

1 ***Messor barbarus* ants as soil bioturbators: implications for granulometry, mineralogical composition and**
2 **fossil remains extraction in Somosaguas site (Madrid basin, Spain)**

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17 **ABSTRACT**

18
19 Few studies have inquired about the relationship between myrmecological activity and the granulometry and
20 mineralogy of sediments of a paleontological site. The objectives of this article are to determine the
21 sedimentological or mineralogical distinctions produced by ants of the species *Messor barbarus* when
22 excavating their nests and extracting grains and vertebrate fossil remains from the Miocene paleontological site
23 of Somosaguas (Madrid, Spain), to evaluate the degree of taphonomic influence this myrmecological activity has
24 on the fossil remains, and to decide whether or not it can be used as a tool for paleontological prospection.
25 Results show that *Messor barbarus* does not alter fossil remains when examined under a 10x binocular
26 magnifying glass. Ants preferentially extract from the ant nest grains of medium sizes (0.25 - 2 mm) compared
27 to the non-ant-modified soils, and also extract a higher quantity of feldspars. These significant granulometric and
28 mineralogical modifications should be considered when carrying out compositional, sedimentological or
29 stratigraphical studies, since these can become biased and alter geological interpretations as provenance or
30 palaeoclimatic signal. Grain size selection could be due to *Messor barbarus*' physical capacities or the use of

31 clay particles as cementing elements in nests. Mineralogical distinction may be related to feldspars' embayments
32 and pits filled with finer material (mainly smectites), making transportation and pheromone impregnation easier.
33 Results show that the ant mounds had increasing concentrations of fossil remains the nearer they were from the
34 main excavation area, therefore the study of ant mounds in potentially fossiliferous zones can indeed be used as a
35 new method of paleontological prospection.

36

37 **Key words:** Bioturbation; Bio-retexturing; Granulometric analysis; Myrmecology; Petrographic analysis; Soils.

38

39 1. INTRODUCTION

40

41 Arthropods make up 90% of urban total fauna (Ruiz Heras et al., 2011; Carpintero and Reyes-López, 2014).
42 Amongst them, ants stand out because of their number and biomass (Hölldobler and Wilson, 1990; Passera and
43 Aaron, 2005). Many studies show how their activities can have a significant effect on human infrastructures
44 (Robinson, 1996; Hill, 1997). Ant activity can bioturbate the surrounding soils, mostly due to colony formation,
45 which is very diverse depending on the different ant species (Tschinkel, 2003). This bioturbation does not only
46 affect soil stratigraphy and geochemistry, but can also increase water infiltration rates, runoff discharge and soil
47 erosion (Lobry de Bruyn and Conacher, 1990; Cerdà and Jurgenson, 2008; among many others), and affect the
48 voids formation and nutrient cycling regulation (Hole, 1981). Although foraging behaviors have been thoroughly
49 studied throughout the genus *Messor* (Plowes et al., 2013), other behavioral mechanisms like different mineral
50 compositions selection by this species must be further studied. Previous studies on bioturbation effects and the
51 selective use of mineral grains by ants had shown mismatches between optical luminescence dating and artifact
52 age (obtained by radiocarbon) in archaeological areas affected by ants' activities (e.g. Rink et al., 2013). Many
53 studies have highlighted the relationship between the development of ant nests and variations in soil chemistry
54 (Culver and Beattie, 1983; Wagner et al., 1997; Frouz et al., 2003; Wagner et al., 2004) or granulometry of
55 extracted sediments (Wang et al., 1995; MacMahon et al., 2000; Nkem et al., 2000; Cammeraat et al., 2002;
56 Dostal et al., 2005; Cosarinsky, 2006; Azcárate and Peco, 2007; Cosarinsky and Roces, 2007) but few studies
57 have been carried out with a more detailed petrological and mineralogical focus when comparing the extracted
58 sediment to the underlying unaltered sediment in fossiliferous areas.

59

60 Sand and sandstone petrography and sedimentology are useful tools to deduce geotectonic setting (Dickinson
61 and Suczek, 1979), lithology and relief of a source area (Basu, 1976; Palomares and Arribas, 1993; Arribas and
62 Tortosa, 2003) or palaeoclimate (Suttner and Dutta, 1986; Weltje, 1994; Fesharaki et al., 2015). Also,
63 petrographic and clastometric analyses are important in soil characterization for environmental contamination,
64 weathering, erosion, pedogenesis, agricultural studies or geoarchaeology (e.g. Courty, 1992; Le Pera et al., 2000,
65 2001; Scarciglia et al., 2005; Zharikova, 2017; Goldberg and Aldeias, 2018). Burrowing and mounding activities
66 of prairie dogs (Whicker and Detling, 1988), gophers (Sherrod and Seastedt, 2001), insects (Liu et al., 2007),
67 worms (Needham et al., 2006) or benthic species (Rhoads and Boyer, 1982) represent local disturbances of soil
68 and sediments characteristics (e.g. O'Brien, 1987). In addition, tunnels or chambers excavated belowground by
69 ants can lead to intense bioturbation, involving mixing and accumulation of soils from different sources and
70 horizons (Nkem et al., 2000; Halfen and Hasiotis, 2010; Rink et al., 2013) and changing soil textural properties
71 (Paton et al., 1995; Folgarait, 1998). Therefore, areas heavily colonized by insects, for example by ants, could
72 lead to misleading compositional or textural observations of the hosting soils and sediments if those
73 modifications are not taken into account.

74
75 Moreover, since ancient times, the ability of ants as gold diggers has generated a great interest in scientists, as is
76 evidenced in the Greek myths described by Herodotus (Herodotus, 2007); but are some current works on
77 termites and their termitaria (mounds constructed by them) which indicate the usefulness of social insects in
78 mineral exploration (Petts et al., 2009). Nevertheless, ant mounds have not been systematically studied in order
79 to be used as criteria for paleontological prospection, even when fossil-collecting behavior has been previously
80 noticed in ants (Turnbull, 1959; Clark et al., 1967; Croft et al., 2004). Here lie the questions that motivated this
81 study: (1) do *Messor barbarus* ants make any kind of distinction, compositional or granulometrical, at the time
82 of sediment extraction while excavating their nests in a palaeontological area? (2) Are the changes generated by
83 the myrmecological action significant when carrying out palaeoenvironmental and palaeoclimatic studies? (3) do
84 *Messor barbarus* ants alter taphonomically the fossil remains they extract from fossiliferous sites? and (4) Can
85 ants' mound sediment study be used as a new tool for paleontological prospection?

86
87 In this article we will determine to what extent *Messor barbarus* ants make a sedimentological or mineralogical
88 distinction when extracting sedimentary particles at a fossiliferous site (Somosaguas fossil site) located
89 northwest of the Madrid Basin (Spain). Sedimentary deposits of the Somosaguas paleontological site have been

90 chosen because they have been intensely studied (Fesharaki et al., 2012 and references therein; Domingo et al.,
91 2017), and therefore the data obtained will be easy to compare (Fig. 1).

92

93 This area presents a high abundance of *Messor barbarus* Linnaeus 1767 (Hymenoptera: Formicidae) nests.
94 *Messor barbarus* is a highly polymorphic grain-collector ant species (Heredia and Detrain, 2000) common on
95 Mediterranean grasslands of Southern Europe and Northern Africa (Detrain et al., 2000). They build complicated
96 nests composed by a big network of galleries and interconnected chambers that can reach 5 meters in depth and
97 in those cases where it does not, the nest can spread out up as much as 25 m² over the surface (Bulot et al.,
98 2014). The nest is excavated and maintained mainly by worker ants that use their mandibles, with a gap range
99 between 0.80 and 2.80 mm (Oliveras et al., 2005), to transport mineral particles and soil pellets outside the nest.
100 The maximum size and weight of materials that a *M. barbarus* worker can transport are still poorly known, but
101 they have been documented carrying soil pellets up to 11 mm (Shipman and Walker, 1980; Durán, 2011) and 50
102 mg (Detrain and Pasteels, 2000), but it can be assumed that the size of soil particles transported by ants depends
103 on the size of their mandibles (Dostál et al., 2005). As a granivore species, *M. barbarus* prefers grasslands and
104 high temperature locations for their nest in order to facilitate soil water evaporation and seed preservation
105 (Bernard, 1958; Rodríguez, 1982; Rodríguez and Fernández Haeger, 1983). Although there are up to ten
106 recognized species of *Messor* in the Iberian Peninsula, it is highly unusual to find two or more different species
107 in the same area (Espadaler and Suñer, 1995) due to the limiting factor of the territory which can influence nest
108 size and new nest formation in those areas where 15% of the land is covered by nests (Nielsen, 1986). Besides
109 *Messor barbarus* it is possible to find two other ant species in the immediate Somosaguas fossil sites
110 surroundings: *Camponotus cruentatus* Latreille, 1802 and *Aphaenogaster senilis* Mayr, 1853. *Camponotus*
111 *cruentatus* is a common species throughout the Mediterranean region where it excavates its nests in dry soils.
112 Their colonies are made up of a few thousand workers which inhabit monodomous nests that rarely exceed 65
113 cm deep and have a surface of 2-4 m² (Boulay et al., 2007). *Aphaenogaster senilis* is an omnivorous species
114 which feeds on a wide range of prey and, to a lesser extent, vegetable remains (Barroso Rodríguez, 2013),
115 distributed all along the Mediterranean basin (Galarza et al., 2012). They form small colonies of 200-1500
116 workers (Barroso Rodríguez, 2013). It is a strongly migratory species. After they migrate, former ant nest retain
117 their whole structure of galleries and chambers which allows reutilization by the same or another colony which
118 reduces the need of excavating a new nest and thus also reduces its impact on the underlying materials (Galarza
119 et al., 2012). Due to its textural characteristics, with poorly and irregularly cemented sediments (Fesharaki,

120 2016), the surroundings of the Somosaguas paleontological site make a favorable area for these organisms to
121 establish their nests.

122

123 As already mentioned ants carry particles to surface mounds during nest construction and continually improve
124 and modify these constructions. Previous literature about these nesting activities have shown the preference of
125 ants to use certain particle sizes for building. Wang et al. (1995) described a preferential selection of grains by
126 *Lasinus neoniger* ants when building their galleries, using the coarse grains infilled by the finer particles as
127 cementing materials, and more recent observations on *Temnothorax albipennis* indicate that when selecting
128 material for wall-building they choose large sand grains as well as smaller ones to construct mixed grain-size
129 walls that are more compact and strong (Aleksiev et al., 2007). Some authors (Wang et al., 1995; Cosarinsky,
130 2006; Cosarinsky and Roces, 2007) have described a preferential selection of grains by ants when building their
131 galleries, using finer particles as cementing materials. *Atta vollenweideri* ants when have the possibility to use
132 sands and also clays they build mixed structures whith sand walls infilled by clay aggregates or pellets
133 (Cosarinsky and Roces, 2007). Similar behaviour have been described for other ant species like *Camponotus*
134 *punctulatus* or *Solenopsis* sp. (Cosarinsky, 2006; Gorosito et al., 2006). Paton et al. (1995) indicate that mounds
135 constructed by *Aphaenogaster* ants are usually depleted in gravel, coarse sand (grains larger than 2.5 mm are
136 absent) and clay when compared with the surrounding soils (Richards, 2009). *Iridomyrmex purpureus* build their
137 galleries using a mixture of silt and saliva (Ettershank, 1968) while *Pogonomyrmex occidentalis* pack soil
138 materials during reinforcement of nets' walls (Halfen and Hasiotis, 2010). Drager et al. (2016) documented silt
139 enrichment in surface mounds of the species *Formica subsericea*. Many other authors have observed an
140 increased percentage of silts and/or clays in the mounds built by different ant species compared to the
141 surrounding soil (MacMahon et al., 2000; Cammeraat et al., 2002; Whitford, 2002; Dostal et al., 2005; Azcárate
142 and Peco, 2007), whereas others have observed that sand fractions are preferentially deposited in the mounds
143 (e.g. Nkem et al., 2000). Possibly many species of ants are able to select different types of material (e.g. clays or
144 coarse sands) to stabilize their nests' walls and mounds in response to local variations in mechanical stability
145 (Cosarinsky and Roces, 2007) being probably this one of the major reasons for their great distribution all around
146 the world (cita). For example in the experiments carried out by Cosarinsky and Roces (2007) *Atta vollenweideri*
147 ants build their nests by coarse sands, fine sands, clays and also mixtures of different grain sizes as a function of
148 material disponibility. Similar observations were made by Tschinkel (2006) when studying the types of materials
149 in which the ant *Solenopsis invicta* build their nests' (clay, dry or wet sands).

150

151 Previous studies have described in detail the modifications on fossils due to termite activity in different parts of
152 the world (e.g. McBrearty, 1990; Backwell et al., 2012), but not the repercussion that ants may have on these.
153 Therefore, we also aim to evaluate to what extent these colonization can influence fossil taphonomy, studied in
154 this site by Polonio and López Martínez (2000) and Domingo et al. (2017), whom described different
155 taphonomic trajectories for fossil remains: from heavily fragmented and rounded bone splinters smaller than 3
156 cm to well-preserved fossil remains.

157

158 Paleontological prospection techniques have become very diverse, ranging from using high-tech indicators such
159 as ultra-violet light (Croft et al., 2004) to more natural ones such as vegetation associations (Monterde et al.,
160 2015). In this study, it is tested whether or not the study on ant mound sediments and their fossiliferous content
161 can be used as a tool for paleontological prospection.

162

163 2. GEOGRAPHICAL AND GEOLOGICAL CONTEXT

164

165 The Somosaguas paleontological site is located inside the campus of the Complutense University of Madrid in
166 Pozuelo de Alarcón, west of Madrid (Fig. 1, López Martínez et al., 2000). The fact that the site is located in such
167 an urban setting makes scientific dissemination easier and more accessible (Fesharaki et al., 2012), with
168 hundreds of passers by walking past every day and many outreach activities taking place at the site throughout
169 the year. This anthropogenic disturbance must be taken into account when analysing the characteristics of the
170 ant-induced modifications on sediments.

171

172 The studied area is at an altitude of about 660 m; presents a Continentalized Mediterranean climate with an
173 average annual rainfall of about 500 mm and an average annual temperature of 14°C (Gómez Oballe, 2016). It
174 has a long summer season and very dry character and the autumns, however, are temperate due to the protective
175 nature of the mountains that surround the city of Madrid (Font Tullot, 1983). These two factors are what
176 contribute to the dry period being so long. As a consequence of the climatic conditions, the mature stage of
177 vegetation in this area would be represented by meso-Mediterranean holm oak forests (Rivas-Martínez, 1987),
178 but as a consequence of the anthropic action, only grasses rich in subnitrophile and ruderal species are developed
179 (Monterde, 2014). In addition, it is an unstable flora subject to continuous changes in terms of its diversity

180 favored by anthropogenic disturbances due to land movement and infrastructures constructions that have
181 multiplied in recent years (Monterde et al., 2015).

182

183 The site includes two main excavation areas, Somosaguas-North (SOM-N), where macrovertebrate fossils
184 excavation takes place organized in grids, and Somosaguas-South (SOM-S), where sediment is extracted and
185 processed to obtain microvertebrate fossil remains (Fig. 2). In addition to these two areas, there are nine
186 excavation trenches, two of which are currently being excavated and another two are used for stratigraphic
187 studies purposes (Díez-Canseco et al., 2012). A total of 25 mammal species have been described and less
188 abundant fossil remains of birds, lizards and testudines have also been found (Hernández Fernández et al., 2006;
189 Fesharaki, 2016). Micromammal fossil remains made it possible to date the site as local biozone E (14 Ma,
190 MN5, middle Aragonian, Middle Miocene; Luis and Hernando, 2000). Based on the abundance and variety of
191 the miocene fauna and the sedimentological, mineralogical and isotopic data, this fossil site has been assigned to
192 a savannah paleoenvironment covered with some vegetation patches and woods, with an intense seasonality
193 leading to predominant dry seasons, and a tendency to increased aridity and decreased temperature coinciding
194 with the end of the Miocene climatic optimum (Böhme, 2003; Hernández Fernández et al., 2006; Carrasco et al.,
195 2008; Domingo et al., 2009; García Yelo et al., 2014; Fesharaki et al., 2015). The observation of the six meter
196 thick sedimentary record of this climatic change makes this site an ideal place to trace the interference of other
197 factors that may affect the palaeoenvironmental and palaeoclimatic studies.

198

199 From a stratigraphic point of view, the Somosaguas paleontological area is made up of two fossiliferous units
200 (T1 and T3) with a barren unit between them (T2), with a total thickness variable between 4.5 and 6 m. The
201 basal unit (T1) is comprised of a matrix supported clayey arkoses which do not show any type of sedimentary
202 structures. The clay content of this unit increases upwards, which can be considered as sandy clay when in
203 contact with the overlying unit (Fesharaki et al., 2007). This unit has a considerable amount of microvertebrate
204 fossil remains (López Martínez et al., 2000). The intermediate unit (T2) shows an alternation of well-sorted
205 micaceous sands and brownish clays. The micaceous sands of this unit show climbing ripples in the lower levels
206 and horizontal lineation upwards. This unit pinches out towards the North and disappears under SOM-N site,
207 where it is reduced to centrimetrical rip-up clasts of micaceous sands, which can be found inside T3 unit
208 (Mínguez-Gandú, 2000). Finally, T3 unit has been classified as a multiepisodic deposit of coarse arkoses with
209 silty-clay matrix. Towards the top of the unit, calcrete levels are observed along with small lenticular levels of

210 organic-rich clays (Fesharaki et al., 2015). Macromammal fossil remains are very abundant in this unit (López
211 Martínez et al., 2000). Previous studies have assigned these levels to distal alluvial fan deposits (T1 and T3) and
212 lake-border areas (T2), produced by processes of mud flow, debris flow, and sheet flood and clay settling
213 respectively (Mínguez-Gandú, 2000; Díez-Canseco et al., 2012).

214
215 From a mineralogical point of view the three units described consist of phyllosilicates, feldspars, quartz and
216 minor amounts of heavy minerals (Fesharaki et al., 2007; Fesharaki, 2016). Also calcite is present in the
217 calcretes levels. Phyllosilicates are mainly micas (biotite and muscovite), smectites (both beidellitic and
218 montmorillonitic end-members are present) and small amounts of kaolinite and mixed-layer illite/smectite
219 (Fesharaki et al., 2007). Beidellites are transformed minerals and show a great compositional variability whereas
220 montmorillonites are mainly neoformed (Fesharaki et al., 2007). The great chemical variability and the presence
221 of low and high charge beidellites are typical characteristics of sediments that have been exposed to the action of
222 pedological processes (Righi et al., 1995; Fesharaki et al., 2007; Fesharaki, 2016). These clay minerals
223 characteristics and other features from inherited minerals indicate successive processes of reworking and soil
224 development in the sediments described in the Somosaguas area (Fesharaki, 2016).

225
226 As mentioned previously these are areas of constant passage of students and visitors throughout the year, and are
227 even more transited during the seasonal paleontological digging activities. For these reasons this “urban”
228 paleontological site and its surroundings have underdeveloped soils without differentiated characteristic horizons
229 (Gómez Oballe, 2016). Soils developed on the T1 and T3 units are Regosols (IUSS Working Group WRB, 2015)
230 formed by an organic A horizon between 0.5 and 4 cm thick, and a C horizon formed on T3 by arkoses with
231 clay-silt matrix, partly infiltrated and generated by processes of neoformation (smectites), and on T1 by clayey
232 arkoses with upward enrichment in clays (Fesharaki, 2005; Gómez Oballe, 2016). Soils are more granular and
233 have a better drainage in T3; and more cohesive, due to the increase of clays, and with a worse drainage in T1
234 (Fesharaki, 2005; Fesharaki et al., 2007; Gómez Oballe, 2016). Finally, diverse processes described by Díez-
235 Canseco et al. (2012) have led to local enrichment in clays in some areas of T3 (elutriation during debris flow
236 episodes), generating darker-colored clays with higher organic matter content which have been called “clay
237 biscuits” by Carrasco et al. (2008). This clay-enriched “biscuits” (average diameter of 10 cm and a thickness of
238 about 0.5 to 1.5 cm) present up to 80 % of smectites and micro-slickensides which gives them vertic
239 characteristics. In any case, the anthills studied have been developed in all cases on soils that would be classified

240 as Regosols (Gómez Oballe, 2016). Preliminary studies indicate the formation of organo-mineral
241 microaggregates formed by smectitic clays, organic matter and quartz-feldspathic grains of silt size (Fesharaki,
242 2005). Probably these are products of the biological action and mainly due ants' load forming behaviour
243 (Cosarinsky and Roces, 2012). Fesharaki et al. (2007) described the presence of clay coatings (smectites) in all
244 the sections of the studied area, with similar mineralogical compositions, that were covering the surface of the
245 detrital minerals. Fesharaki et al. (2015) pointed out the alteration of feldspars and micas to clay minerals (illites
246 and smectites). They described feldspars with different degrees of alteration and transformation to clays resulting
247 in grains of a greater surface with pits and embayments filled with clays.

248

249 3. MATERIALS AND METHODS

250

251 Two field campaigns were carried out during the years 2013 and 2014. Geological cartography of the studied
252 area (Élez, 2005) was merged with the locations of all *Messor barbarus* active mounds visible during the
253 fieldwork throughout two prospection areas (see locations in Fig. 2). All nest mound mapped were measured
254 (diameter and height), and a brief description of their morphology was recorded. All these nest mounds were
255 sampled briefly after mounds were completely formed in order to avoid any exogenous contamination and
256 prevent any granulometric or compositional modification by water or aeolian processes. A total of 18 mounds
257 were sampled (fifteen over T3 and three over T1) collecting all sediment extracted by the *Messor barbarus* ants
258 surrounding each nest entrance.

259

260 All 18 samples were examined under a 10x binocular magnifying glass in search for fossil remains. The fossil
261 remains retrieved were examined for any taphonomic alterations, according to criteria proposed by Backwell et
262 al. (2012) and Fejfar and Kaiser (2005), and compared to those characteristics described by Polonio and López
263 Martínez (2000) and Domingo et al. (2017) for fossil bones from Somosaguas site without myrmecological
264 alteration. A map of the density of fossil remains collected by ants was created with Surfer® 14 (Golden
265 Software, LLC), using Point Kriging as Gridding method, and was compared to the fossil density for the
266 excavation areas obtained with data from the systematic grid excavation of the site for 18 years.

267

268 Ten samples of the sediments extracted by the ants (seven from T3 and three from T1) were selected for the
269 granulometric comparison with previous sedimentological studies (Fesharaki, 2016). For its comparison against

270 data from previous studies the selected samples were treated with hydrogen peroxide (diluted to 30%) until
271 complete removal of any organic material and the fraction smaller than 0.062 mm of each sample was removed.
272 Finally, a dry sieving was applied to all samples, using a battery with a mesh width of between 4 phi and 2 phi,
273 with constant intervals of 0.5 phi, obtaining a total of 13 fractions for their grain size distribution
274 characterization.

275

276 For the compositional characterization, seven sand samples (four from T3 mounds and three from T1) were
277 cemented with epoxy resin and thin sectioned for microscopy observation and analysis. Each thin section was
278 etched and stained using HF and Na-cobaltinitrite to help identify feldspars (Chayes, 1952). The fraction used
279 was 2 phi, for its comparison against data from previous studies (Fesharaki et al., 2015). Point-counting has been
280 carried out as described by Fesharaki et al. (2015).

281

282 From a statistical point of view, many of the samples displayed non-normal distributions so statistical analyses
283 consisted of non-parametric tests (Mann-Whitney and Kolmogorov-Smirnov tests). We set the significance level
284 at $p = 0.05$. Statistical analyses were performed with the paleontological statistics software PAST (Hammer et
285 al., 2001).

286

287 **4. RESULTS AND DISCUSSION**

288

289 **4.1 Mounds Characteristics and Taphonomic Analysis**

290

291 The field observations in this study allowed the detection of seeds and other plant elements along with sediment
292 gathered around the exit of the colony during autumn, while in spring the mounds were primarily composed of
293 sediment extracted from the ant nest (Fig. 3). The nests found in the T3 area had a substantially higher
294 superficial development, with a higher quantity of sediment accumulated at the entrance (mounds), compared to
295 those nests found above T1. Both type of mounds are formed by merely surface deposits of excavated sediments
296 without any kind of cementation, so they can be classified as type-I (Paton et al., 1995), being very susceptible to
297 erosion (Richards, 2009). The mounds at the entrances of the nests had an average diameter of 20 cm ($Sd \pm 3.2$
298 cm) and an average height of 4.7 cm ($Sd \pm 1.8$ cm). As mentioned by Drager et al. (2016) the amount of material
299 moved to the mounds depends on the ants species and the textural characteristics of the soils, because ants

300 display a preference for certain grain sizes when building their nests. The fact that *Messor barbarus* extracts
301 lesser amount of sediments in T1 than in T3 is consistent with previous observations by Whitford and DiMarco
302 (1995), whom report approximately a 30 times higher sediment transport in sandy sediments than in clayey
303 deposits by ants inhabiting Chihuahuan desert. Future studies should further investigate if ant nests are deeper
304 and more extensive in T3 than in T1, as has been observed to happen with plant roots in the same area (Monterde
305 et al., 2015).

306
307 At T3, *Messor barbarus*' nests were much more abundant, with fifteen active nests, compared to only three in
308 T1. The fact that the majority of nests were located over materials belonging to T3 is possibly caused by T1
309 being much more clayey, presenting a higher cohesion and therefore showing a higher resistance to the
310 establishment of new colonies, whilst T3, a less cohesive granular sediment with better soil aeration, is ideal for
311 the abundant colonization by ants (Hölldobler and Wilson, 1990; Baraibar et al., 2011). Costa-Milanez et al.
312 (2017) indicate that the granulometry of sediments and soils imposes restrictions on the establishment of
313 different species of ants according to their body size. This fact would support the observations made in the area
314 of Somosaguas, since the low abundance of *Messor barbarus* is accompanied by the presence of other smaller
315 species in those areas where the T1 unit crops out. In addition, clays are more abundant in the T1 section, so
316 these sediments can preserve environmental moisture better, which could be harmful to the storage and
317 maintenance of seeds that are essential for the *Messor barbarus* survival (Rodríguez, 1982). Therefore, these
318 ants would have a clear preference for the sediments of T3, composed primarily by silts and sands that allow a
319 better evaporation of the water and the preservation of the seeds harvested by them.

320
321 On the other hand, in Figure 2 it can be observed that most of the mounds that indicate active ant nests are
322 located in the vicinity of the Somosaguas-North excavation area, being non-existent in the zones more to the
323 East or South of the prospection area. Similar cases have been described in previous works, indicating that in
324 general there appears to be a random distribution of ant nests with the sole exception that they appear to be more
325 abundant in areas where plant cover is lower (Holec et al., 2006). This could be the explanation for the studied
326 area, since in the vicinity of the Somosaguas-North area, and because of the human activities developed during
327 the excavations, the vegetation is much less abundant (Monterde, 2014).

328

329 Using 10x binocular lens, vertebrate fossil remains were found in 10 of the 15 nests studied in T3 (Table 1).
330 These fossiliferous nests were located within a radius of 10 m around SOM-N site (Fig. 2). The fossil remains
331 found in T3 samples had a length smaller than 0.25 cm. These fossil remains were not taxonomically identifiable
332 and did not show taphonomic signs of alteration due to myrmecological action, like those established by
333 Backwell et al. (2012) or similar marks left by isopteran insects as described by Fejfar and Kaiser (2005). The
334 remains found were angular and sub-angular bone elements, ranging from dark grey to white with black spots,
335 with similar characteristics to those in T3 described by Polonio and López Martínez (2000) and Domingo et al.
336 (2017). One isolated enamel fragment was found in T3H8 (Table 1). In all three T1 samples, micromammal
337 fossil bones were found (well preserved bone elements), although always consisting of disarticulate elements
338 smaller than 1 mm, as described in previous research (Luis and Hernando, 2000). Since the extracted fossil
339 remains show the same taphonomical characteristics as those described by Polonio and López Martínez (2000)
340 and Domingo et al. (2017), we infer that ants have little to no direct taphonomic influence over the remains at
341 optical scale. Up so far, we have not detected direct effects of ants on the fossil remains. In this sense, in the
342 literature about changes that ants and termites actions induce in the chemical characteristics of a soil, one of the
343 characteristics that stand out is the change they cause on pH, decreasing alkaline pH and increasing the more
344 acidic ones (Frouz et al., 2003; Jílková et al., 2012; Morgun and Golichenkov, 2015). These changes can be
345 decisive in the precipitation-dissolution chemistry of mineral phases or the availability of certain ions. For
346 example, an increase in pH can influence the substitution of fossil phosphate by carbonate, or at least the
347 precipitation of calcite on the paleontological remain (Nieto et al., 2002). On the other hand, the decrease of the
348 pH can favor the precipitation of certain clay minerals against others, at the same time that it originates the
349 dissolution of the original bone and its replacement by neoformed clay minerals (Nielsen-Marsh, 2000; Nieto et
350 al. al., 2002). Finally, the structure of the phosphates allows a wide range of ion substitutions, which can be
351 originated through ion exchanges with soils and sediments (Pate et al., 1989). Given that the action of the ants
352 can increase the presence of certain ions and decrease others in the edaphic environment (Nkem et al., 2000,
353 Frouz et al., 2003, Dóstal et al., 2005, Azcárate and Peco, 2007), could influence which ions become part of the
354 fossil remains once buried, and therefore, change their chemistry. Since the chemistry of bones is one of the
355 characteristics used in paleoecological studies, it is important that future researches take into account the
356 possible variations that can be caused by the action of ants or termites on soils that contain these paleontological
357 remains (Pate et al., 1989).

358

359 The fossil remain density map shows the greatest concentration southeast from the main excavation site (Fig. 4),
360 which is consistent with previous taphonomic results, where some levels become poorer in fossil remains
361 towards the northwest, and overall show a lower concentration of remains North of the excavated area (Domingo
362 et al., 2017). Although this is already enough evidence to support the initial hypothesis, future excavations
363 towards the southeast of the main site could confirm the strength and weaknesses of using this technique as a
364 new method for paleontological prospection. This innovative approach is especially suitable for paleontological
365 and archeological sites with some original fragmentation of the macrofauna remains or the presence of
366 microfauna fossils, making it possible to identify areas with a higher density of fossil remains and fructiferous in
367 order to start a preliminary excavation.

368

369 **4.2 Granulometric Analysis**

370

371 Granulometric data obtained from the selected samples are shown in Table 2. Medium sandy fractions (0.25
372 mm) show higher values than any other fractions in all samples (Fig. 5). It is noteworthy that the majority of the
373 samples from T3 do not contain grains with sizes coarser than 2.83 mm, whilst samples from T1 do not show
374 sedimentary particles finer than 0.088 mm. Although the grains and particles finer than 0,062mm were removed,
375 non quantitative observations suggest very little presence of these grain-size fractions, especially in samples
376 from T3 unit.

377

378 Kolmogorov Smirnov tests were carried out to compare all mean clastometric distributions (Table 3). No
379 significant difference was observed between any compared pair (T1 modified *versus* T3 modified; T1 modified
380 vs. T1 unmodified from Fesharaki (2016); T3 modified vs. T3 unmodified from Fesharaki (2016)). This means
381 that the compared pairs of data have similar trends (Fig. 6).

382

383 A Mann Whitney test (Table 4) was also carried out to compare the different fractions of the studied samples
384 with data from non-ant-modified sediments described previously by Fesharaki (2016). Comparing the
385 granulometric data of unmodified sediments of T1 and T3 (Fesharaki, 2016), there are significant ($p < 0.05$)
386 differences in three grain size fractions, being clearly more abundant the fraction of 2mm in T3, and the 0.25 and
387 0.177 mm fractions in T1. The remaining fractions do not present significant differences. This agrees with the
388 field classifications, since T3 is formed by coarse arkoses, while T1 is formed by clayey arkoses.

389
390 Comparison of the grain size distribution of the mounds developed on T1 and T3 shows significant ($p < 0.05$)
391 differences in several fractions. An overrepresentation of the 2mm, 1.41mm and 0.25mm fractions is observed in
392 T1 mound sediments. In T3 mound sediments the fractions of 0.125mm, 0.088mm and 0.062mm are
393 overrepresented. These data indicate a tendency to the homogenization of the grain-size fractions extracted
394 through the bioturbation processes carried out by *Messor barbarus* ants (Tables 3 and 4).

395
396 Comparing the granulometry of the modified and unmodified sediments of T1 it is observed that the finer
397 fractions (0.125mm, 0.088mm and 0.062mm) are significantly underrepresented in the mounds and the same is
398 true for some coarser fractions like the 2.83mm, and practically for the 4mm fraction (with a p value = 0.051).
399 These observations indicate that the coarsest and the finest fractions are not extracted by the *Messor barbarus*. In
400 addition, the intermediate sizes (0.25, 0.5, 0.71, 1mm, and almost 1.41 and 0.35mm) are significantly over-
401 represented in the *Messor barbarus* mounds. Cosarinsky and Rocés (2012) pointed out that *Atta* ants build
402 different types of galleries and chambers with particular types of microstructures depending on the available
403 material (different grain sizes), and they recognized two types of building behaviours. When coarse sands and
404 clays were available *Atta* ants built a combination of these materials linking two sand grains with clay masses of
405 pelletal origin, whereas when fine sands were the available materials they construct their galleries with pelletal
406 materials placing the sand grains in the existing pores (Cosarinsky and Rocés, 2012). These types of behaviour
407 would indicate that ants have the ability to recognize local mechanically unstable zones and respond to
408 instability changing materials and structures to reinforce that locally weak points. This behaviour has been also
409 suggested by Espinoza and Santamarina (2010) when studying the building strategies used by different harvester
410 ants in clay, silt, sand and gravel. Gallery stability may be enhanced by glandular secretions and natural below
411 ground soil cementation (Espinoza and Santamarina, 2010 and references therein). These authors indicate that
412 ants choose particles by size so that the width does not exceed the mandible size. As mentioned in the
413 introduction section many authors have observed preferential selection of grains by ants when building their
414 galleries (Paton et al., 1995; Wang et al., 1995; Cosarinsky, 2006; Aleksiev et al., 2007). For example, *Lasinus*
415 *neoniger* and *Temnothorax albipennis* ants use coarse grains infilled by finer particles as cementing materials to
416 construct their tunnel walls (Wang et al., 1995; Aleksiev et al., 2007). In other cases galleries or chambers
417 excavated belowground are coated with fine material (Cosarinsky, 2006; Cosarinsky & Rocés, 2007). These
418 selective behaviour causes variations in the granulometry of the mounds not only related with each ant species

419 but also as a function of the available grain sizes and other physico-chemical characteristics of the environment
420 in which the mounds are constructed. In this sense Paton et al. (1995) stand out that *Aphaenogaster* ants
421 construct mounds which are usually depleted in gravel, coarse sand (grains larger than 2.5 mm are absent) and
422 clay when compared with the surrounding soils (Richards, 2009). Other researches have highlighted
423 preferentially extraction of silts and clays by different ant species (e.g. Azcárate and Peco, 2007). Finally, others
424 have observed that sands are preferentially extracted (e.g. Nkem et al., 2000). Cammeraat and Risch (2008)
425 indicate that these latter cases could be due to the fact that they occur on vertic soils with a great amount of
426 smectitic clays that are very sensitive to the dispersion by the external agents, and that they would therefore
427 impoverish the mounds in clay particles. This explanation could be valid for the area studied in the present work,
428 since 75% of the clay fraction is composed of smectites (Fesharaki et al., 2007), however, as explained
429 previously, many factors have to be taken into account and many studies are still necessary to clearly understand
430 the preferences of the ants and whether they are related to the different species, their body size or other abiotic
431 factors.

432
433 Finally, comparing the granulometric characteristics of the mounds on T3 (ant-modified samples) with the non-
434 ant-modified T3 sediment data (Fesharaki, 2016), it can be observed that in the mounds the coarser fractions
435 (equal or greater than the 1.41mm fraction) are significantly underrepresented, while the medium-size fractions
436 of 0.25 and 0.35mm are clearly over-represented. This is a trend more or less similar to that observed in T1.
437 Considering that in T3 unit the unmodified sediments show more abundant coarse grains and in T1 the opposite
438 is true, abounding the finer fractions, this trend is consistent with the fact that *Messor barbarus* extracts
439 preferentially medium-size grains.

440
441 Granulometric curves, plotting grain sizes and cumulative frequencies, are a reliable way to compare and
442 contrast results obtained in this study with those of myrmecologically unmodified sediments described by
443 Fesharaki (2016). The curves for T1 show a progressive decrease in sandy fraction content as the nest is further
444 away from superficial contact between T1 and T3 (Fig. 2). This is probably due to the geomorphology of the
445 area and the own stratigraphic characteristics of T1 unit, as it shows a fining upward sequence. These curves also
446 differ from the curve for average values for unmodified sediment since fractions smaller than 0.088mm are
447 absent (Fig. 6a). In T3, although all clastometric curves presented the same pattern, they do not correlate with the
448 tendency of the average unmodified sediments curve, which shows values higher than 2 mm (Fig. 6b).

449 Therefore, mounds' sediments from both units show a deviation in the overall fractions spectrum although have
450 similar trends compared with unmodified sediments (Fig. 6).

451

452 This granulometric distinction can be explained by the ants' own physical capacity to transport material
453 (Hölldobler and Wilson, 1990, Dostál et al., 2005). The grain sizes found in the ant mounds could be limited by
454 *Messor barbarus* average jaw opening, which ranges from 0.80 to 2.80 mm (Olivera et al., 2005), explaining the
455 difficulty for ants to carry grains outside this range of sizes (Reynolds, 1991). This same behaviour is seen in
456 prey selection by *Messor barbarus* in Mediterranean grasslands, where it is partially dependent on seed weight
457 and length (Detrain and Pasteels, 2000; Azcárate et al., 2005). Also, in relation with the size of the grains we can
458 find the answer to the absence of fine grains in the sediments collected, as any sediment of less than 0.088 mm
459 could not be picked up by ants directly and they need to use their forelegs to form load (Cosarinsky and Rocés,
460 2012) and clayey aggregates. However, these clayey aggregates could be very unstable and friable in dry and hot
461 environments such as those prevailing in the Somosaguas area for many months a year (Lucke et al., 2008), so
462 possibly they disaggregate and are dispersed from the mounds by the action wind and water. As mentioned
463 previously, another hypothesis concerning size selection could be the use of smaller sedimentary particles such
464 as clays, which are more cohesive, sometimes along with saliva, as cementing elements of the ant nest's walls
465 (Ettershank, 1968; Wang et al., 1995; Cosarinsky, 2006; Cosarinsky and Rocés, 2007). An intensive colonization
466 of certain areas with this species would generate a great modification of the granulometry (bio-retexturing) of
467 soils and sediments, and consequently of the porosity and pore-size distribution, which can finally result in the
468 modification of the hydrological and aeration characteristics of the soils, influencing other chemical and
469 biological characteristics.

470

471 **4.3 Compositional Analysis**

472

473 The results for the compositional analysis, carried out on four T3 samples and three T1 samples, along with
474 recalculated percentages of quartz (Q), feldspar (F) and rock fragments (R), are shown in Table 5. When
475 compared to results published by Fesharaki et al. (2015) for the unaltered sediment, it is clear that although the
476 ratios seem similar, a higher percentage of feldspar is present in the ants' mounds. To make this compositional
477 difference clearer, both data sets were plotted on a QFR triangular diagram (Fig. 7, Pettijohn et al., 1972),
478 showing that the projected compositions for mounds' sediments are closer to the F vertex, further away from Q

479 vertex and at the same distance to vertex R than the unaltered sediments studied by Fesharaki et al. (2015). This
480 means sediments extracted from the nests, in both areas, have a higher abundance in feldspars and lower in
481 quartz, while the rock fragments are found in relatively the same abundance than in the sediment not
482 myrmecologically modified. Statistical analyses carried out (Mann Whitney test, table 6) reveal significant
483 compositional differences ($p < 0.05$) between modified and unmodified sediments from T3, but not significant for
484 T1, although the quartz and feldspar proportions are near the significancy limit (p value = 0,052). When
485 comparing (Mann Whitney test) myrmecologically-modified sediments from T1 and T3 units, the same ratios of
486 Q, F and R are observed for both sets (Table 6). When this same test is carried out for unmodified sediments
487 (data from Fesharaki, 2016), significantly different ratios of Q, F and R are observed. Therefore, is clear that
488 *Messor barbarus* ants systematically extract the same compositional ratios whether from T1 or T3 units.

489
490 Various hypotheses are proposed according to the compositional results. First of all, since quartz minerals have a
491 high density, ants in terms of energy efficiency, would prefer to carry grains of lesser density, such as feldspar
492 minerals (Reynolds, 1991), which can be found with embayments and pits in the studied area (Fesharaki et al.,
493 2015) additionally making them less dense. Besides, materials with these types of interstices (embayments and
494 pits) could be prioritized by ants, as these are filled with clay minerals such as smectites (Fesharaki et al., 2007;
495 Fesharaki et al., 2015) and could be easier to impregnate with pheromones used as “nest markers” (Karlson and
496 Lüscher, 1959; Hölldobler and Wilson, 1990; Morgan, 2008). This would explain the abundance of feldspars,
497 since they have more interstices than other minerals present in the studied area. The same behavior is observed
498 by ants consistently extracting bone remains instead of tooth enamel fragments (Table 1), which can again be
499 explained because bone remains are porous and have a lesser density. In the majority of the literature dedicated
500 to the analysis of the modifications generated by the ants in the soils, changes in chemical characteristics (e.g.
501 nitrogen, organic and inorganic carbon or phosphorus concentrations) have been exhaustively mentioned
502 (Lafleur et al., 2002; Frouz et al., 2003; Wagner and Jones, 2004), however, the quotations related to
503 modifications of the mineralogical compositions are scarce. Many authors indicate that exists an enrichment in
504 cations (Ca, K,...) in the mounds (e.g. Frouz et al., 2003, Azcárate and Peco, 2007). Since feldspars can be a
505 source of cations such as calcium, sodium or potassium, and their alteration can release these ions to the soil, it
506 would be interesting in future studies to evaluate if part of this enrichment in cations may be related to the
507 preference of ants for extracting feldspars. The fact of making a preferent selection of feldspar not only affects
508 mineralogical composition, but also the geochemical characteristics are modified, since feldspars are more

509 alterable than other minerals present in the study area, and therefore, are a source of Al, K, Na or Ca cations,
510 which are usually exchanged with clay minerals or contribute to the medium to form authigenic minerals.
511 Another possibility would be to consider that just as it seem that somehow ants recognize the fragility of certain
512 structures and use stabilization elements such as clay coatings, they could recognize the grains that are harder
513 and more stable compared to the most altered ones, and therefore less stable, which would explain that they
514 extract feldspars instead of quartz, being the latter more resistant to alteration and harder.

515
516 Finally, although the compositional modification produced by the ants did not end up having a significant
517 change on the petrologic classification of the samples studied in this work, other cases where the compositional
518 field is smaller or data are closer to a compositional limit could have altered significantly its compositional
519 classification and therefore provide erroneous information about geological inferences such as provenance and
520 paleoclimate, altering the geological interpretation of the sedimentary deposit.

521
522 All the ant-induced modifications described are generated during the construction of their mounds contributing
523 to change the physical, chemical and biological characteristics of the sediments in contrast to nearby areas
524 (Drager et al., 2016). Variations in nutrient and plants seeds concentration or the pH or water infiltration rate
525 variations have been described among other characteristics that ant activity may modify (Hölldobler and Wilson,
526 1990; Wagner et al., 2004; Cammeraat and Risch, 2008; Drager et al., 2016; among others). But these
527 modifications also depend on the different species of ants and the textural characteristics of the soil on which
528 they are established (Drager et al., 2016). This work has exposed new data on the behavior of ants of the species
529 *Messor barbarus* in a siliciclastic sediment environment, in relation to their grain size and mineralogical
530 preferences broadening our knowledge about the influence of ants on sedimentary materials. Only with an
531 increase of multidisciplinary investigations we will be able to have a more adjusted knowledge of what entail the
532 processes between geology and ecosystem.

533

534 5. CONCLUSIONS

535

536 The ant species *Messor barbarus* bioturbations does generate a modification in the sediment extracted from its
537 nests. On the one hand, they have a preference towards extracting sediments with a medium-size against finer or
538 coarser grains, which use in their wall building and reinforcement activities (bio-retexturing) or because of

539 energy efficiency; and on the other hand, they prefer to extract feldspar against quartz or rock fragments, due to
540 the lesser density and more clay-infilled interstices present in feldspars facilitating their transportation and
541 impregnation with pheromones. Therefore, it is important to take into account this type of myrmecological action
542 on intensely colonized areas when carrying out granulometric and compositional studies, since ant activity can
543 significantly alter the results and consequently the geological interpretations (i.e. provenance or palaeoclimatic
544 interpretations based on petrographic classes abundance).

545
546 Our data indicate that, taking into account the high original fragmentation of the macrofossils and the size of the
547 microfossils present in the Somosaguas site, they are easily transportable elements by *Messor* ants. In addition,
548 they show a preference for bone remains (less dense and more porous) instead of tooth enamel, the same
549 behaviour observed when selecting preferentially feldspar grains instead of quartz. Besides, the fact that a higher
550 concentration of fossil splinters was found in the mounds closer to the digging area of Somosaguas-North, with a
551 southeastern increasing trend towards the maximum fossil remains concentration, deems the technique of
552 studying ant mounds as a viable method for paleontological prospection. Up to now several works have
553 described the action of extraction of fossil remains by ants and termites, however the Somosaguas site has served
554 as a pilot experimentation area to study the validity of the analysis of ant mounds as a prospecting criterion.
555 Finally, bone splinters extracted from Somosaguas palaeontological site by the *Messor barbarus* ants showed no
556 direct taphonomical signs of myrmecological action once examined under magnifying glasses.

557
558 Further work is still needed to integrate ants' behaviour data with the characteristics of the soils and sediments
559 (in this case arkoses) on which they act and their consequences on the geological materials, and consequently on
560 the degree of alteration that can originate in different geo-ecosystems. There are many other Mediterranean
561 species known to excavate their nests in arkosic sediments like *Aphaenogaster dulcinea*, *A. gibbosa*, *A. ibérica*,
562 *Bothriomyrmex* sp., *Camponotus foreli*, *C. aethiops*, *C. pilicornis*, *Cataglyphys ibérica*, *C. rosenhauri*,
563 *Crematogaster auberti*, *C. scutellaris*, *Formica subrufa*, *Goniomma clanci*, *G. hispanicum*, *Messor bouvieri*, *M.*
564 *capitatus*, *M. structor*, *Pheidole pallidula*, *Plagiolepis pygmaea*, *Tapinoma nigerrimum*, and *T. semilaeve*
565 (Zorilla et al., 1986; Azcarate et al., 2013). Also it would be interesting to study the prospection potential of
566 other ant species in other regions and in palaeontological and archaeological sites with different taphonomical
567 variables such as a lower fragmentation. At the same time, other harvester ants have been pointed out as useful in
568 mineral prospection as many of them excavate complex nest that go several meters deep into the ground. In this

569 sense, ants of the genus *Pogonomyrmex* are good candidates for future research because of their abundance,
570 diversity and the relative wide literature existing about them (Reynolds, 1991; Tschinkel, 2003; Halfen and
571 Hasiotis, 2010, among many others).

572

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583

584 **REFERENCES**

585

586 Aleksiev, A.S., Sendova-Franks, A.B., Franks, N.R. 2007. The selection of building material for wall
587 construction by ants. *Animal Behaviour* 73, 779-788.

588

589 Arribas, J., Tortosa, A. 2003. Detrital modes in sedimenticlastic sand from low-order streams in the Iberian
590 Range, Spain: the potential for sand generation by different sedimentary rocks. *Sedimentary Geology* 159, 275-
591 303.

592

593 Azcárate, F.M., Arqueros, L., Sánchez, A., Peco, B. 2005. Seed and fruit selection by harvester ants *Messor*
594 *barbarus* in Mediterranean grassland and scrubland. *Functional Ecology* 19, 273-283.

595

596 Azcárate, F.M., Peco, B. 2007. Harvester ants (*Messor barbarus*) as disturbance agents in Mediterranean
597 grasslands. *Journal of Vegetation Science* 18, 103-110.

598

- 599 Azcárate, F.M., Seoane, J., Castro, S., Peco, B. 2013. Drove roads: Keystone structures that promote ant
600 diversity in Mediterranean forest landscapes. *Acta oecologica* 49, 107-115.
601
- 602 Backwell, L.R., Parkinson, A.H., Roberts, E.M., D’Errico, F., Hutchet, J.B. 2012. Criteria for identifying bone
603 modification by termites in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 337-338, 72-
604 87.
605
- 606 Baraibar, B., Torra, J., Westerman, P.R. 2011. Harvester ant (*Messor barbarus* (L.)) density as related to soil
607 properties, topography and management in semi-arid cereals. *Applied Soil Ecology* 51, 60-65.
608
- 609 Barroso Rodríguez, A. 2013. Uso del hábitat por la hormiga mediterránea *Aphaenogaster senilis* en Doñana:
610 competencia y explotación de los recursos. PhD Dissertation, Sevilla University (Spain).
611
- 612 Basu, A. 1985. Influence of climate and relief on compositions of sands released at source areas. In: *Provenance*
613 *of Arenites* (Ed. G.G. Zuffa), pp 1-18. Reidel, Dordrecht.
614
- 615 Bernard, F. 1958. Résultats de la concurrence naturelle chez les Fourmis terricoles de France et d’Afrique du
616 Nord: évaluation numérique des sociétés dominantes. *Bulletin de la Société D’Histoire Naturelle D’Afrique du*
617 *Nord* 49, 301-356.
618
- 619 Böhme, M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe.
620 *Palaeogeography, Palaeoclimatology, Palaeoecology* 195, 389-401.
621
- 622 Boulay, R., Cerdá, X., Simon, T., Roldan, M., Hefetz, A. 2007. Intraspecific competition in the ant *Camponotus*
623 *cruentatus*: should we expect the ‘dear enemy’ effect?. *Animal Behaviour* 74, 985-993.
624
- 625 Bulot, A., Dutoit, T., Renucci, M., Provost, E. 2014. A new transplantation protocol for harvester ant queens
626 *Messor barbarus* (Hymenoptera; Formicidae) to improve the restoration of species-rich plant communities.
627 *Myrmecological News* 20, 43-52.
628

- 629 Calvo, J.P., Alonso Zarza, A.M., Garcia del Cura, M.A. 1989. Models of Miocene marginal lacustrine
630 sedimentation in response to varied depositional regimes and source areas in the Madrid Basin (Central Spain).
631 *Palaeogeography, Palaeoclimatology, Palaeoecology* 70, 199-214.
632
- 633 Cammeraat, E.L.H., Risch, A.C. 2008. The impact of ants on mineral soil properties and processes at different
634 spatial scales. *Journal of Applied Entomology* 132, 285-294.
635
- 636 Cammeraat, E.L.H., Willott, S.J., Compton, S.G., Incoll, S.D. 2002. The effects of ants' nests on the physical,
637 chemical and hydrological properties of a rangeland soil in semi-arid Spain. *Geoderma* 105, 1-20.
638
- 639 Carpintero, S., Reyes-López, J. 2014. Effect of park age, size, shape and isolation on ant assemblages in two
640 cities of Southern Spain. *Entomological Science* 17, 41-51.
641
- 642 Carrasco, A., Sacristán, S., Benítez-López, G., Romero-Nieto, D., Fesharaki, O., López Martínez, N. 2008.
643 Aplicaciones paleoclimáticas y paleoambientales de los estudios mineralógicos al yacimiento de vertebrados
644 miocenos de Somosaguas. *Palaeontologica Nova* 8, 135-149.
645
- 646 Cerdà, A., Jurgensen, M.F. 2008. The influence of ants on soil and water losses from an orange orchard in
647 Eastern Spain. *Journal of Applied Entomology* 132, 306-314.
648
- 649 Chayes, F. 1952. Notes on the staining of potash feldspar with sodium cobaltinitrite in thin section. *American*
650 *Mineralogist* 37, 337-340.
651
- 652 Clark, J., Beerbower, J.R., Kietzke, K.K. 1967. Oligocene sedimentation, stratigraphy, paleoecology and
653 paleoclimatology in big badlands of South Dakota (Vol. 5). Field Museum of Natural History. California.
654
- 655 Cosarinsky, M.I. 2006. Nest micromorphology of the neotropical mound building ants *Camponotus punctulatus*
656 and *Solenopsis* sp. *Sociobiology* 47, 329-344.
657

- 658 Cosarinsky, M.I., Roces, F. 2007. Neighboring leaf-cutting ants and mound-building termites: Comparative nest
659 micromorphology. *Geoderma* 141, 224-234.
- 660
- 661 Costa-Milanez, C.B., Majer, J.D., Amorim Castro, P.T., Pontes Ribeiro, S. 2017. Influence of soil granulometry
662 on average body size in soil ant assemblages: implications for bioindication. *Perspectives in Ecology and*
663 *Conservation* 15, 102-108.
- 664
- 665 Courty, M.A. 1992. Soil micromorphology in archaeology. *Proceedings of the British Academy* 77, 39-59.
- 666
- 667 Croft, D.A., Kaye, T., Panko, L. 2004. A new method for finding small vertebrate fossils: ultraviolet light at
668 night. *Palaeontology* 47(4), 795-800.
- 669
- 670 Culver, D.C., Beattie, A.J. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado
671 Montane meadow. *Ecology* 64(3), 485-492.
- 672
- 673 Detrain, D., Pasteels, J.M. 2000. Seed preferences of the harvester ant *Messor barbarus* (Hymenoptera:
674 Formicidae) in a Mediterranean mosaic grassland. *Sociobiology* 35(1), 35-48.
- 675
- 676 Detrain, D., Tasse, O., Versaen, M., Pasteels, J.M. 2000. A field assessment of optimal foraging in ants: trail
677 patterns and seed retrieval by the European harvester ant *Messor barbarous*. *Insectes Sociaux* 47(1), 56-62.
- 678
- 679 Dickinson, W.R., Suczek, C.A. 1979. Plate tectonics and sandstone compositions. *American Association of*
680 *Petroleum Geologists Bulletin* 63, 2164-2182.
- 681
- 682 Díez-Canseco, D., López Martínez, N., Díaz-Molina, M., Benito, M.I. 2012. Stream mouth deposits in the
683 paleontological site of Somosaguas, middle Miocene, Madrid basin. *Spanish Journal of Palaeontology* 27, 93-
684 101.
- 685

- 686 Domingo, L., Cuevas-González, J., Grimes, S.T., Hernández Fernández, M., López Martínez, N. 2009.
687 Multiproxy reconstruction of the palaeoclimate and palaeoenvironment of the middle Miocene Somosaguas sites
688 using herbivore dental enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology* 272, 53-68.
689
- 690 Domingo, M.S., Martín-Perea, D., Domingo, L., Cantero, E., Cantalapiedra, J.L., García Yelo, B.A., Gómez
691 Cano, A.R., Alcalde, G.M., Fesharaki, O., Hernández Fernández, M. 2017. Taphonomy of mammalian fossil
692 bones from the debris-flow deposits of Somosaguas-North (Middle Miocene, Madrid Basin, Spain).
693 *Palaeogeography, Palaeoclimatology, Palaeoecology* 465, 103-121.
694
- 695 Dostál, P., Breznova, M., Kozlickova, V., Herben, T., Kovar, P. 2005. Ant-induced soil modification and its
696 effect on plant below-ground biomass. *Pedobiologia* 49, 127-137.
697
- 698 Drager, K.I., Hirmas, D.R., Hasiotis, S.T. 2016. Effects of ant (*Formica subsericea*) nests on physical and
699 hydrological properties of a fine-textured soil. *Soil Science Society of America Journal* 80, 364-375.
700
- 701 Durán, J.M.G. 2011. Transporte de alimentos líquidos mediante objetos sólidos en *Messor barbarus* (Linnaeus,
702 1767), y reconsideración del denominado “comportamiento de uso de instrumentos” en las hormigas.
703 *Iberomyrmex* 3, 9-20.
704
- 705 Élez, J. 2005. Aplicación GIS 3D a los yacimientos paleontológicos de Somosaguas. Dissertation, Universidad
706 Complutense de Madrid.
707
- 708 Espadaler, X., Suñer, D. 1995. Per què hi ha formigues del Montgrí (Girona) que no es troben a l'illa Meda
709 Gran. *Orsis* 10, 91-97.
710
- 711 Ettershank, G. 1968. The tridimensional gallery structure of the nest of the meat ant *Iridomyrmex purpureus*
712 (SM.) (Hymenoptera: Formicidae). *Australian Journal of Zoology* 16, 715-723.
713
- 714 Fejfar, O., Kaiser, T.M. 2005. Insect bone-modification and paleoecology of Oligocene mammal-bearing sites in
715 the Doupov Mountains, Northwestern Bohemia. *Paleontologia Electronica* 8, 11pp.

- 716
- 717 Fesharaki, O. 2005. Mineralogía y sedimentología del yacimiento paleontológico de Somosaguas (Mioceno,
718 Cuenca de Madrid). Unpublished dissertation, Complutense university of Madrid, Spain.
- 719
- 720 Fesharaki, O. 2016. Análisis Paleoambiental y Paleoclimático de los Yacimientos de Somosaguas y Húmera
721 (Mioceno Medio, Madrid): Sedimentología, Petrología, Mineralogía y Aplicación a Divulgación e Innovación
722 Educativa. PhD Dissertation, Universidad Complutense de Madrid.
- 723
- 724 Fesharaki, O., Arribas, J., López Martínez, N. 2015. Composition of clastic sediments from the Somosaguas
725 Area (Middle Miocene, Madrid Basin): insights into provenance and palaeoclimate. *Journal of Iberian Geology*
726 41(2), 205-222.
- 727
- 728 Fesharaki, O., García Romero, E., Cuevas-González, J., López Martínez, N. 2007. Clay mineral genesis and
729 chemical evolution in the Miocene sediments of Somosaguas, Madrid Basin, Spain. *Clay Minerals* 42, 187-201.
- 730
- 731 Fesharaki, O., Torices, A., García Yelo, B.A., Tejedor Navarro, N., De La Ossa, L., Hernández Fernández, M.
732 2012. The Somosaguas palaeontology project: An envision of Nieves López Martínez for linking science and
733 society. *Spanish Journal of Palaeontology* 27(2), 83-92.
- 734
- 735 Folgarait, P.J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and*
736 *Conservation* 7, 1221–1244.
- 737
- 738 Font Tullot, I. 1983. Climatología de España y Portugal. Servicio Publico Ministerio de Obras Publicas y
739 Transporte. Instituto Nacional de Meteorologia. Madrid, Spain.
- 740
- 741 Frouz, J., Holec, M., Kalcik, J. 2003. The effect of *Lasius niger* (Hymenoptera, Formicidae) ant nest on selected
742 soil chemical properties. *Pedobiologia* 47(3), 205-2012.
- 743
- 744 Galarza, J. A., Jovani, R., Cerdá, X., Rico, C., Barroso, A., Boulay, R. 2012. Frequent colony relocations do not
745 result in effective dispersal in the gypsy ant *Aphaenogaster senilis*. *Oikos* 121, 605-613.

- 746
- 747 García Yelo, B.A., Gómez Cano, A.R., Cantalapiedra, J.L., Alcalde, G.M., Sanisidro, O., Oliver, A., Hernández-
- 748 Ballarín, V., López-Guerrero, P., Fraile, S., Hernández Fernández, M. 2014. Palaeoenvironmental analysis of
- 749 the Aragonian (Middle Miocene) mammalian faunas from the Madrid Basin based on body-size structure.
- 750 *Journal of Iberian Geology* 40(1), 129-140.
- 751
- 752 Goldberg, P., Aldeias, V. 2018. Why does (archaeological) micromorphology have such little traction in
- 753 (geo)archaeology?. *Archaeological and Anthropological Sciences* 10, 269-278.
- 754
- 755 Gómez Oballe, S. 2016. Plantas indicadoras de estratos fosilíferos: El ejemplo del yacimiento paleontológico de
- 756 Somosaguas. Unpublished dissertation, Complutense university of Madrid, Spain.
- 757
- 758 Gorosito, N.B., Curmi, P., Hallaire, V., Folgarait, P.J., Lavelle, P.M. 2006. Morphological changes in
- 759 *Camponotus punctulatus* (Mayr) anthills of different ages. *Geoderma* 132, 249-260.
- 760
- 761 Halfen, A.F. and Hasiotis, S.T. 2010. Neoichnological study of the traces and burrowing behaviours of the
- 762 western harvester ant *Pogonomyrmex occidentalis* (Insecta: Hymenoptera: Formicidae): Paleopedogenic and
- 763 paleoecological implications. *Palaios* 25, 703-720.
- 764
- 765 Hammer, Ø., Harper, D.A.T., Ryan, P.D. 2001. PAST: Paleontological statistics software package for education
- 766 and data analysis. *Palaeontologia Electronica* 4(1), 9pp.
- 767
- 768 Heredia, A., Detrain, C. 2000. Worker size polymorphism and ethological role of sting associated glands in the
- 769 harvester ant *Messor barbarus*. *Insectes sociaux* 47(4), 383-389.
- 770
- 771 Hernández Fernández, M., Cárdbaba, J.A., Cuevas-González, J., Fesharaki, O., Salesa, M.J., Corrales, B.,
- 772 Domingo, L., Élez, J., López-Guerrero, P., Sala-Burgos, N., Morales, J., López Martínez, N. 2006. Los
- 773 yacimientos de vertebrados del Mioceno medio de Somosaguas (Pozuelo de Alarcón, Madrid): implicaciones
- 774 paleoambientales y paleoclimáticas. *Estudios Geológicos* 62, 263-294.
- 775

- 776 Herodotus 2007. Snakes with wings and gold-digging ants. Penguin, London, United Kingdom.
777
- 778 Hill, D.S. 1997. The economic importance of insects. Chapman & Hall, London, United Kingdom.
779
- 780 Hole, F.D. 1981. Effects of animals on soil. *Geoderma* 25, 75-112.
781
- 782 Holec, M., Frouz, J., Pokorny, R. 2006. The influence of different vegetation patches on the spatial distribution
783 of nests and the epigeic activity of ants (*Lasinus niger*) on a spoil dump after brown coal mining (Czech
784 Republic). *European Journal of Soil Biology* 42, 158-165.
785
- 786 Hölldobler, B., Wilson, E.O. 1990. The Ants. The Belknap Press of Harvard, Cambridge.
787
- 788 IUSS Working Group WRB. 2015. World Reference Base for soil resources 2014, updated 2015. International
789 soil classification system for for naming soils and creating legends for soil maps. World Soil Resources Reports
790 No. 106. FAO, Rome.
791
- 792 Jílková, V., Sebek, O., Frouz, J. 2012. Mechanisms of pH change in wood ant (*Formica polyctena*) nests.
793 *Pedobiologia* 55, 247-251.
794
- 795 Karlson, P., Lüscher, M. 1959. "Pheromones": A new term for a class of biologically active substances. *Nature*
796 183, 55-56.
797
- 798 Lafleur, B., Bradley, R.L., Francoeur, A. 2002. Soil modifications created by ants along a post-fire
799 chronosequence in lichen-spruce woodland. *Ecoscience* 9, 63-73.
800
- 801 Le Pera, E., Arribas, J., Critelli, S., Tortosa, A. 2001. The effects of source rocks and chemical weathering on the
802 petrogenesis of siliciclastic sand from the Neto River (Calabria, Italy): implications for provenance studies.
803 *Sedimentology* 48, 357-378.
804

- 805 Le Pera, E., Sorriso-Valvo, M. 2000. Weathering, erosion and sediment composition in a high-gradient river,
806 Calabria, Italy. *Earth Surface Processes and Landforms* 25, 277-292.
807
- 808 Liu, X., Monger, H.C., Whitford, W.G. 2007 Calcium carbonate in termite galleries – biomineralization or
809 upward transport? *Biogeochemistry* 82, 241-250.
810
- 811 Lobry de Bruyn, L.A., Conacher, A.J. 1990. The role of termites and ants in soil modification : A review.
812 *Australian Journal of Soil Research* 28, 55-93.
813
- 814 López Martínez, N., Élez, J., Hernando, J.M., Luís, A., Mazo, A., Mínguez Gandú, D., Morales, J., Polonio, I.,
815 Salesa, M.J., Sánchez, I. 2000. Los fósiles de vertebrados de Somosaguas (Pozuelo, Madrid). *Coloquios de*
816 *Paleontología* 51, 69-86.
817
- 818 Lucke, B., Nikolskii, I., Schmidt, M., Baumler, R., Nowaczyk, N., al-Saad, Z. 2008. The impact of drought in
819 the light of changing soil properties. In (J.M. Sánchez, Ed.) *Droughts: Causes, effects and predictions*. Chapter 2.
820 pp. 69-102. Nova Science Publisher.
821
- 822 Luis, A., Hernando, J.M. 2000. Los microvertebrados fósiles del Mioceno Medio de Somosaguas Sur Pozuelo de
823 Alarcón, Madrid, España. *Coloquios de Paleontología* 51, 87-136.
824
- 825 MacMahon, J.A., Mull, J.F. Crist, T.O. 2000. Harvester ants (*Pogonomyrmex* sp.): their community and
826 ecosystem influences. *Annual Reviews Ecological Systems* 32, 265-291.
827
- 828 McBrearty, S. 1990. Consider the humble termite: Termites as agents of post-depositional disturbance at african
829 archaeological sites. *Journal of Archaeological Science* 17(2), 111–143.
830
- 831 Mínguez Gandú, D. 2000. Marco estratigráfico y sedimentológico de los yacimientos paleontológicos miocenos
832 de Somosaguas Madrid, España. *Coloquios de Paleontología* 51, 183-196.
833

- 834 Monterde, P. 2014. Variabilidad de comunidades vegetales sobre dos suelos contrastados en el yacimiento
835 paleontológico de Somosaguas. Unpublished Dissertation, Complutense University of Madrid, Spain.
836
- 837 Monterde, P., Blanco Segovia, F., De Villepreux, E., Sánchez de Dios, R., Fesharaki, O. 2015. Comunidades
838 vegetales como diferenciadoras de estratos fosilíferos: el ejemplo del área de Somosaguas (Madrid). *Current*
839 *trends in Paleontology and Evolution*, XIII EJIP Conference Proceedings, 191-192.
840
- 841 Morgan, E.D. 2008. Chemical sorcery for sociality: Exocrine secretions of ants (Hymenoptera: Formicidae).
842 *Myrmecological News* 11, 79-90.
843
- 844 Morgun, A., Golichenkov, M. 2015. Contribution of ants in modifying of soil acidity and particle size
845 distribution. *Geophysical Research Abstracts* 17, EGU2015-1070-3.
846
- 847 Needham, S.J., Worden, R.H., Cuadros, J. 2006. Sediment ingestion by worms and the production of bio-clays: a
848 study of macrobiologically enhanced weathering and early diagenetic processes. *Sedimentology* 53, 567-579.
849
- 850 Nielsen, M.G. 1986. Respiratory rates of ants from different climatic areas. *Journal of Insect Physiology* 32(2),
851 125-131.
852
- 853 Nielsen-Marsh, C.M. 2000. Patterns of diagenesis in bone I: The effects of site environments. *Journal of*
854 *Archaeological Science* 27, 1139-1150.
855
- 856 Nieto, J.M., Nocete, F., Sáez, R., Franco, F. 2002. Cambios mineralógicos en restos óseos en función de las
857 condiciones de pH del suelo. *Geogaceta* 31, 181-184.
858
- 859 Nkem, J.N., Lobry de Bruyn, L.A., Grant, C.D., Hulugalle, N.R. 2000. The impact of ant bioturbation and
860 foraging activities on surrounding soil properties. *Pedobiologia* 44(5), 609-621.
861
- 862 O'Brien, N.R. 1987 The effects of bioturbation on the fabric of shale. *Journal of Sedimentary Petrology* 57, 449-
863 455.

- 864
- 865 Oliveras, J., Bas, J.M., Gómez, C. 2005. Reduction of the ant mandible gap range after biotic homogenization
866 caused by an ant invasion (Hymenoptera: Formicidae). *Sociobiology* 45(3), 1-10.
- 867
- 868 Palomares, M., Arribas, J. 1993. Modern stream sands from compound crystalline sources: Composition and
869 sand generation index. In: *Processes controlling the composition of clastic sediments* (Eds. M.J. Johnsson and A.
870 Basu). Geological Society of America Special Papers 284, 313-322.
- 871
- 872 Passera, L., Aaron, S. 2005. *Les fourmis: comportement, organisation sociale et évolution*. Les presses
873 scientifiques du CNRC, Ottawa.
- 874
- 875 Pate, F.D., Hutton, J.T., Norrish, K. 1989. Ionic exchange between soil solutions and bone: toward a predictive
876 model. *Applied Geochemistry* 4, 303-316.
- 877
- 878 Paton, T.R., Humphreys, G.S., Mitchell, P.B. 1995. *Soils. A new global view*. UCL Press, London.
- 879
- 880 Pettijohn, F.J., Potter, P.E., Siever, R. 1972. *Sand and Sandstone*. Springer-Verlag, Berlin.
- 881
- 882 Petts, A.E., Hill, S.M., Worrall, L. 2009. Termite species variations and their importance for termitaria
883 biogeochemistry: towards a robust media approach for mineral exploration. *Geochemistry: Exploration,
884 Environment Analysis* 9, 257-266.
- 885
- 886 Plowes, N.J.R., Johnson, R.A., Hölldobler, B. 2013. Foraging behavior in the ant genus *Messor* (Hymenoptera:
887 Formicidae: Myrmicinae). *Myrmecological News* 18, 33-49.
- 888
- 889 Polonio, I., López Martínez, N. 2000. Análisis tafonómico de los yacimientos de Somosaguas (Mioceno medio,
890 Madrid). *Coloquios de Paleontología* 51, 235-266.
- 891
- 892 Reynolds, T.D. 1991. Movement of gravel by the “Owyhee” harvester ant, *Pogonomyrmex salinus*
893 (Hymenoptera: Formicidae). *Entomological News* 102, 118-124.

- 894
- 895 Rhoads, D.C., Boyer, L.F. 1982. The effects of marine benthos on physical properties of sediments: a
896 successional perspective. In: Animal-sediment relations, the biogenic alteration of sediments (Eds. P.L. McCall
897 and M.J.S. Tevesz). New York, Plenum Press, pp 3-52.
- 898
- 899 Richards, P.J. 2009. *Aphaenogaster* ants as bioturbators: Impacts on soil and slope processes. Earth-Science
900 Reviews 96, 92-106.
- 901
- 902 Righi, D., Terribile, F., Petit, S. 1995. Low-charge to high-charge beidellite in a vertisol from south Italy. Clays
903 and Clay Minerals 43, 495-502.
- 904
- 905 Rink, W.J., Dunbar, J.S., Tschinkel, W.R., Kwapich, C., Repp, A., Stanton, W., Thulman, D.K. 2013.
906 Subterranean transport and deposition of quartz by ants in sandy sites relevant to age overestimation in optical
907 luminescence dating. Journal of Archaeological Science 40, 2217-2226.
- 908
- 909 Rivas-Martínez, S. 1987. Memoria del mapa de series de vegetación de España 1:400.000. ICONA. Ministerio
910 de Agricultura, Pesca y Alimentación. Madrid, Spain.
- 911
- 912 Robinson, W.H. 1996. Urban entomology. Chapman and Hall, London.
- 913
- 914 Rodríguez, A. 1982. Contribución al conocimiento de las hormigas (Hymenoptera, Formicidae) de Sierra
915 Morena Central. Boletín de la Asociación española de Entomología 5, 181-188.
- 916
- 917 Rodríguez, A., Fernández Haeger, J. 1983. Empleo del análisis de clasificación para la detección de grupos de
918 especies afines en una comunidad de hormigas. Studia Oecologica 4, 115-124.
- 919
- 920 Ruiz Heras, P., Martínez Ibáñez, M.D., Cabrero-Sañudo, F.J., Vázquez Martínez, M.A. 2011. Primeros datos de
921 Formícidos (Hymenoptera, Formicidae) en parques urbanos de Madrid. Boletín de la Asociación Española de
922 Entomología 35, 87-106.
- 923

- 924 Scarciglia, F., Le Pera, E., Critelli, S. 2005. Weathering and pedogenesis in the Sila Grande Massif (Calabria,
925 South Italy): From field scale to micromorphology. *Catena* 61, 1-29.
926
- 927 Sherrod, S.K., Seastedt, T.R. 2001. Effect of the northern pocket gopher (*Thomomys talpoides*) on alpine soil
928 characteristics, Niwot Ridge, CO. *Biogeochemistry* 55, 195-218.
929
- 930 Shipman, P., Walker, A. 1980. Bone-collecting by harvesting ants. *Paleobiology* 6(4), 496-502.
931
- 932 Suttner, L.J., Dutta, P.K. 1986 Alluvial sandstone composition and paleoclimate I: Framework mineralogy.
933 *Journal of Sedimentary Petrology* 56, 329-345.
934
- 935 Tschinkel, W.R. 2003. Subterranean ant nests: trace fossils past and future? *Palaeogeography,*
936 *Palaeoclimatology, Palaeoecology* 192, 321-333.
937
- 938 Tschinkel, W.R. 2006. *The fire ants*. Cambridge, M.A: Belknap Press.
939
- 940 Turnbull, W.D. 1959. Ant colony assists fossil collectors in Wioming. *Chicago Natural History Museum*
941 *Bulletin* 30, 6-7.
942
- 943 Wagner, D., Brown, M.J.F., Gordon, D.M. 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia*
944 112, 232-236.
945
- 946 Wagner, D., Jones, J.B. 2004. The contribution of harvester ant nests, *Pogonomyrmex rugosus* (Hymenoptera,
947 Formicidae), to soil nutrient stocks and microbial biomass in the Mojave Desert. *Environmental Entomology* 33,
948 599-607.
949
- 950 Wagner, D., Jones, J.B., Gordon, D.M. 2004. Development of harvester ant colonies alters soil chemistry. *Soil*
951 *Biology and Biochemistry* 36, 797-804.
952

- 953 Wang, D., McSweeney, K., Lowery, B., Norma, J.M. 1995. Nest structure of ant *Lasinus neoniger* Emery and its
954 implications to soil modification. *Geoderma* 66, 259-272.
- 955
- 956 Weltje, G.J. 1994. Provenance and dispersal of sand-sized sediments: Reconstruction of dispersal patterns and
957 sources of sand-sized sediments by means of inverse modelling techniques. PhD dissertation, Utrecht University.
- 958
- 959 Whicker, A.D., Detling, J.K. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38, 778-
960 785.
- 961
- 962 Whitford, W.G. 2002. Ants. In: *Encyclopedia of soil science* (Ed. R. Marcel Dekker), pp 76–79. New York,
963 USA.
- 964
- 965 Whitford, W.G., DiMarco, R. 1995. Variability in soils and vegetation associated with harvester ant
966 (*Pogonomyrmex rugosus*) nests on a Chihuahuan Desert watershed. *Biology and Fertility of Soils* 20, 169-173.
- 967
- 968 Zharikova, E.A. 2017. Geochemical characterization of soils of the eastern coast of the Northern Sakhalin
969 Lowland. *Eurasian Soil Science* 50(1), 34-41.
- 970 Zorilla, J. M., Serrano, J. M., Casado, M. A., Acosta, F. J., Pineda, F. D. 1986. Structural characteristics of an ant
971 community during succession. *Oikos* 47, 346-354.