5 TAPHONOMIC STUDY OF THE LOWER PLEISTOCENE SITE OF TSIOTRA VRYSSI (MYGDONIA BASIN, GREECE): PRELIMINARY RESULTS ON BONE MODIFICATIONS IN EQUID CARCASSES

Anastasia Katsagoni[1, *], George E. Konidaris[2], Domenico Giusti[2], George D. Koufos[1], Dimitris S. Kostopoulos[1], Katerina Harvati[2,3]

[1]*Laboratory of Geology and Palaeontology, School of Geology, Aristotle University of Thessaloniki, Thessaloniki, Greece*
[2]*Paleoanthropology, Institute for Archaeological Sciences and Senckenberg Centre for Human Evolution and Palaeoenvironment, Department of Geosciences, Eberhard Karls University of Tübingen, Tübingen, Germany*
[3]*DFG Centre for Advanced Studies 'Words, Bones, Genes, Tools', Eberhard Karls University of Tübingen, Tübingen, Germany*
**anastasiakat221@gmail.com*

http://dx.doi.org/10.15496/publikation-97671

Keywords: taphonomy; tooth marks; *Equus*; late Villafranchian; carnivores

5.1 INTRODUCTION

The fossiliferous site of Tsiotra Vryssi (TSR; Mygdonia Basin, Greece) is dated to the Lower Pleistocene, between 1.78 and 1.5 Ma, and has yielded a rich late Villafranchian vertebrate fauna, including diverse medium- to very large-sized herbivores (equids, bovids, cervids, giraffids, rhinocerotids, elephantids) and several large carnivorans (hyaenids, canids, ursids, felids) (Konidaris et al., 2015, 2021). Previous spatial taphonomic research has investigated the distribution of the TSR fossils and suggested multiple dispersion events and recurrent spatial rearrangement of a lag, (peri)autochthonous assemblage within a fluvial system (Giusti et al., 2019). Herein, we present preliminary results of our ongoing taphonomic study on carnivore modifications, and we focus on equid postcranial bones, which comprise the bulk of the TSR vertebrate assemblage. For the analysis, we perform a set of standard taphonomic analyses, following the "physical attribute approach" of Domínguez-Rodrigo et al. (2007, 2015a), in which the alterations in the physical attributes of skeletal elements constitute the major component for the interpretation of the taphonomic history of the assemblage. Therefore, besides the skeletal part representation, we focus here on bone surface modifications and bone damage patterns aiming to reveal the main biotic agent responsible for the modification of bones.

5.2 MATERIALS AND METHODS

The studied material comprises all postcranial elements from TSR attributed to the genus *Equus*, which were collected during the excavation seasons of 2014–2019. All specimens are stored at the Mu-

A. Katsagoni: https://orcid.org/0000-0002-8510-6941
G. E. Konidaris: https://orcid.org/0000-0002-7041-233X
D. Giusti: https://orcid.org/0000-0003-1438-4036
G. D. Koufos: https://orcid.org/0000-0001-9669-4884
D. S. Kostopoulos: https://orcid.org/0000-0002-5475-5666
K. Harvati: https://orcid.org/0000-0001-5998-4794

seum of Geology, Palaeontology and Palaeoanthropology of the Aristotle University of Thessaloniki (LGPUT).

Equus is represented at TSR by two species, one of medium and one of large size (Konidaris et al., 2015; Gkeme et al., this volume). Body mass estimations were conducted separately for the medium- and the large-sized species, following the methodology of Eisenmann and Sondaar (1998). For this, we considered only metapodials belonging to articulated limbs that could be confidently classified either as subadult juvenile or adult individuals. This classification was based on the sequence of epiphyseal fusion in modern horses, and in particular, the fusion of the distal epiphysis in the radius (for metacarpals), and the distal epiphysis in the tibia (for metatarsals), which fuse towards the end of the epiphyseal bone fusing sequence (Budras et al., 2011) and are abundant in the articulated elements of the assemblage.

Skeletal part representation was examined by calculating the number of identified specimens (NISP), the minimum number of elements (MNE), and the minimum animal units (MAU). MNE calculations take into consideration anatomical overlap of fragments, size, and ontogenetic age. The minimum number of individuals (MNI) was calculated as well.

The nature of fractures was studied following the methodology of Villa and Mahieu (1991), where fracture angle, outline, and edge are considered. Fresh fractures are generally characterized by oblique angles, curved outlines, and smooth edges, whereas dry fractures generally have right angles, transverse outlines, and jagged edges.

Bone damage patterns are quantified using the classification of long limb bones into “taphotypes” (Domínguez-Rodrigo et al., 2015b: Fig. 1). Each long limb bone is classified into one of the 16 taphotypes (0–15), depending on its preserved portion. Additionally, regression analysis was used to study the correlation of epiphyses abundance with marrow cavity volume and bone density (as in Palmqvist and Arribas, 2001). The data for marrow cavity volume and bone density concerns modern horses and is taken from Outram and Rowley-Conwy (1998) and Lam et al. (1999), respectively.

Carnivore tooth marks were classified into pits, punctures, scores, and furrows, following the criteria set by Pobiner (2007); recorded carnivore damage also includes notches and furrowing (deletion of cancellous bone). Identified tooth marks were measured with a digital caliper to the nearest 1/100 of a millimeter, directly onto the bone surface, under strong light and magnification. The measurements taken are length (maximum dimension) and breadth (maximum dimension transversal to length).

5.3 RESULTS

The mean body mass is calculated at 257 kg for the medium-sized, and 343 kg for the large-sized *Equus* species. They both fall within the size group 4 (150–350 kg) of Palombo (2010), and therefore their skeletal elements are treated here collectively regardless of species attribution. NISP, MNE, and MAU values are given in Table 1. NISP values reveal a greater abundance of limb bones over other elements, while MNE and MAU values show a clear over-representation of tibiae and metapodials, and an under-representation of axial elements and femora. The minimum number of individuals (MNI) is 15.

Fracture variables suggest that most studied fractures occurred when the bones were still in a fresh state. Specifically, curved outlines appear in 67.9% of fractures, smooth edges in 69.8%, and oblique angles in 45.3%. Intermediate outlines and mixed angles are also relatively common (24.5 and 37.7%, respectively).

	NISP	MNE	MAU
Atlas	4	4	4
Axis	3	3	3
3th-7th cervical	14	14	3
Sacrum	1	1	1
Scapula	11	11	6
Pelvis	2	2	2
Humerus	11	11	6
Radius	11	10	5
Ulna	3	3	2
Metacarpal	25	25	13
Femur	7	7	4
Tibia	26	25	13
Metatarsal	23	22	11
Lateral metapodial	53	53	—
Carpals	61	61	—
Astragalus	14	14	7
Calcaneus	13	13	7
Other tarsals	39	39	—
Proximal phalanx	23	23	6
Intermediate phalanx	17	17	4
Distal phalanx	23	23	6
Sesamoids	47	47	—
Metapodial	6	—	—
Total	437	—	—

Table 1: NISP, MNE, and MAU values of *Equus* specimens in TSR.

The implementation of taphotypes (Domínguez-Rodrigo et al. 2015b: Fig. 1) allowes us to quantify the degree and pattern of bone damage in an assemblage. Metapodials from TSR usually belong to taphotype 1, i.e., complete bones (80.0% for metacarpals; 82.6% for metatarsals). On the contrary, taphotype 15, i.e., cylinder, is frequent in humeri (36.4%) and femora (42.9%). The radius frequently lacks the proximal epiphysis and part of the diaphysis (taphotypes 4 and 5; 27.3% and 18.2%, respectively), while complete radii are also relatively abundant (27.3%). Tibiae are rarely preserved complete, with the majority retaining only the distal half, or part of it (26.9% for taphotypes 4 and 5 each). Such a deletion of epiphyses appears to be non-random, rather it shows a degree of selectivity. This pattern is further supported by the regression analysis of abundance of epiphyses with bone marrow content and bone density. There appears to be a statistically significant inverse relationship between abundance of epiphyses and bone marrow content (Fig. 1A), i.e., high-nutritional value epiphyses are missing, and conversely less nutritious epiphyses are preserved. Accordingly, the abundance of epiphyses displays a strong positive correlation with bone mineral density (R^2=0.80),

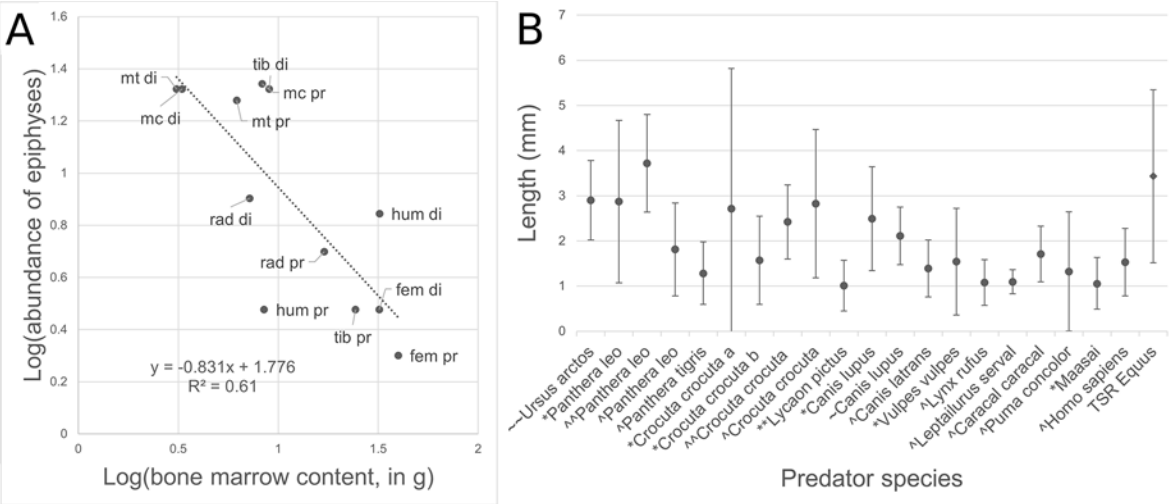

Figure 1: A, Regression analysis between abundance of epiphyses in the *Equus* specimens from TSR and bone marrow content in modern horses (data from Outram and Rowley-Conwy, 1998). B, Mean values and standard deviation intervals of pit length on the diaphysis. Data from: ~~ Domínguez-Rodrigo and Piqueras (2003), * Andrés et al. (2012), ^^ Sala et al. (2012), ^ Delaney-Rivera (2009), ** Yravedra et al. (2014) and ~ Sala et al. (2014), in comparison with *Equus* from TSR.

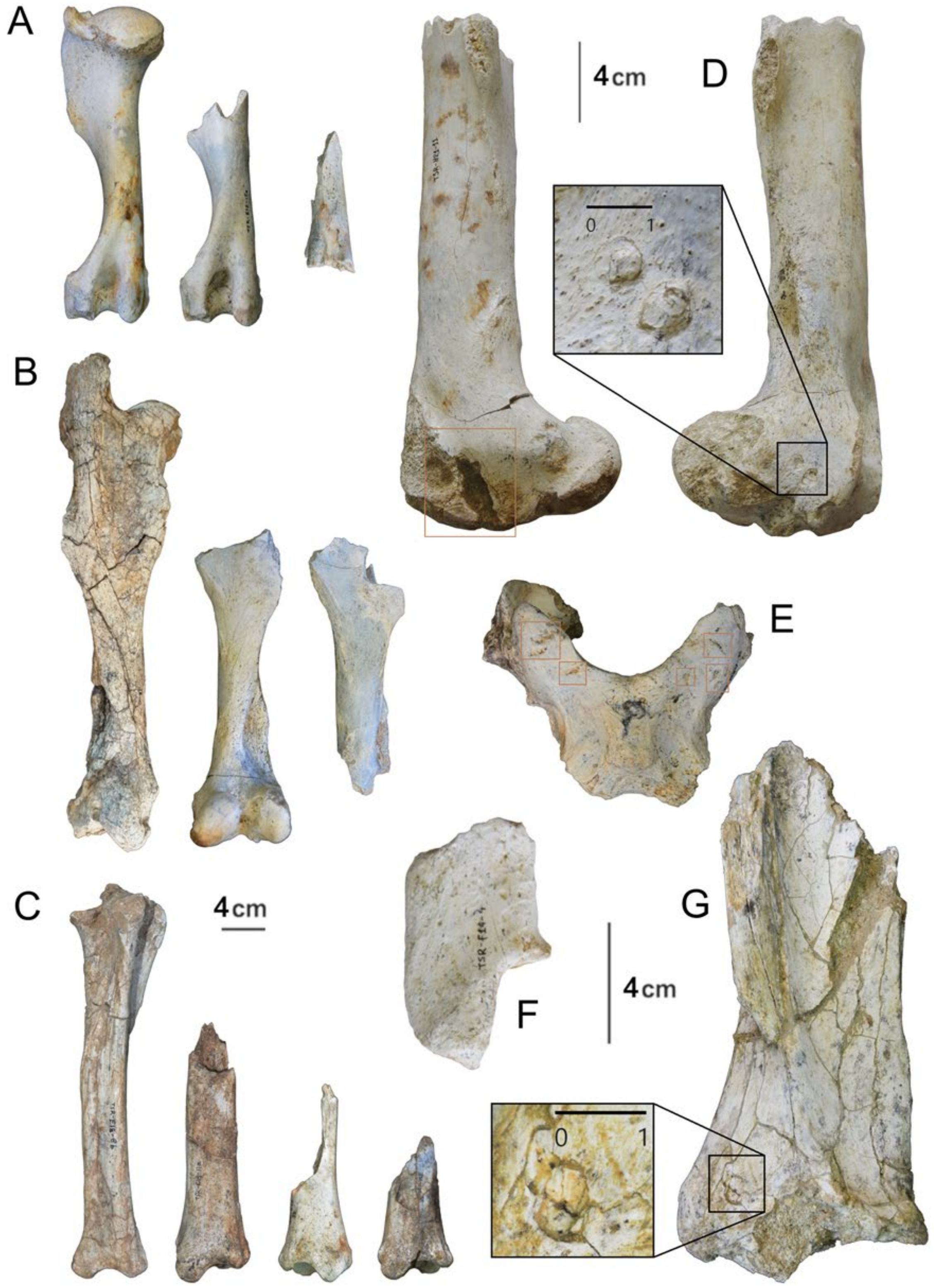

Figure 2: Left: Bone consumption sequence in humerus (A), femur (B), and tibia (C) in the TSR equid assemblage. Right: Examples of carnivore modifications in equid bones: Femur with furrowing and punctures (D), atlas with furrowing, scores, and pits (E), calcanei with furrowing (F), and scapula with jagged edges with a crenulated outline, and puncture (G).

i.e., epiphyses with high mineral density are over-represented.

Carnivore modifications are frequent in the assemblage (Fig. 2), usually in the form of tooth marks, as well as furrowing and notches. The higher percentages of modified elements, displaying any type of carnivore alteration, are recorded in femora (85.7%) and humeri (72.7%); most tibiae (69.2%) are modified as well. Among long limb bones, the least modified elements are metacarpals (16.0%), while metatarsals and radio-ulnae also display relatively low percentages of modification (30.4 and 36.4%, respectively).

Regarding tooth marks, 475 pits, 201 scores, and 12 punctures were recorded. In Figure 1B the mean and standard deviation values of pit length on the diaphysis from TSR are plotted along data from studies conducted with extant predators. The TSR values are comparable to those of some of the largest modern carnivorans, such as lions, hyaenas, and grey wolves. Additionally, a relatively wide range is observed, with the upper limit surpassing that of almost all modern species.

5.4 DISCUSSION

The bone damage patterns in the studied material reveal a significant involvement of carnivorans in the modification of the *Equus* remains from the TSR accumulation. There appears to be preferential deletion of nutrient-dense (with high marrow yield) elements, such as the upper limb bones and axial elements, as well as bone portions, i.e., proximal epiphysis in the humerus, tibia, and radius, and both epiphyses in the femur. Moreover, most fractures are green indicating that the deletion of the aforementioned portions occurred when bones were still fresh and not later during the diagenetic process. Carnivore modification is frequent, especially in the upper limb bones, the majority of which bear tooth marks. The most frequent tooth marks are pits, and their dimensions suggest that they were inflicted by a large-sized carnivoran (Fig. 1B).

Several large carnivorans have been found to date at TSR: the ursid *Ursus etruscus*, the hyaenid *Pachycrocuta brevirostris*, the felid *Megantereon* sp., and several *Canis* sp. morphotypes (two medium- and one large-sized) (Konidaris et al., 2015, 2021; Koufos et al., 2018, Karakosta et al., this volume), while the large carnivoran late Villafranchian fauna of the Mygdonia Basin additionally includes the felids *Panthera gombaszoegensis* and *Homotherium latidens* (Koufos, 2014, 2018). *Ursus etruscus* is regarded an omnivorous carnivoran that consumed both plant and vertebrate matter, the latter possibly consisting mainly of fish (Medin et al., 2017); therefore, it can be rather safely excluded as a candidate for inflicting the heavy bone modifications observed at TSR. Additionally, the level of epiphyseal furrowing and bone deletion (including diaphyseal fragmentation) at TSR is incompatible with a predominantly felid modification. Extant pantherine felids cause generally limited and targeted furrowing in medium/large carcasses, while they usually produce minor/moderate bone deletion (e.g., Pobiner and Blumenschine, 2003; Domínguez-Rodrigo et al., 2012; Rodríguez-Alba et al., 2019; Pobiner et al., 2020), and the same can be hypothesized for the large felids present at TSR. Specifically regarding sabre-tooths, it is suggested that their dental morphology would not allow them to thoroughly exploit carcasses, and therefore cause significant bone modifications (e.g., Valkenburgh and Ruff, 1987; Palmqvist et al., 2011, and references cited therein); but see Marean and Ehrhardt (1995) for *Homotherium* tooth-marking. Modern wolves have the capacity to fracture ungulate bones; however, in wild populations, significant deletion of bone portions is rare in large-sized carcasses and is mainly observed in small-sized prey and medium-sized juvenile carcasses (Haynes, 1982; Yravedra et al., 2011). On the contrary, the

African wild dog is a flesh specialist that causes limited to moderate bone alteration, in particular in terms of bone deletion (Yravedra et al., 2014). Modern hyaenas are by far the most destructive of the extant carnivorans. Hyaena modified assemblages are characterized by an under-representation of axial elements (Binford, 1981; Capaldo, 1998), and high levels of fragmentation of limb bones (Haynes, 1983; Hill, 1989; Domínguez-Rodrigo et al., 2015b). Remarkably, the giant hyaena *Pachycrocuta brevirostris* possessed craniodental adaptations that reveal even greater bone cracking capabilities (Palmqvist et al., 2011). In Venta Micena (Spain; Lower Pleistocene), regarded as a bone accumulation site of *Pachycrocuta*, a preferential deletion of epiphyses in relation to their marrow/fat content and mineral density has been observed, reflected in the consumption sequence of limb elements (Palmqvist et al., 2011, and references cited therein). Specifically, the sequence of consumption is proximodistal in the humerus and tibia, distoproximal in metapodials, and without a clear direction in the femur and radius, but involving the deletion of both epiphyses (Palmqvist et al., 2011). Such a sequence of bone portion consumption, in addition to the degree of bone deletion (Palmqvist and Arribas, 2001: Fig. 2) are common attributes between Venta Micena and TSR.

5.5 CONCLUSIONS

The preliminary taphonomic study on the bone modifications in equid postcranial bones from TSR reveals high levels of gross bone damage and tooth marking, indicating that the main biotic taphonomic signal of the assemblage reflects the action of a large carnivoran that engaged in the intensive exploitation of large ungulate carcasses, similarly to modern hyaenas. Therefore, the study points towards the hyaena *Pachycrocuta brevirostris* (identified at the site) as the primary biotic agent of bone modifications at TSR. This is further corroborated by the similarities with the *Pachycrocuta* bone accumulation site Venta Micena in terms of the preferential deletion of epiphyses with high nutrient content, the degree of bone deletion, and the sequence of bone portion consumption. However, the involvement, even to a minor degree, of other contemporaneous large carnivorans in the alternation of bones cannot be completely ruled out. In order to achieve a more conclusive interpretation of the taphonomic history of TSR, future study directions will focus on the inclusion of the other ungulate size groups, the consideration of additional parameters (e.g., levels of articulation, tooth mark spatial distribution, notches), the investigation of the ontogenetic age profiles, and the examination of the coprolites found at the site.

ACKNOWLEDGMENTS

Excavation at TSR was supported by the ERC Consolidator Grant ERC-CoG-724703 (“CROSSROADS”) and the ERC Starting Grant ERC-StG-283503 (“PaGE”), both awarded to K.H. G.E.K. and K.H. are supported by the Deutsche Forschungsgemeinschaft (DFG Project no. 463225251, “MEGALOPOLIS”). K.H. is also supported by the ERC Advanced Grant ERC-AdG-101019659 (“FIRSTSTEPS”). Research of A.K. at the University of Tübingen was supported by the Erasmus+ exchange program. We thank the reviewers, E. Tsoukala and G. Iliopoulos, for their comments and suggestions.

REFERENCES

Andrés, M., Gidna, A.O., Yravedra, J. and Domínguez-Rodrigo, M., 2012. A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. Archaeological and Anthropological Sciences, 4, pp. 209–219.

Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.

Budras, K.D., Sack, W.O. and Röck, S., 2011. Anatomy of the Horse. Schlütersche, Hannover.

Capaldo, S.D., 1998. Simulating the formation of dual-patterned archaeofaunal assemblages with experimental control samples. Journal of Archaeological Science, 25(4), pp. 311–330.

Delaney-Rivera, C., Plummer, T.W., Hodgson, J.A., Forrest, F., Hertel, F. and Oliver, J.S., 2009. Pits and pitfalls: taxonomic variability and patterning in tooth mark dimensions. Journal of Archaeological Science, 36(11), pp. 2597–2608.

Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. Journal of Archaeological Science, 30(11), pp. 1385–1391.

Domínguez-Rodrigo, M., Egido, R.B. and Egeland, C.P., 2007. Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites. Springer, Dordrecht.

Domínguez-Rodrigo, M., Gidna, A.O., Yravedra, J. and Musiba, C., 2012. A comparative neo-taphonomic study of felids, hyaenids and canids: an analogical framework based on long bone modification patterns. Journal of Taphonomy, 10, pp. 151–169.

Domínguez-Rodrigo, M., Barba, R., Soto, E., Sesé, C., Santonja, M., Pérez-González, A., Yravedra and J., Galán, A.B., 2015a. Another window to the subsistence of Middle Pleistocene hominins in Europe: A taphonomic study of Cuesta de la Bajada (Teruel, Spain). Quaternary Science Reviews, 126, pp. 67–95

Domínguez-Rodrigo, M., Yravedra, J., Organista, E., Gidna, A., Fourvel, J.B. and Baquedano, E., 2015b. A new methodological approach to the taphonomic study of paleontological and archaeological faunal assemblages: a preliminary case study from Olduvai Gorge (Tanzania). Journal of Archaeological Science, 59, pp. 35–53.

Eisenmann, V., Sondaar, P., 1998. Pliocene vertebrate locality of Çalta, Ankara, Turkey. 7. *Hipparion*. Geodiversitas, 20, pp. 409–439.

Giusti, D., Konidaris, G.E., Tourloukis, V., Marini, M., Maron, M., Zerboni, A., Thompson, N., Koufos, G.D., Kostopoulos, D.S. and Harvati, K., 2019. Recursive anisotropy: a spatial taphonomic study of the Early Pleistocene vertebrate assemblage of Tsiotra Vryssi, Mygdonia Basin, Greece. Boreas, 48(3), pp. 713–730.

Gkeme, A.G., Koufos, G.D., Kostopoulos, D.S. and Harvati, K., this volume. The Late Villafranchian equids from the locality Tsiotra Vryssi (Mygdonia Basin, Macedonia, Greece).

Haynes, G., 1982. Utilization and skeletal disturbances of North American prey carcasses. ARCTIC, 35, pp. 266–281.

Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology, 9(2), pp. 164–172.

Hill, A., 1989. Bone modification by modem spotted hyenas, in: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, Orono, Maine, pp. 169–178.

Karakosta, A., Konidaris, G.E., Kostopoulos, D.S., Koufos, G.D. and Harvati, K., this volume. Preliminary study of the canids from the Lower Pleistocene site of Tsiotra Vryssi (Mygdonia Basin, Greece).

Konidaris, G.E., Tourloukis, V., Kostopoulos, D.S., Thompson, N., Giusti, D., Michailidis, D., Koufos, G.D. and Harvati, K., 2015. Two new vertebrate localities from the Early Pleistocene of Mygdonia Basin (Macedonia, Greece): Preliminary results. Comptes Rendus Palevol, 14(5), pp. 353–362.

Konidaris, G.E., Kostopoulos, D.S., Maron, M., Schaller, M., Ehlers, T.A., Aidona, E., Marini, M., Tourloukis, V., Muttoni, G., Koufos, G.D. and Harvati, K., 2021. Dating of the Lower Pleistocene vertebrate site of Tsiotra Vryssi (Mygdonia Basin, Greece): biochronology, magnetostratigraphy, and cosmogenic radionuclides. Quaternary, 4(1), pp. 1–18.

Koufos, G.D., 2014. The Villafranchian carnivoran guild of Greece: implications for the fauna, biochronology and paleoecology. Integrative Zoology, 9(4), pp. 444–460.

Koufos, G.D., 2018. New material and revision of the Carnivora, Mammalia from the Lower Pleistocene locality Apollonia 1, Greece. Quaternary, 1(6), pp. 1–38.

Koufos, G.D., Konidaris, G.E. and Harvati, K., 2018. Revisiting *Ursus etruscus* (Carnivora, Mammalia) from the Early Pleistocene of Greece with description of new material. Quaternary International, 497, pp. 222–239.

Lam, Y.M., Chen, X. and Pearson, O.M., 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. American Antiquity, 64(2), pp. 343–362.

Marean, C.W., Ehrhardt, C.L., 1995. Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth's den. Journal of Human Evolution, 29(6), pp. 515–547.

Medin, T., Martínez-Navarro, B., Rivals, F., Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Figueirido, B., Rook, L. and Palmqvist, P., 2017. Late Villafranchian *Ursus etruscus* and other large carnivorans from the Orce sites (Guadix-Baza basin, Andalusia, southern Spain): Taxonomy, biochronology, paleobiology, and ecogeographical context. Quaternary International, 431, pp. 20–41.

Outram, A., Rowley-Conwy, P., 1998. Meat and marrow utility indices for horse (*Equus*). Journal of Archaeological Science, 25(9), pp. 839–849.

Palmqvist, P., Arribas, A., 2001. Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. Paleobiology, 27(3), pp. 512–530.

Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J.A., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J.M., Espigares, M.P., Ros-Montoya, S. and De Renzi, M., 2011. The giant hyena *Pachycrocuta brevirostris*: Modelling the bone-cracking behavior of an extinct carnivore. Quaternary International, 243(1), pp. 61–79.

Palombo, M.R., 2010. A scenario of human dispersal in the northwestern Mediterranean throughout the Early to Middle Pleistocene. Quaternary International, 223–224, pp. 179–194.

Pobiner, B.L., 2007. Hominin-carnivore interactions: Evidence from modern carnivore bone modification and Early Pleistocene archaeofaunas (Koobi Fora, Kenya; Olduvai Gorge, Tanzania). Rutgers University, New Brunswick.

Pobiner, B.L., Blumenschine, R.J., 2003. A taphonomic perspective on Oldowan hominid encroachment on the carnivoran paleoguild. Journal of Taphonomy, 1(2), pp. 115–141.

Pobiner, B., Dumouchel, L. and Parkinson, J., 2020. A new semi-quantitative method for coding carnivore chewing damage with an application to modern African lion-damaged bones. Palaios, 35(7), pp. 302–315.

Rodríguez-Alba, J.J., Linares-Matás, G. and Yravedra, J., 2019. First assessments of the taphonomic behaviour of jaguar (*Panthera onca*). Quaternary International, 517, pp. 88–96.

Sala, N., Algaba, M., Arsuaga, J., Aranburu, A.

and Pantoja-Pérez, A., 2012. A taphonomic study of the Búho and Zarzamora caves. Hyenas and humans in the Iberian Plateau (Segovia, Spain) during the Late Pleistocene. Journal of Taphonomy, 10(3–4), pp. 477–497.

Sala, N., Arsuaga, J.L., Haynes, G., 2014. Taphonomic comparison of bone modifications caused by wild and captive wolves (*Canis lupus*). Quaternary International, 330, pp. 126–135.

van Valkenburgh, B., Ruff, C.B., 1987. Canine tooth strength and killing behaviour in large carnivores. Journal of Zoology, 212(3), pp. 379–397.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. Journal of Human Evolution, 21(1), pp. 27–4.

Yravedra, J., Lagos, L. and Bárcena, F., 2011. A taphonomic study of wild wolf (*Canis lupus*) modification of horse bones in Northwestern Spain. Journal of Taphonomy, 9(1), pp. 37–65.

Yravedra, J., Andrés, M. and Domínguez-Rodrigo, M., 2014. A taphonomic study of the African wild dog (*Lycaon pictus*). Archaeological and Anthropological Sciences, 6, pp. 113–124.