonso-Zarza et al., 2004).

2.2. Somosaguas fossiliferous area

The Somosaguas fossil sites are found in deposits belonging to the Intermediate Unit of the Miocene sequence of the Madrid Basin. These deposits correspond to the proximal facies of the aforementioned concentric paleogeographic setting and mainly consist of matrix-supported arkosic facies that are interpreted as middle to distal alluvial fan deposits, whose source area was the Central System Range, located 30 km to the northeast of the sites (Hoyos et al., 1985; Fesharaki et al., 2015) (Fig. 1).

The Somosaguas fossiliferous area has two main excavation sites, Somosaguas-North (SOM-N), where the excavation of large-mammal remains takes place, and Somosaguas-South (SOM-S), where sediment is extracted and processed in order to obtain small-mammal remains (Fig. 1). Additionally, there are nine prospection trenches in the nearby

Fig. 3. Content of one of the splinter bags from SOM-N. Splinters are fragmented fossil bones smaller than 3 cm with undetermined anatomic and taxonomic adscription. The total number of bags containing splinters at SOM-N is 814.

Table 1
Large mammal taxa recovered at SOM-N expressed as Number of Identified Specimens (NISP) and percentages. Indet. = indetermined.

	Family/Order	NISP	%
Amphicyon sp.	Amphicyonidae/Carnivora	10	0.15
Hemicyon sp.	Hemicyonidae/Carnivora	1	0.02
Pseudaelurus sp.	Felidae/Carnivora	2	0.03
Carnivora indet.	Carnivora	53	0.80
Anchitherium cursor	Equidae/Perissodactyla	484	7.34
Prosantorhinus douvillei	Rhinocerotidae/Perissodactyla	92	1.40
Retroporcus complutensis	Suidae/Artiodactyla	79	1.20
Micromeryx sp.	Moschidae/Artiodactyla	34	0.52
Heteroprox sp.	Cervidae/Artiodactyla	6	0.09
Tethytragus sp.	Bovidae/Artiodactyla	39	0.59
Ruminantia indet.	Artiodactyla	639	9.69
Artiodactyla indet.	Artiodactyla	10	0.15
Gomphotherium angustidens	Gomphotheriidae/Proboscidea	786	11.92
Indeterminate		4357	66.10
	Total Carnivora	66	1.00
	Total Perissodactyla	576	8.74
	Total Artiodactyla	807	12.24
	Total Proboscidea	786	11.92
	Total Indetermined	4357	66.10
	Total	6592	

area, two of which (Cata-2 and Cata-4) are currently being excavated (Díez-Canseco et al., 2012; Fesharaki, 2016).

The stratigraphic sequence of the Somosaguas paleontological area is made up of two fossiliferous units, T1 and T3, with a non-fossiliferous unit located between them, T2 (Mínguez Gandú, 2000) (Fig. 2). Underlying these three units, six more units have been recently described, which are called from base to top T-5, T-4, T-3, T-2, T-1 and T0 (Díez-Canseco et al., 2012; Fesharaki, 2016). Their description was based on borehole continuous cores and their fossil content has not yet been evaluated. Consequently, only T1 to T3 units will be described here in detail (Fig. 2).

T1 unit consists of clayey arkoses, with the clay content increasing towards the top unit, and has been interpreted as the result of mud-flow deposits. The visible thickness of this unit is 57 cm. The SOM-S fossil site crops out in this type of deposits, which are rich in small-mammal remains (Luis and Hernando, 2000; Mínguez Gandú, 2000).

T2 unit comprises rippled micaceous sandstones interbedded with thin mudstone layers and lacks fossil remains (Mínguez Gandú, 2000).

Table 2
Skeletal element frequencies at SOM-N expressed as Number of Identified Specimens (NISP) and percentages. Indet. = indetermined.

Element	NISP	%
Antler	2	0.03
Skull	72	1.09
Mandible	62	0.94
Tooth	603	9.15
Tooth indet.	1320	20.02
Vertebra	154	2.34
Rib	191	2.90
Clavicle	1	0.02
Scapula	21	0.32
Pelvis	26	0.39
Humerus	14	0.21
Radius	18	0.27
Ulna	8	0.12
Femur	17	0.26
Tibia	34	0.52
Patella	23	0.35
Carpal	171	2.59
Tarsal	144	2.18
Metapodial	149	2.26
Phalanx	185	2.81
Sesamoid	132	2.00
Indeterminate	3245	49.23
Total	6592	
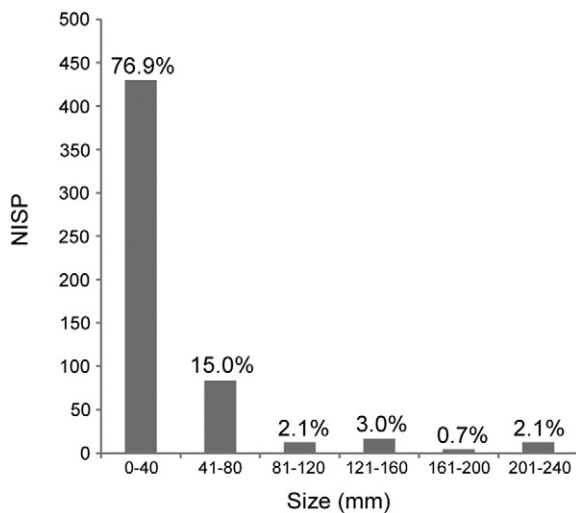
Fig. 4. Bone maximum dimension size frequency at SOM-N. NISP = Number of Identified Specimens. This analysis is performed on the taphonomically analyzed subsample (see 'Materials' section), and splinters <3 cm from this subsample are therefore included.

From a maximum thickness of 200 cm at SOM-S, this unit decreases in thickness towards the north. These deposits are interpreted as stream-mouth lobes or terminal splays of streams when they reach their base level in a pond (Díez-Canseco et al., 2012).

T3 unit consists of poorly-sorted coarse arkosic sandstones and fine conglomerates with a silty-clay matrix, interbedded with irregular clay levels. There are pebbles up to 10 cm in size, although mean size corresponds to that of coarse sands. This unit, interpreted as the result of successive debris-flow deposits (Mínguez-Gandú, 2000; Díez-Canseco et al., 2012; Fesharaki, 2016), reaches a thickness of over 300 cm and contains abundant remains of vertebrates, including mammals as the predominant group, but remains of lizards, turtles and birds are also present. Its large-mammal fossil content constitutes the subject of the present study (SOM-N). T3 unit is also being excavated in the prospection trenches known as Cata-2 and Cata-4.

Cuevas-González (2005) suggested that large arkosic mass-flow alluvial fans from the Madrid Basin formed under an arid climatic regime presenting intense seasonal rain, since mass transport deposits predominate over fluvial facies, which are practically non-existent.

Although bedding planes are not easily recognizable in T3 unit, Elez (2005) performed a three-dimensional reconstruction of the distribution of 1300 remains from this unit and suggested the existence of up to 3 levels where fossils were more concentrated and separated by levels exhibiting an apparent scarcity of fossils. This configuration would be typical of multiple, episodic debris flows (Elez, 2005; Hernández Fernández et al., 2006). Fesharaki et al. (2015) analyzed from a petrographic viewpoint six successive samples from T3 unit

and concluded that the differences in the composition of the clastic materials could point to a multi-episodic process, with sediments deposited by different pulses associated with a sequence of continuous cooling (see also Domingo et al., 2009). Well-defined limits to these episodes cannot be established, given the massive character of the deposits (T3 unit), which are devoid of clear bounding surfaces and major sedimentary structures. The entire stratigraphic sequence displays a dip of 2° to 3° towards the south. This dipping responds to the depositional slope and not to tectonic deformation (Hernández Fernández et al., 2006).

3. Taphonomic background

Polonio and López-Martínez (2000) conducted a preliminary taphonomic study based on material recovered at SOM-N during the first field season (*n* = 211). Highly fragmented, unidentifiable bones (i.e. splinters) were extremely abundant, so the material recovered and observed by these authors mainly belonged to bones larger than 3 cm or smaller than 3 cm but identifiable.

The abovementioned authors observed that the assemblage consisted of remains showing diverse preservational states that included relatively well preserved remains, remains rounded due to abrasion, and highly fragmented remains that were taxonomically and anatomically unidentifiable. There was no contact among the bones in the site. Rather, they were 'floating' in the sedimentary matrix in the same fashion as rock pebbles. Remains were disarticulated and disassociated. The bones showed a trend alignment along the north-south axis. When plunge data were considered, bones were observed to present a mean dip of 15° and a preferential direction of dip towards the south (Polonio and López-Martínez, 2000).

Appendicular skeleton bone fragments, rib fragments and isolated teeth were the most abundant remains in the assemblage. A total of 54% of the remains were taxonomically undetermined. Among the determined specimens, Ruminantia (14%), Proboscidea (12%) and Equidae (12%) were the best represented taxa (Polonio and López-Martínez, 2000). Although there were no quantitative data on the age representation of large mammals at SOM-N, there appeared to be an important presence of juvenile individuals, as evidenced by the presence of long bones with unfused epiphyses, mandibles with decidual dentition as well as infantile and juvenile bone microstructures detected in paleohistological sections (Cuezva and Elez, 2000; Polonio and López-Martínez, 2000; Hernández Fernández et al., 2006).

Regarding the preservation of the bones, fragmentation was the most significant taphonomical alteration detected by Polonio and López-Martínez (2000). Bones showed low integrity, a fact that made bone splinters of different sizes and shapes the most abundant type of remain in the assemblage. Remains did not display features indicative of advanced weathering stages. Given the polishing and rounding of some splinters, the authors indicated that these elements could have undergone intense weathering prior to fragmentation. Bones showed
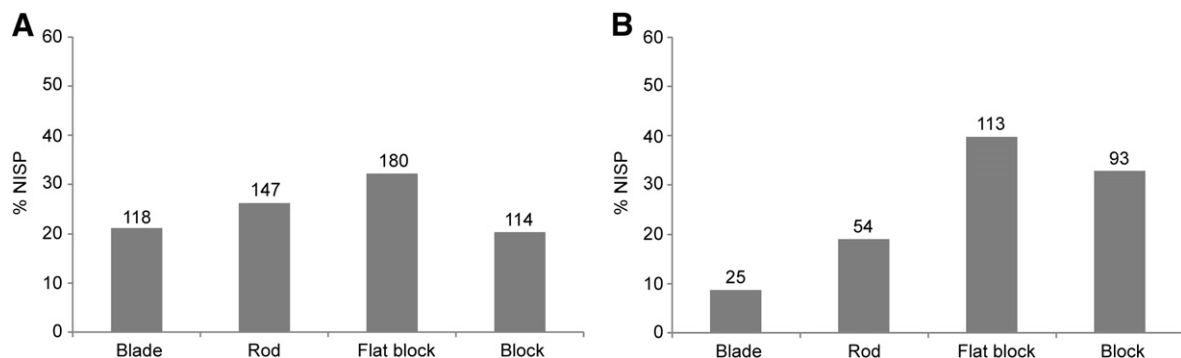
Fig. 5. Fossil shape at SOM-N. The raw NISP (= Number of Identified Specimens) appears above the bars. A. All fossils in the taphonomic subsample. B. Only identifiable fossils. *1.5 column.*
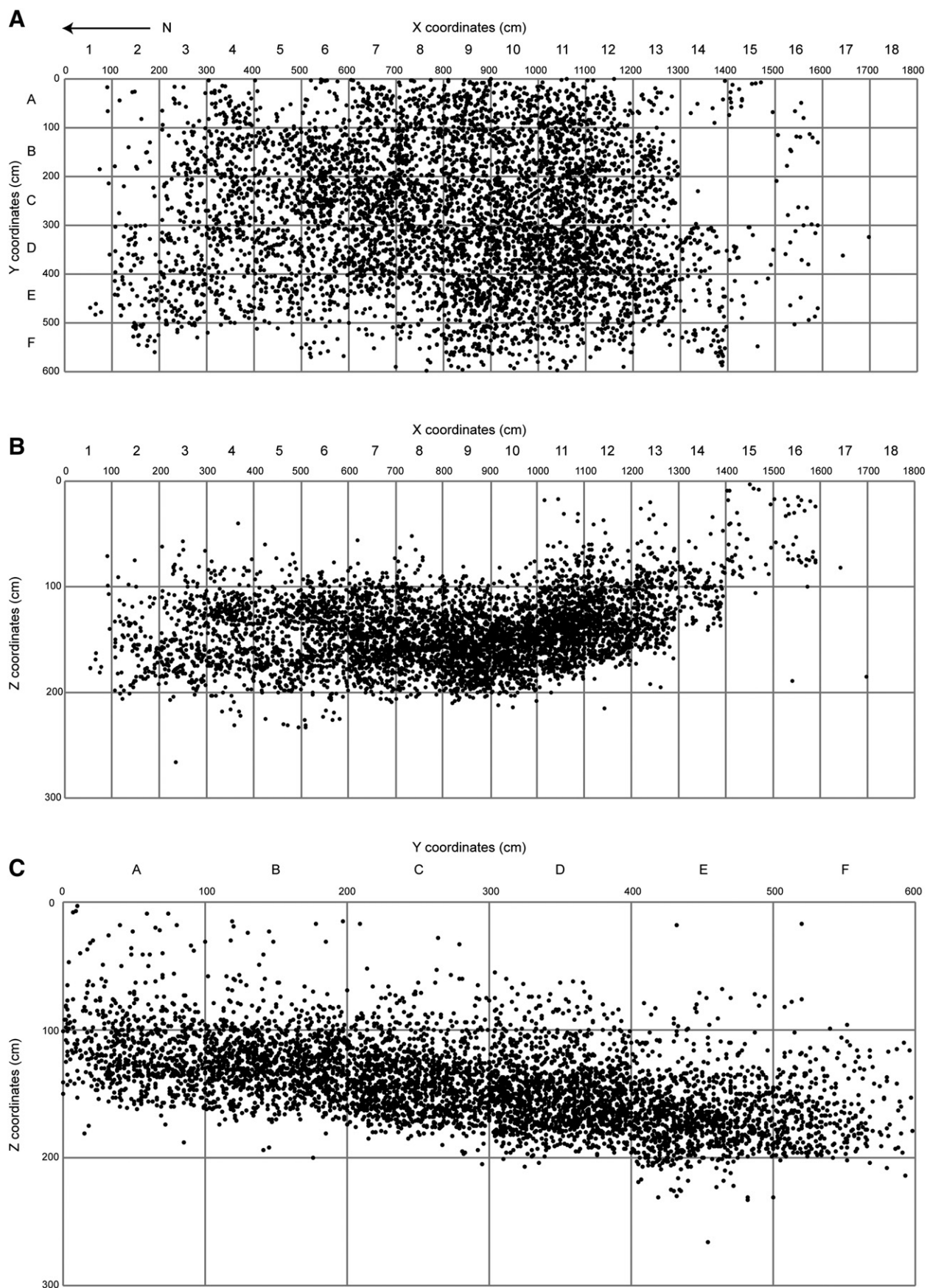
Fig. 6. Spatial distribution of SOM-N fossil remains. Each point corresponds to a skeletal element (splinters <3 cm are not included in this analysis because they are not recorded in the field notes). A. Plan view (X-Y plane). Each one-meter squared excavation grid is labelled with a letter (A-F) and a number (1–18). B. X-Z cross section. Towards the north (left of the plot) there may be two fossil-rich levels separated by a level poorer in remains (vertical scale is exaggerated) C. Y-Z cross section.

no signs of corrosion, digestion, or carnivore and rodent activity. Some elements displayed a powdered texture.

These authors concluded that the SOM-N assemblage comprises remains showing a range of preservational states, from well preserved and almost complete to highly fragmented specimens (although the latter ones predominate). Based on these features and the sedimentology of the site, Polonio and López-Martínez (2000) suggested that mass transport during debris-flow episodes was the agent responsible for the accumulation of the fossiliferous assemblage.

4. Materials

A total of 6592 large-mammal remains has been recovered at SOM-N between 1998 and 2014 (when we were preparing this study, the excavation of 2015 had not taken place). The Somosaguas remains are currently housed in the collections of the Paleontology Department at the Complutense University of Madrid. The remains from field seasons 1998 to 2012 are fully prepared.

As previously mentioned, splinters (i.e. fragmented fossil bones smaller than 3 cm with an undetermined anatomic and taxonomic adscription) are very common at SOM-N (Fig. 3). They are recovered but, due to their great abundance they are not recorded in the field notes and, as a result, in the total account of elements. This could introduce a bias against small, unidentifiable elements, but it is impractical to record all the data on splinters during the field seasons. In any event, direct observation of bone material carried out in this study included splinters, so that we could obtain sound knowledge of the taphonomic alterations present in this type of remains.

The enormous amount of remains collected since the first excavation in 1998 made it unfeasible to make direct taphonomic observations on all of the elements. We therefore performed the direct observation of taphonomic modifications in a subsample of 559 fossil remains (10% of the total material recovered between 1998 and 2012). We randomly selected the subsample but considering material coming from all the field seasons in order to avoid biases derived from the observation of fossils from only some of the field seasons. As previously indicated, we also included splinters in this taphonomic subsample.

Several taphonomic variables can be studied with the use of the information directly available from the field notes (i.e., direct observation of fossil bones is not necessary), such as the anatomical and taxonomical composition of the assemblage or the spatial distribution and orientation of fossils in the site. Thus, we employed the information from all the material to evaluate these taphonomic variables.

5. Methods

SOM-N is excavated following standard techniques commonly used in fossil vertebrate excavations (Eberth et al., 2007a). Information recorded in the field corresponds to the taxonomical and anatomical identification of the remains, the X, Y and Z coordinates, trend and plunge of fossils with a dominant longer axis, and degree of articulation.

The SOM-N site has an area of over 100 m². The excavation area is divided into 1 m² grids. The spatial distribution coordinates (X, Y and Z) are obtained for each fossil from a datum that remains constant year after year. X and Y are surface coordinates, whereas Z represents the depth at which the remains are recovered. These coordinates are measured from the center of each bone. As previously indicated, anatomically identifiable bones of any size, as well as unidentifiable bones larger than 3 cm, were mapped and recorded in the field notes.

Provided that there are no associated or articulated remains at SOM-N, the index we selected to account for taxonomical and anatomical compositions is the Number of Identifiable Specimens (NISP) (Badgley, 1986). In assemblages where formerly articulated remains have been widely dispersed and have accumulated as isolated remains, as it is the case at SOM-N, NISP is the appropriate method to account for taxonomical abundance (Badgley, 1986). Moreover, the limits of the deposit containing SOM-N fossil remains have not yet been established, making NISP the most suitable index for estimating the abundance of the taxa at this site.

Although Polonio and López-Martínez (2000) used Voorhies Groups to analyze the potential of remains to be transported (Voorhies, 1969), we excluded this analysis from our study due to the low integrity of the remains at SOM-N. Voorhies Groups were established according to intact skeletal morphologies (Voorhies, 1969). Additionally, the hydraulics of debris flows differ substantially from those encountered in the experimental flume studies of Voorhies (Voorhies, 1969; Britt et al., 2009).

Rose diagrams were drawn for bones larger than 10 cm to assess the possible existence of preferential orientations. The significance of the bone orientations was evaluated with Rayleigh's tests.

We performed an assessment of sorting by specimen shape by measuring the three major linear dimensions of remains (D1 > D2 > D3), perpendicular to one another as suggested by Zingg (1935). Ratios D2/D1 and D3/D2 are used to classify particles into four morphological categories: blade, rod, flat block and block. Alcalá (1994) indicated that a higher variety and diversity of shapes would be indicative of a limited influence of transport processes, whereas the opposite would imply pre-burial selection of the remains. Nevertheless, Britt et al. (2009) warned about the poor sorting capacity of debris-flow deposits, so all types of shapes can be expected to be present at this type of sites.

Bone modification data (weathering, abrasion, trampling, carnivoran and rodent activity, root action and fragmentation) were obtained following examination of the taphonomic subsample under a binocular microscope. Weathering provides an indication of bone deterioration due to physical and chemical agents and is indicative of the time elapsed between the death of the animal and final burial (Behrensmeyer, 1978). Behrensmeyer (1978) constructed a weathering scale based on the study of modern bones at Amboseli National Park (Kenya), which is characterized by a tropical, semi-arid climate. Bones have been demonstrated to weather much faster in this type of climatic zones than in temperate or arctic zones (e.g., Andrews and Armour-Chelu, 1998; Miller et al., 2013). As previously indicated, a savanna biome in a tropical semiarid climate has been inferred for the Somosaguas area during the Middle Miocene, very different from the Mediterranean continental climate currently existing in this area. We therefore consider that the weathering scale estimated at Amboseli National Park can be applied in our study. Weathering was measured on a scale from 0 (not weathered) to 5 (extremely weathered), where each category relates to a number of years since death: Stage 0 (0–1 yr), Stage 1 (0–3 yr), Stage 2 (2–6 yr), Stage 3 (4–15 yr), Stage 4 and Stage 5 (6–15 yr) (Behrensmeyer, 1978). Abrasion refers to the erosion caused to the bones by means of friction with sedimentary particles. To analyze abrasion, we used the three stages proposed by Alcalá (1994): intact bone (Stage 1), rounded bone (Stage 2) and polished and smoothed bone (Stage 3). Abrasion stage is a proxy of the intensity and/or time of interaction of sediment particles with bones and does not necessarily indicate distance of transport (Behrensmeyer, 1991; p. 309).

As for the breakage analysis, perpendicular and smooth fractures usually occur in recrystallized or permineralized bone and are produced by diagenetic processes, such as sediment pressure or tectonic movements (Lyman, 1994). In turn, spiral and irregular or sawtoothed fractures occur in relatively fresh, collagen-rich bones and can be generated by different agents, including carnivoran activity and trampling (Lyman, 1994). Apart from fracture angle, we accounted for number of fractures, degree of bone completeness and fracture surface as defined by Pesquero et al. (2013). Weathering, abrasion and breakage analyses were performed on 1) the whole taphonomic subsample analyzed and 2) the subsample excluding unidentifiable bone fragments.
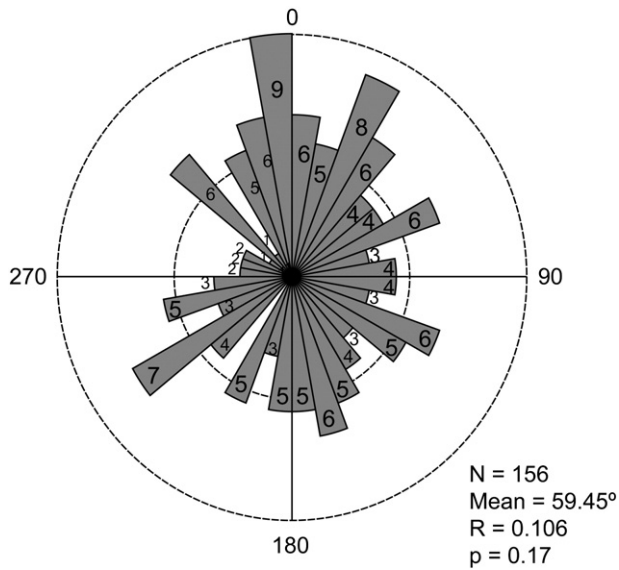
Fig. 7. Long bone (>10 cm) orientation at SOM-N. Rayleigh's test (R) demonstrates that bones are randomly oriented (i.e., *p* = 0.17).

6. Results

6.1. Assemblage data

The number of large-mammal species at SOM-N is 10 (Table 1). The NISP is 6592. Taxonomically unidentifiable elements are represented by 4357 specimens and therefore constitute two thirds of the SOM-N large-mammal assemblage. Of the taxonomically identifiable elements, the proboscidean *Gomphotherium angustidens* is the most abundant taxon (NISP = 786), followed by Ruminantia indet. (NISP = 639) and by the equid *Anchitherium cursor* (NISP = 484). Carnivores are the least abundant large-mammal group, represented by only 66 specimens (1% of the total assemblage; 2.95% of the taxonomically identifiable specimens).

Table 2 shows the skeletal element proportions represented at SOM-N. A total of 49.23% of the remains were anatomically unidentifiable. Unidentifiable teeth (20.02%), most of these heavily fragmented, along with identifiable teeth (9.15%), constitute the most abundant skeletal elements of the assemblage. Moderately abundant elements, making up over a 2% of the assemblage, include vertebrae, ribs, carpal bones, tarsal bones, metapodials, phalanxes and sesamoids (Table 2). No associated or articulated skeletal elements have been found, i.e., the entirety of the skeletal remains were disarticulated and isolated. The SOM-N large-mammal assemblage is dominated (76.9%) by remains displaying a maximum dimension ≤4 cm and fossil bones >8 cm are very scarce (8.1%) (Fig. 4, Supplementary Table 1). The fossil shape categories are represented in Fig. 5 (see also Supplementary Table 2). Splinters are
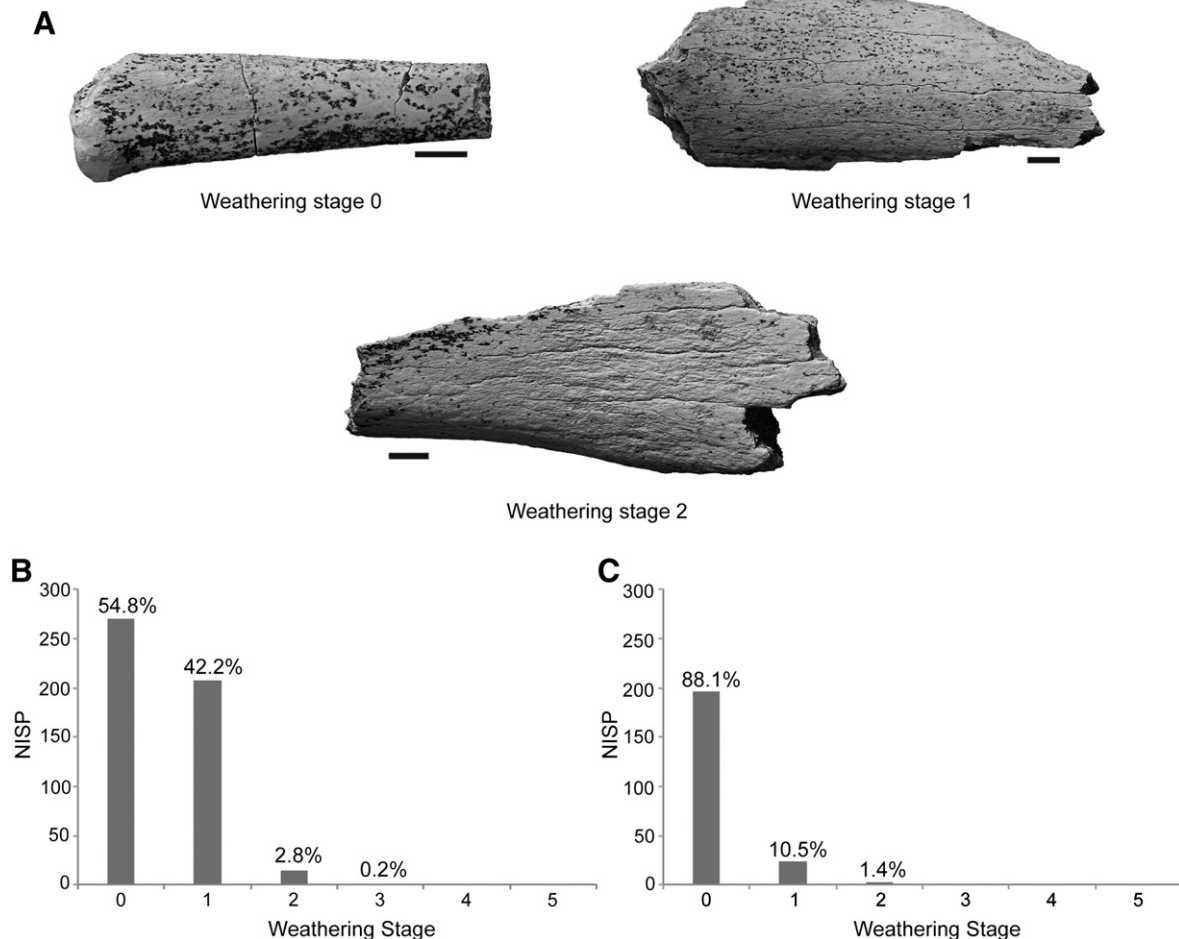
Fig. 8. Bone weathering stages at SOM-N. A. Selected bones displaying weathering stage 0 (indetermined rib fragment SOM-CATA2'10 73), weathering stage 1 that corresponds to bone showing fine cracking (unidentifiable bone fragment SOM-N'06 107) and weathering stage 2 (transitioning to weathering stage 3) that corresponds to bone showing flaking of periosteum (unidentifiable bone fragment SOM-N'05 2423). Scale bars represent 1 cm. B. Weathering stage proportions when all fossils in the taphonomic subsample are considered. C. Weathering stage proportions when only identifiable fossils are considered.

mainly classified in the 'Blade' and 'Rod' categories. Ribs, carpals, tarsals and phalanges were mainly classified as 'Flat block' and 'Rod'. Teeth, depending on their degree of breakage, fell under the 'Flat Block', 'Block' and 'Rod' categories. The very few mandibles that could be studied were classified in the 'Blade' category.

6.2. Spatial data

SOM-N has an excavated area of ~100 m², although the site expands laterally, as demonstrated by the continuity of the deposits and fossils in several prospective trenches excavated in the vicinities of SOM-N. The lateral limits of the fossiliferous deposit have not yet been established. Therefore, the spatial distribution of fossil bones in plan view (X-Y coordinates) is only indicative of the extension of the current excavation area (Fig. 6A). Central grids have been excavated for a greater number of years, and the density of bones is therefore higher in this part of the excavation area compared to the outer rim. In the X-Z cross section, there appear to be two distinct fossil-rich levels towards the North of the site, but these levels are indistinguishable towards the southern area (Fig. 6B). In the Y-Z section, fossil remains are sloped (Fig. 6C), but this morphology only reflects the progression of the excavation. No levels are recognizable in the Y-Z section.

We also analyzed the spatial distribution of anatomically identifiable bones (i.e., we removed all the undetermined bones from the analysis, mainly bone and enamel splinters) to test whether these bones accumulated preferentially in certain parts of the excavation area (Supplementary Fig. 1). We did not observe major differences, and the identifiable bones can therefore be deemed to be uniformly distributed across the whole area and depth.

Mean trend and plunge are 59.45° and 17.64°, respectively. Rayleigh's test indicates that long bones (>10 cm) are randomly oriented (Fig. 7).

6.3. Bone modification data

Bones showing no weathering alteration (Stage 0) predominate at SOM-N, but this stage is more abundant on excluding the unidentifiable bone fragments (Fig. 8, Supplementary Table 3). Weathering Stage 1 is present in 42.2% of the taphonomically analyzed subsample but this percentage decreases to 10.5% when unidentifiable bone fragments are excluded. Bones displaying weathering Stages 2 or higher are very scarce at SOM-N (Fig. 8).

Bones in the three abrasion stages are present at SOM-N (Fig. 9, Supplementary Table 4). When the complete subsample is considered, abrasion stages 2 and 3 are predominant (48.3% and 34.0%, respectively), a fact that indicates that bones show rounding and polishing or smoothening (Fig. 9B). When the unidentifiable bone fragments are excluded from the analysis, abrasion stage 2 is still predominant (52.5%), but in this case, abrasion stage 1 (36.3%), which is indicative of bones showing no signs of rounding or polishing, is more abundant than stage 3 (11.3%) (Fig. 9C).

In general, the SOM-N remains display low integrity; thus, breakage represents the most pervasive taphonomic alteration (Fig. 10, Supplementary Table 5). More than 70% of the bones exhibit three or more fractures, even when unidentifiable bone fragments are excluded from the evaluation (Fig. 10A, E). In terms of the completeness of the original bone morphology, when the whole sample is considered, 74.6% of the remains are represented by less than half of the original bone morphology (Fig. 10B). When the unidentifiable bone fragments are excluded, this percentage decreases to 47.4%, and the complete and almost complete (missing some bone chips) categories reach 37.5% (Fig. 10F).

The most abundant fracture angle category is the combination of perpendicular, spiral and longitudinal fractures (Fig. 10C, G). As for the fracture surface, the combination of smooth and irregular (37.7%) and only irregular (25.8%) categories are predominant when the whole subsample is considered (Fig. 10D). When unidentifiable bone fragments

are excluded, the combination of smooth and irregular fracture surface (45.3%) constitutes the most common category (Fig. 10H).

Six skeletal elements (1.1% of the taphonomically analyzed subsample) exhibit root marks. Most of these were produced by modern roots (Fig. 11). Some remains (<1%) display ~1 mm wide linear marks of varying millimetric to centimetric length (Fig. 12). Some marks are perpendicular to each other (Fig. 12A, B) and others are parallel (Fig. 12C, D). In pre-human fossil sites, these thin linear marks seem to result mainly from sedimentary particle scratching caused by trampling (Behrensmeyer et al., 1986, 1989). No evidence of rodent or carnivore marks or digestion alteration has been observed at SOM-N.

SOM-N remains exhibit a whitish to beige color, only obscured by patches of manganese oxides (Figs. 8, 9, 12, 13). Manganese oxides are common along fractures, but they are also spread throughout the bone surfaces. These oxides are present in both identifiable and unidentifiable bones. SOM-N remains show no evidence of mineral crusting.
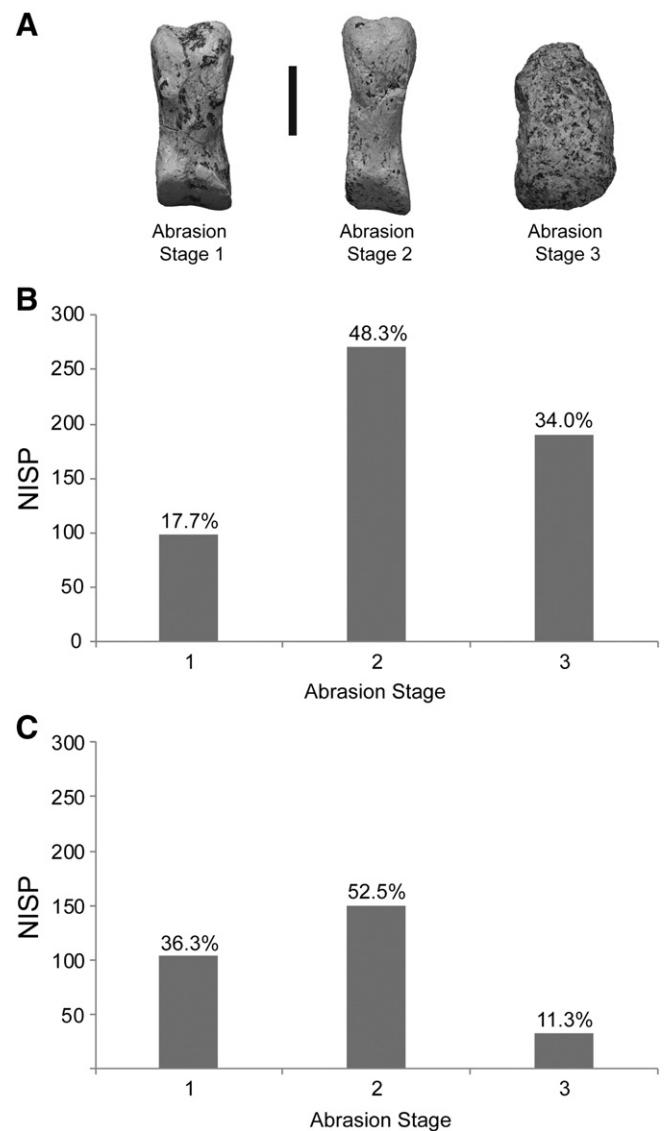
Fig. 9. Bone abrasion stages at SOM-N. A. Selected bones displaying abrasion stage 1 that corresponds to intact bone (*Anchitherium* lateral first phalanx SOM-CATA2'07 1), abrasion stage 2 that corresponds to rounded bone (*Anchitherium* lateral first phalanx SOM-CATA2'10 109) and abrasion stage 3 that corresponds to polished and smoothed bone (unidentifiable bone fragment not numbered). Scale bar represents 1 cm. B. Abrasion stage proportions when all fossils in the taphonomic subsample are considered. C. Abrasion stage proportions when only identifiable fossils are considered.
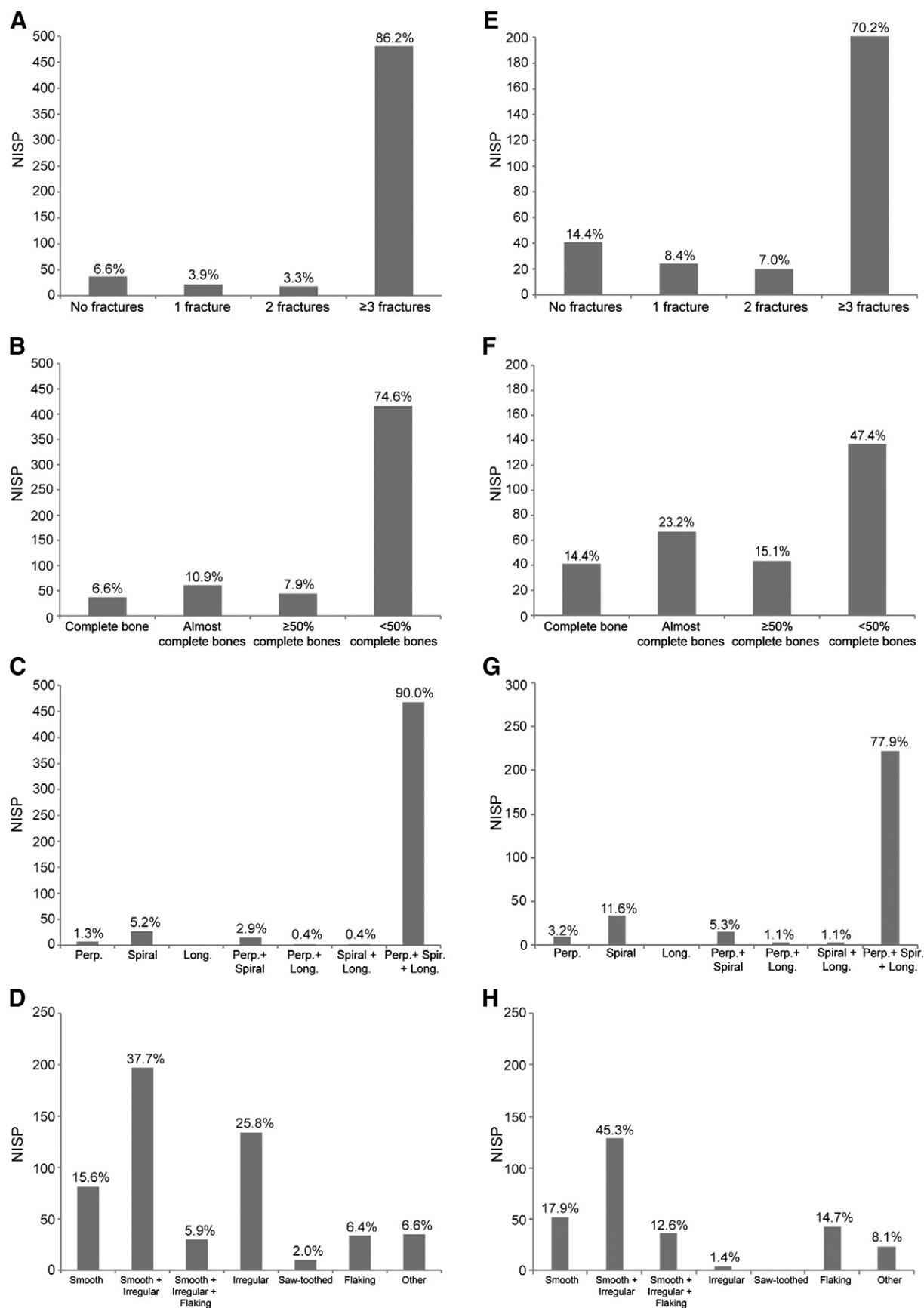
Fig. 10. Bone breakage at SOM-N. In A, B, C and D, all fossils in the taphonomic subsample are analyzed. In E, F, G and H, only identifiable fossils are analyzed. A and E. Number of fractures. B and F. Degree of bone completeness. C and G. Fracture angle. D and H. Fracture surface. 'Other' refers to other fracture combinations too scarce to plot separately.

7. Discussion

7.1. SOM-N taphonomy

Coincident with the results of Polonio and López-Martínez (2000), the best represented taxa at SOM-N correspond to the proboscidean *Gomphotherium angustidens* (11.92% of the assemblage), ruminants, including *Micromeryx* sp., *Heteroprox* sp., *Tethytragus* sp. and Ruminantia indet. (10.89%) and the horse *Anchitherium cursor* (7.34%) (Table 1). Remains that could not be assigned to a specific taxon or to a specific skeletal element are very abundant (66.10% and 49.23%, respectively; Table 1 and Table 2), a fact that is mainly due to intense breakage of the bones. Breakage is the most important taphonomic modification observed in the SOM-N bones (Fig. 10, Supplementary Table 5). Bone splinters of <3 cm are highly abundant at the site (Fig. 3). A high degree of breakage is also evidenced by the fact that the most abundant identifiable bones involve small-sized elements such as teeth, phalanges and carpal and tarsal bones, i.e., long bones generally did not survive and those that survived are mostly incomplete (Table 2). Remains larger than 8 cm, which should be abundant in an assemblage where proboscidean and equids are dominant taxa, make up only 8.1% of the assemblage (Fig. 4, Supplementary Table 1). Although teeth are a very abundant element, in most cases they are broken, as demonstrated by the large amount of teeth that could not be identified (Table 2). We agree with Polonio and López-Martínez (2000) in that most of the breakage of the SOM-N bones and teeth took place prior to burial, as demonstrated by the abundance of splinters, the loss of parts of the broken bones from the site and the low amount of only perpendicular breakages (typical of the diagenetic phase). Behrensmeyer (1982, 1991) demonstrated that hydraulic transport is not an important cause of fracture of fresh bones. We therefore propose that other agents occurring prior to debris-flow transport were responsible for much of the breakage observed in the SOM-N remains. Trampling must be regarded as an important agent of breakage, above all if we take into account that animals such as the proboscidean *Gomphotherium angustidens*, with a body mass of more than two metric tons, were very common dwellers of the Madrid Basin during the Middle Miocene. The previously described thin linear marks present on some of the bones (Fig. 12), might have been caused by trampling, but not all the trampled bones necessarily present this kind of marks (M.

S. Domingo, observation at Amboseli National Park). The extent to which predation and scavenging acted as agents of breakage in the SOM-N remains is unknown. We have detected no marks attributable to these agents, but it is plausible that they were erased by other subsequent taphonomic processes (including trampling). In any event, it has been recognized that hydraulic transport can generate some breakage in weathered or dry bones (Behrensmeyer, 1991). A considerable amount of unidentifiable bones display weathering Stage 1, so dry bones were present in the thanacoenoses prior to debris-flow transport. In the literature we found no empirical data describing the taphonomic modification of bones transported by debris flows, but given that these systems are highly energetic, we cannot rule out that some breakage of collagen-depleted bones resulted during transport.

Although pre-burial fragmentation was more significant than post-burial breakage, some diagenetic breakage also occurred as demonstrated by the presence of bone collapses and in situ fractures in some skeletal elements (Fig. 13A, B, D, F, G). Elements showing this type of breakage are usually large, identifiable bones.

The SOM-N bones were isolated which indicates that, prior to debris-flow transport, the carcasses were subaerially exposed for a sufficiently long time to enable disarticulation by decay, trampling or scavenging (the bones display no marks by scavengers, but it is possible that they disarticulated some carcasses without leaving signs on the bones). Hill and Behrensmeyer (1984) studied the sequence of disarticulation in several African herbivores and determined that complete disarticulation was reached 5 years after the death of the animal. The lack of associated remains may be indicative that, in the original thanatocoenoses, the elements were already disassociated, but it is also feasible that the skeletal elements were scattered by the debris-flow episodes. Weathering stage is used as a tool to infer time elapsed from death until burial. At SOM-N, most of the bones display weathering Stages 0 or 1 (Fig. 8, Supplementary Table 3), which is indicative of a maximum time of exposure of 3 years before burial (Behrensmeyer, 1978). Additionally, a few bones display weathering Stages 2 and 3, which are indicative of times of exposure >2 years and then 4 years before burial, respectively. Furthermore, we cannot rule out the possibility that some of the SOM-N bones were subjected to intense weathering, but that the subsequent taphonomic processes erased the weathering signatures from the bone surface. The concurrence of elements with
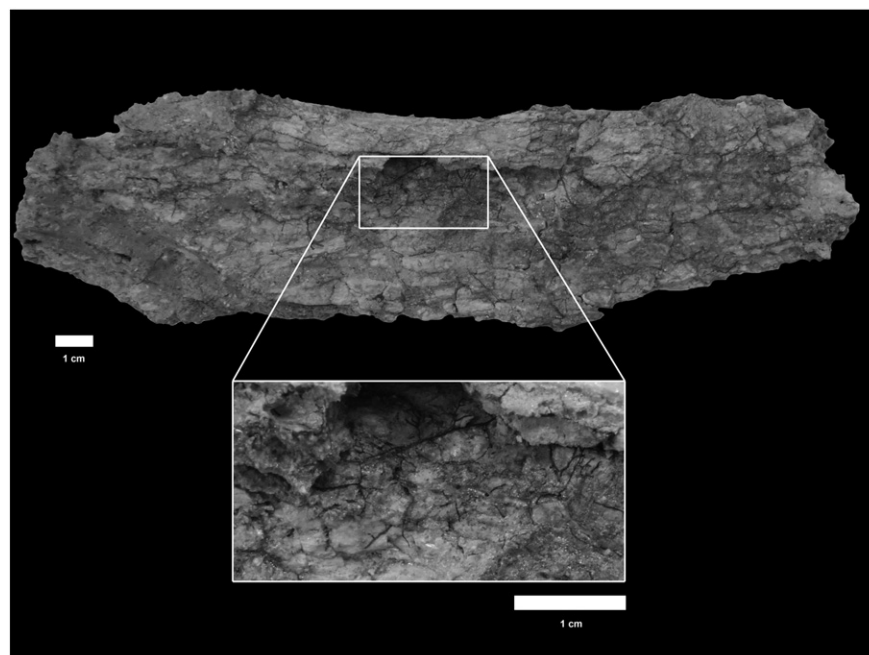

Fig. 11. Unidentifiable fossil SOM-N'04 2042 showing abundant modern root marks.

weathering Stages 0 and 1, together with elements exhibiting weathering Stages 2 and 3, would suggest that debris-flow events did not have an annual character, but were rather more separated in time. This is in agreement with the sedimentological evidence (i.e., embayed quartz grains, low charge beidellites), which points to sedimentation pauses that enabled the weak development of soils in these deposits (Fesharaki et al., 2015). At SOM-N, weathering Stage 1 and above are more abundant in unidentifiable bone fragments than in identifiable bones, which usually display weathering Stage 0 (Fig. 8B, C). This seems reasonable, as more weathered bones are more prone to breakage.

Abraded bone surfaces and abraded bone fractures are abundant in the SOM-N assemblage, although unidentifiable bones display more smoothening and polishing than identifiable bones (Fig. 9B, C, Supplementary Table 4). Abrasion damage has been most commonly attributed to hydraulic transport, but other agents such as wind, weathering, trampling, chewing or chemical and physical erosion during digestion can abrade bone surfaces and fractures (Behrensmeyer, 1991). Abrasion produced by sedimentary particles bombarded by wind tends to be localized in the area being sand-blasted (Lyman, 1994). This is not the case of the SOM-N remains, where abrasion damage is not located in specific areas or on specific surfaces. Bones that have been digested display rounding and polishing produced by digestive acids, but this feature is usually accompanied by other taphonomic modifications, such as the exposure of spongy bone in articular areas and thinning of the bone cortex (see Domingo M.S. et al., 2012 and references therein). We did not detect these features in the SOM-N bones. Rather, we consider that abrasion in the SOM-N remains was caused during trampling or hydraulic transport. As previously indicated, abrasion is a proxy of the intensity and/or time period of interaction with sediment, but not necessarily of distance of transport (Behrensmeyer, 1991). The bones displaying more extreme abrasion stages at SOM-N are unidentifiable, which seems reasonable, as they would have been exposed for a longer time prior to burial and were therefore subjected to intense trampling; moreover, these bones were most likely dry when transported by the debris flow and, were consequently more vulnerable to further abrasion and breakage than fresh bones.

Analysis of the morphology of the bones can provide information on the sorting of the bones during transport. The four morphological categories are present at SOM-N (Fig. 5, Supplementary Table 2), which is indicative of the poor sorting capacity of the debris flows that transported and buried the elements; this was also observed in other debris-flow deposits (e.g., Britt et al., 2009).

As for the spatial distribution of fossils in the deposits, there appear to be two distinct fossil-rich levels towards the North in the X-Z cross section (Fig. 6B). No levels are visible in the Y-Z section (Fig. 6C). Elez (2005) suggested that the SOM-N deposits presented several levels, alternately rich and poor in fossils. It is possible that the amount of fossil remains that we employed in the spatial distribution analysis is so large compared to the one analyzed by Elez (2005) that the levels are not
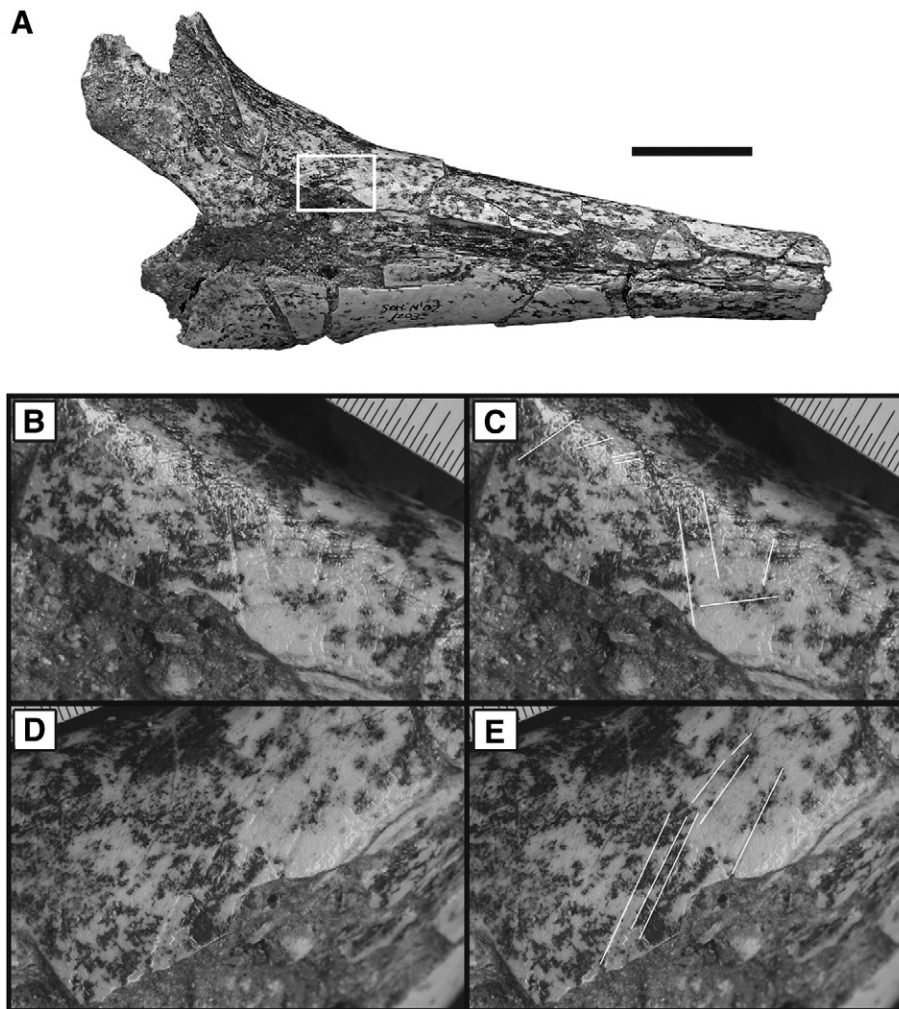

Fig. 12. *Prosantorhinus douvillei* vertebra fragment SOM-N'02 1203 exhibiting fine linear marks. A. General view of the vertebra fragment. The white square marks the area where the linear marks are located. Scale bar represents 2 cm. B-E. Close-up view of the linear marks. Figs. C and E are the same as B and D, respectively, but the linear marks are indicated with white lines to facilitate their observation. Major divisions in the scale shown in B, C, D and E represent 1 mm.

easily recognizable. However, it is worth highlighting that when the sample is reduced by excluding unidentifiable bone fragments, levels are still unrecognizable (Supplementary Fig. 1). Future three-dimensional analyses of the SOM-N coordinates data will shed more light on the geometry of the deposits and will facilitate recognition of different fossiliferous levels, if present.

Contrary to Polonio and López-Martínez (2000), who identified a trend alignment of the bones on the north-south axis, the rose diagram drawn in the present study suggests that SOM-N long bones (>10 cm) are randomly oriented (Fig. 7). The mean plunge of bones calculated in our study, 17.64°, is very close to that of 15° estimated by Polonio and López-Martínez (2000).

Based on the taphonomic evidence, we suggest that the SOM-N assemblage is made up of a mixture of elements with different breakage, abrasion and weathering states, but two endmembers can be suggested: on the one hand, splinters appear to have been the result of elements that were exposed over a longer time period prior to burial and subject to intense breakage and abrasion by trampling and weakened by loss of collagen, a fact that gave rise to further breakage and abrasion during debris-flow transport. On the other hand, we also recovered relatively well preserved skeletal elements (Fig. 13) that would seem to correspond to carcasses that underwent a shorter time of exposure (although sufficiently long to reach complete disarticulation), and lower levels of alteration prior to and during debris-flow transport.
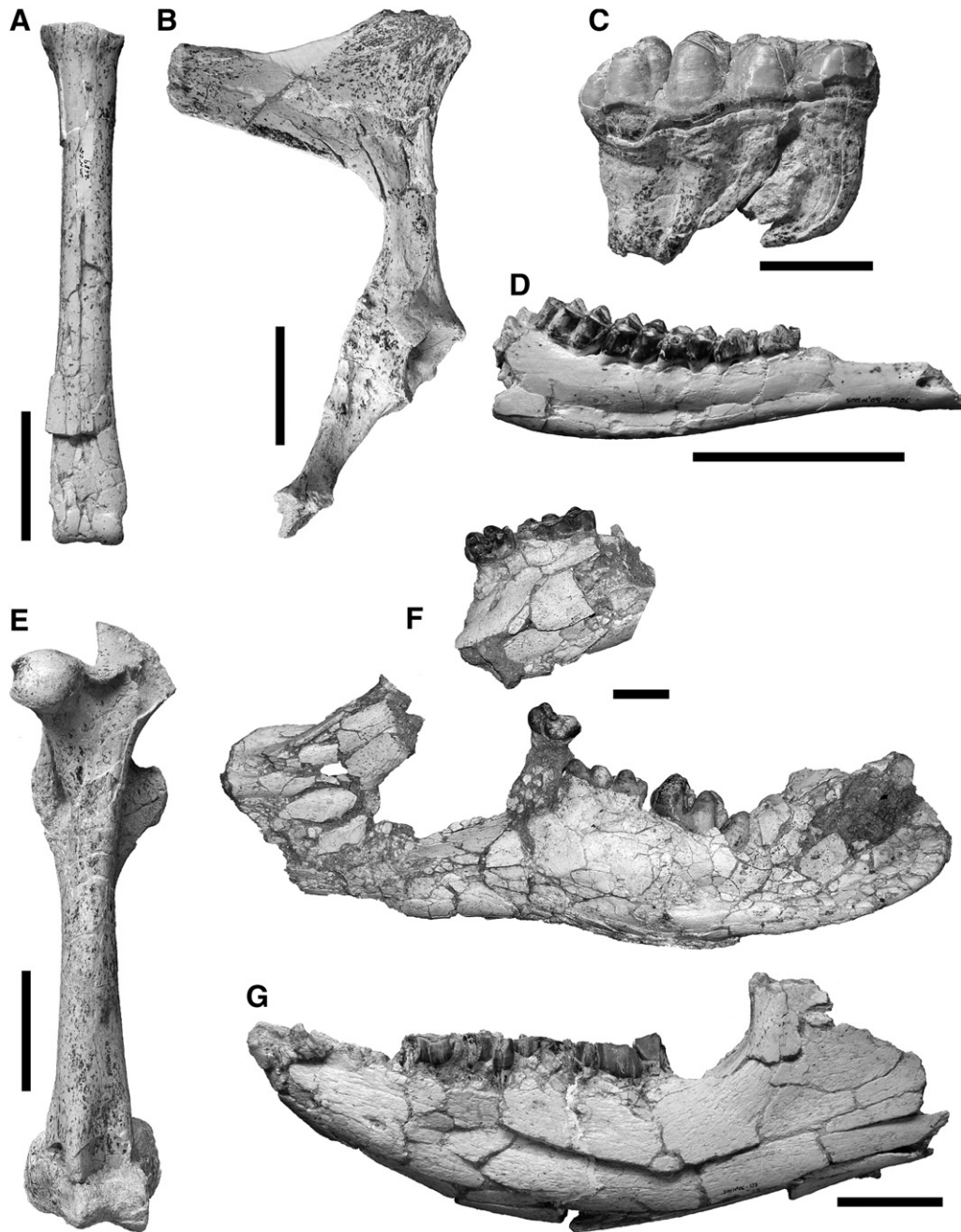
Fig. 13. Well-preserved bones from SOM-N. A. Metapodial of *Anchitherium cursor* (SOM-N'05 2689). B. Hemipelvis of *Anchitherium cursor* (SOM-N'12 438). C. Molar of *Gomphotherium angustidens* (SOM-CATA2'10 98). D. Hemimandible of *Tethytragus* sp. (SOM-N'04 2206). E. Femur of *Anchitherium cursor* (SOM-CATA2'10 30). F. Mandible of *Gomphotherium angustidens* in two fragments (SOM-N'11 395 and SOM-N'11 396). G. Hemimandible of *Prosantorhinus douvillei* (SOM-N'06 339). Note that, although well preserved, these bones have been subjected to collapses and display in situ fractures resulting from diagenetic breakage following burial and mineralization and these breakages are most likely due to sediment pressure. All scale bars represent 5 cm.

Table 3
Taphonomic characteristics of debris-flow hosted assemblages.

	Mammal-dominated				
Locality	Somosaguas-North	Paşalar	Vallparadís Estació (Layer 7)	Collecurti	La Paz
Country	Spain	Turkey	Spain	Italy	Uruguay
Age	Middle Miocene	Middle Miocene	Early Pleistocene	Early Middle Pleistocene	Early Middle Pleistocene
Matrix	Matrix-supported coarse sandstones and fine conglomerate	Poorly sorted sands and gravels	Small-sized pebbles in a matrix-supported mud	Clast-supported to matrix-supported, gravel with sandy, silty clay matrix	Matrix-supported diamictite (matrix is predominantly clayey)
Taxonomic representation[a]	MU_Mu	MU_Mu	MU_Mu	MU_Mo	MU_Mu
Type of death	*Unknown*	Attritional	*Not reported*	Mass mortality event (unrelated to debris flow)	*Not reported*
NISP	6592	*Not reported*	3234	496	130
NISP (unidentifiable)	4357	*Not reported*	726	53	Unidentified fragments are very abundant
MNI	*Not estimated*	*Not reported*	*Not reported*	24	130
Dominant age class	*Not estimated*	Adults are more abundant in medium-sized mammals. Juveniles are equally or more abundant than adults in mega-herbivores.	*Not reported*	Adult	*Not reported*
Bone orientation	No trend alignment	Variable in the different sedimentary facies	No trend alignment	Two trend alignments, horizontal to subhorizontal plunges.	No trend alignment
Representation of bones relative to transport	All types of elements present	*Not reported*	*Not reported*	Hippopotamus sample: larger representation of less easily transportable elements; Non-Hippopotamus sample: larger representation of easily transportable element	All types of elements present
Dominant articulation mode	Isolated	Isolated	Isolated	Associated	Isolated
Dominant weathering stage	0 and 1	All weathering stages represented in unidentifiable bones. WS 0 and 1 are more abundant in identifiable bones.	0 and 1	0 (but more intense in non-Hippopotamus sample)	0 and 1–2
% Abraded remains	82.3	90.0	*Not reported*	0.4% of the Hippopotamus sample; 10% of the non-Hippopotamus sample	5.0
% Broken remains	93.3	Extreme fragmentation	Most of the bones are broken	Mostly post-depositional breakage	70.0
% Carnivore modified	0	0	Abundant marks	0	*Not reported*
% Trampling marks	<1.0	0	*Not reported*	0	*Not reported*
Site category (after Britt et al., 2009)[b]	1	1	*Not reported*	4	1
Reference	This study	Andrews and Ersoy (1990), Andrews (1995)	Madurell-Malapeira et al. (2011)	Mazza and Ventra (2011)	Corona et al. (2012)

[a] MO = Monotaxic (only one taxon at the fossil site), MU_Mo = Multitaxic_Monodominant (multiple taxa but one taxon dominates and account for 50% or more of the NISP or the MNI), MU_Mu = Multitaxic_multidominant (multiple taxa but two or more taxa dominates and account for 50% or more of the NISP or the MNI).
[b] Origination mode of debris-flow hosted assemblages after Britt et al. (2009): 1. Debris-flow transport and burial of pre-existing thanatocoenoses. 2. In situ burial of a pre-existing thanatocoenosis by a debris flow. 3. Death and burial of the biocoenose by a debris flow. 4. Combinations of 1–3.

It is difficult to infer the agent responsible for the death of the individuals in a fossiliferous assemblage such as SOM-N, where breakage, transport and scattering have been intense. The taphonomical evidence at least enables us to ascertain that the debris-flow episodes were not the cause of mortality. Had a debris flow been the main agent of mortality, the assemblage would have shown mass-mortality taphonomic signatures such as the presence of articulated skeletons and non-altered bones, as a consequence of very rapid burial, as well as catastrophic or 'L-shaped' age profiles (Lyman, 1994).

We have not been able to quantify the amount of juvenile vs adult individuals present at SOM-N, as this information is not recorded in the field notes and because we have not conducted a direct observation of the entire fossil collection. Nonetheless, from the start of the excavations, researchers observed the presence of abundant juvenile bones (Polonio and López-Martínez, 2000). Isolated decidual teeth are abundant at SOM-N, but their presence in a fossil site cannot be used as evidence of elevated death rates for juveniles as these teeth are shed during an animal's lifetime and do not imply its death. Nevertheless, we have observed a large amount of skeletal elements with unfused epiphyses and some maxillae and mandibles with decidual teeth,

which together with the presence of juvenile osseous microstructures detected in histological sections (Cuezva and Elez, 2000), point to the death of juvenile individuals.

As previously indicated, a savanna biome has been inferred at SOM-N, which presented a tropical semiarid climatic regime and a very pronounced hydrological seasonality, with an alternation of long dry periods and short wet periods (Cuevas-González, 2005; Hernández Fernández et al., 2006; Carrasco et al., 2008; Domingo et al., 2009; García Yelo et al., 2014). Debris flows result from slope failure and are triggered by diverse causes including rainfall, seismic activity, volcanism, plant denudation or changes in surface and substrate cohesiveness resulting from altered ground water flow patterns (Eberth et al. 2006 and references therein). In the semiarid environment registered at SOM-N, we propose that debris-flow events were generated during times of intense seasonal rainfall. Fluvial facies are almost absent in the Somosaguas fossiliferous levels (Cuevas-González, 2005) and no aquatic fauna, such as fish, amphibians or crocodiles (the turtles from SOM-N are terrestrial), has been recovered (Domingo et al., 2009), which implies a shortage of permanent fresh-water bodies in this area. Polonio and López-Martínez (2000) suggested that droughts

Dinosaur-dominated						
Jirau	Mother's Day Quarry	Jimbo Quarry	Dalton Wells	Puesto Díaz Quarry	Bleriot Ferry	Fox Coulee
Brazil	United States	United States	United States	Argentina	Canada	Canada
Late Pleistocene	Upper Jurassic	Upper Jurassic	Lower Cretaceous	Lower Cretaceous	Upper Cretaceous	Upper Cretaceous
Conglomerate supported by feldspatic clayey-sandy matrix	Massive, sandy siltstone	Muddy-silt matrix- Unit A (debris flow)	Massive-to-vaguely graded, sandy to pebbly mudstone	Massive muddy sandstones	Poorly sorted organic-fragment-rich mudstone	Poorly sorted organic-fragment-rich mudstone
MU_Mo	MU_Mo	MO	MU_Mu	MO	MU_Mo	MU_Mo
Attritional + mass mortality events (unrelated to debris flow)	Mass mortality event (unrelated to debris flow)	Only one individual	Attritional + mass mortality events (unrelated to debris flow)	Mass mortality event (unrelated to debris flow)	Mass mortality event (unrelated to debris flow)	Mass mortality event (unrelated to debris flow)
1405	987 (only identifiable)	Not reported	4211	159	1567	233
1303	Not reported	Not reported	Unidentified bone fragments dominate the assemblage	33	Three fragments for every two identifiable elements	Not reported
48	15 (Diplodocoidea)	1	71	3	9 (Edmontosaurus)	Not reported
Adult	Juvenile	Not reported	Subadults	Adult	Adult	Juvenile
Not reported	Trend alignment; subhorizontal plunge	Trend alignment	No trend alignment; horizontal to subhorizontal plunges	Large bones show trend alignment; small bones show random orientation	Trend alignment; horizontal to subhorizontal plunges	Trend alignment; horizontal to subhorizontal plunges
Larger representation of non-easy to transport elements	Predominance of elements with intermediate transport potential	Not reported	Predominance of elements with complex shapes; reduced occurrence of the most easily to transport elements	Mix of easily transported and non-easily transported elements	Not reported	Not reported
Isolated	Isolated and some associations	Associated	Isolated but some associations	Isolated	Isolated	Isolated
3 (but all stages present)	0	Not reported	0 and 4–5	Not reported	Minimal weathering	Minimal weathering
96.0	10.0	Not reported	Common feature	Low to moderate abrasion	Moderate abrasion	Minimal abrasion
82.0	45.0	Not reported	97.0	Not reported	>90.0	>90.0
1.9	Very low	0	1	Not reported	>10.0	Not reported
15.9	Not reported	Not reported	>6.0	Not reported	>15.0	Not reported
1	2	1	1	1	2	2
Araújo-Júnior et al. (2013)	Myers and Storrs (2007); Storrs et al. (2013)	Lovelace (2006)	Eberth et al. (2006); Britt et al. (2009)	Garrido and Salgado (2015)	Evans et al. (2015)	Evans et al. (2015)

could have constituted a major mortality agent. In view of the climatic regime inferred at SOM-N and the scarcity of stable and long term aquatic conditions in the area, we agree that drought could have played a significant role in the death of individuals —especially juveniles— in the Madrid Basin. In a drought scenario, there would have been intense trampling of the bones of carcasses concentrated around waterholes during the dry season.

To sum up, the present taphonomic study involves the following steps in the formation of the SOM-N assemblage: 1) death of mammals due to different causes (droughts probably played a major role); 2) carcasses were exposed a sufficiently long time to allow decay, defleshing and complete disarticulation; 3) bones underwent different degrees of breakage and abrasion (prior to debris-flow transport) and weathering, depending on the duration of exposure of the carcasses that incorporated in the thanatocoenoses; 4) heavy rainfalls occurred, likely displaying multiannual periodicity, triggering a debris flow that incorporated and buried bones in different preservation states. Debris-flow transport could produce further breakage and abrasion of weathered and dry bones; 5) compaction of skeletal elements and percolation of Mn laden fluids; 6) in modern times, plant roots altered the surface of some bones. As previously mentioned, SOM-N is the result of several debris-flow episodes, and steps 1 to 4 therefore occurred on repeated occasions.

The fauna represented at SOM-N consists of taxa that are well represented in other Aragonian fossil sites from the Madrid Basin (Peláez-Campomanes et al., 2003; Domingo L. et al., 2012a) and they can therefore be considered as common dwellers of the area. We consider the faunal accumulation at SOM-N as parautochthonous (sensu Behrensmeyer and Hook, 1992), as bones were transported, but remain within the habitat area.

7.2. Comparison with other debris-flow hosted vertebrate fossil sites

We surveyed the literature to compile taphonomic data from other debris-flow vertebrate localities; this information is shown in Table 3. We reported only the studies providing detailed taphonomic information.

There is a remarkable scarcity of mammalian-dominated fossil sites hosted in debris-flow deposits (Table 3). Apart from SOM-N, in the literature we only found five localities for the whole Cenozoic, Paşalar (Andrews and Ersoy, 1990; Andrews, 1995) and SOM-N constituting the only pre-Pleistocene sites (both localities are dated from the Middle Miocene). Debris-flow sites dominated by dinosaur remains are more abundant than mammalian-dominated sites (Table 3). It is worth highlighting that, in her analysis of the frequencies of bonebeds as a function of the depositional environment, Eberth et al. (2007b) showed

Table 3 (continued)

	Dinosaur-dominated			Vertebrate-dominated		
Locality	Prehistoric Park	Sun River Bonebed	Kundur	Blagoveschensk	Huizachal Canyon	Ukhaa Tolgod
Country	Canada	United States	Russia	Russia	Mexico	Mongolia
Age	Upper Cretaceous	Upper Cretaceous	Upper Cretaceous	Upper Cretaceous	Middle Jurassic	Upper Cretaceous
Matrix	Poorly sorted organic-fragment-rich mudstone	Calcareous clasts in a matrix of silty mud and sand grains	Muddy matrix with scattered coarse sand particles and pebbles.	Massive claystone with dispersed granules	Mud-rich matrix supported unsorted volcaniclastic intraclasts	Structureless sandstones
Taxonomic representation[a]	MU_Mo	MU-Mo	MU_Mo	MU_Mo	MU_Mu	MU_Mu
Type of death	Mass mortality event (unrelated to debris flow)	Mass mortality event (unrelated to debris flow)	*Not reported*	Attritional	*Not reported*	Mass mortality event (caused by the debris flow)
NISP	1893	592	*Not reported*	*Not reported*	8095	*Not reported*
NISP (unidentifiable)	Four fragments for every identifiable remains	55	*Not reported*	*Not reported*	52.1% (based on a sample of 2035 specimens)	*Not reported*
MNI	2 (Edmontosaurus)	8	*Not reported*	*Not reported*	*Not reported*	505
Dominant age class	Adult	Juvenile	Juvenile and adult	Juvenile and subadult	*Not reported*	*Not reported*
Bone orientation	No trend alignment; horizontal to subhorizontal plunges	Trend alignment; random plunges	Trend alignment; subhorizontal plunge	No trend alignment; subhorizontal plunge	Trend alignment	*Not reported*
Representation of bones relative to transport	*Not reported*	Larger representation of non-easily transported elements	*Not reported*	Predominance of non-easily transported elements	*Not reported*	*Not reported*
Dominant articulation mode	Isolated	Isolated	Articulated	Isolated	Isolated	Articulated
Dominant weathering stage	Minimal weathering	0	*Not reported*	0	*Not reported*	Minimal weathering
% Abraded remains	Minimal abrasion	31.4	*Not reported*	*Not reported*	Common feature	Minimal abrasion
% Broken remains	>90.0	28.0	*Not reported*	Abundant broken remains	Most of the specimens are broken	*Not reported*
% Carnivore modified	<1.0	Low	*Not reported*	<2.0	*Not reported*	*Not reported*
% Trampling marks	*Not reported*	Moderate	*Not reported*	0	*Not reported*	*Not reported*
Site category (after Britt et al., 2009)[b]	2	1	2	1	4	3
Reference	Evans et al. (2015)	Scherzer and Varricchio (2010)	Van Itterbeeck et al. (2005)	Lauters et al. (2008)	Fastovsky et al. (1995)	Dashzeveg et al. (1995), Loope et al. (1998, 1999)

that bonebeds found within the category 'Alluvial-fan/debris-flow/mass-sediment deposits' were very scarce in the fossil record and only eolian deposits hosted a smaller amount of fossil vertebrate assemblages.

Britt et al. (2009) categorized debris-flow sites as a function of their mode of origination as assemblages formed by: 1) debris-flow reworking and burial of pre-existing thanatocoenoses; 2) in situ burial of a pre-existing thanatocoenosis by a debris flow; 3) death and burial of the biocoenoses by debris flow; 4) combinations of 1–3. Most of the debris-flow hosted fossil sites included in Table 3 belong to categories 1 and 2. The SOM-N taphonomic evidence demonstrates that the assemblage belongs to category 1.

In view of the varied taphonomic histories that remains present prior to debris-flow transport (Britt et al. 2009), it is unsurprising that these types of sites only have a few features in common. The shared features of debris-flow hosted localities suggested by Britt et al. (2009) mainly refer to the geological and spatial taphonomical data. SOM-N displays some of these features: the deposits are massive and poorly-sorted coarse-grained sediments, fossil specimens are mostly flat-lying, with a smaller amount subvertically oriented, and elongate elements do not show preferential orientations.

SOM-N shares further taphonomic features with other category 1 sites reported in Table 3, specifically, with Paşalar (Turkey), La Paz (Uruguay), Jirau (Brazil), Dalton Wells (USA) and Blagoveschensk (Russia), such as the abundance of isolated elements and of heavily broken remains (Andrews and Ersoy, 1990; Andrews, 1995; Lauters et al., 2008; Britt et al., 2009; Corona et al., 2012; Araújo-Júnior et al., 2013). Among these sites, abrasion can be considered as an important feature at SOM-N, Paşalar, Jirau and Dalton Wells. Other category 1 sites, however, display important dissimilarities. For example, at the Upper Cretaceous lambeosaurine-dominated locality of Sun River Bonebed (Montana, United States), only 28% of the assemblage shows some degree of breakage (Table 3) (Scherzer and Varricchio, 2010). These authors indicated that the elevated clay content of the debris flow that formed the Sun River Bonebed assemblage likely cushioned large bones, thus preventing extreme breakage (Scherzer and Varricchio, 2010).

Whereas category 1 assemblages show variable taxonomic representations (monotaxic, multitaxic-monodominant and multitaxic-multidominant), category 2 assemblages are always multitaxic-monodominant (Table 3), which indicates that although more than one genus or species are present, one taxon dominates and accounts for 50% or more of the NISP or MNI (Eberth et al., 2007a). Category 2 sites were formed when the debris flow buried in situ the pre-existing thanatocoenoses. Therefore, in principle, debris-flow transport was not long. At monotaxic and multitaxic-monodominant debris-

sites, remains belonging to the dominant taxon usually display homogeneous taphonomic features, because they have undergone the same taphonomic history. The monotaxic and multitaxic-monodominant assemblages at debris-flow sites in categories 1, 2 and 4 reported at our Table 3 are generally the result of mass mortality events that occurred prior to entrainment by the debris flow (i.e., the debris flow is not the agent producing the mass mortality event).

We found only one example representative of category 3 (death caused by the debris flow) in the literature (Table 3). This corresponds to the exceptional Late Cretaceous fossil site of Ukhaa Tolgod (Mongolia). This vertebrate assemblage was entombed by the deposits of dune-sourced sandy mass flows that took place during rainstorms (Dashzeveg et al., 1995; Loope et al., 1998, 1999; Dingus et al., 2008). Although this site lacks a detailed taphonomic description, the taphonomic features reported for this assemblage generally fit well with what we expect to find in a site where death and burial of the biocoenosis were caused by the debris flow: abundance of articulated skeletons and minimal abrasion and weathering (Dashzeveg et al., 1995). Category 3 assemblages display the most homogeneous taphonomic features when compared to debris-flow sites in categories 1, 2 and 4.

Category 4 debris-flow assemblages are represented by the Jurassic site of Huizachal Canyon (Mexico) and the Pleistocene locality of Collecurti (Italy) (Table 3). In both cases, the localities comprise a mixture of assemblages that separately could be assigned to category 1 and category 2 debris-flow sites. At Huizachal Canyon, the presence of delicate specimens such as an articulated pterosaur would be indicative of in situ burials of thanacoenoses (Fastovsky et al., 1995). At the same time, the existence of highly fragmented and disarticulated specimens implies the reworking and burial of pre-existing thanatocoenoses by the debris-flow transport.

The Collecurti assemblage is made up of a combination of disarticulated, polished and weathered remains that belonged to diverse mammals, together with the skeletal elements of *Hippopotamus antiquus* which were found in close association and were practically unaffected by weathering or abrasion (Mazza and Ventra, 2011). The first assemblage (the disarticulated, weathered and polished assemblage) was exposed to different biostratinomic agents for some time at an upslope location and probably fluvially reworked. Subsequently, it was entrained by the debris flow and transported downslope, where it was mixed with the hippopotamus carcasses that were, in turn, buried in situ (Mazza and Ventra, 2011).

We agree with previous authors in that fossil remains found at debris-flow hosted assemblages display highly heterogeneous taphonomic features, sharing only a few consistent patterns (Britt et al., 2009; Scherzer and Varricchio, 2010). This heterogeneity is the consequence of several factors which include: 1) the death mode of the fauna, 2) the time of exposure and biostratinomic processes the remains were subjected to, 3) the time and distance of transport by the debris flow and 4) the lithological features of the debris flow.

Taphonomic studies provide insights into the mode of formation of assemblages, but also into the preservational biases and the paleoecological significance of the faunal association represented. Some depositional contexts show recurring taphonomic patterns but, as observed in this and previous studies, this is not true in the case of debris-flow assemblages. Detailed taphonomic analyses should be a priority at every fossil site regardless of its depositional context, but they become especially relevant at sites comprising a mixture of elements with differing taphonomic signatures and histories, such as debris-flow hosted assemblages.

8. Conclusion

In the present study, we conducted a detailed taphonomic analysis of the SOM-N Middle Miocene large-mammal assemblage to provide insights into the mode of formation and features of fossil sites formed in a debris-flow depositional context. Very few debris-flow sites are known

in the Cenozoic. SOM-N joins Paşalar (Turkey) as the only two examples of Miocene age.

A total of 6592 large-mammal remains have been recovered at SOM-N. The fossils are embedded in matrix-supported and poorly-sorted coarse sandstones and fine conglomerates deposited by different debris-flow events. Intense breakage results in very high percentages of elements that cannot be assigned to a specific taxon or to a specific skeletal element (66.10% and 49.23%, respectively). Bones are found isolated which indicates that, prior to debris-flow transport, the carcasses were subaerially exposed for a sufficiently long time to enable disarticulation by decay, trampling or scavenging. Most of the bones display weathering stages 0 or 1, which is indicative of a maximum exposure time of 3 years before burial, although the presence of bones showing weathering stages 2 and 3 indicates that some bones were exposed for longer time periods. Abraded bone surfaces and abraded bone fractures are abundant. Apart from splinters and bone clasts, which display extreme levels of breakage, there are also some relatively well preserved skeletal elements, which appear to evidence a shorter time of exposure and less alteration prior to and during debris-flow transport.

SOM-N belongs to category 1 debris-flow hosted assemblages in the classification proposed by Britt et al. (2009). Accordingly, the SOM-N assemblage is the result of debris-flow transport and burial of pre-existing thanacoenoses, where biostratinomic agents acted with different intensities. When compared with other debris-flow sites, SOM-N shares some sedimentological and taphonomic features mainly with other category 1 sites such as: the massive and poorly-sorted coarse-grained nature of the sediments, predominance of flat-lying fossil specimens, absence of preferential orientations in elongate elements, and abundance of isolated and heavily broken remains.

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