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New stratigraphically constrained palaeoenvironmental reconstructions for the first human settlement in Western Europe : The Early Pleistocene herpetofaunal assemblages from Barranco Leon and Fuente Nueva 3 (Granada, SE Spain)

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# Quaternary Science Reviews

## New stratigraphically constrained palaeoenvironmental reconstructions for the first human settlement in Western Europe: the Early Pleistocene herpetofaunal assemblages from Barranco León and Fuente Nueva 3 (Granada, SE Spain)

--Manuscript Draft--

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<b>Abstract:</b>	<p>The Early Pleistocene sites of Barranco León and Fuente Nueva 3 (Guadix-Baza Basin, SE Spain) have yielded abundant Oldowan lithic artifacts and one hominin tooth ( <i>Homo</i> sp. in level D1 or D2 of Barranco León), today considered to be among the earliest evidence for a hominin presence in Western Europe, at ca. 1.4-1.2 Ma. Here, for the first time, the stratigraphic succession of these two sites are studied more precisely from a palaeoenvironmental point of view, taking into account the different levels of the depositional sequences to analyze the successive fossil assemblages of amphibians and reptiles. Palaeoenvironmental reconstructions are carried out by applying the “habitat weighting” method, which uses the modern distribution by habitat of amphibian and reptile species in order to interpret past landscapes. The successive herpetofaunal assemblages from Barranco León show a certain tendency towards more arid conditions from level D1 to level E, whereas in Fuente Nueva 3 environmental reconstructions reveal oscillating conditions, with a tendency towards more arid conditions in the basal part of the sequence, up to level 5, where the tendency shifts back to more humid conditions. Our results show that the layers included in this study with the highest density of anthropic evidence (such as levels 5 in FN 3 and levels D1 and D2 in BL) are situated within the late Early Pleistocene climatic and environmental cyclicity, yielding different environmental conditions: a humid, wooded biotope for BL, and a more open and drier biotope in FN 3. This suggests that the hominins of the late Early Pleistocene, although conditioned to some extent by climatic factors, were able to cope with changing environmental conditions, both “interglacial” and “glacial”, in the southwestern extremity of the European continent.</p>

<b>Suggested Reviewers:</b>	<p>Angela Bruch  angela.bruch@senckenberg.de  Palynologist and specialist in Early Pleistocene and hominin dispersal</p>
	<p>José Carrión  carrion@um.es  palynologist and specialist in paleoenvironmental reconstruction in the Iberian Peninsula</p>
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	<p>Danielle Schreve  Danielle.Schreve@rhul.ac.uk  Paleontologist and specialist in Pleistocene paleoenvironmental reconstruction</p>
<b>Response to Reviewers:</b>	

Dear Editor Danielle Schreve,

We are resubmitting here our contribution entitled “New stratigraphically constrained paleoenvironmental reconstructions for the first human settlement in Western Europe: the Early Pleistocene herpetofaunal assemblages from Barranco León and Fuente Nueva 3 (Granada, SE Spain)”.

Most of the changes asked by the reviewers have been done, as commented in the detailed response. Adequation between the text and stratigraphic figures has been discussed again between the different co-authors. A double check of the language editing has been done by our co-author Deborah Barsky.

Some of the suggestions have not been followed, as we think that it is too early or too simplistic to present yet southern Spain as a glacial refugia during the Early Pleistocene, as we have no equivalent section anywhere in Europe.

Conflict of interest were mentioned during the first submission but they reflect more problems with another research group that did not have had any influence on the results we present in this manuscript. As one of this people (the former director of the project) is from our own institute (and acknowledged in the paper), we would like in the final version of the paper that such a petition does not appears as a conflict. We hope this is not a problem at this stage?

Hope you will consider our work for publication.

Sincerely Yours,  
Hugues-Alexandre Blain

Editor and Reviewer comments:

Reviewer #1: In this paper, the authors present a detailed environmental study of some of the most important hominin fossil sites in the Iberian Peninsula. By studying the herpetofauna of each stratigraphic level, they are able to reconstruct the changes in landscape and environment during the formation of these sites. Together with the lithic industry record, this allows them to draw very interesting conclusions regarding human occupation of the area of Orce in the context of a cyclic climate. I believe the methods employed in the study are very useful and successfully depict environmental changes which are in agreement with the stratigraphic succession of the studied sites. The results allow the authors to suggest that hominins could have occupied the area of Orce even during the arid and cold glacial periods. This is a remarkable conclusion, as the influence of the climate in the expansion of early humans in Europe is still an open question, with different authors supporting multiple competing hypotheses on the topic.

Regarding the suitability of the paper in JQSR, the material presented is novel and interesting, certainly suitable for the journal. Additionally, the authors make a good review of what is known from the paleoenvironments of the sites of Barranco León and Fuente Nueva 3. However, I would suggest the authors to undertake a last dive into the available bibliography to make sure that they do not miss any previous works dealing with the environment of the sites. For example, I found no reference to Anadón and Gabàs (2009) which study environmental changes in Barranco León. I understand Anadón et al. (2015) covers similar material, but all previous works in the specific topic should be included. Adding the few missing studies will complete the "review" aspect of their paper and make it, in my opinion, perfectly fitting into JQSR.

Additionally, I have a few comments and suggestions which would improve the paper:

### 1- The geological description of the sites and figure 1c

There is sometimes discrepancy between the description of the stratigraphic levels in the text and their description in figure 1c. Also, the lithological legend is a bit confusing.

**ANSWER: Figure 1C has been updated.**

-Mudstone is described in the legend of figure 1c as the bodies with dark coloration, while limestone is described as bodies with white coloration. No patterns are indicated. But in the stratigraphic column, the colors seem to indicate the actual color of the level, not the lithology? This is confusing. I would suggest to either have the colors represent different lithologies or to add patterns to differentiate between limestone and mudstone.

-Some levels are often described in the text as sands but in the figure they appear as mudstone (for example, levels F2, E of Barranco León, in lines 189-191). Please be consistent with the denominations. If these are indeed sands then depict them in the figure with a dotted symbology (sands) instead of plain (mudstone).

**ANSWER: Adequation and correspondence between Figure 1C and text has been checked in the geological description.**

-The text describes the levels of Barranco León from oldest to youngest (line 188) starting

from level G to level A. However the figure shows level A being the oldest and level G the youngest. Please change the order to the correct one.

**ANSWER: Done**

-The description of Fuente Nueva in the text says that lithic industry is found in layers 2, 3 and 5 (lines 262-264). However, figure 1c indicates that lithics are found in levels 1, 2 and 5. Which one is correct? Also, some levels are described to contain invertebrate fossils in the text, but in the column there is no symbols for them (for example, level 3 of Fuente Nueva).

**ANSWER: Lithics were founded in levels 2 and 5. What was previously attributed to level 3 may in fact proceed from the boundary between levels 2 and 3. Information regarding fauna has been enlarged such as small vertebrates not previously included, but in the case of the herpetological sample from the level 3 of Fuente Nueva (as explained in text), as our sedimentologist thinks that it is impossible that these remains comes from level 3, we renamed this sample as 2sup, maybe located at the 2-3 boundary. A new point as been added to the conclusion concerning this issue: to verify again in the future the base of FN3 stratigraphy in order to understand which of the levels are sterile and which ones are not. We hope that, even raising some doubt about the contextualization of our results, readers will understand the problem raised by many year of ongoing excavation (and subsequent changes in stratigraphical nomenclature) and the honesty of the presentation of our work.**

-Also, in Figure 1c the icon for lithic tools is not in the legend.

**ANSWER: Added**

-In the description of the site of Barranco León there is not a clear explanation of the distribution of the lithic material nor the hominin molar (quite important), this is also not clear in the figure 1c, since it shows level D2 containing no lithics or hominin remains. Please clarify. I understood from the abstract and the caption of figure 6 that the molar cannot be placed either in D1 or D2, but this should be explained in the description of the site.

**ANSWER: Added**

## 2- Previous analyses of the material

It is noted in line 323 that "Part of the material used in this study has already been studied and published in Agustí e al. (2015a)". However, it is not clear what are the differences between the material in that study and this one. I went to check and it seems that in this work the authors present a list with much more material and a slightly different taxonomical list for the herpetofauna for Barranco León. Agustí et al., 2015a report for the levels D1 and D2 the presence of cf. *Dopasia* (instead of *Ophisaurus*) and assign a species to *Coronella*. These are not found in the list by Sánchez-Bandera et al. which includes many new taxa not reported by Agustí et al., 2015a. I am assuming that this is due to an updated classification of the old material and the addition of newer fossils? If so, perhaps all these differences should be briefly explained in the text. Similarly to how

the differences with the studies of Blain, 2005, 2009 and Blain et al., 2011, 2016a are explained.

**ANSWER: OK, main changes are linked with adapting former faunal list to recent taxonomical nomenclature. Unless for Coronella snake, where more material raised some doubt about the secure attribution to this taxa. We now comment all these differences in the manuscript.**

3- I think it would be nice to see the % of the variance represented by each axis in the correspondence analysis in Figure 2.

**ANSWER: Thanks for your observation, we completed the correspondence analyses' figures by adding the % of the variance represented by each axis.**

4- Figures 3-4

Already contain the same values as those presented in figure 5. I think with figure 5 the authors want to represent the data in a more stratigraphical sense. But as it is now figure 5 seems to be mostly repetition of the previous figures. I would suggest the authors to increase the stratigraphical sense in figure 5 by adding simplified versions of the stratigraphical columns and simple explanations of the environmental changes. Perhaps highlighting sequences of aridification and tentatively identifying the possible glacial maximum or periods of transition.

**ANSWER: New figure contains a simplified version of the lithological section, and values are thus referred to a true space dimension (vertical scale).**

5- Glacial maximum hypothesis

In line 713 the authors suggest that level 6 could represent a glacial maximum. And yet level 6 is barely discussed in the text due the low amount of material recovered from it. I get the feeling that the argument is that the low amount of herpetofaunal remains could be caused by the existence of a more extreme environment such as a glacial maximum. If the authors want to raise this possibility then the reasoning for it should be explained. Right now the text is not clear on how they arrive at such idea.

Additionally, since there seems to be not enough evidence supporting the glacial maximum hypothesis, I would advise the authors to clarify in the text that this is a hypothesis they raise which should be tested in future studies in order to confirm it.

**ANSWER: Thank for your comment. In fact glacial maximum is proposed for level 5. We corrected it rephrasing the sentences in order to improve the clarity.**

6- Hominin survival

The discussion ends raising the idea that early hominins in Orce were capable of coping with and adapting to conditions that were both "interglacial" (levels D1 and D2) and "glacial" (levels 3 and 5). This is a remarkable conclusion and I would encourage the authors to expand it a little bit. Does this mean that Orce could have been a glacial refugia for european hominins? Does this fit with the climate reconstructions? How does this fit with the current models for the colonization of Africa.

I understand that the authors will probably tackle these questions in a future papers, as this is a very exciting conclusion. I am just suggesting expanding it a bit here, but I leave it to the discretion of the authors.

**ANSWER: Yes, indeed this idea that early hominins were able to cope with Early Pleistocene glacial periods is very interesting (even if not so impressive from a southern point of view). In our opinion, to be able to speak about a glacial refuge, we must have a whole overview of the fossil record at a continental scale (like for Neanderthals), and for the moment Barranco León has no analogue. We feel that it is too early for been able to speak about a glacial refuge for FN3. Also, the faunal list for each stratigraphical levels (especially in FN3) is not rich enough (low number of taxa and/or taxa represented in the whole Iberian Peninsula) to perform a robust climate reconstruction. We hope that future excavation campaigns will bring more material for each of the lower level.**

#### 7- Figure 6

Figure 6 is a bit confusing. The CA diagram is the same shown in figure 2, but the authors indicate the presence (and abundance) of lithic and hominin fossil material. This is very good and it is discussed in the text. But then, they also add animal silhouettes, which represent the main taxonomical category of large and very large mammals butchered in each level. However, I think the text does not address this point of the discussion. The macrofauna of the sites is discussed in the paragraph in line 616 and 639, but there is no reference to the figure nor mention of which animals were most commonly butchered.

I would suggest the authors to explain the significance of the relationship between butchered animals and the environment. Otherwise, I see no point to including the animal silhouettes in figure 6.

**ANSWER: We corrected that point: we were not referring to butchered animals only but to the most commonly found by the archaeologist (even if still not formally quantified by level yet).**

#### 8- I have made numerous minor remarks in the pdf of the manuscript.

**ANSWER: We added in the new version of the manuscript all the minor remarks suggested in the pdf.**

In conclusion, I believe the present manuscript should be published in JQSR after some corrections and clarifications have been made to the text.

Reviewer #2: This is an interesting manuscript bringing new methods and perspectives into the discussion of earliest human presence in Europe. I have a couple of minor points, which I think are easy to correct/improve.

#### Line 145

"movable ground" - what do you mean here? Be more precise.



**ANSWER: We means ground made of loose material (sand and mud) where some of our taxa (mainly toads) can burrow. We finally decide to remove this information.**

Line 152

**ANSWER: changed**

Line 163

"chronology of this formation runs": formation is a (litho-)stratigraphic term, so I suggest to use words like this: 'the chronostratigraphy of the Baza Formation is ....'

**ANSWER: done**

Line 165

"major geological members": again a member is a lithostratigraphic term, hence 'lithostratigraphic members' (without "major").

**ANSWER: changed**

Line 171, 187, etc.

"lutite" is (in my view) not a precise sedimentological term. It would be better to use 'siltstone' and/or 'mudstone' (also to be consistent with later terminology, e.g. line 259).

**ANSWER: changed**

Line 193/194

"calcites": what you mean here, limestones? Calcite is a mineralogical term, not a sedimentological one.

**ANSWER: changed**

Line 196/197

Which "environmental features ...indicate a freshwater marginal area of the more saline main lake"? In the previous lines you mention petrological and sedimentological features, which have to be translated into "environmental features". What indicates "freshwater" and especially what indicates a "more saline main lake"? Be here more precise and consult Anadón et al. 2015.

**ANSWER: Answered in the manuscript**

Lines 260/261

"These deposits are situated": I would suggest 'be correlated' (biostratigraphy is a correlation tool). Further, Agusti et al. (2010) mention the presence of *Allophaiomys aff. lavocati* (maybe cite here also Agusti & Madurell 2003, which seems to be the primary reference for FN3, but also Agusti et al. 2015 as reference for biozone A. aff. *lavocati*).

**ANSWER: Done**

Lines 333-335

My concern relates to the estimation of MNI for snakes based on vertebra size. I actually have some doubts that this is possible and, if this is indeed possible, I miss a reference and/or technical details (e.g. which measurements, how to measure, statistics, etc.). My concern relates to intra-column variability of centrum-size (did anybody publish research on it?) and how this variability (if present) relates to infra-specific variability. In my opinion, the only way for MNI estimates for snakes are cranial or cervical elements.

**ANSWER: Yes, it can be true for Miocene taxa or tropical area species, but not really in Europe where the snake fauna does not present a big intracolumnar variation between vertebra size. It is to add here that we not only rely on centrum length (that is somewhat variable in a same snake) but on the overall estimation of the vertebral size in a same sample. We understand the doubt of the reviewer, as it is not a formal methodology but more an intuitive approach when studying the material.**

Line 355

What you mean with "synchronic and diachronic" studies? At contemporary and non-contemporary sites?

**ANSWER: We delete the sentence.**

Line 387

Is Bufonidae indet. confidently different from Epidalea calamita and Bufotes viridis s.l.? If not, I would count six amphibian species for BL.

**ANSWER: Bufonidae indet. does not represent any different taxonomical category from the already identified taxa. It just indicates that we were not able to securely attribute such remains neither to Bufo, nor to Epidalea or Bufotes. It has therefore not to be taken into account in the count for the number of species.**

Lines 410/411

I would write '... including aquatic taxa in the analyses and secondly excluding them (without aquatic taxa)...'. State here which taxa you exclude (you bring this quite late in line 444).

**ANSWER: We added the aquatic taxa list in that part of the text, thank you for the observation.**

Further, you use five different terms for water dependence: "fully aquatic" (line 408), "semiaquatic" (line 429), "water taxa" (line 411), "water edge" (Fig. 5, Tab. 2), "water" (Fig. 3 and 4, Tab. 5), without defining them (be consistent in using one term for same meaning). See also below.

**ANSWER: We have simplified it, using 'aquatic' for speaking about the water dependence of the species, and using 'water and water-edge when we speak about the environment (that's last according with the habitat categories we have followed in the present study).**

Lines 413/414

"in which the hominins would have moved": maybe better 'which hominins occupied'.

**ANSWER: Thank you for your comment, we rewrote this sentence following your suggestion.**

**Lines 429+443**

You introduce *Natrix maura* as "semi-aquatic" (line 429) and call it later "full aquatic" (line 443).

**ANSWER: Thank you for the observation, we have corrected it. *Natrix maura* can be described as fully aquatic in comparison with her congeneric species *Natrix natrix/astreptophora*.**

**Chapter 4.3 (Tab. 5)**

You present your "environmental values" (habitat weighting) with two decimal places (e.g. 8.89%). Is this justified from the statistics? Why not give one (or maybe better) no decimals (e.g. 8.9% or 9%)?

**ANSWER: We have simplified values by giving only one decimal in the text in order to facilitate the reading, but we keep the values with two decimals in the tables and figures because we consider that for some of these values it can be important.**

**Line 488**

"little tall vegetation": I assume you mean 'few/scarce arboreal vegetation'?

"In short, this level is characterized by an open landscape, with scarce humid areas and little tall vegetation."

**ANSWER: Thank you for your comment, we have rewrote this sentence.**

**Line 736**

"an additional indication": what are/is the other indication? Please explain. (see also below).

**ANSWER: Done**

**Line 779-781 (Conclusion)**

"further evidence" (see above).

**ANSWER: Done**

"nor probably chronological period": can you explain here (or before in Discussion) why both 'glacials' in BL and FN3 could not be contemporary?

**ANSWER: We have added an explanation in both parts of the text (lines 736 and lines 779-781). Such no-contemporality between the two studied sites is an issue of the new excavations, based on the *Mimomys* evolutionary degree, on numeric dating (even if this last one is not so clear) and on some differences observed by the new studies of the lithics.**

## HIGHLIGHTS

- Amphibians and reptiles are good proxies for the environmental reconstructions.
- Paleoenvironmental conditions are reconstructed by stratigraphic levels.
- The first hominins in Western Europe coped with changing environmental conditions.
- The paleoenvironmental changes are in agreement with the climate oscillations.

1 New stratigraphically constrained ~~paleo~~paleopalaeo environmental reconstructions for the first  
2 human settlement in Western Europe: the Early Pleistocene herpetofaunal assemblages  
3 from Barranco León and Fuente Nueva 3 (Granada, SE Spain)

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81

## 82 **Abstract**

83

84 The Early Pleistocene sites of Barranco León and Fuente Nueva 3 (Guadix-Baza Basin,  
85 SE Spain) have yielded abundant Oldowan lithic artifacts and one hominin tooth (*Homo*  
86 sp. in ~~levelayer~~ D1 or D2 of Barranco León), today considered to be among the earliest  
87 evidence for a hominin presence in Western Europe, at *ca.* 1.4-1.2 Ma. Here, for the first  
88 time, the stratigraphic ~~sequences~~-~~succession~~ of these two sites are studied more precisely  
89 from a palaeoenvironmental point of view, taking into account the different ~~levelsayers~~  
90 of the depositional sequences to analyze the successive fossil assemblages of amphibians  
91 and reptiles. Palaeoenvironmental reconstructions are carried out by applying the “habitat  
92 weighting” method, which uses the modern distribution by habitat of amphibian and  
93 reptile species in order to interpret past landscapes. The successive herpetofaunal  
94 assemblages from Barranco León show a certain tendency towards more arid conditions  
95 from ~~levelayer~~ D1 to ~~levelayer~~ E, whereas in Fuente Nueva 3 environmental  
96 reconstructions reveal oscillating conditions, with a tendency towards more arid  
97 conditions in the basal part of the sequence, up to ~~level 5ayer-7~~, where the tendency shifts  
98 back to more humid conditions. Our results show that the layers included in this study  
99 with the highest density of anthropic evidence (such as ~~levels ayers 3 and-5~~ in FN 3 and



100 ~~levels~~ D1 and D2 in BL) are situated within the late Early Pleistocene climatic and  
101 environmental cyclicality, yielding different environmental conditions: a humid, wooded  
102 biotope for BL, and a more open and drier biotope in FN 3. This suggests that the  
103 hominins of the late Early Pleistocene, although conditioned to some extent by climatic  
104 factors, were able to cope with changing environmental conditions, both “interglacial”  
105 and “glacial”, in the southwestern extremity of the European continent.

106

107 **Key words:** First Human Settlement in Europe; Early Pleistocene; Amphibia;

108 Squamata; Habitat Weighting; Iberian Peninsula

109

## 110 1. Introduction

111

112 The Barranco León (BL) and Fuente Nueva 3 (FN 3) sites are among the oldest and most  
113 significant Oldowan occurrences so far discovered outside Africa (Martínez-Navarro et  
114 al., 1997; Oms et al., 2000a). Moreover, an infant molar attributed to *Homo* sp. from  
115 Barranco León ~~may represent~~ is one of the oldest hominin ~~remains~~ remains ever found so far  
116 in Western Europe (Toro-Moyano et al., 2013). In addition to their exceptionally rich  
117 large- and small-mammal record, these two sites have yielded very rich and well-  
118 documented stone tool assemblages (Barsky et al., 2013, 2015a, 2015b, 2018; Titton et  
119 al., 2018, 2020; Toro-Moyano et al., 2010, 2011), now consisting of around ~~4500~~ 45900 pieces.

120 These assemblages present remarkable features, including an impressive macro-toolkit  
121 made from locally available Jurassic limestone and small-sized flakes and cores knapped  
122 from flint nodules collected in detrital position near or in the sites. Ongoing research on  
123 the lithics from these two sites now distinguishes subtle similarities and differences  
124 between them, highlighting how early hominin behaviors could have been influenced by

125 the availability and formal features of the lithic raw materials they used, as well as by  
126 environmental and chronological differences now recognized between the two site  
127 contexts (Barsky et al., 2015a; Titton et al., 2020).

128

129 Previous works have carried out ~~paleopalaeo~~environmental and ~~paleopalaeo~~climatic  
130 reconstructions of both sites on the basis of studies of their amphibian and ~~squamate~~  
131 reptile assemblages (Blain et al., 2011, 2016a), but without making distinctions by level.

132 The faunal list resulting from these studies was composed of a total of 16 species at BL  
133 and 12 at FN 3 (Blain, 2005, 2009; Blain and Bailon, 2010; Blain et al., 2011, 2016a): in  
134 total seven anurans (*Discoglossus* cf. *jeanneae*, *Pelobates cultripes*, *Bufo bufo* s.l.,

135 *Epidalea calamita*, *Bufo* sp. (*viridis* group), *Hyla* sp., *Pelophylax* cf. *perezii*), four  
136 lizards (*Chalcides* cf. *bedriagai*, *Timon* cf. *lepidus*, small indeterminate lizards and  
137 *Ophisaurus* sp.), and five snakes (*Coronella gironnica*, *Natrix maura*, *Natrix natrix* s.l.,

138 *Zamenis scalaris* and *Malpolon monspessulanus*). On the basis of these assemblages, the  
139 climate was characterized as warm for both sites, with hot summers and mild winters, and  
140 with low precipitation (albeit more abundant than at present) of irregular distribution,

141 concentrated in winter and to a lesser extent in spring, and with a four-month drought  
142 period in the summer and at the beginning of autumn. From a ~~paleopalaeo~~environmental  
143 point of view, both sites were characterized by a terrestrial landscape composed of open

144 environments (mainly dry meadows, rocky-stony areas and Mediterranean scrubland),  
145 although there were some wet wooded areas. Water-linked amphibians and reptiles  
146 suggest the existence of a sunny, permanently aquatic environment ~~with banks made up~~

147 ~~of movable ground~~ (Blain et al., 2011).

148

149 The aim of the present work is to produce some stratigraphically more detailed  
150 ~~paleopalaeo~~environmental reconstructions for each site on the basis of their amphibian  
151 and squamate reptile assemblages, using the remains gathered during the most recent field  
152 campaigns, undertaken from 2015 to 2017 at FN 3 and from 2015 to 2018 at BL. ~~These~~  
153 ~~allow this more detailed stratigraphic approach.~~

154

## 155 2. Stratigraphic setting and chronology

156

157 The Guadix-Baza Basin is located in the southeast of the Iberian Peninsula ([Fig. 1A](#)),  
158 within the Betic Range. This basin was gradually uplifted due to the action of plate  
159 tectonics during [part of the Miocene \(some 8 Ma\), disconnecting from the sea and](#)  
160 [becoming continental](#).— The basin became [a catchment area](#) of [the](#) present-day  
161 Guadalquivir river slightly before 205 ka (Díaz-Hernández and Julià, 2006). ~~The basin~~  
162 was [subsequently](#) infilled by the alluvial Guadix Formation, composed of conglomerates  
163 (Viseras, 1991), and ~~of by~~ the lacustrine and palustrine Baza Formation, covering the  
164 central area (Anadón et al., 1987; Vera et al., 1985). The sites analyzed in the present  
165 work are located in the Baza Formation ([Fig. 1A,B](#)). The chrono[stratigraphy of the Baza](#)  
166 [Formation is](#) ~~logy of this formation runs from the end of the~~ Early Pliocene (Agustí, 1986;  
167 Garcés et al., 1996) to ~~the~~ Middle Pleistocene (Agustí et al., 1987), and is composed of  
168 three ~~major geological lithostratigraphic M~~members (Vera et al., 1985; Oms et al., 1998,  
169 2000b): a [L](#)ower [M](#)member (calcareous surface deposits of a lacustrine and palustrine  
170 origin); an [I](#)ntermediate [M](#)member (fluvial mudstones and sandstones); and an [U](#)pper  
171 [M](#)member (lacustrine and palustrine deposits resulting from an accumulation of silty  
172 calcareous deposits as well as coarser fractions). ~~The archaeo-paleontological sites of BL~~

173 and FN 3 are included in the Upper Mmember. The lithological diversity of this section  
174 includes limestones, lutites, sandstones, conglomerates and breccias (Oms et al., 2011).

176 The archaeo-paleopalaeontological sites of BL and FN 3, ~~which are~~ separated by a  
177 distance of 4.1 km, are located 124 km north of the city of Granada (SE Spain), at  
178 approximately 950 meters above sea level, in the northeastern part of the Guadix-Baza  
179 Basin. In general (see Fig. 1C), the succession containing the archaeo-  
180 paleopalaeontological sites at ~~Fuente Nueva~~ 3 is dominantly palustrine, while ~~in Barranco~~  
181 ~~León~~ is more lacustrine (Oms et al. 2011~~0~~). In both cases (see Fig. 1C),  
182 paleopalaeohydrological conditions were ~~not un~~stable throughout the sections in terms of  
183 water salinity and level~~depth~~. A general overview of the sedimentary conditions is ~~here~~  
184 summarized here in order to better control any bias of paleopalaeoenvironmental data.

### 186 2.1 Barranco León

188 This site is located ~~roughly around~~ 3 km from the village of Orce, which lies on the left  
189 bank of a ravine linked to the Sierra de la Umbría, one of the mountain ranges that delimits  
190 the northeastern part of the Guadix-Baza Basin. The site is located to the south of the  
191 Cañada de Vélez, valley, in a tributary gorge ~~which that~~ presents a geological  
192 sequence~~succession~~ consisting of mudstones, grey to yellow sands, lutites, gravels and  
193 limestones. ~~Its~~ ~~The~~ stratigraphy bounding the site is divided into nine levels. From oldest  
194 to youngest these are ~~as follows~~ (Anadón et al., 2003; Anadón and Gabàs, 2009; Oms et  
195 al., 2011; Fig. 1C): level A, beige calcsiltites to calcarenites; level B, black and dark green  
196 feldspar quartz muddy sands~~level G corresponds to beige colored sands~~; level C, beige  
197 calcsiltites to calcarenites; level D1, greyish gravels with a sandy matrix; level D2,

198 ~~greyish quartz-bioclastic sands, ending in whitish limestones; level E, fine-to-medium-~~  
199 ~~grained quartz and feldspar sands, with reddish, brown and greenish colorations; level F1,~~  
200 ~~black sandy lutites mudstones-;~~ level F2, bioclastic sands of greyish quartz with small  
201 chalk nodules in the upper part; ~~level F1, black sandy lutites;~~ level E, ~~fine to medium-~~  
202 ~~grained quartz and feldspar sands, with reddish, brown and greenish colorations; level~~  
203 ~~D2, greyish quartz-bioclastic sands, ending in whitish limestones; level D1, greyish~~  
204 ~~quartz with a sandy matrix; level C, beige calcites to calcarenites; level B, black and dark~~  
205 ~~green feldspar quartz sands; and finally, level G corresponds to beige-colored sands, level~~  
206 ~~A, beige calcarenites to calcites.~~

207

208 In Barranco León, the main environmental features from levels D1, D2 and E indicate a  
209 ~~marginal~~ freshwater ~~marginal~~ area of the ~~more~~-saline main lake. ~~Theis~~ freshwater was  
210 sourced from the adjacent highlands and ~~got~~-mixed with surface waters and hydrothermal  
211 ones (Anadón et al., 2015). ~~This freshwater~~Its presence must have attracted humans  
212 ~~activities~~ during ~~the~~ relatively lower ~~phasesing~~ of the lake waters. This is consistent with  
213 micromorphologic data ~~by~~ (Rodríguez-Rivas, ~~2004~~9). The faunal content of D1 level  
214 have an obvious component of reworking (para~~autochthonus~~autochthonous), while D2 is  
215 far more ~~autochthonous~~autochthonous and E is fully ~~autochthonous~~autochthonous.

216

217 In archaeo-~~paleo~~palaeontological terms, the most important and ~~interesting~~-significant  
218 levels are D2 and D1. Level D1 ranges from 65 to 0 cm in thickness and gravels consist  
219 mainly of angular pebbles, varying from small quartz clasts to palustrine limestone  
220 boulders (Anadón and Julià, 2010). The formation of level D1 is associated with a sudden  
221 event whereby high-energy water currents brought gravels together with most of  
222 palaeontological and archaeological remains (Oms et al., 2011). Nevertheless, at least a

223 small fraction of the archaeological remains could be *in situ* as shown by the presence of  
224 a re-assembled flint core (Gibert et al., 1998). It is the only event of this nature that has  
225 been documented so far in the BL sequence and its sudden character is also supported by  
226 the absence of lateral accretion surfaces or sedimentary features indicating some type of  
227 recurrence (Oms et al., 2011). Level D2 is roughly 20 cm thick and records background  
228 sedimentation. Both the sands and the microfaunal remains in D2 are reasonably similar  
229 to those found in level D1, apart from the fact that they appear to be *in situ* (Oms et al.,  
230 2011).

231

232 As regards its chronology, the stratigraphic sequence of ~~Barranco-León~~ has been dated  
233 by a variety of techniques, using large-vertebrate and small-mammal assemblages,  
234 ~~paleopalaeo~~paleomagnetic studies and electron spin resonance (ESR). The ESR dating was  
235 applied to optically bleached quartz grains, giving the sequence an age of between  $1.2 \pm$   
236  $0.09$  Ma in the upper part, and  $1.88 \pm 0.19$  Ma at the base. The datings of levels D1 and  
237 D2 yielded an age of  $1.46 \pm 0.17$  Ma (Toro-Moyano et al., 2013). In general, ~~the~~  
238 estimations of the ESR range are ~~in general~~ consistent with the stratigraphy, showing an  
239 overall increase in age with depth, ~~and~~ ascribing the deposits an Early Pleistocene age.  
240 The ~~paleopalaeo~~paleomagnetic study shows reverse polarity throughout the BL stratigraphic  
241 section (Oms et al., 2000a, 2003) belonging to the upper Matuyama chron. ~~In conjunction~~  
242 with the ESR results, this indicates that the sequence of Barranco León was deposited  
243 during the Matuyama Chron ( $0.78 - 2.58$  Ma) (Oms et al., 2003).

244

245 These numerical datesings are supported by the biochronological data. Without taking the  
246 levels into account, the faunal list for large vertebrates consists of *Ursus* sp., *Canis*  
247 *mosbachensis*, *Lycaon* cf. *lycaonoides*, *Vulpes* cf. *praeglacialis*, *Meles* sp., *Pannonictis*

248 cf. *nestii*, *Pachyrocuta brevirostris*, *Homotherium* sp., *Stephanorhinus* cf.  
249 *hundsheimensis*, *Equus altidens granatensis*, *Equus sussenbornensis*, *Hippopotamus*  
250 *antiquus*, *Bison* sp., *Hemitragus* cf. *albus*, *Praemegaceros* cf. *verticornis* and  
251 *Metacervoceros rhenanus* (Martínez-Navarro et al., 2010). This large-mammal  
252 association is characteristic of the Late Villafranchian period (Rook and Martínez-  
253 Navarro, 2010) and is fairly similar to that from the nearby ~~paleopalaeontological~~ site of  
254 Venta Micena, dated to ~~roughly-around~~ 1.4-1.6 Ma (Duval et al., 2010), despite the  
255 presence of *Equus sussenbornensis*, which suggests a slightly more recent age for BL.  
256 The faunal list for small mammals is composed of *Mimomys savini* (showing a  
257 representativity of 80% in relation to the total rodents), *Allophaiomys* aff. *lavocati*,  
258 *Oryctolagus* cf. *lacosti*, Erinaceinae indet., *Crocidura* sp., *Sorex minutus*, *Sorex* sp.,  
259 *Galemys* sp., *Asoriculus gibberodon*, *Apodemus* aff. *flavicollis*, and *Hystrix* sp. (Agustí  
260 and Madurell, 2003; Agustí et al., 2010, 2015a). This assemblage places BL in the  
261 regional *Allophaiomys lavocati* biozone (Agustí and Madurell, 2003; Agustí et al., 2010,  
262 2015b), where level TE9c of the ~~site-of~~ Sima del Elefante ~~site~~ (Atapuerca) is also  
263 ~~located~~situated, biochronologically dated to between 1.5 and 1 Ma (Cuenca-Bescós et al.,  
264 2010, 2013). The evolutionary differences between the *M. savini* populations of BL and  
265 FN 3 have ~~permitted~~allowed to suggest that BL is older than FN 3 (Lozano-Fernández et  
266 al., ~~2014~~ 2015). Finally, combining ~~the~~ data from the numerical datings with the  
267 biochronological and ~~paleopalaeo~~climatic data, Blain et al. (2016a) proposed that BL and  
268 FN 3 had been formed during particularly hot ~~climatic~~ periods around 1.4 Ma, suggesting  
269 a correlation with Marine Isotope Stages 43-49 (i.e. between ~~1.47 and 1.35 Ma~~ ~~1.35 and~~  
270 ~~1.47 Ma~~).

271

272 2.2 Fuente Nueva 3

273

274 ~~The FN 3 site~~ is located to the east of ~~the town of~~ Orce ~~(Granada)~~, on ~~one of the~~ slopes  
275 ~~north~~ of the Cañada de Vélez river valley (Fig. 1B), ~~in the village of Fuente Nueva. The~~  
276 ~~site is some 2 km to the north of the large Sierra Umbría mesozoic reliefs and 900 m to~~  
277 ~~the west of the smaller -Cerro de la Venta hill (see Fig 1B-b). It is made up of mudstones,~~  
278 ~~limestones, silts and sands, containing some freshwater mollusk shells.~~ These deposits  
279 are situated in ~~the~~ biozone ~~in which the presence of~~ *Allophaiomys lavocati* ~~is recorded~~  
280 (Agustí et al., 2010). ~~The general section displays up to~~ ~~Within these deposits,~~ 12 levels  
281 ~~have been distinguished~~ (Oms et al., 2011, ~~see also~~ Anadón et al., 2003), of which levels  
282 2 and ~~3-5~~ are particularly noteworthy presenting abundant remains of lithic industry  
283 ~~(although some 3 bones may, in fact be at the 2/3 boundary). Lithic industries are also~~  
284 ~~found in levels 1 and 5, where~~ ~~In level 5, furthermore,~~ a specimen of *Mammuthus*  
285 *meridionalis* in anatomical connection was found, associated with hyena coprolites  
286 (*Pachycrocuta brevirostris*) and with remains of lithic industry (Espigares et al., 2013;  
287 Toro-Moyano et al., 2010; Martínez-Navarro et al., 1997). ~~Industry rich levels are also~~  
288 ~~rich in fauna, except for level 3 (that has no industry), that in fact are likely to belong to~~  
289 ~~the 2/3 boundary.~~

290

291 The geological composition of each level ~~(from younger to older)~~ was established by  
292 ~~Anadón et al. (2003) and~~ Oms et al. (2011) (Fig. 1C): ~~level 1, the o~~ ~~Units (levels)~~ ~~1-12~~  
293 ~~level 1, 4, 11 and 12 are whitish limestones of mudstone lumpy texture, common calcrete~~  
294 ~~nodules, and post-depositional hydroplastic depositional structures (these last in levels 1~~  
295 ~~and 4). Level 2 is a green to greenish clays that towards the southern part of the excavation~~  
296 ~~gets more carbonatic and whitish. Level 3 is a brown whitish clay with nodular~~  
297 ~~limestone carbonate nodules, the top of which is transitional to level 4. Level 5 is a~~

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298 greenish fine-grained sand that has strong irregularities in thickness and induration.  
299 Thickness variations are due to the compensation of the irregularities of the top of  
300 underlying 4 level, while hardening variations are due to differential cementation, which  
301 is common at the base of -level 5. The top of level 5 becomes brownish and has plenty  
302 of lacustrine invertebrates and locally small (1 cm in diameter) edaphic nodules of around  
303 1 cm in diameter are found. Level 6 are soft dark brown clays in fresh outcrop, that get  
304 whitish when drying. Levels 7 and 9 are greenish-brown dark marly mudstones and levels  
305 8 and 10 are pale-brown greenish -marly mudstones, comprising limestones made up of  
306 nodular lithofacies. This last level is affected by large, post depositional hydroplastic  
307 deformation structures. levels 11 and 12 comprise whitish limestones; levels 8 and 10  
308 consist of pale, greenish brown colored marly lutites; levels 7 and 9, dark, greenish-  
309 brown colored marly lutites; level 6, dark, brown clays; level 5, fine grained, greenish  
310 sands and marly lutites; level 4, limestones strongly affected by hydroplastic  
311 deformations; levels 2 and 3, calcareous lutites containing invertebrate remains, mainly  
312 ostracods, mollusk shells and opercula; and finally level 1, the oldest level, comprising  
313 limestones made up of nodular lithofacies. This last level is affected by large, post-  
314 depositional hydroplastic deformation structures.

315

316 The stratigraphic sequence succession at FN 3 has been dated by means of the large-  
317 vertebrate and small-mammal assemblages, paleopalaeomagnetic studies and ESR. The  
318 data obtained by ESR place the site within a chronological range from 1.67 to 1.34 ~~1.34~~  
319 ~~to 1.67~~ Ma (Duval, 2008; Duval et al., 2012). These results are in broad agreement with  
320 the stratigraphy, showing a general increase in age with depth and assigning the deposits  
321 an Early Pleistocene age. The paleopalaeomagnetic analyses reveal reverse polarity (Oms  
322 et al., 2000a), which, in conjunction with the ESR data, gives attributes the site an age

323 prior to the Jaramillo subchron (1.07-0.99 Ma) (Oms et al., ~~2000~~, 2003, [Alvarez et al.](#),  
324 [2015](#)). The taxonomic list of large mammals published by Martínez-Navarro et al.  
325 (2010), ~~leaving the different levels out of account~~ for all levels combined, is composed of  
326 *Ursus* sp., *Canis mosbachensis*, *Lycaon* cf. *lycaonoides*, *Vulpes* cf. *praeglacialis*, *Meles*  
327 sp., *Pannonictis* cf. *nestii*, *Mustelidae* indet. (small-sized), *Pachycrocuta brevirostris*,  
328 *Lynx* sp., *Felidae* indet., *Mammuthus meridionalis*, *Stephanorhinus* cf. *hundsheimensis*,  
329 *Equus altidens granatensis*, *Hippopotamus antiquus*, *Bison* sp., *Ammotragus europaeus*,  
330 *Hemitragus* cf. *albus*, *Praemegaceros* cf. *verticornis* and *Metacervoceros rhenanus*.  
331 Notable by comparison with BL is the abundance of *M. meridionalis* remains. This large-  
332 vertebrate assemblage is also characteristic of the Late Villafranchian period (Rook and  
333 Martínez-Navarro, 2010) and reasonably similar to that present at the nearby  
334 ~~paleopaleo~~ontological site of Venta Micena, despite the presence of *Ammotragus*  
335 *europaeus*, which suggests a more recent age for the site of FN 3, as likewise suggested  
336 for BL. The taxonomic list of rodents is composed of *Hystrix major*, *Allophaiomys* aff.  
337 *lavocati*, *Mimomys savini* and *Mimomys* sp. (Agustí and Madurell, 2003; Agustí et al.,  
338 2010, 2015b, 2019). This rodent assemblage fits within the *Allophaiomys lavocati*  
339 biozone (Agustí and Madurell, 2003; Agustí et al., 2010), the same biozone as BL. As  
340 commented above, the evolutionary stages of *Mimomys savini* suggest that FN 3 is more  
341 recent than BL (Lozano-Fernández et al., ~~2014~~ [2015](#)).

342

### 343 **3. Material and Methods**

344

#### 345 *3.1 Fieldwork*

346

347 The amphibian and squamate fossil remains used for this study consist of disarticulated  
348 elements collected by ~~means of the~~ water screening of sediment obtained during  
349 archaeological excavations at both sites, during ~~the~~ field campaigns from 2015 to 2017 in  
350 FN 3 and from 2015 to 2018 in BL. The total amount of water-screened sediment has  
351 been evaluated to be approximately 8.3 tons, 6.2 tons for BL and 2.1 tons for FN 3 (Table  
352 1). All the sediment was water-screened during the successive summer field seasons using  
353 superimposed 10, 5 and 0.8 mm mesh screens and bagged by excavation layer. In  
354 subsequent years, the microfossils were processed, sorted and classified into broad  
355 categories at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES,  
356 Tarragona, Spain).

357

### 358 3.2 Systematic study

359

360 Part of the material used in this study (from levels D1 and D2 from BL) ~~was~~ already  
361 ~~been~~ studied and published in Agustí et al. (2015a). Updated classification of this old  
362 material leads to a revision of the specific attribution of the fossils attributed to the genus  
363 *Coronella* (*Coronella* cf. *girondica* becomes cf. *Coronella* sp.) and the nomenclature for  
364 fossil anguils (*Dopasia* becomes *Ophisaurus*) and extant snakes (*Rhinechis scalaris*  
365 becomes *Zamenis scalaris*). Fossil amphibians and reptiles used in other studies (Blain,  
366 2005, 2009; Blain et al., 2011, 2016a) come from older excavations, where the levels  
367 were not yet individualized and consequently have not been included in this work.  
368 Systematic attribution basically follows the osteological criteria established by Szyndlar  
369 (1984), Bailon (1991, 1999), Barahona and Barbadillo (1997), Holman (1998), Gleed-  
370 Owen (1998), Blain (2005, 2009) and Blain et al. (2008, 2011).

371

372 The fossils were grouped by the minimum number of individuals (MNI) method,  
373 determining the number of individuals for a particular species represented in each site by  
374 counting a diagnostic element. In the case of snakes, which are virtually only represented  
375 by vertebrae, the MNI was assessed for each sample taking into account the size of the  
376 dorsal vertebrae (i.e. centrum length).

### 378 *3.3 Analyses of species interrelationships*

379  
380 To analyze the changes in the faunal composition as well as the interrelationships between  
381 the various fossil species and their possible paleopalaeoenvironmental and  
382 chronostratigraphic implications, first a binary data matrix was generated based on the  
383 presence/absence of the taxa recorded for each level throughout the sequence under study,  
384 where 'presence' is represented by '1' and 'absence' by '0'. Where the taxa could not be  
385 identified to species level (Anura indet., Bufonidae indet., Ophidia indet., cf. Colubrinae  
386 indet. and *Natrix* sp.), they are not included. However, Lacertidae indet. is included in  
387 spite of being taxonomically indeterminate, on account of ~~its~~ their significance for ~~the~~  
388 assessing the environmental reading context (as they represent a ~~dude to all the lacertidae~~  
389 species have terrestrial indicator not documented in FN 3 and BL by any other lower  
390 taxonomic category) ~~habits and because we have not recovered any other lacertidae~~  
391 remains.

392  
393 A correspondence analysis (CA) was applied to the resulting data matrix, a method  
394 recommended for comparing and highlighting the proximity or difference between the  
395 taxa (assigned to the rows in the matrix) in different associations or concurrences  
396 (assigned to the columns) (Greenacre, 2010), grouping them more closely together the

397 greater the degree of concurrence. This statistical analysis ~~makes it possible to relates~~  
398 different taxa through their recorded concurrences, ~~and has yielded solid results in~~  
399 ~~synchronic and diachronic regional studies~~ (Bisbal-Chinesta and Blain, 2018). The  
400 software PAST3 was used to perform the statistical analysis (Hammer et al., 2001).

401

#### 402 3.4 *PaleoPalaeo*environmental reconstruction

403

404 The *paleopalaeo*environmental reconstruction of the sites of BL and FN 3 was carried out  
405 using the habitat weighting method (Blain et al., 2008). As the amphibians and reptiles of  
406 the Pleistocene of the Iberian Peninsula are considered specifically identical to present-  
407 day populations, the current distribution of the habitat of the species can be used to obtain  
408 the habitat weightings (Blain, 2005). This method is based on the distribution of each  
409 species in the habitat or habitats they presently occupy in the Iberian Peninsula. These  
410 habitats are divided into five major categories: open-dry, open-humid, woodland and  
411 woodland-edge, rocky and water-edge (Table 2). Each species may have a maximum  
412 weighting of 1.00, obtained on the basis of its habitat preferences. If a species shows  
413 preferences for more than one of the defined types of habitat, the resulting weighting is  
414 proportional to a greater or lesser preference (Blain et al., 2008, 2011).

415

416 *PaleoPalaeo*environmental inferences were based on current chorological data (mainly  
417 geographical distribution and ecological requirements) for the extant herpetofauna of the  
418 Iberian Peninsula, available in general atlases (Gasc et al., 1997; Pleguezuelos and  
419 Martínez Rica, 1997; Pleguezuelos et al., 2002), in regional works (Pleguezuelos, 1989;  
420 Fernández-Cardenete et al., 2000) and in biogeographical studies (Antúnez et al., 1988;  
421 Real et al., 2001).

422

## 423 4. Results

424

### 425 4.1 Amphibians and squamate reptiles from Barranco León and Fuente Nueva 3

426

427 Slightly less than 2000 bones of amphibians and squamate reptiles, including toads and  
428 frogs, lizards and several snakes, are recognized in this study (Tables 3 and 4). With the  
429 material from the new field seasons, the faunal list recorded at BL in the present study is  
430 composed, without taking the levels into account, of a total of 14 species: ~~seven~~six  
431 anurans (*Discoglossus* sp., *Pelobates cultripes*, ~~Bufonidae indet.~~, *Epidalea calamita*,  
432 *Bufo* *viridis* s.l., *Hyla* sp. and *Pelophylax* cf. *perezi*), two lizards (an indeterminate  
433 large-sized lizard and *Ophisaurus* sp.) and five snakes (*Malpolon monspessulanus*, *Natrix*  
434 *maura*, *Natrix natrix* s.l., cf. *Coronella* sp. and *Zamenis scalaris*). By contrast, the faunal  
435 list recorded for FN 3 is somewhat poorer, consisting of seven species: three anurans  
436 (*Discoglossus* sp., *Pelobates cultripes* and *Pelophylax* cf. *perezi*), one lizard (an  
437 indeterminate large-sized lizard) and three snakes (*Malpolon monspessulanus*, *Natrix*  
438 *maura* and cf. *Coronella* sp.). The amphibian and reptile species identified in the present  
439 study coincide with those identified in previous studies (Blain, 2005, 2009; Blain et al.,  
440 2011, 2016a), apart from the fact that the taxonomic lists obtained are poorer, especially  
441 for the site of FN 3. In the above-cited studies, the presence of various species of bufonids  
442 is recorded (*Bufo bufo* s.l., *Epidalea calamita* and *Bufo* *viridis* s.l.), ~~yet~~although we  
443 did not identify any remains belonging to this family in FN 3.

444

445 In general, the sequences of BL and FN 3 show a predominance of anurans over reptiles.

446 Particularly abundant is the frog *Pelophylax* cf. *perezi*, a green frog that is very typical of

447 the aquatic environments of the Iberian Peninsula and is most abundant in the areas with  
448 the greatest Mediterranean influence. The taxon with the second greatest record in the  
449 sequence as a whole is the genus *Discoglossus* sp., currently represented in the Iberian  
450 Peninsula by the endemic species *Discoglossus galganoi*, another thermophilic species  
451 typical of warm environments with a Mediterranean influence. Indeed, as both sites are  
452 situated on the banks of a ~~paleopalaeo~~lake, there is an over-representation of ~~fully~~-aquatic  
453 species (*Discoglossus* sp., *Pelophylax* cf. *pPerezi* and *Natrix mMaura*; Blain et al., 2011,  
454 2016a). For this reason, the ~~paleopalaeo~~environmental reconstruction for each of the  
455 levels under study was produced firstly, including these taxa in the analyses (with ~~water~~  
456 ~~aquatic~~ taxa) and secondly, excluding them (without ~~water-aquatic~~-taxa), with a view to  
457 gaining a better view of the environmental characteristics of the landscapes around the  
458 ~~paleopalaeo~~lake, since this would have been the ecosystem in which the hominins would  
459 have ~~lived~~ in the Early Pleistocene.

460

461 The rest of the recorded herpetofauna also shows affinities for Mediterranean  
462 environments, and most of the species still have present-day representatives in the region  
463 of Orce. The only taxa not currently represented in the Iberian Peninsula are the anuran  
464 *Bufo viridis* s.l. and the anguid *Ophisaurus* sp. (Blain et al., 2016b; Blain and Bailon,  
465 2019).

466

#### 467 4.2 Analyses of species interrelationships at Barranco León and Fuente Nueva 3

468

469 The correspondence analysis (Fig. 2A), pertaining to the taxa, shows two main groups,  
470 one formed by the aquatic binomial *Discoglossus* sp. and *Pelophylax* cf. *perezi*, the  
471 predominant species in the herpetological record, and a second group made up of the rest

472 of the taxa, mainly terrestrial ones, though also including some species partially  
473 associated with aquatic environments (as is the case with the amphibians and the  
474 ~~semiaquatic-aquatic~~ snake *Natrix maura*). In the diagram (Fig. 2A), this latter grouping  
475 shows an ascending internal arrangement, such that the lower part includes the taxa with  
476 preferences for open, dry environments (such as *Malpolon monspessulanus* and *Pelobates*  
477 *cultripes*), ~~by~~ Contrastingly, with the taxa grouped in the upper right-hand quadrant,  
478 ~~which~~ show tendencies that are more hydrophilic and more typical of environments with  
479 greater plant cover (such as *Hyla* sp. and *Natrix natrix* sensu lato), compared to the other  
480 species in the record.

481

482 At the level of concurrences, FN 3 displays an environment that is more aquatic than BL,  
483 levels 2 and 6 being the ones in which the aquatic factor is most predominant. This  
484 observation is completely consistent with the sedimentology and the invertebrate record  
485 (Fig. 1C). The fact that FN 3 is an in situ accumulation (there is no traction except for  
486 some sands in level 5) is also observed in the aquatic character of the herpetofauna. The  
487 rest of the levels show the presence of terrestrial environments, yet without ever  
488 impinging upon the preeminence of aquatic environments.

489

490 The correspondence analysis, from which we excluded the ~~fully~~-aquatic species  
491 (*Discoglossus* sp., *Pelophylax* cf. *perezi* and *Natrix maura*) (Fig. 2B), shows BL to be  
492 more associated with terrestrial environments, ~~and ones settings~~ with greater plant cover  
493 than FN 3, its three analyzed levels being grouped together in the upper right-hand  
494 quadrant of the diagram. It further allows us to analyze the environmental tendencies of  
495 both sites in ~~the~~ light of the specificities of each stratigraphic sequence ~~of each one.~~ This  
496 input of non-typically aquatic species in all Barranco-León levels (particularly D1 and



497 [D2](#)), is also consistent with the slightly reworked character observed in macrovertebrates.

498 The 'y' axis of the graph shows that the variables are distributed mainly in ~~function~~  
499 ~~relation to~~ greater humidity (upper part of the graph) or greater aridity (lower part of  
500 the graph). Accordingly, the levels of both sites tend to present a certain tendency to  
501 increased aridity as they progress from older to more recent.

502  
503 Having ascertained the relationships between the different species of amphibians and  
504 reptiles identified at a qualitative level by their ethological and biological attributes, we  
505 proceed to analyze the taxonomic groupings applying the habitat weighting method, ~~with~~  
506 ~~in order to view to~~ obtaining an environmental interpretation at a quantitative level.  
507 ~~Finally, t~~The two interpretations are ~~finally~~ analyzed ~~in conjunction~~ together.

#### 509 4.3 ~~Paleo~~Palaeoenvironmental reconstructions for Barranco León

511 ~~It was~~ Enough identifiable amphibian and reptile remains were recovered only from levels  
512 D1, D2 and E of the BL site ~~of BL~~ that ~~enough identifiable amphibian and reptile remains~~  
513 ~~were recovered~~. A minimum number of 179 individuals (MNI) were identified on the  
514 basis of the 1656 bone remains recovered (Table 3). The results by level are shown in  
515 Figure 3 and Table 5.

##### 517 4.3.1 Level D1

518  
519 Level D1 has higher humidity values ~~for humidity~~ than levels D2 and E. The highest  
520 values are those ~~for of~~ an open-humid environment (28.33%), followed by those ~~for of~~  
521 open-dry (25.765%), wooded (25.656%), water-edge (11.767%) and rocky (8.989%)

522 environments. The resulting landscape in this level would have been composed of more  
523 arid and rocky areas together with areas of ~~warm,~~ humid Mediterranean-type woodland.

524

#### 525 *4.3.2 Level D2*

526

527 Level D2 appears rather similar to level D1, but has fairly homogeneous values as regards  
528 aridity and humidity. The highest values correspond to open-dry ~~environments~~ (28.33%)  
529 and woodland environments (28.33%), followed by ~~those for~~ open-humid (23.33%),  
530 rocky (10.83%) and water-edge (9.247%) environments. The landscape presented ~~by~~ in  
531 level D2 ~~would have been~~ was similar to that of level D1, but ~~less humid~~ drier, consisting  
532 of arid, rocky areas alternating with others ~~zones of with warm,~~ humid woodlands.

533

#### 534 *4.3.3 Level E*

535

536 Level E shows a predominance of open-dry (46%) and rocky (13%) environments, in  
537 stark contrast with open-humid (18%) and water-edge (13%) environments and with  
538 some shrub vegetation (13%). In short, this level is characterized by an open landscape,  
539 with scarce humid areas and ~~little~~ sparse tall vegetation.

540

#### 541 *4.3.4 Environmental characterization of the stratigraphic sequence of Barranco León*

542

543 ~~Putting-Combining together~~ the paleopalaeo environmental results for the three levels and  
544 without taking the aquatic species into account (Table 5), we obtain a predominance of  
545 open-dry (33.3%) and somewhat stony or rocky (10.94%) environments, with a lateral

546 presence of humid (23.22%) and water-edge areas (10.328%) with ~~a certain amount~~  
547 ~~of some~~ shrub vegetation (23.3%).

548  
549 The stratigraphic sequence of BL displays a tendency towards greater aridity, with an  
550 increase in open-dry landscapes and a simultaneous decrease in arboreal density  
551 (woodland) and open-humid and water-edge environments. Levels D1 and D2 are the  
552 most humid and the richest in vegetation in the sequence under study, with D2 slightly  
553 more arid. In level E there is an increase in open, arid environments (which rise from  
554 28.33% to 46%), whereas there is a drop in more closed, wetter environments.

#### 556 4.4 ~~Paleo~~Palaeoenvironmental reconstructions for Fuente Nueva 3

557  
558 ~~At the site of FN 3, a minimum number of 66 individuals were identified on the basis of~~  
559 ~~the 285 bone remains recovered from the levels 2, 4, 5, 6, 7 and the sample 2sup (Table~~  
560 ~~4). At the site of FN 3, levels 2, 3, 4, 5, 6 and 7 were studied. A minimum number of 66~~  
561 ~~individuals were identified on the basis of the 285 bone remains recovered (Table 4). The~~  
562 results are displayed by level in Figure 4 and Table 5.

##### 564 4.4.1 Level 2

565  
566 The bone remains of amphibians and reptiles recovered from this level are too few (NR  
567 = 3) to ~~be able to~~ apply the habitat weighting method. These remains represent just two  
568 individuals, belonging to aquatic species (*Discoglossus* sp. and *Pelophylax* cf. *perezii*).

569 The ~~poverty scarcity of remains from~~ level 2 ~~can be due~~may in certain measure be due  
570 to the fact that, as one of the lowest archaeological levels, it has not yet been fully

571 ~~excavated possible to excavate it extensively~~, thus resulting in less sediment being washed  
572 than in the other, overlying levels (Table 1).

573

#### 574 4.4.2 Level 3 Sample 2sup

575

576 The results of the ~~paleo~~palaeo environmental analyses for level 3 sample 2sup reveal a  
577 predominance of open-dry (50%) and rocky (15%) environments, in stark contrast to  
578 open-humid environments (35%). ~~Among In~~ the material under study, we did not identify  
579 any species showing preferences for woodland habitats. The landscape ~~presented by in~~  
580 level 3 sample 2sup can be characterized as open, dry and stony or rocky, with high aridity  
581 and a scarcity of wooded areas.

582

#### 583 4.4.3 Level 4

584

585 In spite of having washed 200 kg of sediment from this archaeologically sterile level  
586 (Table 1), the herpetofaunal bone remains recovered ~~from this level~~ are too scarce and  
587 too indeterminate to apply the habitat weighting method. As a result, it was not possible  
588 to take level 4 into consideration within the present study.

589

#### 590 4.4.4 Level 5

591

592 Level 5 displays a predominance of ~~the an~~ open-dry environment (65%), with low values  
593 for the open-humid (17.5%), rocky (10%) and aquatic (7.5%) environments. No species  
594 typical of woodland habitats were identified. This level is characterized by an open, arid  
595 and rather dry landscape, with ~~small limited~~ rocky areas.

596

597 4.4.5 Level 6

598

599 ~~We were unable to apply the habitat weighting method to this level~~ because the 33 bone  
600 remains recovered from this level ~~it~~ all belong to aquatic species (*Discoglossus* sp. and  
601 *Pelophylax* cf. *perezi*). ~~we were unable to apply the habitat weighting method.~~

602

603 4.4.6 Level 7

604

605 Level 7 exhibits the same value (25%) for all the habitats under consideration in the  
606 present study, with the exception of the aquatic habitat (0%). Given these results, it is  
607 difficult to characterize the landscape presented by this level. ~~However, the values~~  
608 ~~obtained are consistent with the overall characterization of the site of FN 3.~~

609

610 4.4.7 Environmental characterization of the stratigraphic sequence of Fuente Nueva 3

611

612 Putting together the ~~paleo~~paleopalaeoenvironmental results for the six levels and leaving out  
613 of account the aquatic species (Table 5), we ascertain a predominance of open dry  
614 (46.~~767~~) and somewhat rocky (16.~~767~~) environments, with a lateral presence of more  
615 humid areas such as meadows (25.~~833~~) and waterside areas (2.5%), with scarce tall  
616 vegetation (8.~~333~~).

617

618 In its lower part, the stratigraphic sequence of FN 3 shows a certain tendency towards  
619 greater aridity, with values for open dry environments increasing by 15% between ~~level~~  
620 ~~sample 2sup3~~ and level 5, whereas humid environments decrease by 17.5%. In the upper

621 part between level 5 and level 7, however, the environmental tendency changes, with a  
622 7.5% increase in humid environments and a 40% reduction in open dry environments.

623

624

#### 625 4.5 Comparison between Barranco León and Fuente Nueva 3

626

627 The amphibian and squamate reptile assemblages from the archaeo-~~paleopalaeo~~palaeontological  
628 sites of BL and FN 3 testify to the presence of a ~~major-large~~ body of water that has already  
629 been recorded at a geological level (i.e. a ~~paleopalaeo~~lake), ~~as well as by-and-through~~  
630 other proxies such as pollen analyses (Jiménez Moreno, 2003) and ~~the composition of the~~  
631 large-mammal assemblages (Martínez-Navarro et al., 2003, 2010). The aquatic species  
632 *Pelophylax* cf. *perezi*, *Discoglossus* sp. and *Natrix maura* are by far the prevalent ones  
633 ~~over-compared to~~ the rest of the species at both sites. The landscapes surrounding the lake  
634 display some rather irregular environmental features. Open landscapes are well  
635 represented, with species characteristic of arid, rocky areas such as *Pelobates cultripes*,  
636 *Epidalea calamita* and *Malpolon monspessulanus*. In ~~parallel~~addition, *Ophisaurus* sp.,  
637 Bufonidae indet., *Hyla* sp. and *Natrix natrix* s.l. suggest the existence of ~~warm~~, humid  
638 shrubland areas with soft soils.

639

640 The environmental interpretation suggested by this graded series of landscapes is the  
641 existence, throughout the stratigraphic sequence recorded at BL and FN 3, of a permanent  
642 body of water whose limits with the bordering terrestrial environments (waterside  
643 woodland and hygrophilous vegetation, Mediterranean shrubland, flood plains, sandy  
644 areas, etc.) change over the course of the sequence. In theory, therefore, the number of  
645 remains from terrestrial species ~~will-risero~~ with the regression of the ~~water-lake-~~

646 ~~shorebody~~, while ~~ce~~reas in periods of aquatic transgression their presence ~~will be~~was  
647 reduced.

648

649 A comparison of the two sites (Fig. 5) brings to light a predominance of woodland areas  
650 in BL, with more humid, water-edge environments. In FN 3, by contrast, ~~there is a~~  
651 preponderance of open, drier, more arid and rocky environments is evidenced. Three of  
652 the archaeologically most significant levels (levels D2 and D1 of BL and level 5 of FN  
653 3) are characterized by open, more humid environments, with a greater presence of the  
654 aquatic element and, in the case of BL, with a greater representation of wooded areas and  
655 mild environmental conditions that would have been favorable for hominins.

656

## 657 **5. Discussion and comparisons**

658

659 The present work makes it possible, for the first time, to place the previously obtained  
660 ~~paleo~~palaeoenvironmental results within a more detailed stratigraphic context. Overall,  
661 our data ~~are is~~ consistent with the general data obtained from the previous studies of the  
662 amphibian and reptile assemblages, which describe the landscape surrounding the  
663 ~~paleo~~palaeolake as a mosaic made up of humid woodland and of drier areas with shrubs  
664 as well as more open, rocky habitats (Blain, 2005, 2009; Blain and Bailon, 2010; Blain et  
665 al., 2011, 2016a). Nonetheless, ~~this~~ study ~~we present~~ reveals certain differences between  
666 the various levels that may be associated with the inherent climatic cyclicity of the end of  
667 the Early Pleistocene. As ~~has been~~ demonstrated above, the successive amphibian and  
668 reptile assemblages of BL show a certain tendency towards increased aridity, whereas FN  
669 3 records a tendency towards aridity from the basal part of the stratigraphic sequence as  
670 far as level 7, ~~where the environment becomes more humid again~~. 5, corresponding to the

671 aridity maximum-in aridity, and after which (level 7) the environment becaomes more  
672 humid again.

673

674 There are few proxies with which we can compare our results in detail, since practically  
675 all the previous studies have considered a single faunal list for each of the sites, without  
676 providing data by level. A preliminary study of the chelonian remains recovered from BL  
677 identified three species: *Testudo* sp., *Emys* cf. *orbicularis* and *Mauremys* cf. *leprosa*  
678 (Bailon, 2010). The latter two testify to the presence of humid areas with permanent still  
679 waters rich in vegetation, coinciding with the results we inferred primarily from the  
680 presence of fully aquatic species (*Pelophylax* cf. *perezi*, *Discoglossus* sp. and *Natrix*  
681 *maura*) as well as species with a preference for habitats with plant cover such as *Hyla* sp.  
682 and *Natrix natrix* s.l. As far as large mammals are concerned, the various studies carried  
683 out are consistent with the results of our work. These reveal that the landscapes  
684 surrounding the lake consisted of a mixed environment with a preponderance of open  
685 plains and with some wooded areas (Martínez-Navarro et al., 2003; Abbazzi, 2010). The  
686 presence of ~~wet~~ humid woodlands around both sites is well supported by the occurrence  
687 of large cervids such as *Praemegaceros* cf. *verticornis* and *Metacervocerus rhenanus*.  
688 Large herbivores such as *Mammuthus meridionalis* and *Stephanorhinus* cf.  
689 *hundsheimensis* as well as the prevalence of *Equus altidens* suggest wet, open meadows.  
690 The occurrence of *Hippopotamus antiquus* provides evidence supporting the presence of  
691 large water ~~edges~~ areas. New, as yet unpublished dental mesowear analyses of ungulates  
692 and mammoths from both sites indicate largely browse-dominated diets for most of the  
693 species, with *Equus altidens* being the only notably grass-dominated feeder (Saarinen,  
694 personal observation). This observation is consistent with the interpretation of  
695 Mediterranean woodland and perhaps some more open shrubland



696 ~~paleopalaeo~~environments, and the presence of wetlands, but it does not suggest the  
697 presence of extensive grasslands. Nevertheless, further studies are needed in order to  
698 more clearly delimit that broad scenario.

699

700 To date, only the microvertebrates and isotopic values of biogenic lacustrine carbonates  
701 have been studied by-in accordance to each level. On the basis of a reduced number~~very~~  
702 ~~limited sample~~ of amphibians, reptiles and micromammals (83 individuals in total) from  
703 levels D1 and D2 of the BL site, Agustí et al. (2015a) undertook a  
704 ~~paleopalaeo~~environmental characterization of these levels by means of the habitat  
705 weighting method. The results demonstrated the existence of significant bodies of water  
706 at the time when both levels were being formed and showed that an open landscape was  
707 always present in the area around the lake. The results from level D1 revealed a  
708 predominance of woodland elements (35%), followed by open humid (27.1%), rocky  
709 (20%), and open dry elements (17.9%). The results for level D2, by contrast, showed open  
710 humid elements (41.2%) to be predominant, followed by woodland elements (30%) and  
711 open dry elements (27.1%) with a few small mammals characteristic of rocky habitats  
712 (3.8%). These results hinted at a possible tendency towards more humid conditions with  
713 a greater prevalence of woodland elements moving upwards from the base of the  
714 stratigraphic sequence. The results for these levels in the present study, which also  
715 includes an analysis of level E, likewise show an increase, albeit only a slight one, in  
716 woodland elements (~~25.756~~ % in level D1 as opposed to 28.33% in D2). By contrast, the  
717 amphibian and reptile assemblages indicate a tendency towards slightly more arid  
718 conditions in level D2 compared with D1. The difference in these values between the two  
719 levels is hardly significant, making it difficult to interpret. However, taken in conjunction  
720 with those for level E, with 46% open-dry elements and 13% woodland elements, the

721 results reveal more clearly that the stratigraphic sequence of BL shows a tendency  
722 towards more arid conditions with a lower woodland density. A complementary proxy at  
723 BL section are isotopic ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) values of biogenic lacustrine carbonates (Anadón  
724 et al., 2015). Such palaeoenvironmental data display similar conditions for both C, D and  
725 E units, but a slight positive shift in oxygen values is observed in the D to E transition.  
726 This could suggest a slight evolution to more concentrated waters, i.e. with more  
727 evaporation and/or less rainfall, as it would be expected for a relative interglacial (wet) to  
728 glacial (dry) transition.

729

730 As far as the site of FN 3 is concerned, new data ~~on~~-from rodents ~~from~~-collected during  
731 the most recent field seasons (Agustí et al., 2019), provide an interesting new point of  
732 comparison for our study. According to Agustí et al. (2019), there are two elements that  
733 are almost omnipresent at FN 3. These are *Mimomys savini* and *Mimomys* sp., a new  
734 species yet to be defined which is also present at the Early Pleistocene site of Quibas  
735 (Murcia, Spain). *Mimomys savini* is the direct ancestor of *Arvicola*, the water vole, and  
736 as such, it can be presumed to have aquatic habits implying the presence of water. By  
737 contrast, *Mimomys* sp. is a hypsodont species without tooth roots that is practically absent  
738 from BL, yet it is the only arvicolid present at Quibas, where there is scarcely a trace of  
739 water. Accordingly, we assume it to be an ubiquist form or one adapted to open  
740 environments. Together with the presence of *Allophaiomys* aff. *lavocati*, this suggests an  
741 interpretation of FN 3 as representing a habitat that is more open and less aquatic than  
742 BL, a result consistent with our study. According to Agustí et al. (2019), moreover, the  
743 presence of *Apodemus* aff. *sylvaticus* in level 5 indicates a more wooded habitat than  
744 those in levels 4, 6 and 7, where the murid present is *Castillomys rivas*, characterized by  
745 its stephanodont dentition. These latter data cannot be confirmed by our study, since many

746 of the levels of FN 3 lack any amphibians and reptiles typical of wooded environments,  
747 certainly due in large measure to the poverty of our samples in terms of number of remains  
748 and/or individuals.

749

750 Putting our results within a broader ~~paleopalaeo~~environmental and ~~paleopalaeo~~climatic  
751 context also reveals a knowledge gap in quantitative data for the end of the Early  
752 Pleistocene. Nevertheless, a recent pollen study ~~has analyzed~~ is available from the  
753 Palominas Core (Baza Basin; i.e. some 40 km from FN 3 and BL), ~~with a view to~~ casting  
754 light on the climatic conditions in the southeast of the Iberian Peninsula in the Early  
755 Pleistocene (Altoñaguirre et al., 2019, 2020). The quantitative results obtained by means  
756 of the coexistence approach show that the vegetation of the Iberian Peninsula ~~in~~ during  
757 the Early Pleistocene was controlled by cyclical climate changes. ~~Woodland flourished~~  
758 ~~during the warm, humid phases whereas during the cold, dry phases the landscape was~~  
759 ~~dominated by steppes, savannahs and open woods. In the southeast of the Iberian~~  
760 ~~Peninsula, the vegetation during these dry phases consisted primarily of herbaceous~~  
761 ~~elements, whereas the humid phases saw an increase in the arboreal component, creating~~  
762 ~~wooded steppe or Mediterranean woodlands. In the southeast of the Iberian Peninsula,~~  
763 ~~during the cold, dry phases, the landscape was dominated by steppes, savannahs and open~~  
764 ~~woodlands~~ and the vegetation consisted primarily of herbaceous elements, whereas  
765 ~~during the warm, humid phases, the woodland flourished and the vegetation~~  
766 ~~saw~~ experienced an increase in the arboreal component, creating wooded steppe or  
767 Mediterranean woodlands. For the multi-cyclic sequence at Palominas, the results show  
768 first and foremost that the “interglacial” periods were much warmer than at present,  
769 whereas the “glacial” periods were characterized by temperatures ~~identical~~ more similar  
770 to ~~current~~ modern ones. They also reveal that the oscillations in precipitation recorded

771 between the “interglacial” and “glacial” phases were not extreme, which could have  
772 facilitated the development of mosaic environments in the glacial phases of the Iberian  
773 Peninsula. In short, Altoaguirre et al. (2019, 2020) suggest that there were long warm,  
774 humid periods, interspersed with short periods of a more temperate and above all drier  
775 climate, visible in particular in the Upper and Lower Sections of Palominas, whereas in  
776 the Middle Section of Palominas the climate was cooler and humid during interglacials  
777 (Altoaguirre et al., 2020: fig. 8).

778  
779 These data shed light on the small differences observed between the different levels of  
780 BL and FN 3. The analyzed stratigraphic sequence of BL displays a tendency towards  
781 increased aridity from level D1 to level E, which might be interpreted —within the  
782 environmental cyclicality of the Early Pleistocene —as a tendency towards a “glacial”  
783 period. Likewise, in FN 3, the initial tendency towards aridity, culminating in level 5,  
784 would also correspond to a tendency towards a “glacial” period, followed in the more  
785 humid level 7 by a return to environmental conditions in line with an “interglacial” period  
786 (Fig. 6-5). In this case, level 6-5 of FN 3 might represent a period of “glacial maximum”  
787 as it is the driest and less wooded landscape of the whole sequence. It should be  
788 highlighted here that the low number of remains in level 4 of FN 3 precludes establishing  
789 whether the tendency towards aridity between levels 3 and 5 was continuous or whether  
790 the dearth-scarcity of herpetofaunal remains in level 4 should be interpreted as another  
791 “glacial” period, in which case the FN 3 sequence would also represent a multi-cyclical  
792 paleopalaeoenvironmental model.

793  
794 The present study also permits a more detailed approach to the quantitative  
795 paleopalaeoclimatic data obtained by applying the mutual ecogeographic range method

796 to the amphibians and reptiles from the earlier field seasons at BL and FN 3 (Blain et al.,  
797 2011, 2016a). In methodological terms, the mixture of levels at the two sites means that  
798 the richer levels (normally corresponding to “interglacials”) hide the lower diversity of  
799 the levels that are poorer (corresponding to the “glacials”), where there tend not to be any  
800 taxa indicative of a cold climate. As a result, the presence of “glacial” periods in the  
801 sequences of FN 3 and BL was not detected in previous studies, ~~yet~~ nor is it in  
802 contradiction with our new ~~paleo~~paleopalaeo environmental data. The higher temperature and  
803 precipitation values ~~were~~ obtained for BL, corresponding to the assemblages from levels  
804 D1 and D2 ~~and squaring correlate~~ well with the presence of more developed wooded areas.  
805 Meanwhile, the lower temperature and precipitation values obtained at FN 3 (though  
806 higher than the present-day values for the study area) are consistent with a more open,  
807 dry landscape typical of a “glacial” period or at least an “interglacial/glacial” transition  
808 period, corresponding to levels 5 and 7.

809  
810 A further ~~final~~ aspect of this study is that the ~~paleo~~paleopalaeo environmental data obtained  
811 from the amphibians and reptiles from each level provide an additional indication, apart  
812 from those already given suggested by based on the some –evolutionary differences  
813 between the *Mimomys savini* populations of both sites– that – environmentally and  
814 probably also chronologically – the sites of BL and FN 3 do not correspond to the same  
815 period. The joint analysis of the amphibian and reptile assemblages of the two sites leads  
816 us to infer certain ~~paleo~~paleopalaeo environmental similarities between level 5 of FN 3 and  
817 level E of BL. Corresponding to the most arid phases in the sequence, these might  
818 represent or lie very close to the brief “glacial maxima” of the Early Pleistocene (Fig. 6).  
819 By focusing on the levels with the highest degree of anthropic activity and the greatest  
820 archaeological significance (~~levels sample 2sup3~~ and level 5 of FN 3 and levels D1 and

821 D2 of BL), it can be seen that they are situated within different environmental (and  
822 probably also climatic) conditions, lending support to the notion that the hominins of the  
823 Early Pleistocene, though conditioned to a certain extent by the climate (see Agustí et al.,  
824 2009, 2015a), were capable of coping with and adapting to conditions that were both  
825 “interglacial” (levels D1 and D2) and “glacial” (~~levels-sample 2sup3~~ and level 5) in the  
826 southwest of the European continent.

827

## 828 **6. Conclusions**

829

830 In this study, the successive fossil assemblages of amphibians and reptiles from the Early  
831 Pleistocene sites of Barranco León and Fuente Nueva 3 (Granada, Spain) are for the first  
832 time studied from a paleopalaeo environmental point of view, taking into account the  
833 different layers of the depositional sequences. Our conclusions are as follows:

834

835 1. The successive herpetofaunal assemblages from Barranco León show a certain  
836 tendency towards more arid conditions from layer-level D1 to layer-level E, whereas the  
837 environmental reconstructions of Fuente Nueva 3 reveal oscillating conditions, showing  
838 a tendency towards more arid conditions in the basal part of the sequence up to layer-level  
839 7, where this tendency shifts back to more humid conditions.

840

841 2. The joint analysis of the amphibian and reptile assemblages from the two sites leads us  
842 to infer certain paleopalaeo environmental resemblances between level 5 of FN 3 and level  
843 E of BL. Corresponding to the most arid phases of the sequence, these might represent or  
844 be very close to the brief periods of “glacial maximum” of the Early Pleistocene.

845

846 3. The layers ~~used in this study~~ with the highest density of anthropic evidence used in this  
847 study (such as ~~sample 2suplayers 3~~ and level 5 in FN 3 and ~~layers levels~~ D1 and D2 in  
848 BL) ~~are situated within the late Early Pleistocene climatic and environmental cyclicality,~~  
849 yielding different environmental conditions: a humid, wooded biotope for BL, and a more  
850 open, drier biotope for FN 3.

851  
852 4. This suggests that the hominins of the late Early Pleistocene, although conditioned to  
853 some extent by climatic factors, were able to cope with changing environmental  
854 conditions, both “interglacial” and “glacial”, in the southwestern extremity of the  
855 European continent.

856  
857 5. The ~~paleopalaeo~~environmental data obtained for each of the levels provides further  
858 evidence that the sites of BL and FN 3 correspond to neither the same environmental  
859 context nor probably the same chronological period (in accordance with ~~thesome~~  
860 evolutionary differences ~~between~~ observed in the *Mimomys savini* populations of both  
861 sites).

862  
863 6. As perspective of future, the sterility of level 3 concerning small-vertebrates has to be  
864 checked again, as well as the correct stratigraphic position of the sample 2sup.

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889

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## 1229 **Figures and Tables**

1230

1231 **Figure 1.** A: Location of the Guadix-Baza Basin in the context of the Cenozoic basins of  
1232 the Iberian Peninsula. B: Geological units around Orce and location of the Barranco León  
1233 and Fuente Nueva 3 sites. C: Barranco León and Fuente Nueva 3 sections with indications  
1234 of the levels and environmental conditions of deposition documented by sedimentology  
1235 and invertebrate organisms.

1236

1237 **Figure 2.** Graphic representation of correspondence analyses of fossil assemblages from  
1238 Barranco León and Fuente Nueva 3 (Guadix-Baza Basin, SE Spain). **A:** correspondence  
1239 analysis including ~~water-edge~~aquatic taxa (in blue: *Discoglossus* sp., *Pelophylax perezii*

1240 and *Natrix maura*); **B**: correspondence analysis without ~~water-edgeaquatic~~ taxa.  
1241 Abbreviations: D sp., *Discoglossus* sp.; Pc, *Pelobates cultripes*; Ec, *Epidalea calamita*;  
1242 Bv, *Bufo viridis* s.l.; H sp., *Hyla* sp.; Pp, *Pelophylax* cf. *perezi*; L. indet., Lacertidae  
1243 indet.; O sp., *Ophisaurus* sp.; Mm, *Malpolon monspessulanus*; Nm, *Natrix maura* ; Nn,  
1244 *Natrix natrix* s.l.; C sp., cf. *Coronella* sp.; Zs, *Zamenis scalaris*. For data matrix see  
1245 Supplementary Material (Appendix 1).

1246

1247 **Figure 3:** Quantitative reconstruction of landscapes according to the habitat weighting  
1248 method (see text and Table 2) for the Early Pleistocene site of Barranco León (Granada,  
1249 Spain), with (left) and without (right) ~~water-edgeaquatic~~ taxa included in the analyses.

1250

1251 **Figure 4:** Quantitative reconstruction of landscapes according to the habitat weighting  
1252 method (see text and Table 2) for the Early Pleistocene site of Fuente Nueva 3 (Granada,  
1253 Spain), with (left) and without (right) ~~water-edgeaquatic~~ taxa included in the analyses.

1254

1255 **Figure 5:** Habitat interpretation for the stratigraphic sequences of the Early Pleistocene  
1256 sites of Barranco León and Fuente Nueva 3 (Granada, Spain), based on amphibian and  
1257 squamate assemblages. From bottom to top: archaeological levels excavated during the  
1258 2015–2018 field seasons. Adjacent columns show the distribution of open-dry, open-wet,  
1259 woodland, rocky and ~~water-edgeaquatic~~ dwellers, expressed as a percentage, ~~and the~~  
1260 ~~rightmost column shows the minimum number of individuals (MNI) throughout the~~  
1261 ~~sequence.~~

1262

1263 **Figure 6:** Hominin activities at the Early Pleistocene sites of Barranco León and Fuente  
1264 Nueva 3 (Granada, Spain) put into the ~~paleopalaeo~~ environmental context obtained from

1265 the amphibian and squamate reptile fossil assemblages without considering ~~water-~~  
1266 ~~edge~~aquatic species. Lithic elements represent knapping and percussive activities (size in  
1267 accordance with the density of recovered artifacts); animal silhouettes represent the main  
1268 taxonomical category of large and very large mammal ~~butchered~~ in the level. The human  
1269 tooth from Barranco León cannot confidently be ascribed to level D1 or D2.

1270

1271 **Table 1:** Main archaeological characterization throughout the stratigraphic sequence of  
1272 Barranco León and Fuente Nueva 3 (Granada, Spain) and indication of the weight of  
1273 water-screened sediment by level from the 2015 to 2018 excavation campaigns. \* Some  
1274 samples have been labelled as pertaining to level 3 during the excavation process, but  
1275 according to sedimentological studies, characterizing level 3 as sterile, they must  
1276 probably come from the upper part of level 2. In order to not mix such samples with those  
1277 labelled as level 2, we provisionally rename them here as 2sup.

1278

1279 **Table 2:** Distribution by habitat(s) of the amphibians and reptiles recovered as fossils in  
1280 the Early Pleistocene of Barranco León and Fuente Nueva 3 (Granada, Spain). (x)  
1281 indicates that weighting was not possible because the taxon was probably extinct (*Bufo*  
1282 *viridis* s.l. and *Ophisaurus* sp.) or because the higher taxonomic category contained  
1283 species with different requirements (Lacertidae indet.).

1284

1285 **Table 3:** Distribution of amphibian and squamate remains throughout the stratigraphic  
1286 sequence of Barranco León (Granada, Spain) in terms of number of remains (NR) and  
1287 minimum number of individuals (MNI).

1288



1289 **Table 4:** Distribution of amphibian and squamate remains throughout the stratigraphic  
1290 sequence of Fuente Nueva 3 (Granada Spain) in terms of number of remains (NR) and  
1291 minimum number of individuals (MNI).

1292

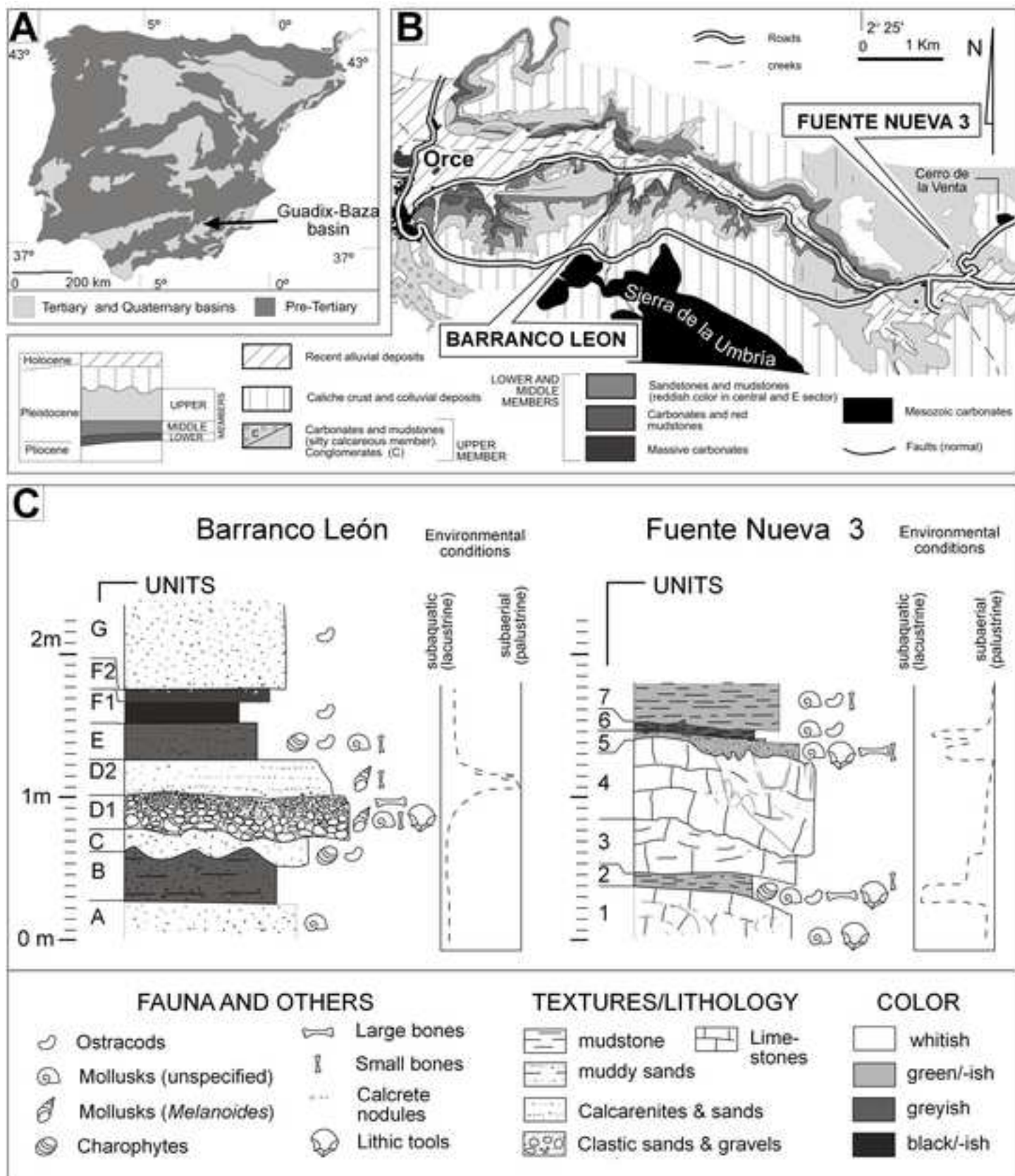
1293 **Table 5:** Distribution of the frequency of different habitats at the Barranco León and  
1294 Fuente Nueva 3 sites (Granada, Spain). This is based on the amphibian and squamate  
1295 contents of the different levels ~~and sublevels~~, according to their habitat preferences as  
1296 defined in Table 2.

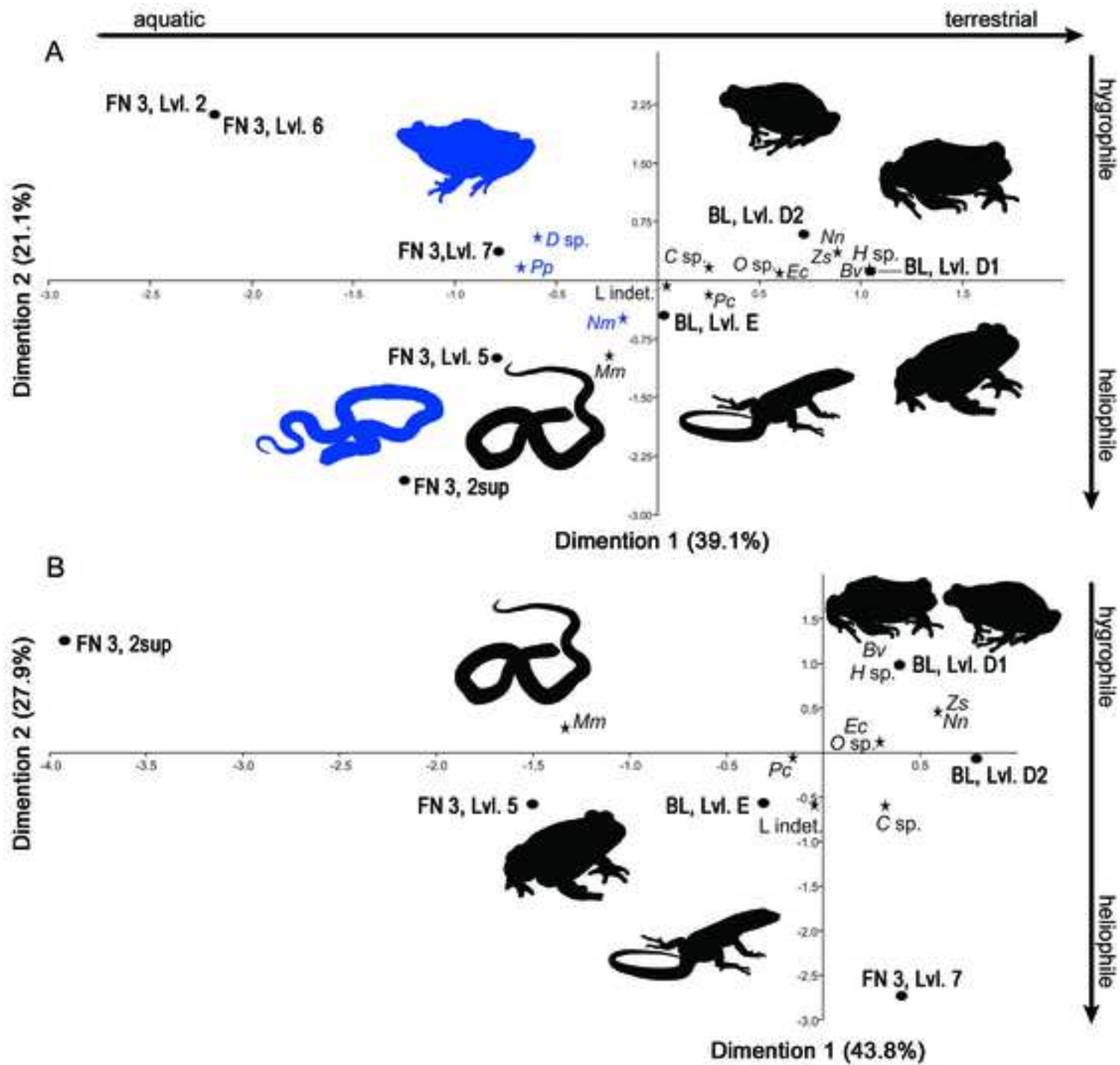
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1298 Supplementary Information

1299 **Appendix 1.** Data matrix of presence (1) and absence (0) for the successive ~~levelsayers~~  
1300 of the Early Pleistocene sites of Barranco León and Fuente Nueva 3 (Granada Spain). In  
1301 bold: aquatic taxa excluded from the second analysis.

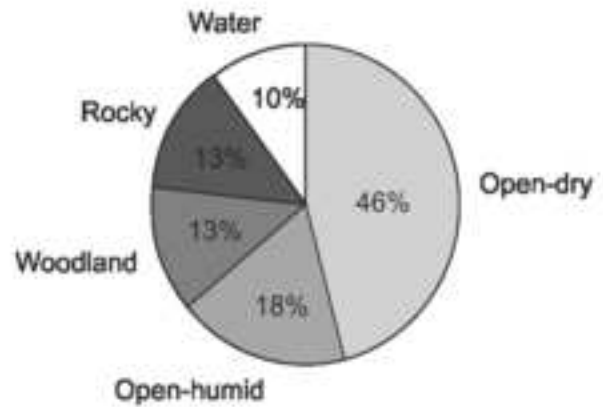
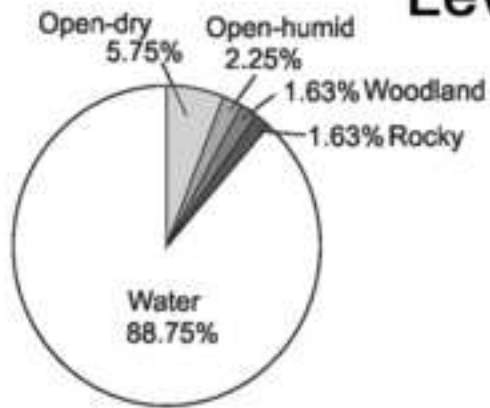
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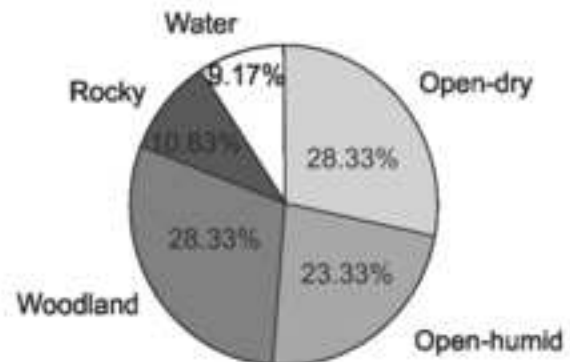
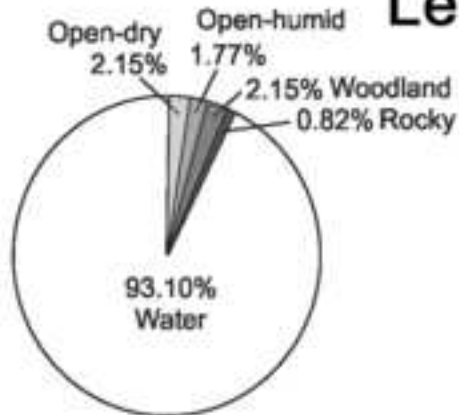


# Barranco León

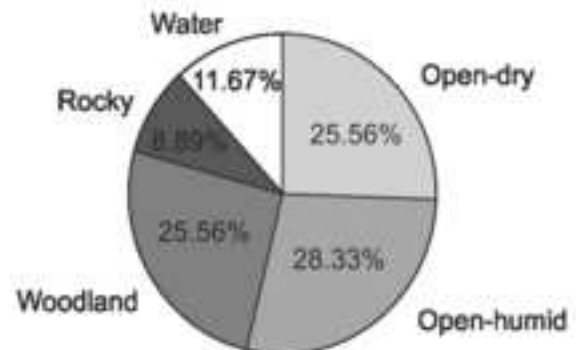
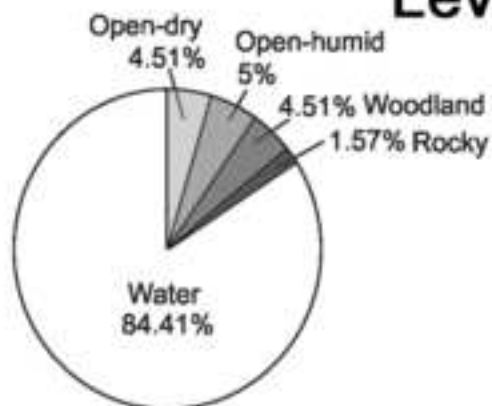
## Level E



## Level D2

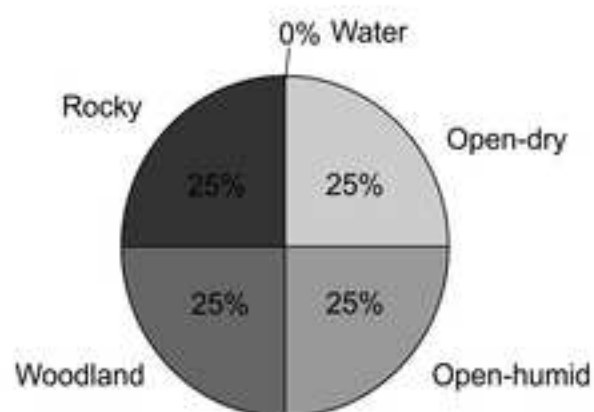
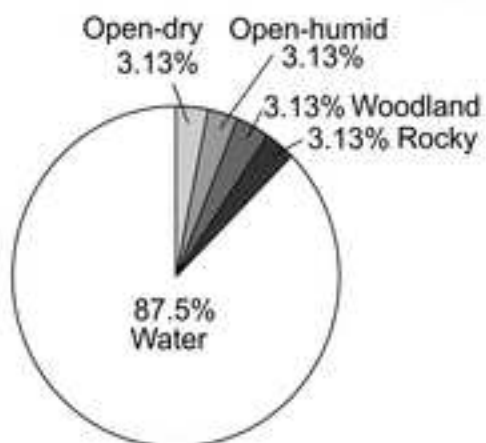


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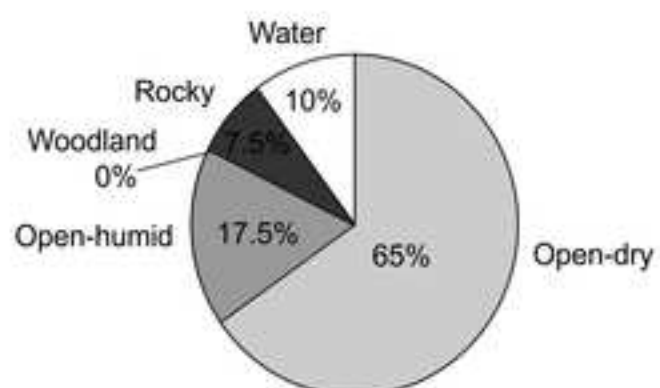
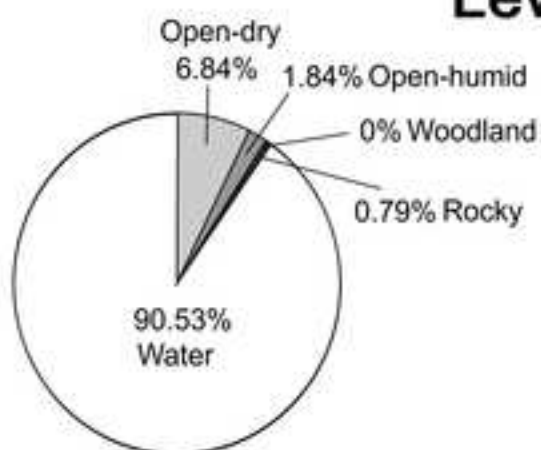


# Fuente Nueva 3

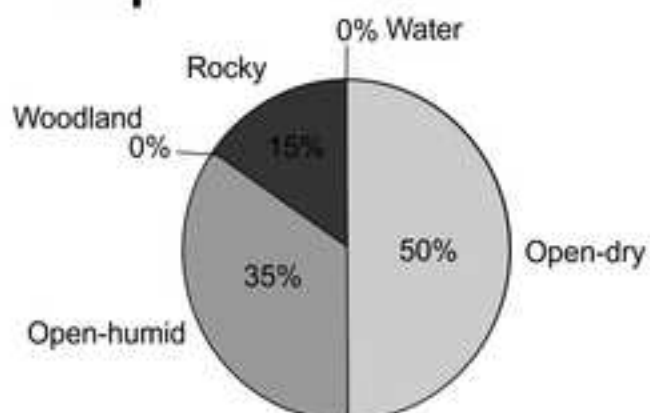
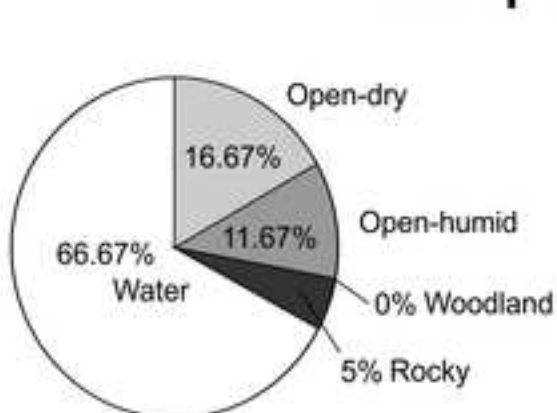
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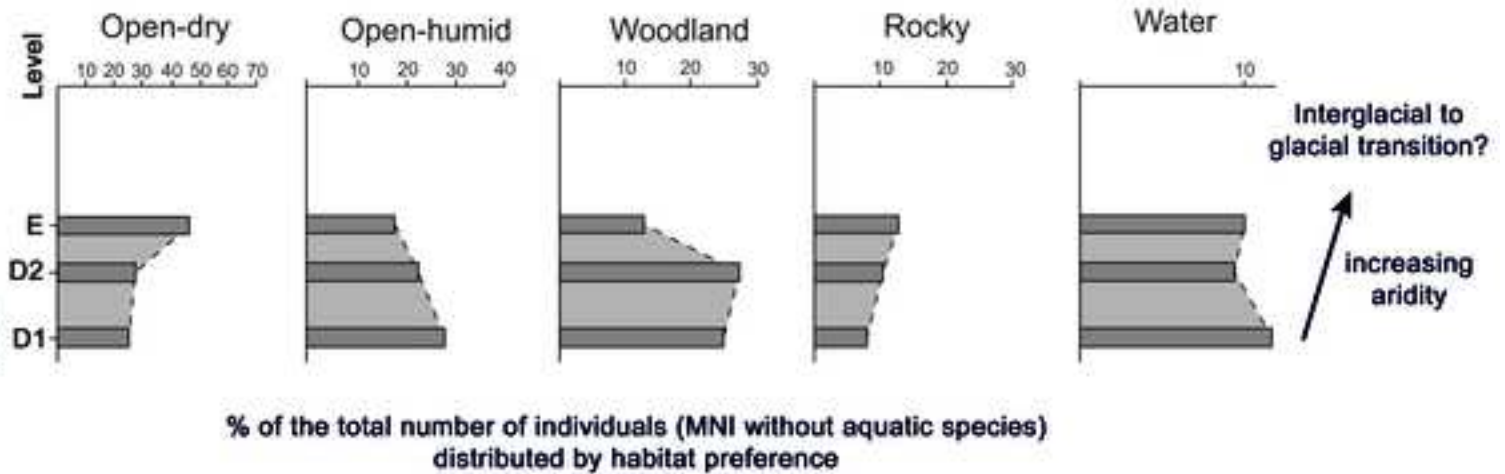
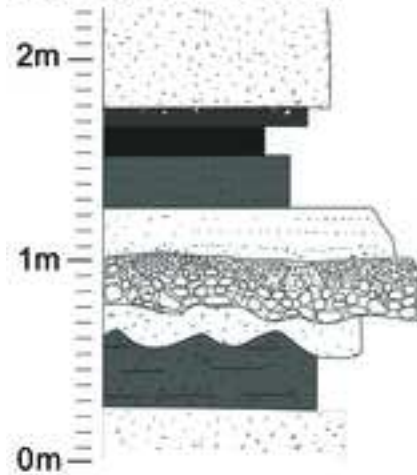
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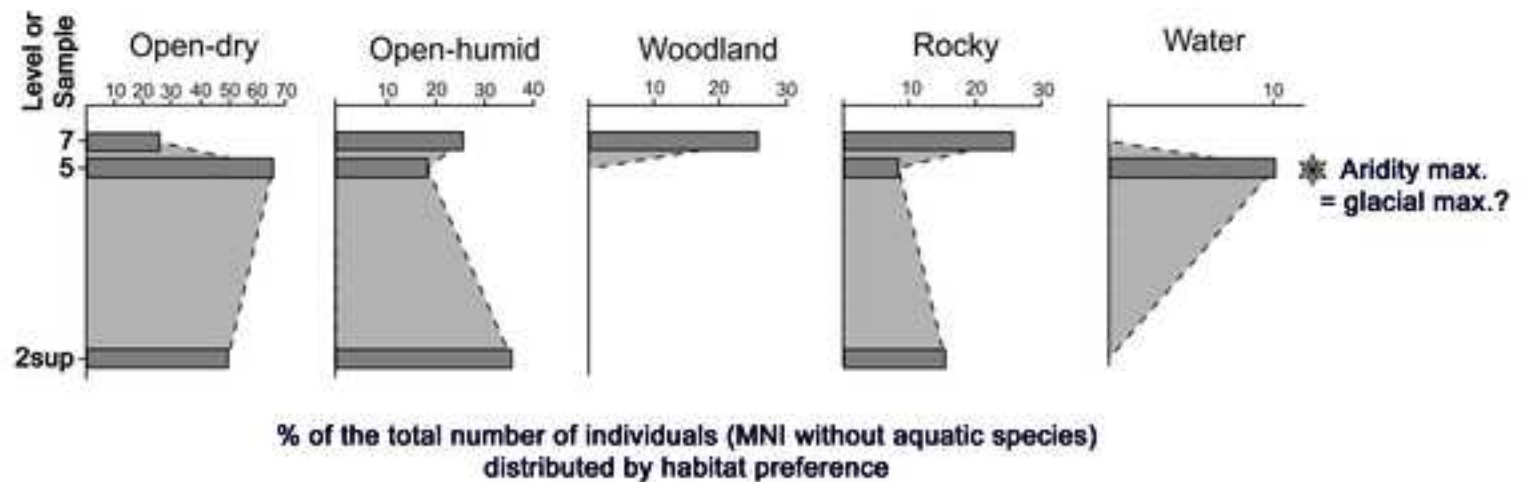
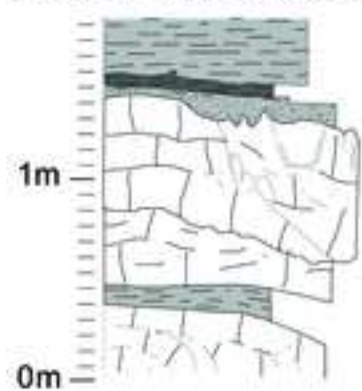
## Sample 2sup

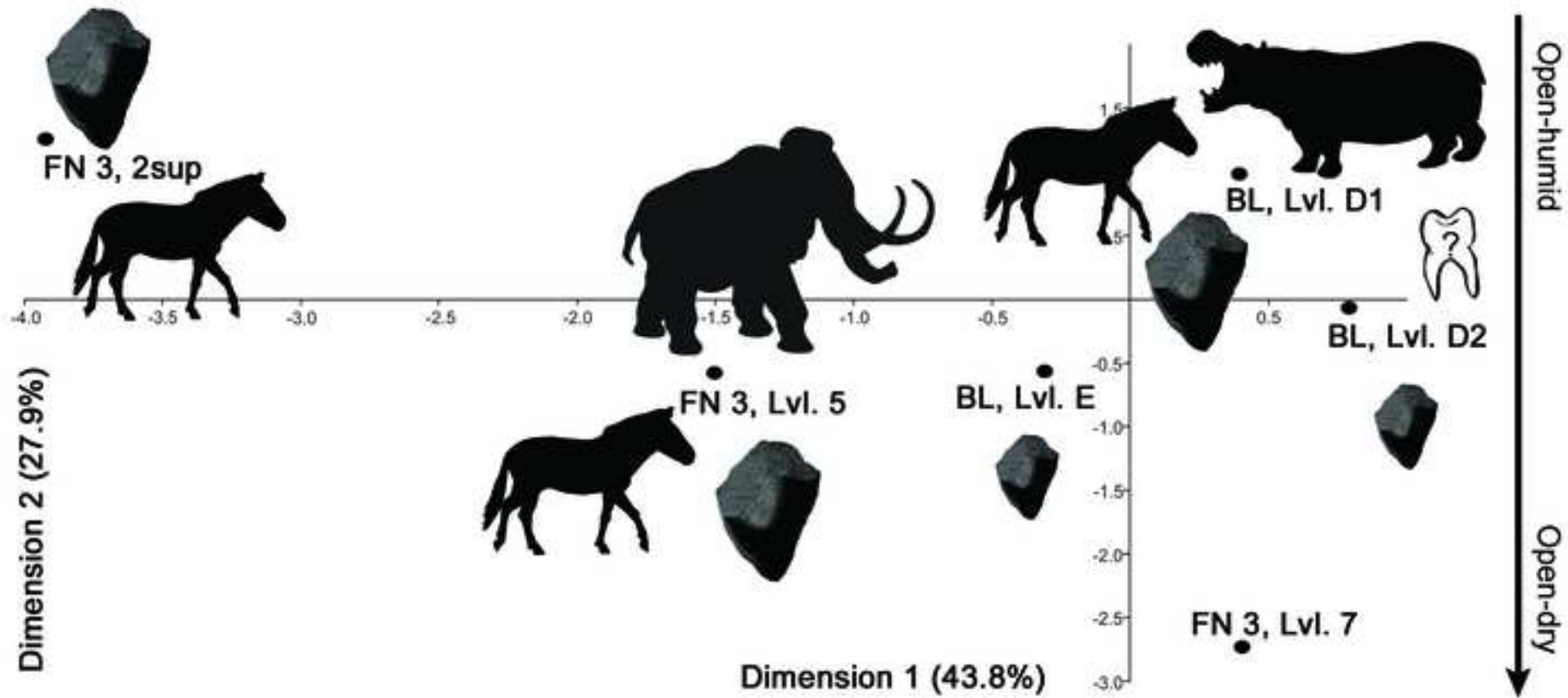


## Barranco León



## Fuente Nueva 3







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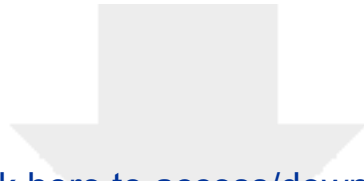
**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Author statement

**Christian Sánchez-Bandera:** Investigation; Formal analysis; Writing- Original draft preparation. **Oriol Oms:** Investigation; Formal analysis; Writing- Reviewing and Editing. **Hugues-Alexandre Blain:** Conceptualization, Methodology, Supervision; Funding acquisition. **Iván Lozano-Fernández:** Supervision, Writing- Reviewing and Editing. **Josep Francesc Bisbal-Chinesta:** Formal analysis; Writing. **Jordi Agustí:** Writing; Validation; Funding acquisition. **Juha Saarinen:** Writing; Validation. **Mikael Fortelius:** Writing; Validation. **Stefania Tibbon:** Reviewing and Editing; Validation. **Alexia Serrano-Ramos:** Reviewing and Editing; Validation. **Carmen Luzón:** Validation. **José Solano-García:** Reviewing and Editing; Validation. **Deborah Barsky:** Writing- Reviewing and Editing; Validation. **Juan Manuel Jiménez-Arenas:** Project administration; Funding acquisition; Supervision.



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