

Déjà vu: A reappraisal of the taphonomy of quarry VM4 of the Early Pleistocene site 1 of Venta Micena (Baza Basin, SE Spain"

Paul Palmqvist (✉ ppb@uma.es)

University of Malaga

M. Patrocinio Espigares

University of Malaga

Juan A. Pérez-Claros

University of Malaga

Borja Figueirido

University of Malaga

Antonio Guerra-Merchán

University of Malaga

Sergio Ros-Montoya

University of Malaga

Guillermo Rodríguez-Gómez

Universidad Complutense de Madrid

José Manuel García-Aguilar

University of Malaga

Alejandro Granados

University of Malaga

Bienvenido Martínez-Navarro

IPHES-CERCA, Institut Català de Paleoecologia Humana i Evolució Social

Research Article

Keywords: VM4, Baza palaeolake, skeletal remains

Posted Date: November 3rd, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-1016187/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

1 **Déjà vu: A reappraisal of the taphonomy of quarry VM4 of the Early Pleistocene site**
2 **of Venta Micena (Baza Basin, SE Spain)**

3
4 Paul Palmqvist^{a*}, M. Patrocinio Espigares^a, Juan A. Pérez-Claros^a, Borja Figueirido^a,
5 Antonio Guerra-Merchán^a, Sergio Ros-Montoya^a, Guillermo Rodríguez-Gómez^{b,c}, José
6 Manuel García-Aguilar^a, Alejandro Granados^a, Bienvenido Martínez-Navarro^{d,e,f}

7
8 ^a Departamento de Ecología y Geología, Universidad de Málaga, Campus de Teatinos, 29071-Málaga,
9 Spain. ppb@uma.es, mpespigares@uma.es, johnny@uma.es, frafigcas@uma.es, antguerra@uma.es,
10 sergiorosm@uma.es, chemacyanos@msn.com, a.granados@uma.es

11 ^b Departamento de Geodinámica, Estratigrafía y Paleontología, Universidad Complutense de Madrid. C/
12 José Antonio Novais 12, 28040-Madrid, Spain. guillerwilson@gmail.com

13 ^c Centro UCM-ISCIll de Evolución y Comportamiento Humanos, Avd/ Monforte de Lemos, 5, Pabellón 14,
14 28029-Madrid, Spain.

15 ^d IPHES-CERCA, Institut Català de Paleoecologia Humana i Evolució Social, C/ Marcel·lí Domingo s/n,
16 Campus Sescelades, Edifici W3, 43007 Tarragona, Spain. bienvenido.martinez@icrea.cat

17 ^e Area de Prehistoria, Universitat Rovira i Virgili (URV), Avda. Catalunya 35, 43002 Tarragona, Spain.

18 ^f ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain.

19 * Corresponding author

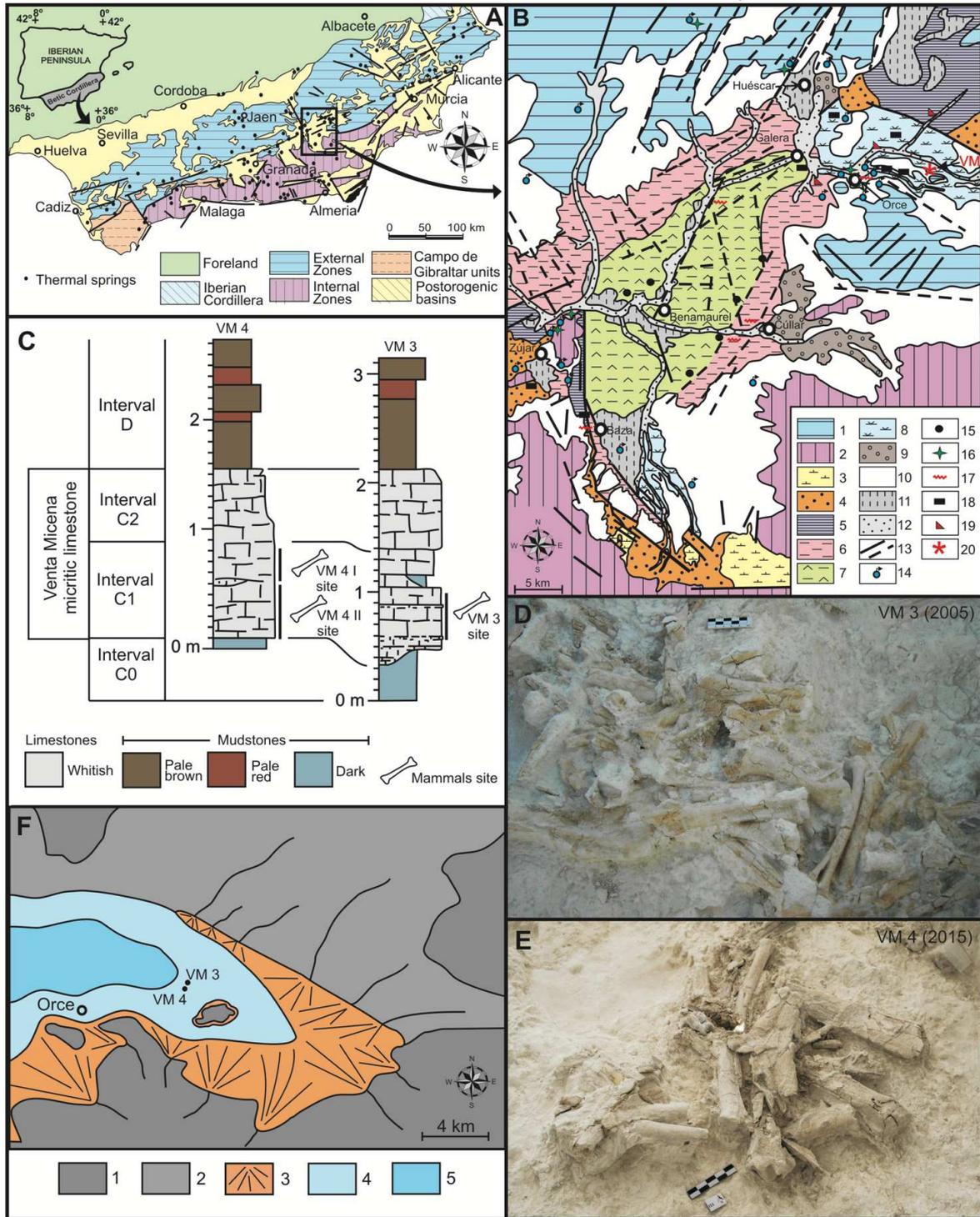
20
21 **Abstract**

22 Venta Micena, an Early Pleistocene site of the Baza Basin (SE Spain), preserves a rich and
23 diverse assemblage of large mammals. VM3, the main excavation quarry of the site, has
24 been interpreted as a den of the giant hyaena *Pachycrocuta brevirostris* in the plain that
25 surrounded the Baza palaeolake. Taphonomic analysis of VM3 has shown that the hyaenas
26 scavenged the prey previously hunted by the hypercarnivores, transported their remains to
27 the communal den, and consumed the skeletal parts according to their marrow contents and
28 mineral density. In a recent paper¹, a small sample of remains unearthed from VM4, an
29 excavation quarry ~350 m distant from VM3, are analysed. The authors indicate several
30 differences in the taphonomic features of this assemblage with VM3, and even suggest that
31 a different carnivore could have been the agent involved in the bone accumulation process.
32 Here we make a comparative analysis of both quarries and analyse more skeletal remains
33 from VM4. Our results indicate that the assemblages are broadly similar in composition,
34 except for slight differences in the frequency of megaherbivores, carnivores and equids
35 according to NISP values (but not to MNI counts), the degree of bone weathering, and the
36 intensity of bone processing by the hyaenas. Given that VM4 and VM3 were not coeval
37 denning areas of *P. brevirostris*, these differences suggest that during the years when the
38 skeletal remains were accumulated by the hyaenas at VM3, the rise of the water table of the
39 Baza palaeolake that capped with limestone the bones was delayed compared to VM4,
40 which resulted in their more in-depth consumption by the hyaenas.

41
42 **Introduction**

43 VM4¹ is an excavation quarry of the Early Pleistocene (Calabrian, Late Villafranchian) site
44 of Venta Micena (VM), which lies in the NE sector of the Baza Basin (Guadix-Baza
45 Depression, Province of Grenade, SE Spain; Fig. 1). This inland basin preserves a thick
46 (>400 m) and relatively continuous record of continental sediments of Plio-Pleistocene age
47 composed of lacustrine and fluvial deposits, as well as dark clays and silicites associated

48 to hot springs. Hydrothermal activity (Figs. 1A-B) provided a mild and productive
 49 environment for the terrestrial fauna, which remains were preserved in many fossil localities
 50 across the basin²⁻⁴. VM preserves a worldwide unique fossil record (Figs. 1D-F): for
 51 example, >24,000 skeletal remains of large mammals have been unearthed from a surface
 52 of ~400 m² during the last decades in several excavation quarries, including VM2, VM3, and
 53 VM4, which represents a mean density of fossils of >60/m² 5-11. Although this density is not
 54 homogeneously recorded across the 80-120 cm thick VM stratum, which outcrops along
 55 ~2.5 km¹², it suggests that tens of millions of fossils were preserved in the micritic limestones
 56 of the lithological unit⁷.



57
 58 **Figure 1.** A: Geological context of the Guadix-Baza Depression in the Betic Cordillera, SE Spain. The box
 59 encloses the Baza subbasin. The points indicate the thermal springs (N = 122) that are nowadays active in the
 60 Betic Cordillera, with a range of water output temperatures of 18–60 °C. B: Tectono-sedimentary map of the

61 Baza subbasin with indication of those points that preserve geochemical, mineralogical, or lithological evidence
62 of thermal activity during the Neogene-Quaternary. 1, External Zones; 2, Internal Zones; 3, Tortonian marine
63 deposits; 4, Plio-Pleistocene alluvial and fluvial deposits; 5, Late Turolian–Ruscinian lacustrine deposits; 6,
64 Middle Villafranchian fluvio-lacustrine deposits; 7, Middle Villafranchian lacustrine marls and evaporites; 8,
65 Late Villafranchian lacustrine deposits; 9, Middle Pleistocene alluvial and lacustrine deposits; 10, Late
66 Pleistocene glacial surface; 11, Holocene fluvial terrace; 12, Modern fluvial sediments; 13, Faults (solid lines;
67 striped lines indicate those faults covered by sediments that have been inferred from aerial photographs); 14,
68 Thermal springs nowadays active; 15, Sulphur deposits; 16, Travertine buildings; 17, Palaeoseismites; 18,
69 Black levels; 19, Silicites; 20, Location of the Venta Micena site. C: Stratigraphic series of VM4 and VM3
70 quarries. D: View of one grid of quarry VM3 during the summer excavation of 2005, which was codirected by
71 B. Martínez-Navarro and P. Palmqvist. E: View of one grid of quarry VM4 during the summer excavation of
72 2015. F: Palaeogeographical context of the Orce-Venta Micena sector of the Baza Basin during the Late
73 Villafranchian [1, External Zones; 2, Pliocene sediments (emerged relief); 3, Alluvial and fluvial sediments; 4,
74 Extension of the lake during a highstand stage; 5. Extension of the lake in a lowstand stage]. The location of
75 excavation quarries VM4 and VM3 of Venta Micena is shown.

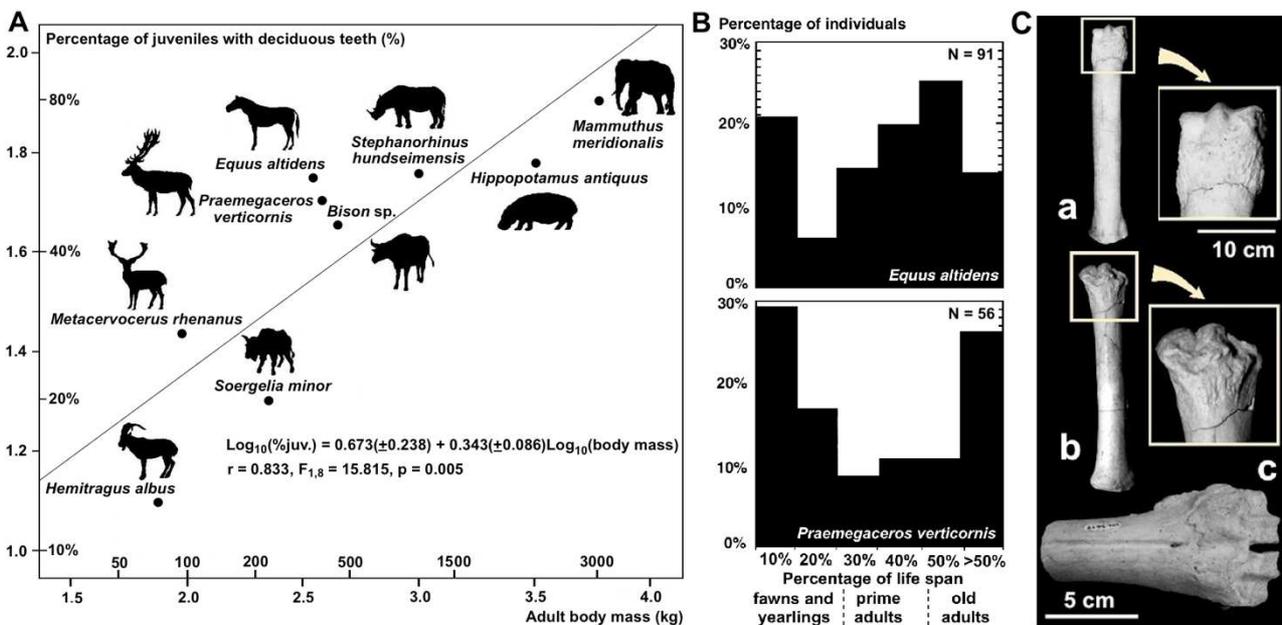
76 During the last decades, taphonomic studies of VM3, the main quarry excavated at
77 the site^{4–10,13}, have shown that: (i) the excavated surface (~220 m²) has provided 6,331
78 identifiable skeletal remains from 339 individuals distributed among 24 mammalian taxa,
79 1,819 anatomically identifiable bones that could not be determined taxonomically (e.g.,
80 diaphyseal fragments and small cranial fragments) and several thousands of bone shafts
81 (Table 1); (ii) the fossils range in size from isolated teeth and phalanges of small carnivores
82 to mandibles of elephants; (iii) girdle/limb bones and, to a lesser extent, cranial elements
83 predominate over ribs and vertebrae; (iv) herbivore taxa dominate the assemblage, both in
84 number of identifiable specimens (NISP) and minimal number of individuals (MNI); (v) the
85 age estimated for the individuals includes calves and juveniles with deciduous teeth as well
86 as prime and past prime adults with fully erupted permanent dentition; (vi) more common
87 herbivores, such as horse *Equus altidens* and megacerine deer *Praemegaceros* cf.
88 *verticornis*, show high frequencies of non-adults, >45% in both cases; and (vii) among
89 carnivores, only adult individuals have been recovered, with the exception of the giant (~110
90 kg)¹⁰, short-faced hyaena *Pachycrocuta brevirostris*, which is represented by 50% of non-
91 adults, and a few juveniles of the wild dog *Lycaon lycaonoides*, the wolf *Canis orcensis* and
92 the bear *Ursus etruscus* (Table 1).

93 Taphonomic analyses have shown that *P. brevirostris* was the bone accumulating
94 agent at VM3 and that most losses of palaeobiological information were a consequence of
95 the selective destruction of skeletal remains by the hyaenas during the period when the
96 bones were exposed before burial^{7–10}. Analysis of mortality patterns for ungulate species
97 deduced from juvenile/adult proportions and tooth-wearing classes⁶ indicates that the
98 hyaenas scavenged the skeletal remains from carcasses of animals previously hunted upon
99 by hypercarnivores such as sabre-tooths *Homotherium latidens* and *Megantereon whitei*,
100 jaguar *Panthera* cf. *gombaszoegensis*, and wild dog *Lycaon lycaonoides*. This inference is
101 based on: (i) the positive relationship in herbivorous taxa between the percentage of
102 juveniles and the body mass estimated for the adults, which indicates the selection of young,
103 more vulnerable individuals in the largest prey species (Fig. 2A); (ii) the finding of U-shaped,
104 attritional mortality profiles in the ungulates better represented in the assemblage, horse and
105 megacerine deer (Fig. 2B); and (iii) the presence of abundant autopodial bones with
106 osteopathologies that limited the ability of the animals to escape from predators (Fig. 2C)^{6,7,9}.

107

Species	Venta Micena-4				Venta Micena-3			
	NISP	MNI (cj/as)	% non-adults	CI (p = 0.05)	NISP	MNI (cj/as)	% non-adults	CI (p = 0.05)
<i>Mammuthus meridionalis</i>	4	2 (1/1)	50.0	1.3 – 98.7	58	5 (4/1)	80.0	28.4 – 99.5
<i>Stephanorhinus</i> aff. <i>hundsheimensis</i>	14	5 (4/1)	80.0	28.4 – 99.5	103	7 (4/3)	57.1	18.4 – 90.1
<i>Equus altidens</i>	124	12 (7/5)	58.3	27.7 – 84.8	2,937	91 (51/40)	56.0	45.3 – 66.4
<i>Hippopotamus antiquus</i>	17	1 (0/1)	0.0	0.0 – 97.5	63	5 (3/2)	60.0	23.1 – 88.2
<i>Bison</i> sp.	43	3 (1/2)	33.3	0.8 – 90.6	831	51 (23/28)	45.1	31.1 – 59.7
<i>Hemibos</i> aff. <i>gracilis</i>	4	1 (0/1)	0.0	0.0 – 97.5	1	1 (0/1)	0.0	0.0 – 97.5
<i>Soergelia minor</i>	13	1 (0/1)	0.0	0.0 – 97.5	302	20 (4/16)	20.0	5.7 – 43.7
<i>Hemitragus albus</i>	19	3 (1/2)	33.3	0.8 – 90.6	285	16 (2/14)	12.5	1.6 – 38.6
<i>Praeovibos</i> sp.	–	–	–	–	1	1 (0/1)	0.0	0.0 – 97.5
Bovidae indet., small size (cf. <i>Rupicapra</i>)	–	–	–	–	1	1 (0/1)	0.0	0.0 – 97.5
<i>Praemegaceros</i> cf. <i>verticornis</i>	61	7 (3/4)	42.9	9.9 – 81.6	881	56 (26/30)	46.3	33.0 – 60.3
<i>Metacervocerus rhenanus</i>	35	6 (2/4)	33.3	4.3 – 77.7	460	33 (9/24)	27.3	13.3 – 45.5
Cervidae indet., small size (cf. <i>Capreolus</i>)	–	–	–	–	1	1 (0/1)	0.0	0.0 – 97.5
Herbivore indet.	1,158	–	–	–	646	–	–	–
Total herbivores	1,492	41 (19/22)	47.4	31.0 – 64.2	6,570	287 (125/162)	43.6	37.7 – 49.5
<i>Homotherium latidens</i>	1	1 (0/1)	0.0	0.0 – 97.5	15	2 (0/2)	0.0	0.0 – 84.2
<i>Megantereon whitei</i>	1	1 (0/1)	0.0	0.0 – 97.5	52	3 (0/3)	0.0	0.0 – 70.8
<i>Panthera</i> cf. <i>gombaszoegensis</i>	1	1 (0/1)	0.0	0.0 – 97.5	1	1 (0/1)	0.0	0.0 – 97.5
<i>Lynx</i> cf. <i>pardinus</i>	3	1 (0/1)	0.0	0.0 – 97.5	12	2 (0/2)	0.0	0.0 – 84.2
<i>Pachycrocuta brevirostris</i>	15	2 (0/2)	0.0	0.0 – 84.2	122	18 (9/9)	50.0	26.0 – 74.0
Viverridae indet.	–	–	–	–	1	1 (0/1)	0.0	0.0 – 97.5
<i>Lycaon lycaonoides</i>	8	2 (0/2)	0.0	0.0 – 84.2	63	9 (1/8)	11.1	0.3 – 48.3
<i>Canis orcutensis</i>	15	1 (0/1)	0.0	0.0 – 97.5	96	8 (1/7)	12.5	0.3 – 52.7
<i>Vulpes alopecoides</i>	1	1 (0/1)	0.0	0.0 – 97.5	11	2 (0/2)	0.0	0.0 – 84.2
<i>Ursus etruscus</i>	11	1 (0/1)	0.0	0.0 – 97.5	33	4 (1/3)	25.0	0.6 – 80.6
<i>Meles meles</i>	–	–	–	–	1	1 (0/1)	0.0	0.0 – 97.5
Carnivore indet.	30	–	–	–	47	–	–	–
Total carnivores	86	11 (0/11)	0.0	0.0 – 28.5	454	52 (12/40)	22.6	12.3 – 36.2
Large mammal indet.	–	–	–	–	1,126	–	–	–

109 **Table 1.** Number of identified specimens (NISP) and minimal number of individuals (MNI) of herbivore and
 110 carnivore species in Venta Micena (data for the excavation quarry of VM4 published by Luzón et al.¹, which
 111 include the fossils unearthed during the years 2005 and 2019–2020; data for VM3 updated from ref.⁹). This
 112 table shows the abundance of young individuals (i.e., calves and juveniles: cj) and adults (i.e., prime adults
 113 and senile individuals: as). For each species, the percentage of calves and juvenile individuals over the MNI
 114 count shows the 95% confidence interval (CI) estimated using a binomial approach: $p \pm z[p(1-p)/n]^{1/2}$, where
 115 p is the proportion of successes in a Bernoulli trial process and z is the $1-\alpha/2$ quantile of a standard normal
 116 distribution.
 117



118 **Figure 2.** Evidence of prey selection in VM3. A: least-squares regression between the logarithms of the mean
 119 body masses (X-axis) of adult individuals of the herbivore species of Venta Micena, estimated from postcranial
 120 measurements (data from refs.^{6,43}), and the logarithms of the percentage of calves and juvenile individuals
 121 over the MNI estimates of each species (Y-axis), calculated from teeth counts (data from Table 1). B: mortality
 122 profiles deduced from crown height measurements in horse *Equus altidens* and megacerine deer
 123

124 *Praemegaceros verticornis* (updated from ref.⁶). C: three examples of osteopathologies detected in VM3: a,
125 horse metatarsal with osteophytic overgrowths in the distal epiphysis; b, horse metacarpal showing an intense
126 deformation of the distal epiphysis; c, severe osteoarthritis in a third-four metacarpal of megacerine deer.

127 Analysis of skeletal representation for ungulate taxa in VM3 has shown that the
128 hyaenas selectively transported herbivore carcasses and body parts to their maternity den
129 as a function of the mass of the ungulates scavenged. This resulted in the transport as whole
130 carcasses of small-to-medium sized species like goat *Hemitragus albus* and fallow deer
131 *Metacervocerus rhenanus*, while in the case of large-sized species (e.g., horse and *Bison*
132 sp.) the carcasses were dismembered by the hyaenas, which preferentially transported the
133 limbs that provided larger marrow yields⁸. Later, the fracturing and consumption of major
134 limb bones by the hyaenas at their den was highly selective, correlating with their marrow
135 contents and mineral density. This resulted in well-defined patterns of consumption for the
136 limb bones (e.g., a proximodistal sequence in the humerus and tibia, and a distoproximal
137 one in the radius, femur, and metapodials)^{7,9,10}. As a result of these taphonomic biases, the
138 assemblage records marked differences in the abundance of different skeletal remains from
139 each ungulate species as well as among taxa.

140 In a recent paper, Luzón et al.¹ address the taphonomy of VM4, focusing their study
141 on a subset of the bone assemblage unearthed from this quarry, which taphonomic features
142 compare with those published for VM3^{6–10,13}. Despite the overall similarity between the bone
143 assemblages of VM4 and VM3 (Table 1, Figs. 3-4), Luzón et al.¹ contribute interesting new
144 data for VM4, which we discuss in detail below, and indicate several differences with respect
145 to the assemblage preserved at VM3, which was conclusively accumulated and modified by
146 *P. brevirostris*^{6–10}. Moreover, they even suggest the possibility that a different carnivore was
147 the taphonomic agent involved in the site formation process at VM4¹. For this reason, we
148 perform here a comparative taphonomic study of VM4 and VM3, to shed light on the
149 similarities and differences between the bone assemblages from both quarries, as well as
150 on the bone accumulating and modifying agent at VM4.

151 In this paper, we: (i) compare the taphonomic data provided by Luzón et al.¹ for VM4
152 with those available in the larger assemblage from VM3, and also with new data from an
153 analysis by M.P. Espigares of 3,729 fossils unearthed from VM4 during the years 2013–
154 2015; (ii) discuss on the taphonomic agent responsible of the accumulation and modification
155 of skeletal remains at VM4; (iii) provide clues on the palaeoecology of the assemblages of
156 large mammals from VM4 and VM3; and (iv) propose a new model for the generation of the
157 huge amount of fossils preserved across the VM stratum. Due to space limitations, the points
158 (ii) and (iii) are addressed in the Supplementary Information.

159

160 **Results: Taphonomy of the VM4 bone assemblage**

161 **Patterns of species abundance.** In their analysis of the fossil assemblage of VM4, Luzón
162 et al.¹ indicate that herbivorous taxa comprise the bulk of the fauna. Their data, compiled in
163 Table 1, show that herbivore remains represent 94.2% (1,492/1,578) of NISP and 78.8%
164 (41/52) of MNI values for large mammals. These figures are close to those of VM3, 93.5%
165 (6,570/7,027) and 84.4% (287/340), respectively (Table 1). A χ^2 test shows that these
166 differences are not statistically significant ($p > 0.3$ in both cases). Among herbivores, Luzón
167 et al.¹ indicate that *E. altidens* is the species most abundantly preserved, both in frequency
168 of remains and number of individuals, followed by cervids, bison, caprines, and
169 megaherbivores (i.e., elephant, rhino, and hippo). This is also the situation in VM3 according
170 to data compiled in Table 1: for example, the NISP value of *E. altidens* represents 31.8%
171 (124/390) of the remains of large mammal identified in VM4 and 49.6% (2,937/5,924) in
172 VM3. Although this difference is statistically significant ($\chi^2 = 46.408$, $p < 0.0001$), the
173 frequencies of horse based on MNI estimates, 29.3% (12/41) in VM4 and 31.7% (91/287) in

174 VM3, are similar ($\chi^2 = 0.096$, $p > 0.75$). The difference based on NISP values seems high,
 175 but it falls within the range expected from variations in abundance data from different years
 176 for the ungulate prey more common in Serengeti, where the frequencies of Thomson's
 177 gazelle, wildebeest, and zebra fluctuated in the late sixties between 18.9–56.3%, 21.3–
 178 42.8%, and 11.1–15.7%, respectively^{14,15}. Finally, *P. brevirostris* is the species most
 179 represented among carnivores in both assemblages according to NISP values (Table 1),
 180 26.8% (15/56) in VM4 and 30.0% (122/407) in VM3 ($\chi^2 = 0.241$, $p > 0.6$), followed by canids,
 181 ursids and felids.

182

Taxa	NISP values			Σ partial rows	MNI values			Σ partial rows
	VM4 (a)	VM4 (b)	VM3		VM4 (a)	VM4 (b)	VM3	
Megahervivores								
<i>(Mammuthus meridionalis + Hippopotamus antiquus + Stephanorhinus aff. hundsheimensis)</i>	35 (17.68) 4.326 ***	68 (40.88) 4.633 ***	224 (268.56) -3.018 **	327	8 (3.47) 2.667 **	6 (4.94) 0.536 --	17 (22.65) -2.360 *	31
<i>Equus altidens</i>	124 (183.42) -6.010 ***	331 (424.05) -6.436 ***	2,937 (2,785.83) 4.144 ***	3,392	12 (13.78) -0.595 --	20 (19.62) 0.110 --	91 (89.86) 0.268 --	123
Large bovids (<i>Bison</i> sp. + <i>Hemibos</i> aff. <i>gracilis</i> + <i>Praeovibos</i> sp.)	47 (51.37) -0.669 --	70 (118.77) -5.106 ***	833 (780.23) 2.190 *	950	4 (7.40) -1.431 --	9 (10.53) -0.554 --	53 (48.22) 1.428 --	66
Caprines (<i>Soergelia minor</i> + <i>Hemitragus albus</i>)	32 (35.31) -0.599 --	34 (81.64) -5.889 ***	587 (536.31) 2.484 *	653	4 (5.04) -0.519 --	5 (7.18) -0.932 --	36 (32.88) 1.101 --	45
<i>Praemegaceros</i> cf. <i>verticornis</i>	61 (59.32) 0.242 --	155 (137.14) 1.759 --	881 (900.96) -0.779 --	1,097	7 (8.63) -0.644 --	14 (12.28) 0.586 --	56 (56.26) -0.072 --	77
<i>Metacervocerus rhenanus</i>	35 (29.58) 1.063 --	52 (68.38) -2.197 *	460 (449.25) 0.571 --	547	6 (4.93) 0.537 --	5 (7.02) -0.873 --	33 (32.15) 0.304 --	44
<i>Pachycrocuta brevirostris</i>	15 (8.87) 2.140 *	27 (20.50) 1.550 --	122 (134.69) -1.201 --	164	2 (2.69) -0.458 --	4 (3.83) 0.099 --	18 (17.50) 0.237 --	24
Other carnivores	71 (34.45) 6.684 ***	234 (79.64) 19.300 ***	332 (525.17) -9.474 ***	637	9 (6.05) 1.353 --	11 (8.61) 0.944 --	34 (39.45) -1.774 --	54
Σ partial columns	420	971	6,376	$\Sigma\Sigma = 7,767$ $\chi^2 = 570.43$ ***	52	74	338	$\Sigma\Sigma = 464$ $\chi^2 = 15.65$ --

183 **Table 2.** Contingency tables for the abundance of large mammals in the assemblages of the two excavation
 184 quarries of Venta Micena compared in this study, VM4 (a: data published by Luzón et al.¹ for the fossils
 185 unearthed during the years 2005 and 2019–2020; b: unpublished data analysed by M.P. Espigares for the
 186 fossils of 2005 and 2013–2015) and VM3 (updated from ref.⁹). Separate tables are provided for the number of
 187 identifiable specimens (NISP, left table) and the estimates of minimum number of individuals (MNI, right table).
 188 The cells of each contingency table show the observed frequencies (OF), the frequencies expected from a
 189 random distribution (EF, between brackets), the adjusted residuals (normal deviates) and the level of statistical
 190 significance according to a two-tailed t-test (--: $p > 0.95$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). The tables
 191 also include the cumulative χ^2 -values [$\Sigma_i \Sigma_j (OF - EF)^2 / EF$] with $(r - 1) \cdot (c - 1) = 14$ degrees of freedom.

192 The distribution of NISP and MNI values among taxa in VM4 and VM3 was further
 193 analysed using an approach based on contingency tables. The table for NISP values shows
 194 a significant χ^2 value (Table 2, left part). This results from some differences in taxa
 195 abundance between the assemblages compared, which are reflected in the adjusted
 196 residuals: remains of megaherbivores and carnivores (excluding hyaenas) are represented
 197 in VM4 by higher frequencies than those expected from a random, homogeneous
 198 distribution, while they are underrepresented in VM3. This applies to the estimates obtained
 199 for VM4 using the data of Luzón et al.¹ and our own data (Tables S1–S2). The NISP values
 200 estimated for *P. brevirostris* by Luzón et al.¹ suggest a higher frequency of this carnivore in
 201 VM4 than in VM3, as indicated by the adjusted residual. However, the abundance of hyaena
 202 remains in our dataset for VM4 does not depart significantly from the expectations, as
 203 happens in VM3. Given that the database of Luzón et al.¹ includes less than half of the
 204 remains of large mammals included in our database (Table S2), this suggests that the high
 205 frequency of *P. brevirostris* reported in VM4 results from poor sampling. The remains of
 206 other carnivores are more abundantly represented in VM4 than in VM3. However, it must
 207 be noted that a study of 24 dens of the three living hyaenas showed that the abundance of
 208 carnivore remains is highly variable, even among dens of the same species¹⁶. The

209 distribution of MNI values among taxa in VM4 and VM3 (Table 2, right part) does not differ
210 from the expectations of a random distribution according to the low χ^2 value of the
211 contingency table. Only the adjusted residual for megaherbivores, which are slightly over-
212 represented in VM4 according to the data of Luzón et al.¹, is statistically significant, while
213 their abundance in VM3 is slightly lower than expected. Moreover, the probabilities of
214 obtaining in the randomization tests the cumulative χ^2 values observed for the NISP and
215 MNI values of each species ($p < 0.001$ and $p > 0.97$, respectively; Fig. S4) are equivalent to
216 those obtained with their groupings in Table 2.

217 In summary, the comparison of the faunal assemblages from both excavation
218 quarries (Tables 1–2) only shows some minor differences in taxa abundance for horse,
219 megaherbivores, and carnivores other than the hyaena, as well as the presence in VM3 of
220 some remains of two small ungulates (a roe deer-sized cervid and a chamois-sized bovid)
221 and two small carnivores (Table 1), which are not reported by Luzón et al.¹. Given their
222 comparatively low number of specimens studied at VM4, it is reasonable to expect that the
223 latter taxa, which are poorly represented in VM3, will also appear in future excavations.

224

225 **Age mortality profiles.** Luzón et al.¹ indicate that two megaherbivores, elephant
226 *Mammuthus meridionalis* and rhino *Stephanorhinus* aff. *hundsheimensis*, show frequencies
227 of non-adults that are close to, or even higher than, those of adults, as happens in VM3
228 (Table 1). However, the low MNI counts for these species in VM4 do not allow to state this:
229 for example, elephants are represented by a juvenile and an adult, which gives a frequency
230 of 50% of non-adults; with a sample size of only two individuals, the 95% confidence interval
231 calculated with a binomial approach for this percentage is 1.3–98.7% (Table 1). In *S.*
232 *hundsheimensis*, the frequency of non-adults, 80% (4/5), has also a very wide confidence
233 interval (28.4–99.5%). In three species of medium-to-large sized ungulates, *E. altidens*, the
234 ancestor of water buffalo *Hemibos* aff. *gracilis* and *P. verticornis*, Luzón et al.¹ report similar
235 frequencies of adults and non-adults, while they indicate that *Bison* sp. shows a lower
236 frequency of juveniles (Table 1). This is true for horse and deer (58.3% and 42.9% of non-
237 adults, respectively), but *Hemibos* is only recorded by one adult individual, which means
238 that the percentage of non-adults for this species is not reliable. Luzón et al.¹ calculate the
239 percentage of 33% non-adult bison over a sample of only three individuals, of which one is
240 a juvenile: the confidence interval for non-adults (0.8–90.6%) comprises the frequencies for
241 horse and megacrine deer (Table 1), which rules out their suggestion of a lower frequency
242 of juveniles for this bovid. In contrast to VM4, the abundances of non-adult horse, bison and
243 megacrine deer are similar in VM3 (Table 1), where they are represented by higher MNI
244 counts (which makes their percentages reliable). A similar reasoning can be applied to the
245 claim of Luzón et al.¹ that adults outnumber calves and juveniles among smaller herbivores
246 such as the Ovibovini *Soergelia minor*, the Caprini *Hemitraus albus* and the cervid
247 *Metacervocerus rhenanus*: in these species, MNI counts are very low to calculate reliably
248 the percentage of juveniles (see their confidence intervals in Table 1). In fact, Luzón et al.¹
249 acknowledge this limitation when they write that “the total number of individuals in each
250 species is too low to draw reliable conclusions on the resulting patterns” and “a prime-
251 dominant, L- or U-shaped mortality profile cannot be clearly discerned”. The situation in VM3
252 is quite different (Table 1): MNI counts for the two ungulates better represented in the
253 assemblage, *E. altidens* and *P. verticornis*, allowed to reconstruct U-shaped attritional
254 mortality profiles (Fig. 2B), which evidenced that the hypercarnivores focused on young and
255 old individuals in the case of large prey^{6,7}.

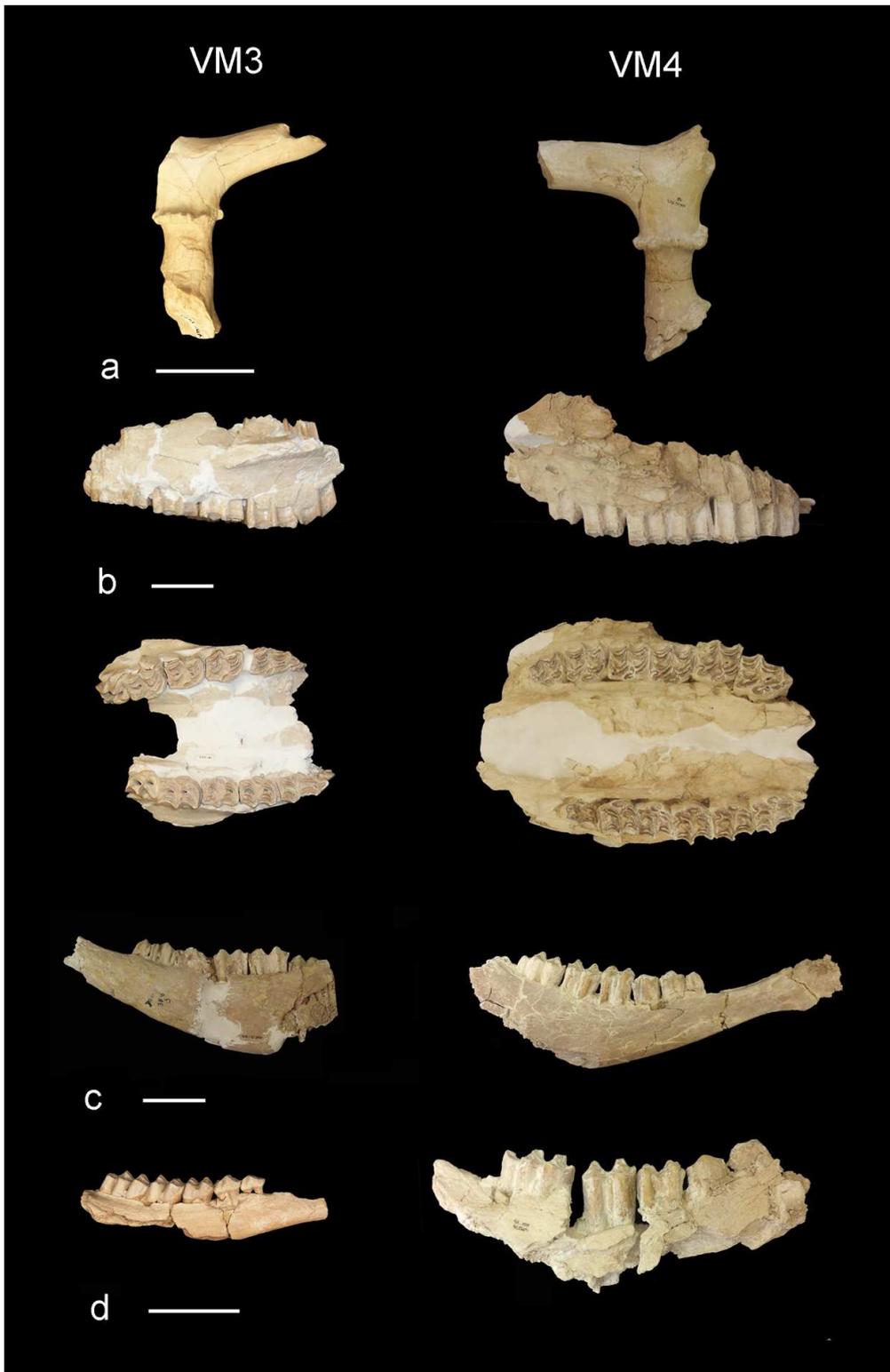
256

257 **Patterns of skeletal abundance.** The limitations and inaccuracies cited above result from
258 the small sample analysed by Luzón et al.¹ in VM4 (1,578 remains of large mammals of

259 which only 420 could be determined taxonomically and anatomically, compared to 8,150
260 and 6,331 remains in VM3, respectively: Table 1). These limitations apply also to their
261 inferences on the skeletal profiles of ungulates. For example, they indicate that species of
262 herbivore size class 2 (50–125 kg: *M. rhenanus*, *H. albus*, and *S. minor*) show biased
263 skeletal profiles, with a predominance of teeth and elements of the forelimb over those of
264 the hindlimb. In VM3, these ungulates also show higher frequencies of teeth than of bones,
265 which has been interpreted as evidence of the transport by *P. brevirostris* of small-to-
266 medium sized ungulates as whole carcasses to their denning site, where the giant hyaenas
267 fractured the bones for accessing their medullary cavities and this resulted in their
268 underrepresentation compared to teeth^{7–10}. In the case of the major limb bones of these
269 species in VM4, the elements of the forelimb (12.9%, 13 bones out of 101 determined
270 remains) are twice as abundant as those of the hindlimb (6.9%, 7 bones), but these
271 percentages do not differ statistically ($\chi^2 = 2.028$, $p = 0.1544$), which indicates the effects of
272 limited sampling. In the species of herbivore size class 3 (125–500 kg), Luzón et al.¹ indicate
273 that they are well represented by all anatomical elements (e.g., craniodental elements
274 account for ~30% of the remains, while both axial and appendicular elements show
275 frequencies >20%). This pattern is like the one reported in VM3 for medium-to-large sized
276 ungulates^{7–10}. However, Luzón et al.¹ indicate a bias in the disproportionate amount of
277 posterior limb remains compared to anterior limb specimens, which in their opinion contrasts
278 with the more balanced representation of these elements observed in VM3. Specifically, the
279 number of forelimb bones (13.8%, 54 out of 392 bones) is about half the abundance of
280 hindlimb bones (25.3%, 99 bones). This difference is statistically significant ($\chi^2 = 16.460$, p
281 < 0.0001) because the sample size studied here is larger than in the former case. Moreover,
282 Luzón et al.¹ do not report in Table S4a of their appendix on the presence of astragali or
283 calcanei, highly mineralised bones well represented in the faunal assemblage of VM3^{5,7,9,10}.
284 Given that they are not absent from VM4 (our own dataset for VM4 includes nine calcanei
285 and 20 astragali out of 78 autopodial bones: Table S1), their inclusion would further increase
286 the frequency of hindlimb bones. On the other hand, they indicate the presence of 25
287 pelvises, which outnumber all major limb bones except the tibia (in our dataset, the number
288 of pelvises is 16). Compared to the limb bones, the pelvis is a flat anatomical structure
289 composed of three poorly mineralised bones, which uses to be fractured by the hyaenas for
290 accessing its internal nutrients. As a result, it is usually recorded as fragments that preserve
291 the acetabulum⁷. This suggests that the high number of pelvises reported by Luzón et al.¹
292 probably represent pelvis fragments, which explains in part the overabundance of hindlimb
293 elements. In VM3, *E. altidens* and *Bison* sp. are better represented by limb bones than by
294 cranial and axial elements⁸. The living hyaenas do not cooperate to transport large portions
295 of a carcass, which limits the individuals in what they can move¹⁷. Given the size of the
296 carcasses of the adult individuals of these species, which exceeds what even a hyaena as
297 large as *P. brevirostris* could transport, the overabundance of limb elements of horse and
298 bison indicates the dismemberment of the carcasses and the selective transport to the
299 denning site of the limbs due to their high marrow yields^{8,10}. In the case of the horse,
300 hindlimbs predominate over forelimbs in VM3, because the femur and tibia provide more
301 marrow than the humerus and radius, respectively, and this resulted in the preferential
302 transport of hindlimbs by the hyaenas to their den⁸. Therefore, the pattern of skeletal
303 representation noted by Luzón et al.¹ in VM4 for the size category of the horse, the species
304 better represented in the assemblage, agrees also with the expectations from VM3.

305 Figures 3 and 4 show examples of the patterns of preservation of cranial and
306 postcranial remains of ungulates in VM4 and VM3, which are strikingly similar. The data
307 compared above on species abundances and skeletal representation suggest that the small
308 differences outlined by Luzón et al.¹ between both quarries result from random oscillations
309 emerging from the small sample studied at VM4. Surprisingly, they only analyse
310 taphonomically the fossils of large mammals of the years 2005 and 2019–2020 (1,578

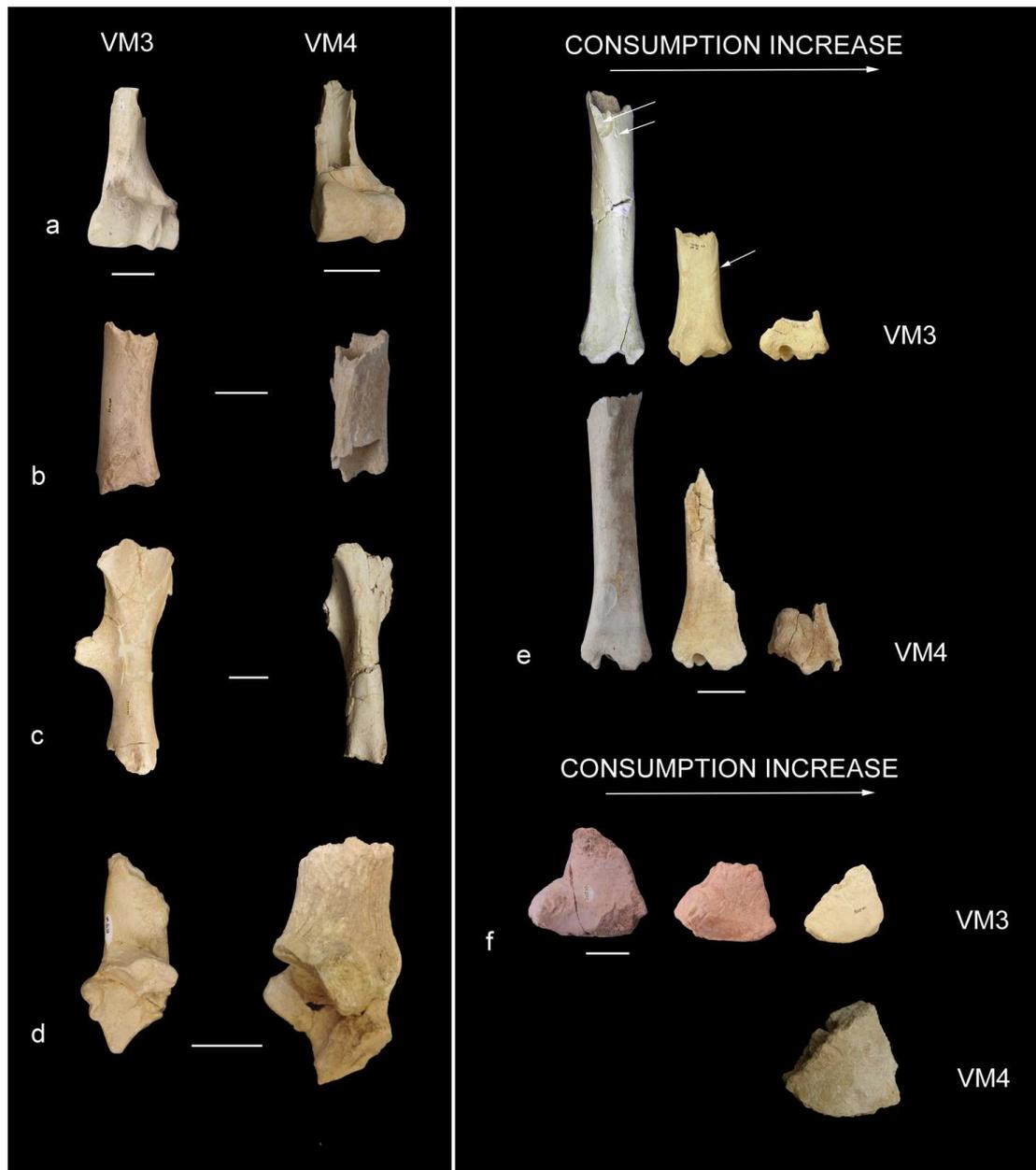
311 remains), but do not include those unearthed during the years 2013–2015 (3,729 remains).
312 Their inclusion would raise the number of specimens studied to 5,338 specimens, a figure
313 more in accordance with the information available for VM3 (the site they intend to compare
314 their results with), which would make their analyses more robust. Moreover, it is difficult to
315 understand why Luzón et al.¹ do include 4,219 skeletal remains in the analysis of spatial
316 patterns with random forest algorithms, which allowed them to assign confidently most of
317 these fossils to any of the two bone accumulations identified at VM4, but do not use such
318 data for analysing the patterns of species abundances and skeletal representation.



319
320 **Figure 3.** Cranial remains from quarries VM3 (left) and VM4 (right) of Venta Micena showing similar patterns
321 of consumption by the hyaenas^{6–10}: a, antler fragments of *Metacervocerus rhenanus*; b, maxillae of *Equus*

322
323
324

altidens in labial (upper photographs) and occlusal views (lower photographs); c, jaw fragments of *Bison* sp.; d, jaw fragments of *M. rhenanus* (left) and *Bison* sp. (right). Scale bars represent 5 cm.



325

326 **Figure 4.** Postcranial remains from quarries VM3 (left) and VM4 (right) of Venta Micena showing similar
327 patterns of bone consumption by the hyaenas^{6–10}: a, distal humeri of *Bison* sp. (left) and *Equus altidens* (right);
328 b–c, femur diaphyseal fragments of large sized herbivores; d, calcanei of Bovini (left) and *Hippopotamus*
329 *antiquus* (right); e, sequences of consumption of tibiae from large-sized ungulates (upper sequence: VM3,
330 lower sequence: VM4); f, sequences of consumption of lunate bones of *Mammuthus meridionalis* (upper
331 sequence: VM3, lower sequence: VM4; the difference of size is because the lunate of VM4 is from an adult
332 individual while those of VM3 are from juveniles). Scale bars represent 5 cm.

333 **Patterns of bone weathering.** Luzón et al.¹ indicate that 90.8% (1,461/1,609) of the
334 specimens analysed of VM4 show weathering stage (ws) 0 (bones with no sign of cracking
335 or flaking, preserving their cortical surface intact), which indicates less than one year of
336 subaerial exposure before burial¹⁸, while the remaining 9.2% of elements show ws 1 (cracks
337 poorly developed and longitudinally oriented in the long bones: 0–3 years) or ws 2
338 (outermost concentric layers of bone showing mosaic flaking and deeper split line cracks:
339 2–6 years)¹⁸. In the case of VM3, the estimates calculated over a substantially larger sample
340 of skeletal remains (4,921 bones, updated from ref.⁹) are the following: 75.9% ws 0, 23.4%
341 ws 1, 6.3% ws 2, and 0.04% ws 3 (bone surface with patches of rough, homogeneously

342 weathered compact bone where all the external, concentrically layered bone has been
 343 exfoliated: 4–15 years of exposure)¹⁸. Half of the bones of VM3 classified within ws 1 show
 344 shallow split line cracks due to insolation in only one side or in a part of their outer surface,
 345 while the other shows ws 0 (Fig. 5d). For this reason, they could equally well have been
 346 classified within the latter category, which would raise the frequency of elements with ws 0
 347 to ~88%, a figure more in accordance with the data of Luzón et al.¹. A similar proportion of
 348 the few remains classified in VM3 within ws 2 display ws 1 in a part or a side. If they are
 349 considered within the latter category, this would raise the percentage of bones with ws 1 to
 350 ~12%, a figure also closer to that of Luzón et al.¹. In summary, these estimates suggest that
 351 the skeletal remains of VM3 show a slightly more advanced degree of weathering than those
 352 of VM4, which tentatively indicates that part of the bones preserved at VM3 were exposed
 353 during a longer time before burial. However, most bones from both quarries were buried
 354 very shortly after the death of the animals, less than one year. Moreover, the medullary
 355 cavities of the bones fractured by the hyaenas in VM3 are infilled by mud flows, but those
 356 preserved complete do not show infillings, even in the areas close to large nutrient foramina.
 357 This indicates that they were buried with the greasy periosteum intact, which suggests a
 358 subaerial exposure of few months⁷.



359
 360 **Figure 5.** Examples of bone remains and a hyaena coprolite from the excavation quarry VM4 of Venta Micena:
 361 a, diaphysis of a digested long bone of bird; b, bone fragment showing gnaw marks made by a porcupine

362 (*Hystrix* sp.); c, coprolite of *Pachyrocuta brevirostris*; d, third-fourth metacarpal of a large Bovini showing a
363 different degree of bone weathering in its proximal and distal part (this bone, preserved complete, shows some
364 diagenetic fractures orthogonal to the major axis, which resulted from sediment compaction); e, bone flake
365 with micronotches and tooth marks; f, fragment of a radius of a large-sized ungulate (the upper view shows
366 the presence of a double opposing notch, the lower one shows one notch, pits and scores); g, proximal radius
367 of megacerine deer *Praemegaceros* cf. *verticornis* fragmented and consumed by the hyaenas [the enlarged
368 photographs show pits (1) and crenulated edges (2)]; h, ulna of hippo *Hippopotamus antiquus* consumed by
369 the hyaenas, showing several pits; i, notch in an indeterminate bone fragment. Scale bars represent 2 cm.

370 **Elements in anatomical connection.** According to Luzón et al.¹, many bones of VM4 are
371 anatomically connected (e.g., a humerus-radius and a femur-tibia, fibula, and talus of rhino
372 *S. hundsheimensis*, both sets located some meters distant; a group of seven dorsal
373 vertebrae of *M. meridionalis*; an almost complete forelimb and two complete hindlimbs of *L.*
374 *lycaonoides*, also separated by a short distance; and two hemipelvises of *E. altidens*). During
375 the field excavation seasons of 2013–2015, which they do not study, other elements of the
376 same rhino skeleton (e.g., a humerus-radius and a femur-tibia, fibula, talus, and three
377 metapodials as well as a cervical section including the axis and two cervical vertebrae; Figs.
378 6a–c) were found. In addition, some vertebrae of *M. meridionalis* (Fig. 6d), a complete
379 forelimb of a small-sized felid (Fig. 6e), two complete hindlimbs of a large canid, probably *L.*
380 *lycaonoides* (Fig. 6f), a skull of *P. brevirostris*, and two hemipelvises of *E. altidens* (Fig. 6g)
381 were unearthed. Surprisingly, these fossils are not cited by Luzón et al.¹. Although there are
382 also elements of VM3 in anatomical connection (e.g., several skulls showing the mandible
383 articulated with the cranium, two hemipelvises of a juvenile horse, some groups of lumbar
384 vertebrae and several groups of autopodial elements)^{7,9,19}, their frequency is lower than in
385 VM4. However, many bones of VM3 are disarticulated but spatially associated to others with
386 which they were anatomically connected in origin^{7,9} (Fig. S3). Again, this difference
387 suggests that the bones preserved at VM3 were exposed during a longer time before their
388 burial, which resulted in more weathering and a higher degree of modification by the
389 hyaenas. Most probably, the reason was that the breeding season in the denning site of *P.*
390 *brevirostris* in VM3 prolonged a little longer than in VM4 before the rise of the water level of
391 the lake covered the area and capped with limestone the bone assemblage.

392

393 **Patterns of skeletal completeness.** Luzón et al.¹ affirm that the skeletal remains of VM4
394 show a moderate degree of fragmentation. This claim is contradicted by data provided in
395 their Table 2: ~36% of the remains measure <3 cm and >55% of limb bones show green
396 fractures, which evidence their breakage in fresh state by the hyaenas. In VM3, a substantial
397 proportion of the remains are also small shaft fragments and one third of them measure <3
398 cm, like in VM4. Isolated epiphyses and diaphyseal bone shafts are very abundant and
399 outnumber the bones preserved complete in VM3^{9,10}: 80.5% (963/1,196) of the major limb
400 bones of equids, bovids, and cervids are represented by isolated bone portions that show
401 green fractures (mostly spiral or longitudinal fractures) and only 19.5% are preserved
402 complete^{7,9}. These fractures were produced by the hyaenas during the biostratigraphic stage,
403 when the bones were still fresh and retained their marrow contents. Green fractures
404 predominate over diagenetic fractures resulting from sediment compaction, which are found
405 in 22.5% of the bones of VM3⁹. The latter tend to be orthogonally oriented to the major axis
406 in the long bones and are delimited in all cases by both bone portions (i.e., there is no
407 fracture defining the end of one specimen), which shows that the assemblage is not
408 reworked⁷.



409

410 **Figure 6.** Several elements found in anatomical connection in the excavation quarry VM4 of Venta Micena: a-
 411 c, *Stephanorhinus* aff. *hundsheimensis* (a: hindlimb; b: axis, first and second cervical vertebrae; c: second,
 412 third, and fourth metacarpals); d, group of five dorsal vertebrae of elephant *Mammuthus meridionalis*; e,
 413 forelimb of an indeterminate felid of small size; f, hindlimb of a large-sized canid; g, two hemipelves of horse
 414 *Equus altidens*.

415 **Bone transport.** There is no evidence of transport by water currents in VM3, because the
 416 bones: (i) show a random pattern in their spatial orientation; (ii) have no rounded or polished
 417 edges; (iii) show no traces of abrasion from rolling or similar movements within a current;
 418 and (iv) detritics are nearly absent from the sediment, which composition is 90-98% pure
 419 micritic limestone precipitated in water ponds emplaced on a caliche palaeosol of diagenetic
 420 origin^{7,9}. In the case of VM4, Luzón et al.¹ also indicate the absence of bones with rounded
 421 surfaces, which helps them to discard fluvial currents as responsible of the accumulation of
 422 skeletal remains. However, they affirm that ~40% of specimens show evidence of hydraulic
 423 abrasion. Given that it is difficult to explain the presence of bones that were abraded but not
 424 rounded, they suggest the following *ad hoc* hypothesis: while the currents were weak for
 425 displacing the remains, abrasion resulted from circulating waters that moved the sediment
 426 over the bones, which originated their abrasion¹. However, detritics are absent from the
 427 whole VM stratum⁷ and it is difficult to explain the finding at VM4 of microvertebrate remains,
 428 which should have been transported by water currents of low energy. Luzón et al.¹ indicate
 429 that the fossil remains of the two levels of accumulation described in VM4 show patterns of
 430 preferential orientations towards the NE. This is also difficult to explain, because they
 431 discard the role of hydraulic currents in the transport and deposition of bones. Concerning
 432 bone dip, only 4% of the remains show azimuth values over 45°, while 79% of bones are
 433 found relatively flat along the topography of the excavated surface¹. As a result, they suggest
 434 gravity as the likely cause for the observed patterns of bone inclination at VM4¹, a hypothesis
 435 previously suggested for VM3⁷. In the case of VM3, rose diagrams show no preferential

436 patterns of alignments in the orientation of the skeletal remains, while dip angles greater
437 than 30° are poorly represented and bones showing a vertical or subvertical inclination are
438 very scarce⁹.

439

440 **Carnivore tooth marks.** Luzón et al.¹ indicate that carnivore alterations were only observed
441 in 4.5% of those bones with a well-preserved cortical surface and that only three bones
442 showed 3–6 tooth marks. The frequency of tooth-marked remains in the larger sample of
443 VM4 analysed here is slightly higher, 5.5% (177/3,227) (Table S3). The marks include
444 scores, pits, notches, crenulated edges, and furrows made by the hyaenas (Table S4, Fig.
445 5). Of these marks, ~60% appear in limb bone shafts. In addition, one bone shows marks
446 made by a porcupine (Fig. 5b). In the case of VM3, 29.4% (1,555/5,288) of the remains
447 analysed show carnivore tooth marks⁹. These bones belong to all ungulate species identified
448 in the site and there are also some tooth-marked bones of *Pachycrocuta*, both of adult and
449 non-adult individuals. Many cranial fragments and most limb bones of VM3 show striations
450 and biting marks, the preserved epiphyses have furrows and punctures, and the diaphyses,
451 as well as the skull bones, show scoring and pitting. Pits, scores, and notches are the marks
452 most frequently recorded, although crenulated edges and furrows are also abundant^{7,9}. The
453 proportion of tooth-marked bones in VM3 was in all probability even higher, as many limb
454 bones of the assemblage that do not preserve tooth marks show fracture patterns that
455 evidence that they were broken in fresh state by the hyaenas⁹, and this also applies to VM4.
456 A significant part of the tooth marks preserved in VM3 were probably produced by juvenile
457 hyaenas, which deciduous teeth are more cutting than the permanent premolars of adults,
458 which are progressively blunted by bone cracking, and this results in inconspicuous tooth
459 marks⁷. However, a minor implication of some small or medium-sized carnivore like the wolf
460 *C. orcensis*²⁰ cannot be discarded. Among modern hyaena dens, the frequency of tooth
461 marked bones is highly variable¹⁶: 29.0–53.5% in spotted hyaenas, 22.1–100% in brown
462 hyaenas, and 6.0–56.2% in striped hyaenas (the lower limit for this species is contentious,
463 because it corresponds to a den where the bones are highly weathered). These frequencies
464 are higher than in VM3 and VM4, but many fossil bones of the site are pending of restoration
465 and evidence of gnawing by juvenile hyenas is usually very subtle.

466 The higher proportion of tooth-marked bones in VM3 agrees with a longer exposure
467 of the skeletal remains than in VM4, which would explain why they were exploited more
468 thoroughly by the hyaenas. As discussed earlier, this is also suggested by the more
469 advanced degree of bone weathering and by the lower frequency of articulated elements.
470 According to Luzón et al.¹, bones with salivary and gastric alterations are absent in VM4,
471 but they are recorded in VM3 at very low frequencies (0.34% and 0.15% of 5,288 specimens
472 analysed, respectively)⁹. This suggests that their absence from VM4 results from the small
473 sample of remains studied. In fact, our analysis of the specimens from the excavation
474 seasons not studied by Luzón et al.¹ showed the presence of two bones with evidence of
475 digestion (0.06% of the specimens analysed; Fig. 5a) and two others with salivary alterations
476 resulting from licking (Table S4). In the study of 24 hyaena dens cited above¹⁶, evidence of
477 acid or gastric edging of bones was detected in only eleven skeletal remains (six from
478 spotted hyaena, four from brown hyaena and one from striped hyaena assemblages). These
479 low numbers are not surprising, because neither striped hyaenas nor brown hyaenas
480 regurgitate bones.

481 Finally, Luzón et al.¹ indicate that hyaena coprolites are absent in VM4, but a small
482 coprolite was unearthed during the excavation of 2014 (Fig. 5c). The hyaena den of VM3
483 also preserves some coprolites represented by isolated pellets with diameters of 3–6 cm⁷.

484

485 **VM4 and VM3: coeval or successive bone accumulations?** According to Luzón et al.¹,
486 VM4 is in the context of a series of short-time events (they identify two of them in VM4, while
487 only one was recognized in VM3⁷) followed by rapid sedimentation, as indicated by the low
488 degree of bone weathering, the low frequency of tooth-marked bones, and the presence of
489 skeletal remains anatomically connected. In the case of VM3, the more advanced
490 weathering, the higher frequency of bones with bite marks and the lower proportion of
491 elements in anatomical connection suggest that the deposition of limestone that capped the
492 bone assemblage after the rising of the water table of the Baza palaeolake was delayed
493 compared to VM4.

494 The bone assemblage accumulated in the hyaena den of VM4 is positioned ~350 m
495 distant from VM3 (Fig. 1F). This distance is very short for considering the possibility of two
496 neighbouring hyaena clans: in Serengeti, where spotted hyaenas engage in prolonged
497 clashes with neighbouring clans, the radius of the permanent territory defended by a clan
498 around the communal den fluctuates between 2.6 and 5.7 km²¹. This suggests that VM4
499 and VM3 were not coeval but correspond to separate events of accumulation during different
500 years. More specifically, a study of a spotted hyaena clan in Masai Mara showed that the
501 hyaenas used 57 different sites for communal denning during a period of ten years, with an
502 average distance between the dens used consecutively of 1.5 ± 0.1 km²². The distance
503 between VM4 and VM3 is five times shorter than the one expected when the adult spotted
504 hyaenas move their cubs to a new denning site, which suggests that VM4 and VM3 do not
505 represent a residential move of the same hyaena clan. Therefore, the most parsimonious
506 interpretation is that the bone assemblages preserved at both denning sites were
507 accumulated by the hyaenas during the dry seasons of different years in the emerged plain
508 that surrounded the lake surface covered by permanent waters (Fig. 1F). During the interval
509 of time in which the accumulation of the bone assemblage of VM3 took place, the rising of
510 the water table in the rainy season probably occurred some months later than during the
511 years that correspond to the two accumulations of bone remains detected in VM4¹.
512 Following this interpretation, the remains accumulated at the denning site of VM4 were
513 capped with limestone (which protected them from weathering) somewhat earlier than those
514 of VM3, which explains the minor taphonomic differences between both sites cited above.
515 This interpretation also helps to clarify why the whole VM stratum, which outcrops along
516 ~2.5 km, seems to be littered with fossils of large mammals, as it is difficult to conceive a
517 “megadenning site” of *P. brevirostris* that extended over several squared kilometres. In our
518 model, the VM stratum would represent successive deposits of micritic limestones in the
519 plain that surrounded the Baza palaeolake during several lowstand-highstand cycles, each
520 corresponding to the dry and rainy seasons of one year (Fig. S2d). Each year, the hyena
521 clans that inhabited the Baza Basin would randomly select their denning sites on this plain.
522 After enough years, the surface seasonally submerged of the plain that surrounded the lake
523 would be almost entirely covered by fossils of large mammals, which were preserved in the
524 micritic limestones of the VM stratum.

525

526 **Concluding remarks**

527 Taphonomic analysis of the remains of large mammals preserved at VM4 shows that this
528 bone assemblage is very similar to the one preserved at VM3, the main excavation quarry
529 of Venta Micena, from which many thousands of fossils were unearthed during the last
530 decades. Contingency tables show that the only significant differences between both sites
531 are the frequencies of skeletal remains of megaherbivores, slightly overrepresented at VM4,
532 and of horse *E. altidens*, a species more abundant in VM3. These variations in prey
533 abundance are not unexpected in natural ecosystems according to survey data from
534 different years. Many differences between VM4 and VM3 reported by Luzón et al.¹,
535 particularly those related to the abundance of juvenile individuals, result from poor sampling,

536 which is reflected in low NISP and MNI estimates for most species. Our study, based on a
537 larger dataset, shows no major differences in the taphonomic signatures of VM4 and VM3
538 except for a somewhat longer time of exposure at VM3, which resulted in a more in-depth
539 consumption by the hyaenas of the bones accumulated. Therefore, the results obtained in
540 this study suggest that the bone assemblages of VM4 and VM3 were produced in non-
541 coeval denning areas of *P. brevirostris* in the plain that surrounded the Baza palaeolake.

542

543 **Materials and methods**

544 In this study, we analysed 8,831 vertebrate fossil remains from VM3 unearthed during the
545 field excavation seasons performed between the years 1982 and 2005. Most of these
546 specimens were taphonomically analysed by M. P. Espigares⁹. The materials from VM4
547 analysed here consist of 3,961 vertebrate remains (mostly large mammals) recovered
548 during systematic excavations in the years 2005 and 2013–2015.

549 Anatomical and taxonomic data were determined using atlases of comparative anatomy^{23–}
550²⁶ and palaeontological publications on the Orce sites. Species of large mammals (mean
551 mass estimates from refs.^{6,43}) were distributed among size categories following refs.^{27,28}:
552 small size (S), <23 kg; medium-to-small size (SM): 23–114 kg, medium size (M): 114–227
553 kg, medium-to-large-size (ML): 227–340 kg; large size (L): 340–907 kg; very large size (VL):
554 >2,721 kg (size classes 5 and 6 from refs.^{27,28} are grouped in this study). Elements that do
555 not preserve taxonomically diagnostic features were classified to order, infraorder, family,
556 or tribe level, and were then assigned to a size category.

557 The faunal assemblages of VM3 and VM4 were taphonomically analysed following
558 the standard methodology^{29–31}. Numbers of identified specimens (NISP), minimum numbers
559 of elements (MNE) and minimum numbers of individuals (MNI) were calculated for all taxa.
560 Four age groups were established for the specimens: immature individuals, subdivided in
561 calves and juveniles, and adults, classified as adults *sensu strictum* (i.e., yearlings and prime
562 adults) and past-prime adults (i.e., senile individuals). Criteria for estimating age at death
563 included patterns of tooth replacement and degree of tooth wearing for deciduous and
564 permanent teeth, as well as degree of epiphyseal fusion for limb bones.

565 Bone cortical surfaces were analysed with a stereoscopic binocular microscope
566 (Olympus SZ 11) and a digital microscope (DINO-LITE Modell AM4115TL). In the case of
567 VM4, surface modification was analysed in only a part of the assemblage, because many
568 bones are badly conserved and need restoration. Carnivoran activity was identified based
569 on refs.^{32–37}. Most tooth marks identified were pits, notches, and scores; furrowing and
570 crenulated edges were present but in lower percentages. Bone breakage patterns were
571 classified according to ref.³⁸. Weathering and other bone surface modifications were
572 identified and described following refs.^{18,30,39,40}.

573 The abundance of each species of large mammals identified in VM4 and VM3 was
574 tested statistically using two contingency tables, one for NISP values and another for MNI
575 estimates. In the case of VM4, data provided by Luzón et al.¹ were used. However, given
576 that their study only analysed the fossils from the excavation seasons of the years 2005
577 (245 skeletal elements) and 2019–2020 (1,364 remains), we also included in this
578 comparison unpublished data analysed by M.P. Espigares on 3,974 fossils unearthed during
579 the years 2005 and 2013–2015 (see Tables S1–2). Data for VM3 were updated from ref.⁹.
580 The limitations posed on this analysis by the low sample sizes reported by Luzón et al.¹ for
581 most taxa in VM4 made necessary to group several species according to taxonomic affinities
582 (e.g., large bovids, caprines, and other carnivores apart from *P. brevirostris*) or size
583 categories (e.g., megaherbivores).

584 Each contingency table has r rows (species or group of species) and c columns (their
585 raw abundances in the two datasets for VM4 and in VM3). The statistic for testing against
586 independence between species abundances and assemblages is: $\chi^2 = \sum_{i=1}^r \sum_{j=1}^c (O_{ij} -$
587 $E_{ij})^2/E_{ij}$, where O_{ij} is the observed frequency of species i in assemblage j for the ij -th cell (i.e.,
588 n_{ij}) and E_{ij} represents the expected frequency for this cell under the null hypothesis of
589 independence (i.e., a random, homogeneous distribution of species among the
590 assemblages). The latter is computed as: $E_{ij} = (\sum_{i=1}^r n_{i.} \cdot \sum_{j=1}^c n_{.j}) / \sum_{i=1}^r \sum_{j=1}^c n_{ij}$, where $n_{i.}$ and
591 $n_{.j}$ are the total number of cases that show the i -th and j -th attributes [partial sums for rows
592 (species) and columns (assemblages) in the table, respectively]. When the null hypothesis
593 holds, χ^2 is approximately distributed as a chi-square variable with $(r - 1) \cdot (c - 1)$ degrees of
594 freedom.

595 The individual cells of the contingency tables were also analysed independently with
596 the method of adjusted residuals¹⁰. This allows the determination of which species or groups
597 of species (rows) are significantly over-represented in each assemblage (columns). Let $e_{ij} =$
598 $(O_{ij} - E_{ij})/E_{ij}^{1/2}$. The mean of this variable equals zero and its variance is $v_{ij} = (1 - n_{i.}/n) \cdot (1 -$
599 $n_{.j}/n)$. The adjusted residuals are $d_{ij} = e_{ij}/v_{ij}^{1/2}$, and they result from standardization (i.e., z-
600 score normalization) of e_{ij} values. Adjusted residuals are approximately normally distributed
601 $[N(0,1)]$ when there is no association between the rows and columns of the contingency
602 table. However, a situation of dependency generates residuals that are higher in absolute
603 value than the standard normal deviate for a specific level of confidence (e.g., 1.96 for $p <$
604 0.05). For this reason, when the absolute value of the adjusted residual (d_{ij}) for a given cell
605 is higher than this deviate, the null hypothesis of independence is rejected for this cell (a
606 positive value indicates an over-representation of the i -th species in the j -th assemblage
607 compared to the expectations from a random distribution of species among assemblages,
608 while a negative one points to an under-representation).

609 A randomization test for contingency tables was also used to compare species
610 abundances in the assemblages of VM4 and VM3 without the need of grouping the species
611 with low frequencies in larger categories⁴¹. It is worth noting that MNI estimates are more
612 adequate for describing the relative frequencies of species in those assemblages that show
613 a high degree of fragmentation⁴². Given that most bones of VM3 and VM4 were subject to
614 ravaging by the hyaenas, the use of MNI counts seems the best choice for comparing both
615 assemblages. According to data from Luzón et al.¹, sample sizes were fixed for VM4 in 390
616 (NISP values) and 52 (MNI counts). The frequencies considered for VM3 were 6,331 and
617 339, respectively (these numbers refer to those remains identified taxonomically: see Table
618 1). This allowed to generate an empirical distribution of the χ^2 statistic by simulating a set of
619 random samples ($n = 10^4$) according to the marginal frequencies of each species.

620

621 Acknowledgments

622 This work has been granted by projects CGL-2016-78577-P, CGL-2016-80975-P, and
623 PID2019-111185GB-I00 of the Spanish Ministry of Science, Innovation and University,
624 'Junta de Andalucía' (FEDER) project UMA18-FEDERJA-188, 'Generalitat de Catalunya'
625 grant GENCAT 2017SGR 859, and by Research Group RNM-146 from 'Junta de Andalucía'.
626 The permission to the study of the fossil collections from Venta Micena and other sites of
627 Orce has been provided by 'Consejería de Cultura y Patrimonio Histórico' of Grenade (ref.
628 BC.03.174/19). G. Rodríguez-Gómez is granted by an "Atracción de Talento" postdoctoral
629 contract (2019-T2/HUM-13370) from 'Comunidad de Madrid/Universidad Complutense' for
630 developing the project "Estudios paleoecológicos en los yacimientos de Orce y de la sierra
631 de Atapuerca". A. Granados enjoys a FPI predoctoral grant from the Spanish Ministry of
632 Science, Innovation and University.

633 **References**

- 634 1. Luzón, C. *et al.* Taphonomical and spatial analyses from the Early Pleistocene site of
635 Venta Micena 4 (Orce, Guadix-Baza, Basin, southern Spain). *Sci. Rep.* **11**, 13977.
636 <https://doi.org/10.1038/s41598-021-93261-1> (2021).
- 637 2. García-Aguilar, J. M., Palmqvist, P. A model of lacustrine sedimentation for the Lower
638 Pleistocene deposits of Guadix-Baza basin (southeast Spain). *Quat. Int.* **243**, 3–15 (2011).
- 639 3. García-Aguilar, J. M. *et al.* Hydrothermal activity and its paleoecological implications in the
640 Latest Miocene to Middle Pleistocene lacustrine environments of the Baza Basin (Betic
641 Cordillera, SE Spain). *Quat. Sci. Rev.* **96**, 204–221 (2014).
- 642 4. García-Aguilar, J. M. *et al.* A reassessment of the evidence for hydrothermal activity in the
643 Neogene-Quaternary lacustrine environments of the Baza Basin (Betic Cordillera, SE Spain)
644 and its paleoecological implications. *Quat. Sci. Rev.* **112**, 226–235 (2015).
- 645 5. Martínez-Navarro, B. *Revisión sistemática y estudio cuantitativo de la fauna de*
646 *macromamíferos del yacimiento de Venta Micena (Orce, Granada)*. (PhD dissertation
647 thesis, Universitat Autònoma de Barcelona, 1991).
- 648 6. Palmqvist, P., Martínez-Navarro, B. & Arribas, A. Prey selection by terrestrial carnivores
649 in a lower Pleistocene paleocommunity. *Paleobiology* **22**, 514–534 (1996).
- 650 7. Arribas, A. & Palmqvist, P. Taphonomy and paleoecology of an assemblage of large
651 mammals: hyaenid activity in the Lower Pleistocene site at Venta Micena (Orce, Guadix-
652 Baza Basin, Granada, Spain). *Geobios* **31**, 3–47 (1998).
- 653 8. Palmqvist, P. & Arribas, A. Taphonomic decoding of the paleobiological information locked
654 in a Lower Pleistocene assemblage of large mammals. *Paleobiology* **27**, 512–530 (2001).
- 655 9. Espigares, M. P. *Análisis y modelización del contexto sedimentario y los atributos*
656 *tafonomícos de los yacimientos pleistocénicos del borde nororiental de la cuenca de Guadix-*
657 *Baza*. (PhD dissertation thesis, University of Granada, 2010).
- 658 10. Palmqvist, P. *et al.* The giant hyena *Pachycrocuta brevirostris*: modelling the bone-
659 cracking behavior of an extinct carnivore. *Quat. Int.* **243**, 61–79 (2011).
- 660 11. Martínez-Navarro, B., Ros-Montoya, S., Espigares, M. P., Madurell-Malapeira, J. &
661 Palmqvist, P. Los mamíferos del Plioceno y Pleistoceno de la Península Ibérica. *Revista PH*
662 **94**, 206–249 (2018).
- 663 12. Anadón, P., Julià, R., de Deckker, P., Rosso, J.C. & Soulié-Märsche, I. Contribución a
664 la Paleolimnología del Pleistoceno inferior de la cuenca de Baza (sector Orce-Venta
665 Micena). *Paleontología i Evolució, Spec. Mem.* 35–72 (1987).
- 666 13. Arribas, A. *Análisis y Modelización de la Tafonomía del Yacimiento de Venta Micena*
667 *(Orce, Granada) y su estudio comparativo con otras localidades españolas del Plio-*
668 *Pleistoceno continental*. (PhD dissertation thesis, Universidad Complutense de Madrid,
669 1999).
- 670 14. Hendrichs, H. Schätzungen der Huftier-Biomasse in der Dornbusch-Savanne nördlich
671 und westlich der Serengeti-Steppe in Ostafrika nach einem neuen Verfahren und
672 Bemerkungen zur Biomasse der anderen pflanzenfressenden Tierarten. *Säugetierk. Mitt.*
673 **18**, 237–255 (1970).
- 674 15. Schaller, G. B. *The Serengeti lion*. (Chicago University of Chicago Press, 1972).
- 675 16. Kuhn, B. F, Berger, L. R. & Skinner, J. D. Examining criteria for identifying and
676 differentiating fossil faunal assemblages accumulated by hyenas and hominins using extant
677 hyenid accumulations, *Int. J. Osteoarchaeol.* **20**, 15–35 (2010).
- 678 17. Cruz-Urbe, K. Distinguishing hyena from hominid bone accumulations. *J. Field Archaeol.*
679 **18**, 467–486 (1991).
- 680 18. Behrensmeier, A.K. Taphonomic and ecologic information from bone weathering.
681 *Paleobiology* **4**, 150–162 (1978).
- 682 19. Palmqvist, P., Arribas, A. & Martínez-Navarro, B. Ecomorphological study of large canids
683 from the Lower Pleistocene of southeastern Spain. *Lethaia* **32**, 75–88 (1999).

- 684 20. Martinez-Navarro, B. *et al.* A new species of dog from the Early Pleistocene site of Venta
685 Micena (Orce, Baza Basin, Spain). *C. R. Palevol* **20**, 297–314 (2021).
- 686 21. Hofer, H. & East, M. L. The commuting system of Serengeti spotted hyaenas: how a
687 predator copes with migratory prey. II. Intrusion pressure and commuters' space use. *An.*
688 *Behav.* **46**, 559–574 (1993).
- 689 22. Boydston, E.E., Kapheim, K.M. & Holekamp, K.E. Patterns of den occupation by the
690 spotted hyaena (*Crocuta crocuta*)., *Afr. J. Ecol.* **44**, 77–86 (2006).
- 691 23. Pales, L. & Lambert, C. Atlas ostéologique des mammifères I, herbivores et carnivores.
692 (Paris CNRS, 1971).
- 693 24. Schmid, E. *Atlas of animals bones for prehistorians archaeologist and quaternary*
694 *geologists.* (Amsterdam Elsevier, 1972).
- 695 25. Barone, R. *Anatomie comparée des mammifères domestiques, T. 1 Osteologie.* (Paris
696 Vigot Frères, 1976).
- 697 26. Pales, L. & Garcia, M.A. *Atlas ostéologique des mammifères II, carnivores et homme,*
698 *herbivores.* (Paris CNRS, 1981).
- 699 27. Brain, C.K. *The hunters or the hunted? An introduction to African cave taphonomy.*
700 (Chicago University of Chicago Press, 1981).
- 701 28. Bunn, H.T. *Meat-eating and human evolution: studies on the diet and subsistence*
702 *patterns of Plio-Pleistocene hominds in East Africa.* (PhD dissertation thesis, University of
703 California Berkeley, 1982).
- 704 29. Brain, C.K. The contribution of Namib Desert Hottentots to an understanding of
705 australopithecine bone accumulation. *Sci. Pap. Namib Desert Res. Stat.* **39**, 13–22 (1969).
- 706 30. Lyman, R.L. *Vertebrate Taphonomy.* (New York Cambridge University Press, 1994).
- 707 31. Reitz, E. & Wing, E.S. *Zooarchaeology.* (New York Cambridge University Press, 1999).
- 708 32. Haynes, G. Evidence of carnivore gnawing on Pleistocene and recent mammalian
709 bones. *Paleobiology* **6**, 341–351 (1980).
- 710 33. Binford, L.R. *Bones: Ancient Men and Modern Myths.* (New York Academic Press,
711 1981).
- 712 34. Shipman, P. Early hominids lifestyle: hunting and gathering or foraging and scavenging
713 in *Animals and Archaeology, vol 1: Hunters and their Prey* (eds. Clutton-Brock, J. & Grigson,
714 C.). BAR ser. **163**, 31–49 (1983).
- 715 35. Blumenschine, R.J. Percussion marks, tooth marks, and experimental determination of
716 the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai
717 Gorge, Tanzania. *J. Hum. Evol.* **29**, 21–51 (1995).
- 718 36. Capaldo, S.D. & Blumenschine, R.J. A quantitative diagnosis of notches made by
719 hammerstone percussion and carnivore gnawing on bovid long bones. *Am. Antiq.* **59**, 724–
720 748 (1994).
- 721 37. Blumenschine, R.J. & Marean, C.W., Capaldo, S.D. Blind test of interanalyst
722 correspondence and accuracy in the identification of cut marks, percussion marks, and
723 carnivore tooth marks on bone surfaces. s.l. *J. Archaeol. Sci.* **23**, 493–507 (1996).
- 724 38. Villa, P. & Mahieu, E. Breakage patterns of human long bones. *J. Hum. Evol.* **21**, 27–
725 48 (1991).
- 726 39. Fiorillo, A.R. Taphonomy of Hazard Homestead Quarry (Ogallala Group), Hitchcock
727 County, Nebraska. *Contributions to Geology Univ. Wyoming* **26**, 57–97 (1988).
- 728 40. Fernández-Jalvo, Y. & Andrews, P. Experimental effects of water abrasion on bone
729 fragments. *J. Taphon.* **1**, 147–163 (2003).
- 730 41. Howell, D.C. Chi-Square Test: Analysis of Contingency Tables. [ed.] M. Lovric. s.l.:
731 Springer-Verlag, Heidelberg, *International Encyclopedia of Statistical Science*, 250–253.
732 (2011).
- 733 42. Marshall, F. & Pilgram, T. NISP vs. MNI in quantification of body-part representation.
734 *Am. Antiq.* **58**, 261–269 (1993).

735 43. Rodríguez-Gómez, G., Palmqvist, P., Ros-Montoya, S., Espigares, M.P. & Martínez-
736 Navarro, B. Resource availability and competition intensity in the carnivore guild of the
737 Early Pleistocene site of Venta Micena (Orce, Baza Basin, SE Spain). *Quat. Sci. Rev.* **164**,
738 154–167 (2017).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [TaphonomyofVM4SupplementaryInformation.pdf](#)