

Recursive anisotropy: A spatial taphonomic study of the Early Pleistocene vertebrate assemblage of Tsiotra Vryssi, Mygdonia Basin, Greece

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Abstract

By applying advanced spatial statistical methods, spatial taphonomy complements the traditional taphonomic approach and enhances our understanding of biostratigraphic and diagenetic processes. In this study, we elaborate on a specific aspect - spatial anisotropy - of taphonomic processes. We aim to unravel the taphonomic history of the Early Pleistocene vertebrate assemblage of Tsiotra Vryssi (Mygdonia Basin, Macedonia, Greece). Circular statistics are used for the fabric analysis of elongated elements; geostatistics (directional variograms), wavelet and point pattern analyses are applied for detecting anisotropy at the assemblage level. The anisotropy of magnetic susceptibility (AMS) of sedimentary magnetic minerals is as well investigated. The results of our analyses, integrated with preliminary remarks about the differential preservation of skeletal elements, sedimentological and micromorphological observations, suggest multiple dispersion events and recurrent spatial re-arrangement of a lag, (peri)autochthonous assemblage, consistent with the cyclical lateral switching of a braided fluvial system. Furthermore, this study offers an important contribution to the building of a spatial taphonomic referential framework for the interpretation of other fossil vertebrate assemblages, including archaeo-palaeontological ones.

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1. Introduction

Since the first definition of taphonomy as “the study of the transition (in all its details) of animal remains from the biosphere into the lithosphere” (Efremov, 1940), the spatial properties of taphonomic processes received special attention. Concerned about thanatocoenosis, Efremov (1940) indicated as chief part of a taphonomic study, among others, the analysis of “the spatial distribution of animal remains and their distribution relatively to the planes of stratification”. More recent research on early hominid evolution (Behrensmeyer, 1975a; Boaz and Behrensmeyer, 1976; Hill, 1976) extended the original definition of taphonomy beyond its role as a “new branch of paleontology” (Efremov, 1940) to include also formation and modification processes of the archaeological record. Despite some misrepresentations in the archaeological adaptation of the original concept (e.g., the ontological difference between natural and cultural formation processes; Domínguez-Rodrigo et al., 2011; Lyman, 2010), in the last decades taphonomy has widened its theoretical and methodological framework towards an integrative and multidisciplinary investigation that aims to reconstruct the past in all its details, incorporating any signal of the processes, both natural and cultural, that modified the original properties of the organic and inorganic components (Domínguez-Rodrigo et al., 2011).

If taphonomy evolved towards an evolutionary and systemic approach that embraces multiple taphonomic levels of organisation (i.e., basic taphonomic elements, taphonomic groups [taphons], taphonomic populations and taphoclades; Fernández-López, 2006), likewise, the study of the spatial properties of taphonomic processes extended from the analysis of the spatial distribution of animal remains in relation to the stratigraphic setting, towards a multilevel quantitative investigation of the spatial behaviour of different taphonomic entities (*sensu* Fernández-López, 2006). Therefore, spatial taphonomy (Domínguez-Rodrigo et al., 2017; Giusti and Arzarello, 2016), encompasses the spatial properties of basic entities (i.e., taphonomic elements, constitut-

28 ing the fossil record), as well as higher level entities (e.g., taphonomic groups or pop-
29 ulations). Indeed, at multiple scales and levels of organisation, the spatial patterns ob-
30 served in any palaeontological or archaeological assemblage retain valuable informa-
31 tion about taphonomic accumulation and re-elaboration processes (*sensu* [Fernández-](#)
32 [López et al., 2002](#)). Spatial taphonomic data, appropriately recorded, can be quantita-
33 tively analysed within a statistical framework in order to reliably draw inferences about
34 taphonomic processes, in turn with consequences for palaeoecological reconstructions
35 ([Fernández-Jalvo et al., 2011](#)), biochronological estimates and the interpretation of past
36 human behaviours.

37 In this study, we elaborate on a specific aspect - anisotropy - of the spatial prop-
38 erties of taphonomic entities, with implications for the interpretation of taphonomic
39 processes. Anisotropy, as opposed to isotropy, is generally defined as the property of
40 a process of being directionally dependent. Spatial anisotropic patterns can be seen as
41 products of physical anisotropic processes, such as fluvial or eolian processes, which
42 modified at multiple scales and levels of organisation the original spatial properties of
43 taphonomic entities.

44 At the level of basic taphonomic elements, anisotropy, expressed as preferential
45 orientation of fossils or artefacts, is among the key variables used for interpreting site
46 formation and modification processes. Especially in terrestrial alluvial environments,
47 anisotropy is one of the proxies traditionally used to discriminate autochthonous vs. al-
48 lochthonous assemblages ([Petraglia and Nash, 1987](#); [Petraglia and Potts, 1994](#); [Schick,](#)
49 [1987](#); [Toots, 1965](#); [Voorhies, 1969](#), among others). The orientation of elongated ele-
50 ments, prone to preferentially align along the flow direction, would eventually indicate
51 the action of water-flows and suggest substantial transport prior to burial. Nevertheless,
52 anisotropy has been equally documented in autochthonous assemblages subjected to
53 low-energy water-flows ([Cobo-Sánchez et al., 2014](#); [Domínguez-Rodrigo et al., 2012,](#)
54 [2014d](#)); hence, it can be a necessary but not sufficient condition to differentiate al-
55 lochthony from autochthony ([Lenoble and Bertran, 2004](#)). Moreover, besides water-
56 flow processes, anisotropy has been as well observed in association with a wide range
57 of other biostratinomic processes, such as slope processes ([Bertran and Texier, 1995](#))
58 and trampling ([Benito-Calvo et al., 2011](#)).

59 Although the anisotropy of basic taphonomic elements have been long studied,
60 the anisotropy of higher level taphonomic entities received by far less attention (see
61 [Markofsky and Bevan, 2012](#) for a directional analysis of archaeological surface distri-
62 butions). Here we address this research gap and conduct a spatial taphonomic study
63 of anisotropy both at the level of fossil specimens and at the assemblage level. The
64 present study uses a comprehensive set of spatial statistics (fabric analysis, geostatistics,
65 wavelet analysis, point pattern analysis) in order to identify directional trends that
66 may not be readily apparent. Indeed, beyond the traditional approach of eye-spotting
67 spatial patterns, spatial statistics allow one to adopt a more formal, quantitative ap-
68 proach.

69 Furthermore, at the scale of sedimentary particles, anisotropy is investigated by
70 means of anisotropy of magnetic susceptibility (AMS). AMS refers to the property of
71 elongated magnetic crystals to orient parallel to the flow direction when transported
72 as sedimentary clasts. In sedimentology, AMS analysis is widely applied in order
73 to determine paleoflows in a range of depositional environments, including turbidite
74 systems, contouritic drifts, beaches, deltas and tidal flats ([Felletti et al., 2016](#); [Liu et al.,](#)
75 [2001](#); [Lowrie and Hirt, 1987](#); [Novak et al., 2014](#); [Parés et al., 2007](#), among others).

76 Therefore, integrating the results of our multiscale and multilevel analysis of anisotropy
77 with preliminary remarks about differential taphonomic preservation, sedimentologi-
78 cal and micromorphological observations, we aim to disentangle the taphonomic his-
79 tory of the fossiliferous locality Tsiotra Vryssi (Mygdonia Basin, Macedonia, Greece;
80 [Konidaris et al., 2015](#)).

81 Finally, this study offers an important contribution to the building of a spatial tapho-
82 nomic referential framework for the interpretation of other fossil vertebrate assem-
83 blages, including archaeo-palaeontological ones ([Domínguez-Rodrigo et al., 2017](#)).

84 **2. The palaeontological site of Tsiotra Vryssi (TSR)**

85 Tsiotra Vryssi (TSR) is located in the Mygdonia Basin (Macedonia, Greece), about
86 45 km Southeast of Thessaloniki (Fig. 1). TSR was discovered in 2014 by a joint
87 research team from the Aristotle University of Thessaloniki and the Eberhard Karls

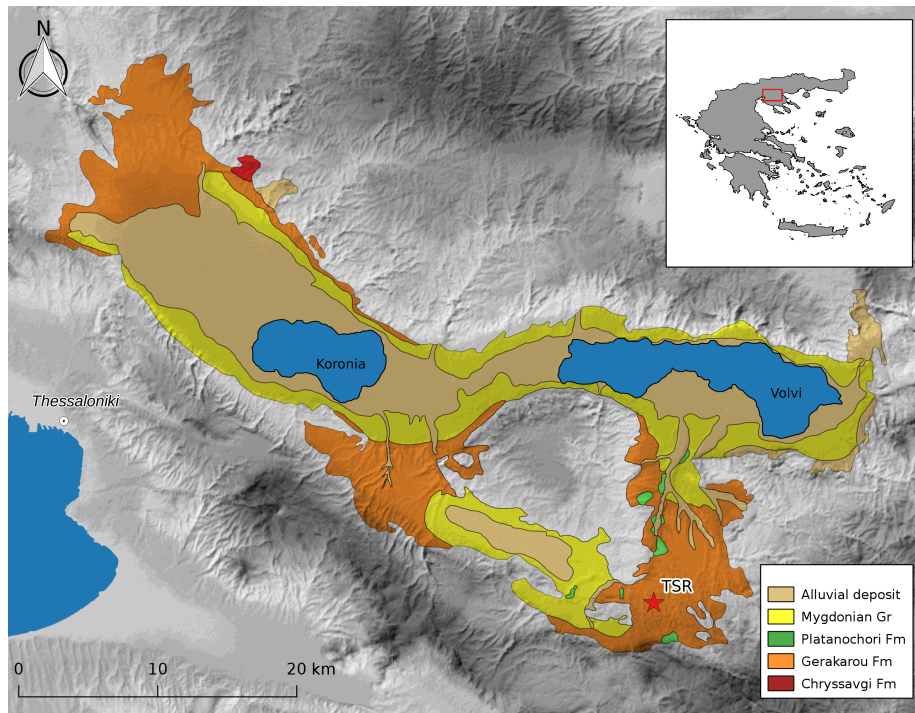


Figure 1: Geological setting of the Mygdonia Basin (Macedonia, Greece) showing the Neogene and Quaternary lithostratigraphic units and the location of Tsiotra Vryssi (TSR), modified after Koufos et al. (1995)

88 University of Tübingen during systematic field surveys in the basin. After the first
 89 collection of fossils from the exposed natural section and the test excavation carried
 90 out in 2014, systematic excavation of the site took place in 2015 and is still ongoing
 91 (Fig. 2a).

92 To date, the excavation covers about a 10 m-thick stratigraphic interval from the
 93 upper Gerakarou Formation (Fig. 1), a suite of continental clastic deposits of mainly
 94 fluvial origin and inter-layered paleosols (Konidaris et al., 2015; Koufos et al., 1995).
 95 The TSR fauna occurs mainly within a c. 1 m-thick interval of silts (uppermost part
 96 of unit Geo2, see Fig 3) and comprises several mammalian taxa, as well as some birds
 97 and reptiles, whose preliminary biochronological correlation is consistent with a late
 98 Villafranchian (Early Pleistocene) age (Konidaris et al., 2016, 2015).

99 Two main depositional units are identified (Geo 1 and Geo 2, from younger to older;

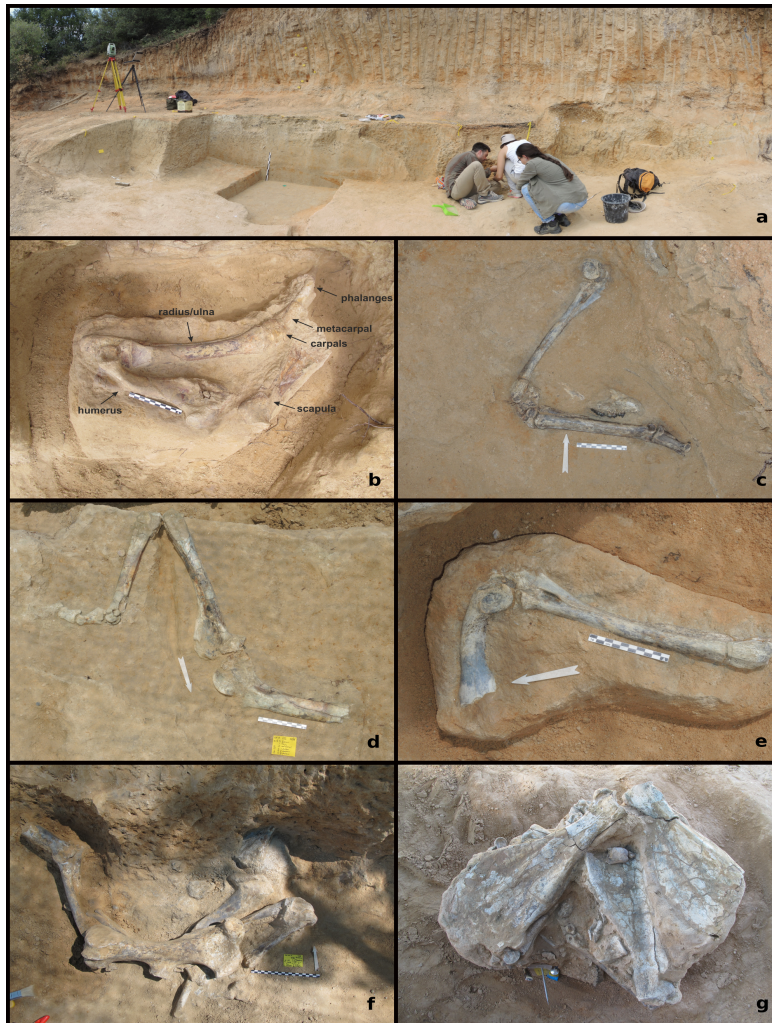


Figure 2: Panoramic view (2017) of the excavation area of Tsiotra Vryssi. Pictures of articulated specimens (a, b, c, d) and clusters of bones (e, f).

100 Fig. 3). The fossiliferous unit Geo 2 begins with ~1.5 m (Geo 2b in Fig. 3) of cross-
101 stratified gravelly sands organised into dm-thick beds with a range of planar to trough-
102 cross laminations. Noteworthy, Geo 2b can be followed laterally for at least 150m in the
103 E-W direction, suggesting an extensive setting of deposition. Above a sharp contact,
104 a few tens of cm of well-sorted, structure-less fine sands follow, which rapidly grade
105 upward into the deposit forming the matrix of the main TSR fossil assemblage (Geo
106 2a in Fig. 3). This is represented by ~1 m of poorly sorted silts (moderately rich in
107 mica grains), locally intercalated by cm-thick lenses of medium-coarse grained sands
108 and relatively more clayey in the uppermost 30 cm of the deposit. Apart for alignment
109 of isolated sand to granule grade clasts and some crude parallel lamination in coarse
110 lenses, the deposits appear overall structure-less. Typically, Geo 2a has a very pale
111 brown colour with a few (less than 10%) pink to reddish yellow mottles, whereas the
112 topmost part of Geo 2a has a strong brown to dark yellowish brown matrix with about
113 the 15-20% of reddish yellow mottles. This change in colour is associated with the
114 occurrence of very small calcareous nodules and common to abundant Mn-Fe-bearing
115 nodules with diameter less than 1 cm (see micromorphological analysis in Section 4.5).

116 Geo 1b is represented by an up to 2 m-thick bed set of cross-stratified gravelly
117 sands and gravels, similar to those observed in Geo 2b (Fig. 3). It sits on top of a basal
118 erosion, down-cutting deeply into older sediments (Geo 2a) and shallowing toward the
119 West. In the same direction, the Geo 1b beds tend to be thinner, finer grained and
120 less extensive laterally, suggesting less energetic hydrodynamic conditions. Though
121 poorly exposed, the younger Geo 1a is represented by a monotonous 3 m-thick section
122 of poorly silty sands devoid of coarse intercalations, which rapidly grades into clayey
123 silts of a distinctive pale brown colour.

124 Overall, the stratigraphic position of TSR in the fluvio-terrestrial Gerakarou Forma-
125 tion (Koufos et al., 1995) and the specific sedimentary sequence of the site indicate
126 that the TSR assemblage formed in a relatively low energy fluvial environment. A pre-
127 liminary visual inspection of the vertical and horizontal distribution of the fossil finds
128 (Fig. 4) suggests a densely preserved association of fossils (about 24 elements/m²), ho-
129 mogeneously distributed within the study area. Apparent anisotropy is also suggested
130 at assemblage level.

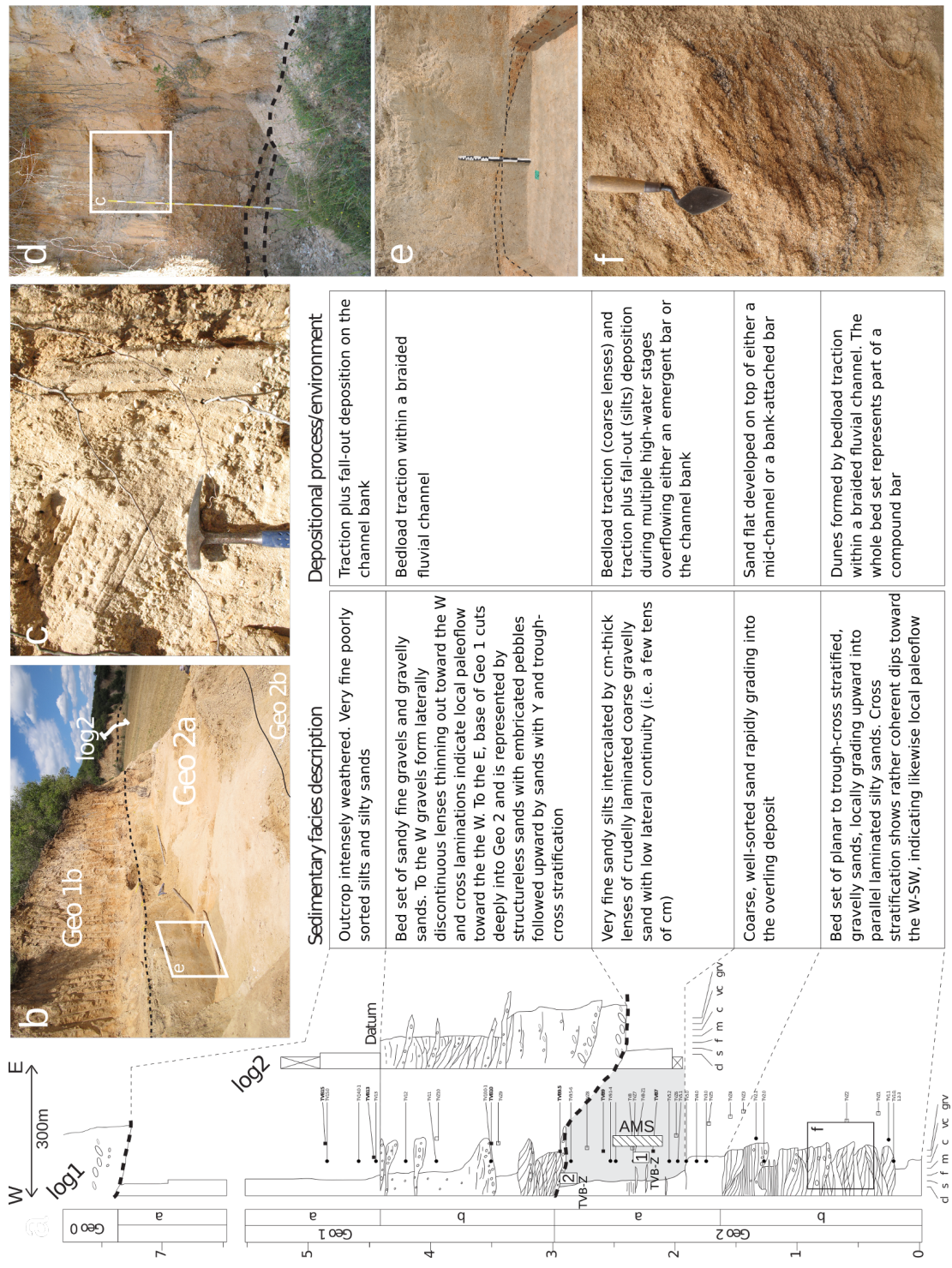


Figure 3. Stratigraphic sedimentary logs (log1 and log 2) with location of main erosional surfaces bounding depositional units Geo 1 and Geo 2, block samples TVB-Z 1 and 2 collected for micromorphology analysis and interval sampled for anisotropy of magnetic susceptibility analysis (AMS); b) WNW-ESE oriented panoramic view of the excavation site and location of the stratigraphic log2 in the background; c) and d) are details of the lower half of log2 showing the basal erosion of Geo 1b followed upward by inclined laminations; e) the middle part of Geo 2a (i.e., the fossiliferous unit) sampled for AMS analysis. Note the presence of cm-thick sand lenses of sands with Fe-hydroxide stains; f) detail of cross stratifications from the top of Geo 2b.

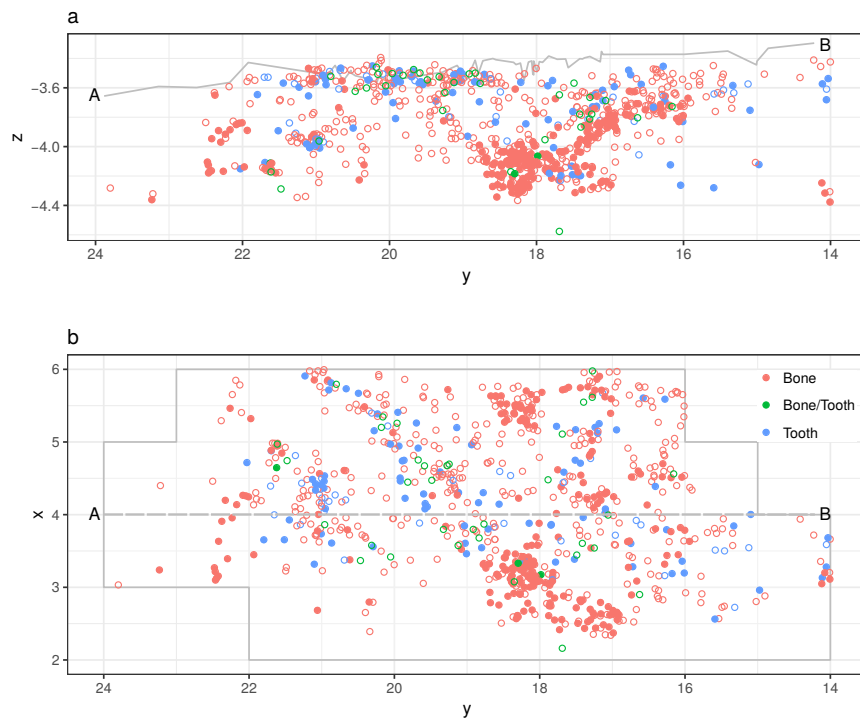


Figure 4: Vertical (a) and horizontal (b) distribution of the sampled fossil specimens from Tsiotra Vryssi (excavations 2015-2017). Filled circles mark complete specimens, hollow circles mark fragmented ones. Grey continuous line in a) marks the Geo 1/2 erosional contact, as recorded at the AB transect marked in b).

131 In such a fluvial depositional context, questions arise with respect to the specific
132 character of the TSR fossil assemblage, the number of depositional events (single or
133 multiple) and the degree of transportation of the fossil record (autochthonous vs. al-
134 lochthonous assemblage).

135 **3. Material and methods**

136 *3.1. Data collection and sub-setting*

137 Since 2015 a grid of 1 m² units was set up and a total station was used in or-
138 der to record the spatial provenience of collected (i.e., diagnostic bones and teeth,
139 and carnivore modified bones) and not collected remains (i.e., non-diagnostic bone
140 fragments with length ≥ 50 mm; Fig. 2a). Non-diagnostic, or non-carnivore modified
141 bone fragments with length < 50 mm were not recorded. This dimensional thresh-
142 old was chosen because small bone fragments show more random orientations than
143 longer specimens (Domínguez-Rodrigo et al., 2014d). Orientation (plunge and bear-
144 ing) of clearly elongated specimens (i.e., specimens with length at least twice the width)
145 was measured with a 1 degree accuracy, using a compass and inclinometer (Eberth
146 et al., 2007; Fiorillo, 1991; Voorhies, 1969, among others). Strike and dip measure-
147 ments were taken along the symmetrical longitudinal a-axis (SLA) of the specimens
148 (Domínguez-Rodrigo and García-Pérez, 2013), using the lowest endpoint of the a-axis
149 as an indicator of the vector direction. The dimensions (length and maximum width)
150 of the recorded finds were measured on-site with a millimetric measuring tape.

151 The present spatial taphonomic study analysed a sample of stratified specimens (n
152 = 797) from the fossiliferous unit Geo 2a, whose spatial coordinates were recorded
153 with the total station. The area of analysis comprises the 34 m² excavated from 2015
154 until 2017. The sample included mostly macromammal remains (n = 707, 89%), unde-
155 termined isolated bone fragments (n = 70), birds (n = 12) and turtle (n = 8) remains. A
156 sub-sample (n = 249) was further subset for the fabric analysis described below. Strat-
157 ified specimens from Geo 2a collected during the test excavation of 2014, or subse-
158 quently found in plaster-jackets with concentration of bones during the lab preparation
159 were excluded due to the lack of precise spatial coordinates. The very small sample (n

160 = 4) of micromammal remains was also not included in the spatial and faunal analyses.
161 Faunal analysis was conducted on a sub-sample of complete or fragmented, isolated
162 or articulated macromammal remains (n = 707). Further sub-setting strategies are de-
163 scribed below.

164 As for the AMS analysis, we collected 18 cylindrical oriented samples ($\emptyset = 2.5$
165 cm) from the middle part of the fossiliferous unit Geo 2a (Fig. 3). AMS analysis was
166 performed at the Alpine Laboratory of Paleomagnetism in Peveragno (Italy) using a
167 AGICO KLY-3 Kappabridge susceptibility meter (15-positions, manual oriented).

168 In order to investigate the micromorphological properties of the Geo 2a unit (i.e.,
169 sedimentary structures and pedogenetic features), two blocks of undisturbed sediment
170 were collected from the excavation area; one (TVB-Z 1) from the middle part of the
171 unit and the other (TVB-Z 2) from the topmost 30 cm of it (Fig. 3). The blocks were
172 later consolidated for preparation of thin sections following the methods described in
173 [Murphy \(1986\)](#)).

174 3.2. *Spatial anisotropy*

175 Different methods have been developed in neighbouring disciplines to detect spa-
176 tial anisotropy. Here we use circular statistics for the fabric analysis of taphonomic el-
177 ements; geostatistics (directional variograms), wavelet analysis and point pattern anal-
178 ysis for detecting anisotropy at the assemblage level.

179 3.2.1. *Fabric analysis*

180 The first controlled experiments and analyses of the orientation and dispersal of
181 disarticulated mammal bones as indicators of the depositional context, carried out by
182 [Toots \(1965\)](#) and [Voorhies \(1969\)](#), led to an increasing number of studies on the effects
183 of water flows on natural and anthropogenic faunal assemblages ([Aramendi et al., 2017](#);
184 [Benito-Calvo and de la Torre, 2011](#); [Cobo-Sánchez et al., 2014](#); [de la Torre and Benito-
185 Calvo, 2013](#); [Domínguez-Rodrigo et al., 2014a, 2012, 2014d](#); [Fiorillo, 1991](#); [Nash and
186 Petraglia, 1987](#); [Organista et al., 2017](#); [Petraglia and Nash, 1987](#); [Petraglia and Potts,
187 1994](#); [Schick, 1987](#), among others).

188 Whereas most of these studies have been conducted on disarticulated long bones
189 or elongated bone fragments - which were observed to preferentially align their a-
190 axes along the direction of the flow - relatively few have investigated the hydraulic
191 behaviour of articulated skeletal elements. Flume experiments conducted by [Coard](#)
192 [and Dennell \(1995\)](#) and [Coard \(1999\)](#) demonstrated that articulated bones display a
193 greater transport potential than disarticulated ones when the articulated elements align
194 themselves. However, they also noted that skeletal parts with a higher number of artic-
195 ulated elements, such as complete limbs, may show weak preferential orientation when
196 assuming disorganised spatial configuration, i.e., when not aligned. Therefore, articu-
197 ulated bones, although relatively common at TSR (Fig. 2a,b,c,d), were not included in
198 the fabric analysis.

199 In this study we applied circular statistics to a subset of 249 non-articulated, elon-
200 gated bone specimens, having length ≥ 20 mm ([Domínguez-Rodrigo et al., 2014d](#)).
201 No distinction of skeletal elements was made, due to the high percentage (91%, $n =$
202 227) of fragmented remains in the analysed sample - mostly appendicular ($n = 122$),
203 undetermined ($n = 93$), axial and cranial ($n = 12$) fragments - and due to the low per-
204 centage (9%, $n = 22$) of complete bones - 17 limb bones, 4 scapulae and a rib.

205 We applied Rayleigh and omnibus tests of uniformity, such as Kuiper, Watson and
206 Rao ([Jammalamadaka et al., 2001](#)), to test the isotropic orientation of the fossil speci-
207 mens. Whereas the Rayleigh test assumes a unimodal distribution and assess the sig-
208 nificance of the sample mean resultant length (\bar{R}), the omnibus tests detect multimodal
209 departures from the null hypothesis of circular isotropy.

210 Rose and equal area Schmidt diagrams were used as exploratory data analysis tools
211 to visualise the sample distribution. Compared to the widely used rose diagrams, which
212 plot the circular distribution of the bearing values, the Schmidt equal area diagram
213 informs about the distribution of the three-dimensional orientation (plunge and bearing)
214 of the elements ([Fiorillo, 1988](#)). Points plotting at the margin of the globe indicate
215 planar fabric, whereas points towards the centre have higher dip angles.

216 The Woodcock diagram ([Woodcock and Naylor, 1983](#)), based on three ordered
217 normalised eigenvalues (S_1, S_2, S_3), was used to discriminate between linear (cluster),
218 planar (girdle) and isotropic distributions. In the Woodcock diagram, the C parameter

219 ($C = \ln(S_1/S_3)$) expresses the strength of the preferential orientation, and its signifi-
220 cance is evaluated against critical values from simulated random samples of different
221 sizes. A perfect isotropic distribution would plot at the origin, with equal eigenvalues
222 ($S_1 = S_2 = S_3 = 1/3$). On the other hand, the K parameter ($K = \frac{\ln(S_1/S_2)}{\ln(S_2/S_3)}$) expresses
223 the shape of the distribution, and it ranges from zero (uni-axial girdles) to infinite (uni-
224 axial clusters).

225 In a fluvio-lacustrine environment a cluster distribution would suggest a strong
226 preferential orientation of the sample, such as in the case of channelised water flows
227 (Petraglia and Potts, 1994), whereas a girdle distribution a weaker preferential orienta-
228 tion, spread over a wider range of directions. Overland flows have been interpreted to
229 produce such a pattern (Organista et al., 2017). On the other hand, a isotropic distribu-
230 tion would suggest that post-depositional disturbance by water flows was not strong
231 enough to preferentially orient the assemblage (Domínguez-Rodrigo et al., 2014a).
232 However, a variety of taphonomic processes can produce similar patterns. Fabric anal-
233 ysis, although very informative, has low power by itself. In order to overcome the
234 intrinsic limitations of the fabric analysis, a multivariate approach to site formation and
235 modification processes should be employed (Lenoble and Bertran, 2004).

236 3.2.2. Geostatistics

237 Geostatistics refer to a body of concepts and methods typically applied to a limited
238 sample of observations of a continuous variable, for example environmental variables.
239 Geostatistics thus aim to estimate the variance and spatial correlation of known ob-
240 servations and predict, using interpolation methods such as Kriging, unknown values
241 of the variable at non-observed locations. Moreover, by using directional variograms,
242 geostatistics enable the identification of spatial anisotropy (i.e., directional patterns).
243 Since the vast majority of spatial statistics assume stationarity and isotropy, it is well
244 understood that a misinterpretation of spatial anisotropy may result in inaccurate spatial
245 modelling and prediction.

246 Although well known in ecological studies, only a relatively small number of stud-
247 ies have explicitly applied geostatistics to the study of site formation and modifica-
248 tion processes, using directional variograms to investigate the specimens size spa-

249 tial distributions (Domínguez-Rodrigo et al., 2014a,c), or to specifically detect spatial
250 anisotropy of archaeological assemblages (Bevan and Conolly, 2009; Markofsky and
251 Bevan, 2012).

252 In order to investigate spatial anisotropy in the distribution of the TSR fossil as-
253 semblage and identify spatial continuity in some directions more than others, we used
254 directional variograms and variogram maps. The studied sample includes 797 recorded
255 specimens (isolated or articulated, complete or fragmented bones and teeth) unearthed
256 from Geo 2a and included in the 34 m² window of analysis (Fig. 4). The same sample
257 was used for the wavelet and point pattern analyses.

258 Specifically, plotting the semi-variance between the variable values of sampled
259 point pairs as a function of distance (spatial lag) between these pairs, directional var-
260 iograms are used to model the spatial variation at multiple scales and different direc-
261 tions. Three parameters (*nugget*, *range* and *sill*) are estimated from an experimental
262 variogram to fit a theoretical omnidirectional variogram. The *nugget* is used to account
263 for spatial variability at very short distances. The *range* indicates the maximal dis-
264 tance up to which there is spatial correlation. At longer distances the semi-variance
265 levels off forming the *sill*, indicating independence between pairs of sample separated
266 by that minimum distance (Dale and Fortin, 2014; Lloyd and Atkinson, 2004). Thus,
267 we plotted the experimental directional variogram against the theoretical omnidirec-
268 tional variogram. A directional semi-variance lower than the fitted omnidirectional
269 variogram indicates continuity in the analysed direction. We selected for our analysis
270 the N-S (0°), E-W (90°), NE-SW (45°) and NW-SE (135°) geographical directions. In
271 addition to the directional variograms, variogram maps are visual representations of the
272 semi-variance: the anisotropy is represented by an ellipse, its axes being proportional
273 to the variation expected in each direction. Thus, the direction of maximum anisotropy
274 corresponds with the major axis of the ellipse (Legendre and Legendre, 2012).

275 3.2.3. Wavelet analysis

276 As a second method for the detection of spatial anisotropy at the assemblage level
277 we used the wavelet analysis. Wavelet analysis, commonly applied in mathematics for
278 signal processing, has relatively wide application in palaeoclimatology and palaeocol-

279 ogy, but is seldom used in studies on site formation processes (Markofsky and Bevan,
280 2012).

281 Unlike the geostatistics approach to the analysis of spatial anisotropy, which is
282 based on a transformation of point values into a continuous surface, the wavelet ap-
283 proach does not apply any transformation, but identifies the elements (points) of a
284 pattern merely by their location. In this regard, the wavelet analysis does not suffer
285 from the arbitrary choice of a surface smooth parameter, as in the case of geostatistics.

286 For each specific point of the pattern, a wheel of 360 sectors of 1° is used to measure
287 the average variance in the angles between point pairs (Rosenberg, 2004). The signif-
288 icance of the wavelet analysis is evaluated against 199 Monte Carlo simulations of the
289 observed pattern under the null hypothesis of randomness. The variance is plotted as a
290 function of angle measurements. Direction is measured anti-clockwise from East (i.e.,
291 0° is East, 90° is North). When the distribution of the observed values (dashed line)
292 wanders above the simulated values (continuous line), the pattern shows significant
293 anisotropy in that direction.

294 3.2.4. Point pattern analysis

295 A spatial point pattern is the outcome of a random spatial point process. Any nat-
296 ural phenomenon which results in a spatial point pattern, such as a distribution pattern
297 of fossils, can be viewed as a point process (Baddeley et al., 2015). Therefore, the
298 analysis of a spatial point pattern ultimately addresses the nature of the point process
299 that generated the pattern. Point pattern analysis has been specifically applied to the
300 study of site formation and modification processes by a relatively small number of
301 studies (Domínguez-Rodrigo et al., 2014a, 2017, 2014c; Giusti and Arzarello, 2016;
302 Giusti et al., in press; Lenoble et al., 2008; Organista et al., 2017). However, this ana-
303 lytical method has never been used to detect anisotropy in the distribution patterns of
304 archaeological or palaeontological assemblages. Nevertheless, detecting anisotropy is
305 an essential part of any spatial analysis. Standard statistical tools in spatial point pat-
306 tern analysis rely on crucial assumptions about the point process itself: a point process
307 is assumed to be stationary and/or isotropic if its statistical properties are not affected
308 by shifting and/or rotating the point process.

309 In order to further assess the presence of anisotropy in the distribution pattern of the
310 TSR assemblage, we specifically applied the point pair distribution function ($O_{r_1,r_2}(\Phi)$;
311 [Baddeley et al., 2015](#)). The function estimates the probability distribution of the direc-
312 tions of vectors joining pairs of points that lie more than r_1 and less than r_2 units
313 apart. With selected different distances r_1 and r_2 , the function estimates the multiscale
314 variation of anisotropy. Results are visualised in rose diagrams, where the direction is
315 measured counter-clockwise from East (0°).

316 At the supra-element assemblage level, spatial anisotropy is expected to be detected
317 in a fluvial depositional environment, and most likely to share the same preferential
318 orientation with taphonomic elements. Characteristic elongated lag deposits are typical
319 patterns observed in association with water-flows dragging materials in one direction,
320 the same as the main orientation of the elements ([Domínguez-Rodrigo et al., 2012](#)).

321 3.3. Anisotropy of magnetic susceptibility (AMS)

322 The anisotropy of magnetic susceptibility (AMS) is a technique used to identify
323 preferred orientation of magnetic minerals in rocks and unconsolidated sediments ([Hrouda,](#)
324 [1982](#); [Tarling and Hrouda, 1993](#)). It is based on the principle that, when a magnetic
325 field is applied to a sample, the induced magnetisation depends on the bulk orienta-
326 tion of its magnetic constituents. In turn, the AMS magnitude depends on both the
327 anisotropy of individual magnetic particles and the degree of their alignment. Particle
328 anisotropy can be related to either crystalline (anisotropy along a specific crystal plane
329 or axis) or shape (anisotropy along the long axis of the particle) characteristics. Since
330 in most magnetic minerals forming sedimentary particles the long crystallographic axis
331 is the easiest to magnetise (e.g., magnetite), the shape anisotropy is generally dominant,
332 with few exceptions (e.g., haematite).

333 The magnetic susceptibility is represented by three symmetric tensors describing
334 an ellipsoid with three susceptibility axes named K1 to K3 and ordered by decreasing
335 susceptibility. The orientation of the ellipsoid is evaluated projecting the ellipsoid axes
336 on an equal-area projection stereogram. Thus, the shape of the ellipsoid is evaluated
337 using the Flinn or Jelinek scatter plots. In a Flinn (F/L) diagram the foliation along
338 the horizontal axis ($F = K_2/K_3$; [Stacey et al., 1960](#)) is plotted against the lineation

339 along the vertical axis ($L = K1/K2$; [Balsey and Buddington, 1960](#)). Values of $F/L < 1$
 340 indicate oblate ellipsoids (i.e., disc-shaped), whereas values of $F/L > 1$ indicate prolate
 341 ellipsoids (i.e., cigar-shaped) with the axial ratios increasing with distance from the
 342 origin. Alternatively, the AMS magnitude and shape can be visualised on the Jelinek
 343 shape plot ([Jelinek, 1981](#)), by using the corrected anisotropy degree

$$Pj = exp \sqrt{2[(lnK1 - k)^2 + (lnK2 - k)^2 + (lnK3 - k)^2]}$$

344 where

$$k = \frac{lnK1 + lnK2 + lnK3}{3}$$

345 and the shape parameter

$$T = \frac{lnL - lnF}{lnL + lnF}$$

346 where samples are prolate for $-1 < T < 0$ or oblate for $0 < T < 1$.

347 In sediments, oblate ellipsoids with imbrication angles less than 20° are considered
 348 diagnostic of primary depositional processes ([Hamilton and Rees, 1970](#); [Hrouda, 1982](#);
 349 [Lanza and Meloni, 2006](#); [Liu et al., 2001](#); [Tarling and Hrouda, 1993](#)). In turn, prolate
 350 ellipsoids mostly relate to post-depositional deformation (e.g., rocks recording tectonic
 351 or metamorphic strain), especially when the magnetic anisotropy is high ([Hrouda and](#)
 352 [Janák, 1976](#)).

353 3.4. Differential preservation

354 Differential preservation, or taphonomic survival, refers to the proportion of tapho-
 355 nomic elements being preserved after the action of environmental factors ([Fernández-](#)
 356 [López, 2006](#)). Selective preservation arises from the differential modification of tapho-
 357 nomic entities, by interaction of inherent properties of the entities with the external
 358 environmental factors. Skeletal elements representation is among the key variables po-
 359 tentially indicative of the selective action of water-flows ([Behrensmeier, 1975b](#); [Kauf-](#)
 360 [mann et al., 2011](#); [Voorhies, 1969](#), among others). Other variables, not considered

361 in this preliminary study, include breakage patterns, disarticulation patterns and bone
362 surface modifications.

363 The pioneering flume experiments by Voorhies (1969) on disarticulated, complete
364 sheep and coyote bones resulted in a three-group classification of fluvial transport sus-
365 ceptibility of skeletal elements, subsequently elaborated by Behrensmeyer (1975b).
366 Since shape and structural density have been found to influence the transportability of
367 skeletal elements (Behrensmeyer, 1975b; Boaz, 1982), assemblages subject to moder-
368 ate to high-energy water-flows typically show an under-represented number of smaller,
369 less dense bones. The Voorhies Group I (rib, vertebra, sacrum, sternum) is the most
370 easily affected by fluvial transport; thus its presence or absence in the fossil assemblage
371 informs about the degree of disturbance by water-flows. In turn, the proportion between
372 the represented Voorhies Groups provides evidence for the degree of preservation of the
373 assemblage (Behrensmeyer, 1975b). We included in the Voorhies groups only com-
374 plete, non-articulated macromammal bones (plus rami of mandibles, and maxillae) of
375 adult individuals - the very few specimens of juvenile individuals, having different hy-
376 draulic behaviour, were excluded. Our grouping criteria followed the classification
377 reported in Lyman (1994, Tab.6.5). Carpals, tarsals and sesamoids were included in
378 Voorhies Group I/II, as the phalanges; maxillae in Group II/III, as the mandibular rami.
379 The studied sample included 147 specimens of Perissodactyla (n = 59), Artiodactyla
380 (n = 41), Carnivora (n = 12) and indeterminate taxa (n = 35). The distribution of deter-
381 minate Voorhies Groups was further categorised in 5 size classes, following the body
382 mass (BM) classification of Palombo (2010, 2016), modified for *Ursus etruscus* after
383 Koufos et al. (in press). The first group (BM1), not present so far in our collection,
384 includes mammals weighing less than 10 kg; BM2 ranges from 10 to 59 kg (*Canis*
385 *etruscus*); BM3 from 60 to 249 kg (*Ursus etruscus*, medium-sized Cervidae); BM4
386 from 250 to 1000 kg (*Equus*, *Bison*, *Praemegaceros*). We excluded from the Voorhies
387 Groups specimens attributed to BM5, that includes very large mammals over 1000 kg
388 weight (Rhinocerotidae and Elephantidae). Nevertheless, their skeletal element rep-
389 resentation was analysed following the Fluvial Transport Index (FTI) classification of
390 Frison and Todd (1986). Undetermined taxa or BM classes - yet in the BM2-BM4
391 range - were also included in the analysis (named NA in Fig. 10).

392 Closely related to the Voorhies Groups, the ratio of complete isolated teeth/vertebrae
393 (T/V) is another indicator of the depositional environment (Behrensmeyer, 1975b).
394 High-energy fluvial deposits, such as channel-fills and -lag deposits, tend to have high
395 T/V ratio, whereas a low T/V ratio characterises low-energy fluvial deposits, such as
396 that of floodplain deltaic and lacustrine settings (Lyman, 1994).

397 Complementary to the hydraulic behaviour of complete, isolated faunal remains
398 classified in the Voorhies Groups, the skeletal part representation of fragmented bones
399 provides another indication of the assemblages degree of preservation (Domínguez-
400 Rodrigo et al., 2017, 2014d; Pante and Blumenschine, 2010). Vertebrae and ribs, being
401 mostly cancellous, fragile and comparatively less dense, are more susceptible to frag-
402 mentation and transportation, even in low-energy conditions, with respect to cranial
403 and appendicular elements, which are more dense and likely to survive in lag assem-
404 blages (Domínguez-Rodrigo et al., 2017). In order to integrate the Voorhies Groups,
405 we analysed a sub-sample of 400 isolated macromammal specimens, composed of 315
406 bone and tooth fragments, 78 complete teeth, 1 antler, and 6 appendicular bones of
407 juvenile or BM5 specimens.

408 Finally, the distribution of articulated bones was analysed by anatomical regions. A
409 sub-sample of 50 articulated macromammal units of 154 bone elements were classified
410 as axial (vertebrae, ribs) or appendicular (humeri, femura, radii, tibiae, metapodials,
411 carpals/tarsals and phalanges) units.

412 3.5. Reproducible research

413 The subset of the raw data collected for this study, necessary to reproduce the re-
414 ported results, is licensed, except where otherwise specified, under the CC-BY license
415 and publicly available on an open-access repository at the DOI: [zenodo/osf?](https://zenodo.org/doi/10.5281/zenodo.10000000). The
416 repository includes in addition metadata description and the code used to process and
417 reduce the data-set. The analyses were performed in R: a language and environment
418 for statistical computing (R Core Team, 2017); except for the wavelet analysis, per-
419 formed using the PASSaGE software, version 2 (Rosenberg and Anderson, 2011). The
420 commented R code needed to reproduce the reported analyses is released under the
421 MIT license in the same repository. We provide as well a detailed description of the

Table 1: Values and p – values of circular uniformity test statistics.

Sample n	mean dir.	Rayleigh		Kuiper		Watson		Rao	
		\bar{R}	p	V_n	p	U^2	p	U	p
249	148°	0.165	0.001	2.3791	<0.01	0.3957	<0.01	186.5181	<0.001

422 procedure used in PASSaGE.

423 4. Results

424 4.1. Anisotropy of basic taphonomic elements

425 Circular statistics were applied for the fabric analysis of basic taphonomic ele-
 426 ments, i.e., isolated, not articulated elongated complete bone specimens or bone frag-
 427 ments. Tab. 1 summarises the results of the circular uniformity tests. The Rayleigh
 428 test, which assumes a unimodal distribution, confirmed (p – value = 0.001) the sig-
 429 nificance of the sample mean resultant length ($\bar{R} = 0.165$). The value of \bar{R} close to 0
 430 indicates that the data are evenly spread around the mean direction ($\bar{\theta} = 148$, SE), with
 431 relatively high standard deviation ($\hat{\sigma} = 1.89$) and angular variance ($V = 48$). On the
 432 other hand, the Schmidt and rose diagrams (Fig. 5a) showed a multimodal distribution,
 433 mostly concentrated in the SE quadrant and with secondary peaks to the N and SW.
 434 Accordingly, the Kuiper, Watson and Rao omnibus tests, all rejected the null hypothe-
 435 sis of uniformity at the 99% confidence level, thus suggesting a significant anisotropic
 436 multimodal distribution of the fossil sample. Moreover, the Schmidt diagram (Fig. 5a)
 437 showed a planar fabric of the sample distribution, with points plotting predominantly
 438 on the edge of the equal area hemisphere, thus indicating 0-to-low degree of dip (mean
 439 plunge=12°; variance=1.5°).

440 In the Woodcock diagram (Fig. 5b), the C value (1.89) is higher than the critical
 441 S1/S3 test value (1.44) for $N=300$ at 99% confidence level. Thus, the data sample sig-
 442 nificantly rejects the hypothesis of randomness in favour of a strong organised sample.
 443 The K value (0.11) plots the data sample close to $K = 0$, indicating uniaxial girdles
 444 (planar fabric).

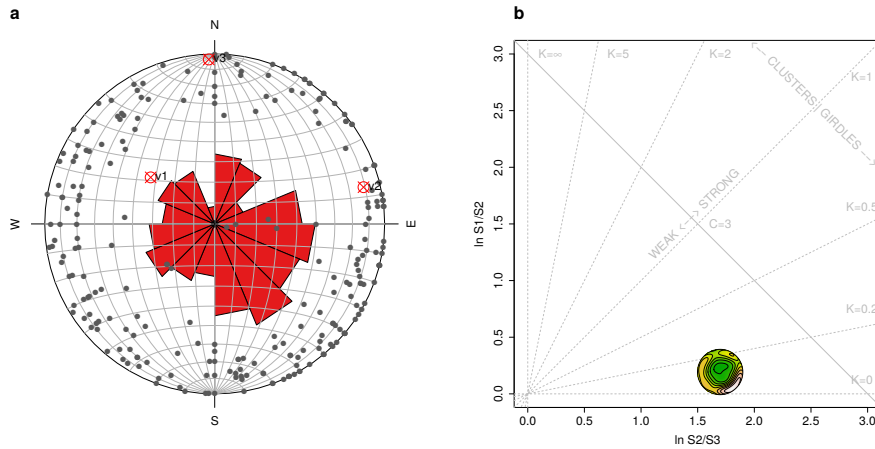


Figure 5: Rose and equal area Schimdt diagrams (a). Woodcock diagram (b).

445 4.2. Anisotropy of the taphonomic population

446 Geostatistics (directional variograms and variogram map), wavelet and point pat-
 447 tern analyses were used for detecting anisotropy at the assemblage level. Fig. 6a shows
 448 the kernel smooth density estimation ($\sigma = 0.17$) of the sample distribution in the study
 449 area. A preliminary visual examination suggests a NW-SE oriented clustering of the
 450 assemblage, although interfered with secondary NE-SW oriented dispersion. Fig. 6b
 451 shows the variograms in the four main geographical directions (N-S, E-W, NE-SW,
 452 NW-SE), plotted against the omnidirectional fitted variogram. As a rule of thumb, in
 453 order to determine the spatial structure of the sampled data, only the first two-thirds of
 454 the variogram are interpreted (Dale and Fortin, 2014). The omnidirectional variogram
 455 (red line) indicates that at short distance lags, the semi-variances are close to zero,
 456 indicating very strong spatial structure (correlation). With longest distance lags, the
 457 semi-variance rise to a plateau (*sill*) of lack of spatial correlation. The semi-variance
 458 of the NW-SE (135°) direction is lower than in the omnidirectional variogram, start-
 459 ing well before the *sill*, thus indicating continuity (spatial correlation) in that direction.
 460 Minor directional trends are also detected in the N-S (0°), and to a lesser extent in the
 461 NE-SW (45°) directions. This result is clearly confirmed by the diagonal striping in the
 462 variogram map (Fig. 6c). The map shows a major ellipse oriented NW-SE, with minor

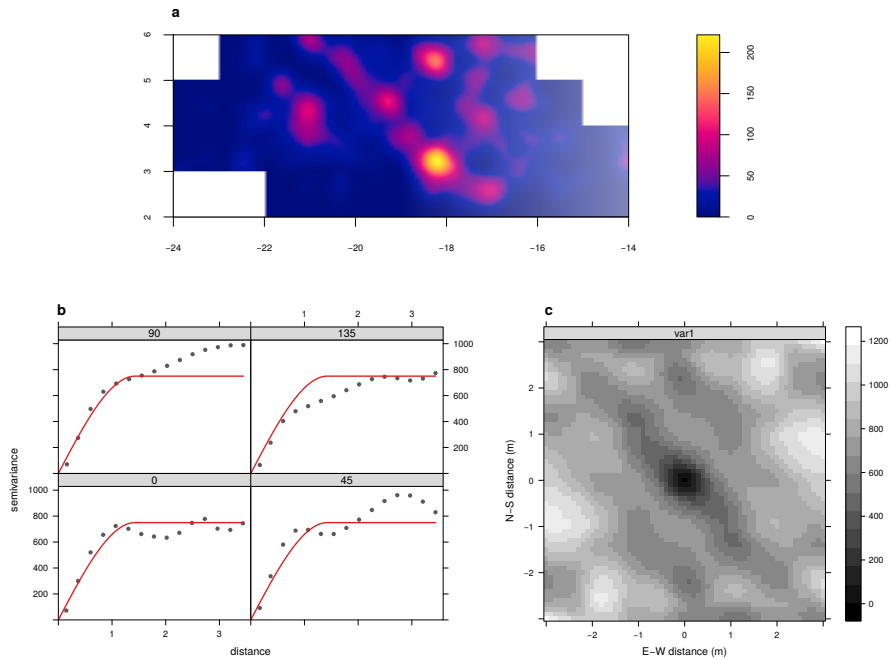


Figure 6: Kernel smoothed intensity function of the fossil assemblage (a). Directional variograms (4 clockwise directions from N-S, 0°) shown as grey points alongside the fitted omnidirectional variogram shown as a continuous red line (b) and variogram map (c).

463 parallel structures.

464 As for the wavelet analysis, Fig. 7 plots the variance as function of the direction,
 465 ranging anti-clockwise from 0° (E) to 180° (W). A major peak is evident at 135° (NW),
 466 wandering way above the expected values for a random (isotropic) pattern. A sec-
 467 ondary significant peaks, although of much less intensity, is present at 85° (N). In
 468 accordance with the directional variograms, the wavelet analysis indicates a signifi-
 469 cant anisotropy in the NW-SE direction. Moreover, it suggests minor occurrence of
 470 points (specimens) in the N-S direction, as also indicated by the geostatistics analysis.
 471 However, in contrast with the directional variograms, the angular wavelet graph does
 472 not support significant preferential orientation in the NE range (angles between 0° and
 473 90°).

474 Fig. 8 shows the results of our point pattern analysis and specifically the point

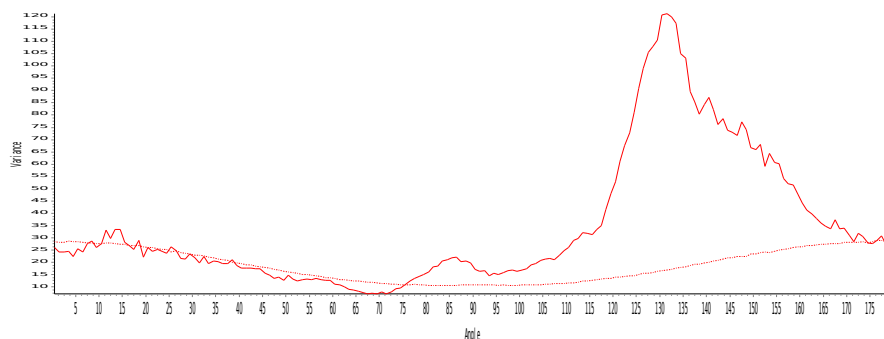


Figure 7: Angular wavelet graph. Angles range from 0° (E) to 180° (W). Peaks of variance (continuous line) indicate the direction of maximum anisotropy. Dashed line marks the Monte Carlo simulated null hypothesis of isotropy.

475 pair distribution function $O_{r_1, r_2}(\Phi)$ for a range of distances $r_1 = 0.01$ m and $0.25 <$
 476 $r_2 < 1.5$ m. The plot illustrates the multiscale variation of anisotropy, from a uniform,
 477 isotropic pattern (for $r_2 = 0.25$ m), to increased anisotropy in the NW-SE direction.
 478 The maximum anisotropy is observed for $r_2 = 1$ m, as elements at a maximum distance
 479 of 1 m show the strongest directional pattern. With increased distances of $r_2 > 1$ m, the
 480 rose diagrams suggest the addition of a second orthogonal NE-SW directional trend,
 481 which reflects the parallel alternation of NW-SE bands in the assemblage distribution.

482 4.3. Anisotropy of magnetic susceptibility

483 In Fig. 9a, the AMS of the whole sample set ($n = 18$) is investigated. The equal-
 484 area projection of the three susceptibility axes K1-K3 (left-hand side of Fig. 9a) in-
 485 dicates high variability of the axes orientation, with confidence angles of the K1 and
 486 K2 mean directions largely overlapping. This result suggests no preferential orien-
 487 tation of the axes. However, the Flinn and Jelinek plots (right-hand side of Fig. 9a)
 488 reveal the presence of 7 samples with prolate ellipsoids, thus suggesting the action of
 489 post-depositional deformation processes which could have obliterated the primary de-
 490 positional pattern. Therefore, in order to overcome possible post-depositional noise,
 491 further AMS analysis focused only on a sub-set of samples showing oblate ellipsoids
 492 ($n = 11$). In Fig. 9b, the equal-area projection shows a well defined clustering of the
 493 axes, with the maximum anisotropy axis K1 aligned along the NW-SE direction and the

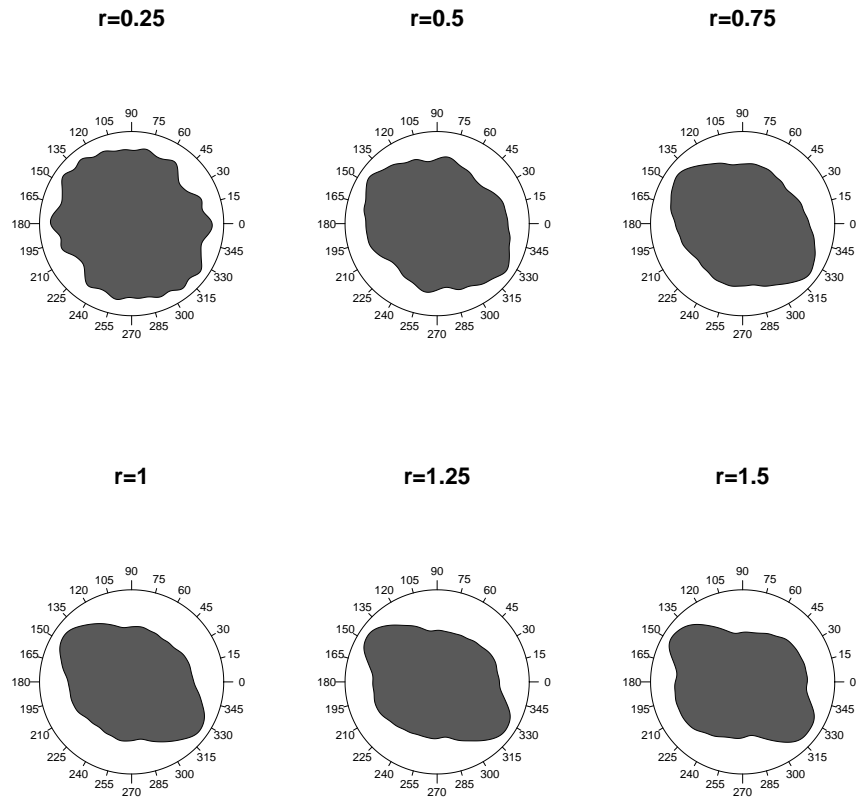


Figure 8: Rose diagrams of the point pair distribution function for a range of distances ($0.25 < r < 1.5$ m). Direction is measured counter-clockwise from East (0°).

494 K3 imbrication angles varying within a wide range of angles (from 4° to 85°). Because
495 high K3 imbrication angles may result from post-depositional rehash of sediments, fur-
496 ther analysis were conducted on a selection of 5 samples with K3 imbrication angles
497 less than 20° (Hamilton and Rees, 1970; Hrouda, 1982; Lanza and Meloni, 2006; Liu
498 et al., 2001; Tarling and Hrouda, 1993). In Fig. 9c, the equal-area projection indicates
499 again a NW-SE orientation of the maximum anisotropy axis K1. Despite the small
500 sample size, the AMS analysis suggests a weak anisotropy of magnetic sedimentary
501 grains along a NW-SE direction.

502 4.4. Differential preservation

503 Fig. 10a shows the distribution at the family level of the whole sampled material.
504 Determined taxa included Perissodactyla, Artiodactyla, Carnivora and Proboscidea,
505 together with a number of undetermined bone fragments (44%). The histogram shows
506 the prominent presence of Equidae over other taxa (27%), followed by Bovidae (11%)
507 and Cervidae (5%). However, it is worth noting the presence of very large mammals
508 (body mass class BM5), such as Elephantidae and the rhinocerotid *Stephanorhinus* sp.,
509 and to a less extent, of carnivores, such as *Canis etruscus* and *Ursus etruscus*.

510 The distribution of the Voorhies Groups plotted by body mass classes is shown
511 in Fig. 10b. BM1 is so far not present in the TSR assemblage, while BM2 includes
512 the *C. etruscus*, BM3 includes the medium-sized Cervidae and *Ursus etruscus*, BM4
513 the medium- and large-sized *Equus* sp., *Bison* sp. and the large-sized cervid *Prae-*
514 *megaceros* sp. Notably, the Voorhies Group III is represented in Fig. 10b only by the
515 crania of the carnivores *Canis* and *Ursus*. Moreover, the fossil record of *U. etruscus* in-
516 cluded maxilla fragments (Voorhies Group II/III), isolated teeth, 2 articulated vertebrae
517 and an ulna fragment. Specimens from the BM4 grouped mostly in II/III, II, I/II and
518 showed lack of Voorhies Group I and III. On the other hand, the bulk of undetermined
519 BM specimens plotted in Voorhies Group I/II, with some occurrence in Group I, II, and
520 to a less extent in Group II/III.

521 Fig. 10c shows the side-by-side distribution of complete and fragmented isolated
522 macromammal skeletal elements. Firstly, the skeletal element distribution of complete
523 specimens suggests a very high teeth/vertebra ratio (7.8). The ratio (3) is lower, but

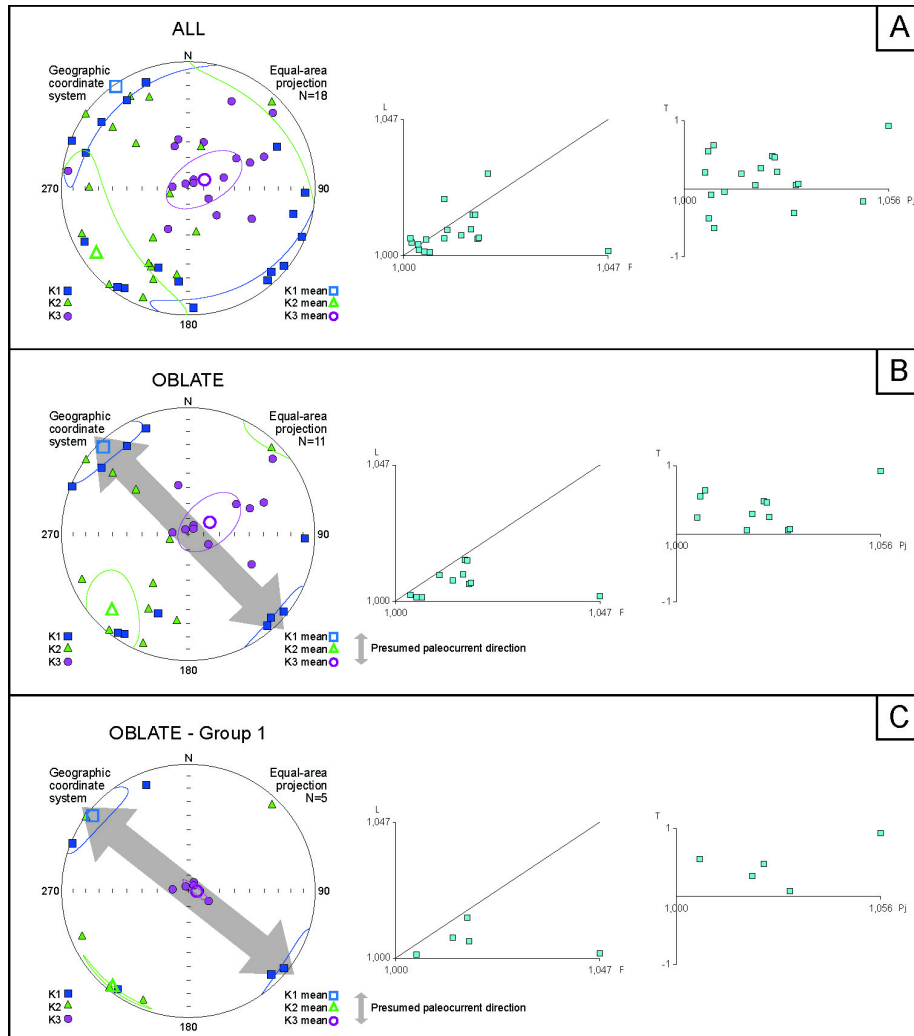


Figure 9: Equal-area projection stereogram (left-hand side) of the anisotropy axes K1, K2 and K3 (with $K1 > K2 > K3$) and Flinn and Jelinek plots (right-hand side) for a) all the samples; b) samples with oblate-shaped anisotropy ellipsoid; c) samples with K3 imbrication angle less than $20-25^\circ$.

524 still relatively high when considering isolated, fragmented specimens. Limb bone and
525 undetermined fragments represent the majority of the fragmented, isolated specimens,
526 as compared to axial skeletal parts.

527 Accordingly, the prominent presence of appendicular skeletal elements over axial
528 is also showed in the distribution of articulated specimens (Fig. 10d), which account
529 for 22% of the sampled assemblage. Articulated lower limb elements (metapodes,
530 carpals/tarsals, phalanges) represent the majority of bones, often articulated to frag-
531 mented upper elements (radii, tibiae, humeri, femora). Interestingly, some of the latter
532 elements present carnivore gnawing marks (Fig. 2e).

533 4.5. *Micromorphology*

534 The TVB-Z 1 block (Fig. 3) consists mostly of poorly sorted sandy silts, composi-
535 tionally dominated by metamorphic quartz and accessory metamorphic minerals. From
536 bottom to top, several sharp grain size breaks occur, which partition the sampled inter-
537 val into mm-thick normally graded laminae, displaying an upward increase of matrix
538 content (Fig. 11a). This includes clay infilling pore spaces (Fig. 11a) and suggests
539 either flow velocity fluctuations or multiple waning depositional events. Birefringent
540 illuvial clay coatings are also present along some voids (Fig. 11b), thus indicating in-
541 cipient pedogenesis, likely due to temporary subaerial exposure (Kühn et al., 2010).

542 Most of the thickness of the TVB-Z 2 block (Fig. 3) displays similar characteris-
543 tics to the TVB-Z 1 block, except for the presence of rolled soil clasts (pedorelicts;
544 Fig. 11c), likely eroded from nearby locations (Cremaschi et al., In press). Conversely,
545 the uppermost part of the sample (Fig. 11d) displays moderate clay illuviation along
546 voids, sparse voids most likely related to bioturbation and impregnating redoximor-
547 phic features (Lindbo et al., 2010). The latter include Fe oxide hypocoatings on the
548 groundmass, Fe/Mn oxide nodules with regular outline developed on quartz grains,
549 and fragmented clay coatings. Altogether, these features suggest that, after deposi-
550 tion, Geo 2a underwent moderate pedogenesis due to a relatively prolonged phase of
551 subaerial exposure in a warm and possibly humid climate or while still saturated with
552 water.

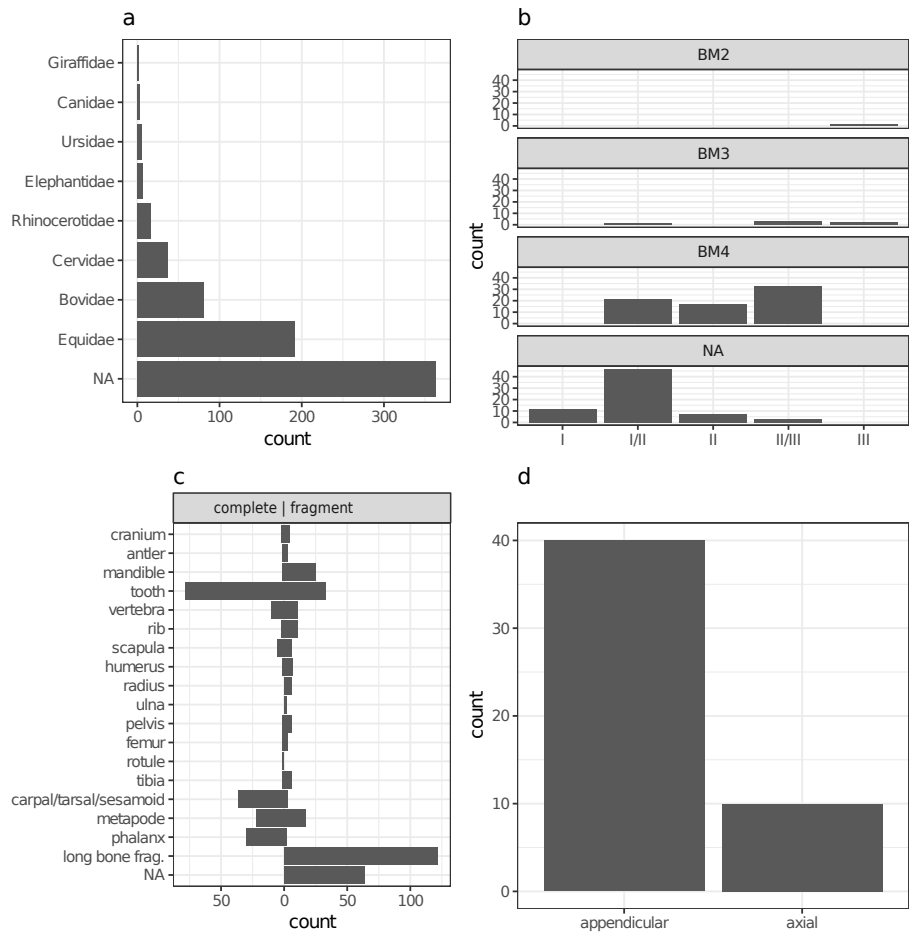


Figure 10: Distribution at the family level of the whole sampled material (a). Voorhies Groups distribution of the complete, isolated macromammal bones (plus rami of mandibles and maxillae) by body mass (BM) (b). Side-by-side distribution of complete/fragmented isolated macromammal skeletal elements (c). Skeletal region distribution of articulated macromammal specimens (d).

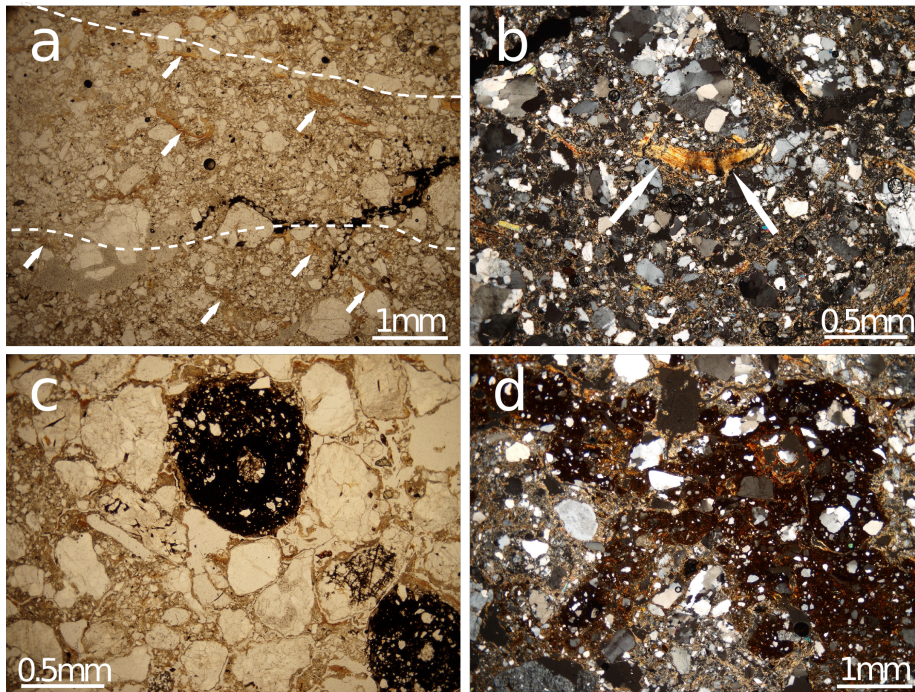


Figure 11: Microphotographs showing a) clast alignments (dashed white lines), crude normal grading and clays infilling pore spaces (arrows) from block TVB-Z 1 in parallel polarised light (PPL); b) illuvial clay coating a planar void from sample TVB-Z 1 in cross polarised light (XPL); c) rolled pedorelict (a Fe/Mn nodule developed on quartz grain) from topmost part of block TVB-Z 2 (PPL); d) Fe oxide hypococoatings on the groundmass and illuvial clay coating of voids from topmost part of block TVB-Z 2 (XPL).

553 5. Discussion

554 Spatial taphonomy has recently emerged as a new methodological framework com-
555 plement to the traditional taphonomic approach (Domínguez-Rodrigo et al., 2017). By
556 using spatial statistical methods, spatial taphonomy aims to investigate the multiscale
557 and multilevel spatial properties of different taphonomic entities (*sensu* Fernández-
558 López, 2006). Indeed, taphonomic alteration processes work simultaneously, at dif-
559 ferent scales, on entities of different level of organisation, from the basic taphonomic
560 elements (bone specimens), to higher level taphonomic groups (taphons) or popula-
561 tions (assemblages). For example, dispersion processes of taphonomic elements may
562 modify their spatial location, orientation and removal degree. At the same time, disper-
563 sion of taphonomic elements may also cause changes in the density, spatial distribution
564 and representatives of elements of each taphon or taphonic population (Fernández-
565 López, 2006). Thus, beside the traditional taphonomic approach, the results of spatial
566 taphonomy are of great importance for investigating the natural or cultural processes
567 of dispersal and accumulation of faunal or cultural remains, in turn with consequences
568 for palaeoecological reconstructions, biochronological estimates and past human be-
569 havioural inferences.

570 In this regard, this study offers an initial contribution to the development of a so far
571 non-existent referential framework for the spatial taphonomic interpretation of palaeon-
572 tological or archaeological assemblages (Domínguez-Rodrigo et al., 2017). Indeed,
573 the taphonomic study of non-human related bone assemblages has great importance
574 for archaeological research as well. As an example, water-flow processes are recog-
575 nised to be among the most important natural processes in the formation and modifi-
576 cation of a significant percentage of the vertebrate fossil and archaeological sites alike
577 (Behrensmeier, 1975a, 1982, 1988; Coard, 1999; Coard and Dennell, 1995; Petraglia
578 and Nash, 1987; Petraglia and Potts, 1994; Schiffer, 1987; Voorhies, 1969, among
579 others). Under the effect of water-flows, assemblages may adopt a variety of forms,
580 ranging from (peri)autochthonous rearranged assemblages and biased lag assemblages
581 to transported, allochthonous assemblages (Behrensmeier, 1988; Domínguez-Rodrigo
582 and García-Pérez, 2013). One fundamental assumption behind reliable inferences on

583 past human behaviour is the pristine preservation of the depositional context. There-
584 fore, it is essential, in order to fully comprehend the archaeological record, to test
585 within a referential framework alternative taphonomic hypotheses.

586 In this study, taphonomic dispersion and accumulation processes were analysed
587 focusing on a specific aspect - anisotropy - of the spatial properties of taphonomic enti-
588 ties. A multilevel analysis of anisotropy was conducted at the level of basic taphonomic
589 elements and at the assemblage level. Anisotropy, defined as the preferential orienta-
590 tion of skeletal elements, constitutes a fundamental part of any taphonomic study ([Ara-](#)
591 [mendi et al., 2017](#); [Benito-Calvo and de la Torre, 2011](#); [Cobo-Sánchez et al., 2014](#);
592 [de la Torre and Benito-Calvo, 2013](#); [Domínguez-Rodrigo et al., 2014a, 2012, 2014d](#);
593 [Fiorillo, 1991](#); [Nash and Petraglia, 1987](#); [Organista et al., 2017](#); [Petraglia and Nash,](#)
594 [1987](#); [Petraglia and Potts, 1994](#); [Schick, 1987](#); [Toots, 1965](#); [Voorhies, 1969](#), among
595 others). However, spatial anisotropy at supra-element level of taphons or assemblages
596 is an often neglected taphonomic criterion that should be reconsidered, especially in
597 spatial taphonomic analyses of fluvial dispersion and accumulation processes. Never-
598 theless, standard spatial statistics rely on crucial assumptions about the isotropy of the
599 spatial processes responsible for the observed spatial pattern ([Baddeley et al., 2015](#)).

600 We investigated the multilevel spatial anisotropy and selective composition of the
601 fossiliferous deposit of Tsiotra Vryssi, from the fluvial Gerakarou Formation of the
602 Mygdonia Basin, Greece. Specific research questions regarded the character and num-
603 ber of depositional processes and the degree of re-elaboration of the fossil record. Spe-
604 cific aspects of our results are discussed below.

605 *5.1. Recursive anisotropy*

606 Recursive anisotropy emerged at the level of basic taphonomic elements and at the
607 assemblage level. Fabric analysis, geostatistics, wavelet and point pattern analyses all
608 pointed to a preferential NW-SE orientation of the assemblage and the sub-sample of
609 elongated bone specimens.

610 Fabric analysis, or the analysis of the orientation (plunge and bearing) of elongated
611 elements, can provide valuable insight into taphonomic processes, allowing discrimi-
612 nation between different orientation patterns (isotropic, linear or planar). We analysed

613 a sub-sample of not articulated, clearly elongated bone specimens, mostly limb bone
614 fragments. Articulated units were excluded from the fabric analysis since experimental
615 studies by [Coard and Dennell \(1995\)](#) and [Coard \(1999\)](#) reported that articulated units
616 with a higher number of elements, such as complete limbs, may show weak preferen-
617 tial orientation when not aligned, as they often occur at TSR (Fig. 2c,d,e). Otherwise,
618 the authors concluded that articulated bones showed a greater than expected hydraulic
619 transport potential. Thus, their conspicuous presence in the TSR fossil record (about
620 22%) would not necessarily suggest an autochthonous deposit.

621 The results of the circular uniformity test statistics (Tab. 1) agreed upon rejecting
622 the null hypothesis of uniformity, suggesting a significant anisotropic distribution of the
623 fossil sample. The Schimdt and Woodcock diagrams in Fig. 5 indicated planar fabric
624 (0-to-low degree of dip) and a girdle pattern, with preferential orientation towards the
625 SE. In girdle distribution elements orient over a wider sector of angles than cluster dis-
626 tributions, yet showing higher anisotropy than random distributions. Whereas cluster,
627 linear patterns are associated with channelised water-flows ([Petraglia and Potts, 1994](#)),
628 girdle, planar patterns have been interpreted as products of overland flows (runoff;
629 [Organista et al., 2017](#)). The preferential orientation of the sampled elongated bones
630 suggests that the TSR fossil deposit most likely underwent relatively high-energy, but
631 non-channelised NW-SE water-flows. However, anisotropy does not itself discriminate
632 between allochthonous and autochthonous deposits. Autochthonous lag assemblages
633 undergoing minimal re-sedimentation could also exhibit significant anisotropic spatial
634 patterns ([Domínguez-Rodrigo et al., 2012, 2014b, 2017, 2014c](#)). Since a wide range of
635 different taphonomic processes can produce similar patterns, an unequivocal discrim-
636 ination based only on fabric observations is seldom possible, and other taphonomic
637 criteria should be considered ([Lenoble and Bertran, 2004](#)).

638 Geostatistics, wavelet and point pattern analyses were applied in order to detect
639 anisotropy of the TSR fossil assemblage. All these different methods agreed on iden-
640 tifying a preferentially NW-SE oriented distribution. Four directional variograms and
641 a variogram map (Fig. 6b,c) were calculated from a kernel density estimation of the
642 assemblage spatial distribution (Fig. 6a). Small, dense clusters of fossils, although
643 occurring at different elevations in the 1m-thick vertical distribution (Fig. 4a), con-

644 catenate along a prevailing NW-SE direction. Secondary minor directions (N-S and
645 NE-SW) were identified in the directional variograms (Fig. 6b). In the same manner,
646 the wavelet graph (Fig. 7) and the rose diagrams (Fig. 8) also detected a strong pref-
647 erential NW-SE directional distribution. Similar elongated lag deposits are typically
648 associated with water-flows dragging material in one direction (Domínguez-Rodrigo
649 et al., 2012).

650 These observations are in agreement with the AMS results. Despite the small sam-
651 ple size, the AMS results suggest relatively strong anisotropy, with a mean K1 axis
652 oriented NW-SE and a mean K2 axis oriented NE-SW, although with much smaller
653 confidence angles (Fig. 9). Since K1 (i.e., the axis of maximum anisotropy) should
654 reflect the bulk orientation of the elongated axis of the ferro/paramagnetic sedimentary
655 particles, it might be concluded that AMS hints at a NW-SE oriented anisotropy.

656 Thus, the observed recursive multilevel anisotropy patterns most probably points
657 to the action of NW-SE oriented water-flows, at the specific location of the TSR site.
658 However, both analyses of isotropy at element level (fabric analysis) and assemblage
659 level (geostatistics, wavelet and point pattern analyses) suggested some degree of noise
660 in the prevalent NW-SE distributions toward other directions, especially to the or-
661 thogonal NE-SW direction. Whereas long bones can roll orthogonally to the main
662 direction of the flow (Voorhies, 1969), noise in the main directional trend at assem-
663 blage level may indicate multiple depositional processes, or secondary reworking post-
664 depositional processes. Moreover, the relatively high average density of preserved ele-
665 ments ($24/m^2$) occur in small, well defined clusters (Figs. 2f,e, 4 and 6a). Such spatial
666 aggregation of taphonomic elements may be the result of a combination or the sum of
667 different taphonomic processes (Fernández-López et al., 2002). On the other hand, the
668 formation of gaps in the spatial distribution and clusters of elements in correspondence
669 with topographic depression may as well be associated with lag deposits (Petraglia and
670 Potts, 1994). This is likely to happen on top of rippled surfaces or small dunes in the
671 channel-belt. However, there is no evidence of such structure at TSR.

672 5.2. Differential preservation

673 According to the evolutionary and systemic theory of taphonomy, taphonomic al-
674 teration is not only conceived as a destructive process, but it also has positive effects
675 with the preservation and creation of new taphonomic groups. In this sense, the dif-
676 ferential destruction (or taphonomic sieve) of taphonomic entities is just a particular
677 case of taphonomic alteration, as it is the differential modification that gives rise to
678 selective preservation (Fernández-López, 2006). Intrinsic and extrinsic taphonomic
679 factors determine the differential preservation of taphonomic entities. In this study we
680 integrated our spatial taphonomic approach with a preliminary study of the differential
681 preservation of fossil elements.

682 In the BM4 class of mammals, the relatively high abundance of skeletal elements
683 belonging to the Voorhies Groups I/II, II and II/III (Fig. 10b) suggests minor winnow-
684 ing of the assemblage, with preservation of the densest elements that are above the
685 threshold of transportability (Behrensmeyer, 1988). Indeed, skeletal elements in the
686 Voorhies Group I (ribs, vertebrae, sacrum, sternum) tend to be transported more easily
687 by saltation or flotation in relatively low-energy currents (Voorhies, 1969). The under-
688 representation of the Voorhies Group III (crania and complete mandibles) in the BM4
689 class is balanced by the high occurrence of cranial elements in the Group II/III (rami
690 of mandibles and maxilla fragments). Thus, the distribution in Fig. 10b suggests, more
691 than the taphonomic sieve of the Voorhies Group III, a higher fragmentation rate of
692 cranial elements in the BM4 class of mammals (*Equus*, *Bison*, *Praemegaceros*). On
693 the other hand, the Voorhies Group III is better represented in the BM classes 2 and
694 3, which include smaller mammals, i.e., *C. etruscus*, *U. etruscus* and medium-sized
695 cervids. The presence of better preserved carnivore cranial elements, as well as the
696 presence of a partial articulated skeleton of a wolf-sized carnivore, would suggest an
697 autochthonous or para-autochthonous assemblage (Behrensmeyer, 1988).

698 Although excluded from the Voorhies Group analysis, it is worth noting the pres-
699 ence of several mostly complete skeletal elements of Elephantidae (e.g., ribs, scapula,
700 humerus and several articulated carpals, metacarpals and phalanges) with different FTI
701 values, comparable to elements of the Voorhies Group II and III (Frison and Todd,
702 1986). Their distribution suggests that the assemblage was winnowed of the elements

703 with highest FTI, which are comparable to elements of the Voorhies Group I. This is
704 also the case for the other excluded megaherbivore, the rhinocerotid *Stephanorhinus*,
705 which is represented by several teeth and limb bones.

706 Overall, the very high teeth/vertebra ratio (7.8) also supports the hypothesis of a lag,
707 winnowed assemblage. Moreover, the actual presence of a high number of limb and
708 undetermined bone fragments, together with complete appendicular and axial elements
709 (Fig. 10c) supports also some degree of sorting (taphonomic sieve) of the smallest,
710 cancellous fragments. Segregation of axial elements from epiphyses and shafts has
711 been observed even in low-energy fluvial environments (Domínguez-Rodrigo et al.,
712 2017).

713 On the other hand, as noted earlier, the conspicuous presence of articulated spec-
714 imens in the TSR fossil assemblage does not necessarily suggest an autochthonous
715 deposition, since articulated bones may as well show a great hydraulic transport po-
716 tential (Coard, 1999; Coard and Dennell, 1995). Nevertheless, it is worth noting that
717 the distribution of articulated units at TSR shows a significant presence of appendicu-
718 lar elements over axial ones (Fig. 10d). Thus, the under-representation of articulated
719 axial elements also indicates a winnowed, lag assemblage formed by the densest and
720 most resilient elements, with sieve and transport of part of the lighter and more can-
721 cellous elements. However, carnivore ravaging alike tends to eliminate or at least lead
722 to under-representation of those skeletal elements (the less dense, axial elements) in
723 the transport group most prone to be transported by water (Domínguez-Rodrigo et al.,
724 2012; Voorhies, 1969). Interestingly, a preliminary analysis of the bone breakage pat-
725 terns suggests that carnivores had some active role in the modification and possibly in
726 the accumulation of bones at TSR (Fig. 2e; Konidaris et al., 2015).

727 In conclusion, considering the results of our spatial taphonomic analysis, pro-
728 cesses of taphonomic dispersion, such as fluvial accumulation processes, would have
729 likely separated and disseminated the most cancellous taphonomic elements, favouring
730 the persistence of taphons constituted by allochthonous elements (Fernández-López,
731 2006). Carnivores could have likely been primary accumulation agents. However, the
732 recursive anisotropic spatial patterns, at the level of taphonomic elements and at the
733 assemblage level, as well as the clustering pattern in relatively small, dense, aggre-

734 gations of elements aligned in parallel NW-SE oriented bands, suggest that the TSR
735 deposit resulted from multiple taphonomic dispersion events, with winnowing of less
736 dense, lighter elements and spatial anisotropic re-arrangement of a lag, autochthonous
737 assemblage accumulated over the migrating banks of a NW-SE oriented fluvial system.
738 As suggested by [Organista et al. \(2017\)](#), it is likely for secondary over-bank flows to
739 aggregate bones dispersed over the bank surface into topographic depressions, where
740 they accumulate and acquire greater stability.

741 Noteworthy, both Geo 1 and Geo 2 show fining upward trends and facies sequences
742 similar to those typical of braided rivers ([Miall, 1977](#)). In such a sequence, the lower
743 coarser-grained part would represent one or more sets of sinuous-crested medium-scale
744 bedforms (i.e., small dunes) forming by bedload traction in the deeper reaches of chan-
745 nels, whereas the upper muddy part is dominantly deposited by decantation either on
746 top of in-channel or bank-attached emerging bars or in floodplains, occasionally pro-
747 vided with coarse material at high-water stages ([Miall, 1982](#)). Therefore, the excavated
748 section can be viewed as the product of cyclical lateral switching of a braided fluvial
749 system.

750 **6. Conclusions**

751 Spatial taphonomy is the systemic, multiscale and multilevel study of the spatial
752 properties of taphonomic processes. Indeed, taphonomic alteration processes work
753 simultaneously, at different scales, on entities of different levels of organisation, from
754 the basic taphonomic elements (bone specimens), to higher level taphonomic groups
755 (taphons) or populations (assemblages). In this study we elaborated on a specific aspect
756 - anisotropy - of the spatial properties of taphonomic processes, investigating an often
757 neglected aspect of the spatial distribution of taphonomic populations.

758 A multilevel analysis of anisotropy was conducted for the Early Pleistocene fossil-
759 iferous locality Tsiotra Vryssi, from the fluvial Gerakarou Formation of the Mygdonia
760 Basin, Greece. Differential preservation of skeletal elements was also analysed in order
761 to unravel the character and number of depositional processes and the degree of
762 re-elaboration of the TSR fossil record. The results of the analyses suggested repeated

763 taphonomic dispersion processes, with winnowing of less dense, lighter elements and
764 spatial anisotropic re-arrangement of a lag, autochthonous assemblage possibly accu-
765 mulated over the migrating banks of a NW-SE oriented fluvial system.

766 We believe that this study contributes towards the development of a referential
767 framework for the spatial taphonomic interpretation of other palaeontological, as well
768 as archaeological, localities.

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