



Insights on the Early Pleistocene Hominin Population of the Guadix-Baza Depression (SE Spain) and a Review on the Ecology of the First Peopling of Europe

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OPEN ACCESS

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Specialty section:

This article was submitted to
Paleontology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 22 February 2022

Accepted: 14 March 2022

Published: 21 April 2022

Citation:

Palmqvist P, Rodríguez-Gómez G, Bermúdez de Castro JM, García-Aguilar JM, Espigares MP, Figueirido B, Ros-Montoya S, Granados A, Serrano FJ, Martínez-Navarro B and Guerra-Merchán A (2022) Insights on the Early Pleistocene Hominin Population of the Guadix-Baza Depression (SE Spain) and a Review on the Ecology of the First Peopling of Europe. *Front. Ecol. Evol.* 10:881651. doi: 10.3389/fevo.2022.881651

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The chronology and environmental context of the first hominin dispersal in Europe have been subject to debate and controversy. The oldest settlements in Eurasia (e.g., Dmanisi, ~1.8 Ma) suggest a scenario in which the Caucasus and southern Asia were occupied ~0.4 Ma before the first peopling of Europe. Barranco León (BL) and Fuente Nueva 3 (FN3), two Early Pleistocene archeological localities dated to ~1.4 Ma in Orce (Guadix-Baza Depression, SE Spain), provide the oldest evidence of hominin presence in Western Europe. At these sites, huge assemblages of large mammals with evidence of butchery and marrow processing have been unearthed associated to abundant Oldowan tools and a deciduous tooth of *Homo* sp. in the case of BL. Here, we: (i) review the Early Pleistocene archeological sites of Europe; (ii) discuss on the subsistence strategies of these hominins, including new estimates of resource abundance for the populations of Atapuerca and Orce; (iii) use cartographic data of the sedimentary deposits for reconstructing the landscape habitable in Guadix-Baza; and (iv) calculate the size of the hominin population using an estimate of population density based on resource abundance. Our results indicate that Guadix-Baza could be home for a small hominin population of 350–280 individuals. This basin is surrounded by the highest mountainous reliefs of the Alpine-Betic orogen and shows a limited number of connecting corridors with the surrounding areas, which could have limited gene flow with other hominin populations. Isolation would eventually lead to bottlenecks, genetic drift and inbreeding depression, conditions documented in the wild dog population of

the basin, which probably compromised the viability of the hominin population in the medium to long term. This explains the discontinuous nature of the archeological record in Guadix-Baza, a situation that can also be extrapolated to the scarcity of hominin settlements for these ancient chronologies in Europe.

Keywords: early *Homo*, Western Europe, subsistence strategies, Barranco León, Fuente Nueva 3, population size

INTRODUCTION

The chronology of the first hominin settlements in Europe has been subject to debate and controversy. Until the mid 1990s most paleoanthropologists believed that there was no significant habitation before 0.6–0.5 Ma (e.g., Aragón, Bilzingsleben, Boxgrove, Ceperano, Mauer, and Verteszöllos), with most sites concentrating on ≤ 0.45 Ma (e.g., Atapuerca's Sima de los Huesos, Petralona, Schönningen, Swanscombe, and Steinheim) (Carbonell and Rodríguez, 1994; Roebroeks and van Kolfschoten, 1994), an increase in the number of occupations that coincided with interglacial MIS 11 (Blain et al., 2021). This “young chronology” was shortly challenged by new findings in Europe (Carbonell et al., 1995; Ascenzi et al., 1996; Bermúdez de Castro et al., 1997; Martínez-Navarro et al., 1997), the Caucasus (Gabunia and Vekua, 1995) and China (Wanpo et al., 1995; Larick and Ciochon, 1996), as well as by the geochronological re-evaluation of the evidence from Java (Swisher et al., 1994; Larick et al., 2001; Hyodo et al., 2011), which all indicated an earlier hominin arrival in Eurasia, during late Early Pleistocene times (Arribas and Palmqvist, 1999). However, although the archeological record in Europe has improved over the last decades, it remains highly fragmentary for these ancient chronologies and many sites lack high-resolution chronostratigraphic frameworks, which raises doubts on the age of the earliest hominin settlements. For example, a re-evaluation of the magnetostratigraphic and radiometric age constraints on several key sites bearing hominin remains and/or lithic tools from southern Europe led Muttoni et al. (2010, 2013) to propose that the first hominin dispersal in Western Europe took place during the Matuyama reverse polarity chron, between the Jaramillo normal polarity subchron and the Brunhes-Matuyama boundary.

Ancient evidence of hominin presence in Western Europe, The Caucasus, the Levantine Corridor, and Northern Africa is now well documented in a number of Early Pleistocene archeological localities (see **Figure 1** and references therein). This provides a chronological scenario for the oldest hominin settlements in Eurasia in which the Caucasus (Dmanisi, ~ 1.8 Ma) and southern Asia were occupied ~ 400 ka before the first peopling of Europe (Arribas and Palmqvist, 1999; Dennell and Roebroeks, 2006; Mosquera et al., 2013). It has been proposed that this delay could result from competition with other carnivores: hominin survival at the middle latitudes, where plant resources are scarce during the cold season, would depend on the regular scavenging of ungulate carcasses (Turner, 1992; Palmqvist et al., 2022a). For this reason, Rodríguez-Gómez et al. (2017a) estimated the level of competition for meat among the members of the carnivore guild of Venta Micena (VM), a site dated by biochronology and paleomagnetism to

1.6–1.5 Ma with no conclusive evidence on hominin presence (Arribas and Palmqvist, 2002; Martínez-Navarro, 2002; Palmqvist et al., 2005). This study provided estimates on meat availability and competition intensity for VM that were higher and lower, respectively, than those obtained for Barranco León (BL) and Fuente Nueva 3 (FN3) (Rodríguez-Gómez et al., 2016a). Given that BL and FN3 are 200–100 ka younger than VM, this suggests that the delay in the colonization of Europe was not a matter of ecological opportunity and other factors (e.g., climatic and/or geographic barriers to dispersal) should be considered (Rodríguez-Gómez et al., 2017a).

The Early Pleistocene Archeological Sites of the Guadix-Baza Depression

Barranco León and FN3 lie in the NE sector of the Baza Basin (Guadix-Baza Depression, SE Spain; **Figure 2A**), in the vicinity of the town of Orce (**Figure 2B**). This sedimentary depression is an inland basin that covers an area of $\sim 4,000$ km² and is surrounded by mountainous reliefs of the Betic Chains, with heights of up to 3,479 m in the Mulhacén peak. The continental Plio-Pleistocene record of the basin is composed of lacustrine and fluvial deposits that show a complex sedimentary architecture (both laterally and vertically) as a result from active tectonics and orbitally induced climatic cycles (García-Aguilar and Palmqvist, 2011). The sediments include limestones, marls, shales, sands, and conglomerates, as well as dark clays and silexites associated to the archeopaleontological sites (García-Aguilar et al., 2014, 2015). The basin was in connection with the Mediterranean Sea during Late Miocene times by the ‘Almanzora Corridor’ and became continental at the end of the Tortonian (Guerra-Merchán, 1990, 1993; Soria et al., 1999; but see also Husing et al. (2010)). Since these times, it was subject to isostatic uplift with an average uplift rate of ~ 200 m/Ma, as estimated from Late Neogene coastal marine conglomerates and coral reefs (Braga et al., 2003). As a result, the glacial surface (i.e., the uppermost horizontal infilling level) stands now 1,000 m on average above sea level. During the Plio-Pleistocene, the basin developed a network of endorheic drainage, being subject to: (i) intense tectonic subsidence relative to the surrounding mountains, which facilitated the accumulation of a thick (~ 550 m) and relatively continuous sedimentary record; and (ii) hydrothermal activity (**Figures 2A,B**), which provided a mild and productive environment for the terrestrial fauna (García-Aguilar et al., 2014, 2015). The thermal springs were a major determinant in the establishment of biodiversity ‘hot spots’ for the large mammal fauna, which remains were preserved in many sites like BL and FN3 (Palmqvist et al., 1996, 2005, 2022b; Arribas and Palmqvist, 1998; Viseras et al., 2006; Arribas et al.,

2009; Maldonado-Garrido et al., 2017; Ros-Montoya et al., 2017; Martínez-Navarro et al., 2018).

The stratigraphy of BL (**Figure 2C**) spans the middle terrigenous and upper silty calcareous members of the Baza Formation (Vera et al., 1984). The middle member consists of alluvial red clays, sandstones and conglomerates while the upper one is dominated by limestones, sandstones, carbonate silts, and dark mudstones (Turq et al., 1996; Arribas and Palmqvist, 2002) deposited in a shallow lacustrine system with an alternation of oligo- to mesohaline waters (Anadón et al., 1994; Anadón and Gabàs, 2009). The excavated layers show sediments associated with a swampy environment, except level D (formerly BL5; Arribas and Palmqvist, 2002), which shows fluvial features and encases most of the archeological assemblage (Toro-Moyano et al., 2013). The sub-horizontal stratigraphy of FN3 (**Figure 2C**) shows two sedimentary cycles deposited in a lutitic-carbonate, lacustrine-to-swampy environment, each with limestones at the top of the sequence separated by clays, fine sands and marly lutites, which cluster in two main units, the Lower and Upper Archeological Levels (Turq et al., 1996; Martínez-Navarro et al., 1997; Espigares et al., 2013, 2019).

The age of BL-D (**Figures 2C,E**) and FN3 (**Figures 2C,D**) was estimated in 1.43 ± 0.38 and 1.19 ± 0.21 Ma, respectively, using biochronology, magnetostratigraphy and the U-series/electron spin resonance (ESR) dating method applied to optically bleached quartz grains and fossil teeth (Duval et al., 2012; Toro-Moyano et al., 2013). An age of 1.50 ± 0.31 Ma was derived for FN3 based on cosmogenic nuclides (Álvarez et al., 2015). Other age estimates were derived from a biometric approach that considered an orthogenetic, rectilinear pattern of size increase in the lower molar teeth of the arvicolid *Mimomys savini* (Lozano-Fernández et al., 2013, 2014), but this “vole-clock” was questioned (Martin, 2014; Palmqvist et al., 2014, 2016). The absence of suids from BL and FN3 provides also a useful biochronological inference (Martínez-Navarro et al., 2015): suids are absent from Europe between 1.8 and 1.2 Ma, until the arrival of an evolved form of *Sus strozzi* during the Epivillafranchian (Cherin et al., 2018, 2020). This species is first recorded in level TE9 (Atapuerca), dated at 1.22 ± 0.16 Ma by cosmogenic nuclides (Carbonell et al., 2008), and later in other sites of Jaramillo age like Untermassfeld, Vallonnet, or Vallparadís (Moullé et al., 2006; Madurell-Malapeira et al., 2010, 2014; Cherin et al., 2018, 2020).

Excavations through the last three decades in BL and FN3 have unearthed huge Oldowan assemblages composed of cores, flakes and debris that represent the whole reduction sequence (Tixier et al., 1995; Turq et al., 1996; Martínez-Navarro et al., 1997; Oms et al., 2000; Palmqvist et al., 2005; Barsky et al., 2010, 2016; Toro-Moyano et al., 2011, 2013; Espigares et al., 2013; Tilton et al., 2018, 2021; Yravedra et al., 2021). The tools are associated to skeletal remains of vertebrates, mostly large mammals (>6,500 specimens in BL and >9,000 in FN3). Espigares et al. (2019) showed that of those bones with their cortical surface well preserved (4,249 in BL and 3,852 in FN3), 64 (0.8%) exhibited cut marks and 163 (2%) showed percussion marks resulting from bone fracturing by the hominins for accessing their marrow contents. Similarly, a recent study of 2,857 bone remains from

FN3 unearthed during the excavation seasons of the years 2017–2020 has shown that 25 (0.9%) bear cut marks and 16 (0.6%), percussion marks (Yravedra et al., 2021). These frequencies are close to those recorded at Pirro Nord, where 1.1% of the remains are cut-marked and 0.6% show evidence of intentional bone breakage (Cheheb et al., 2019).

The anthropogenic marks of BL and FN3 provides clues on the subsistence strategies of the hominins that first dispersed in Europe (Espigares et al., 2013, 2019; Toro-Moyano et al., 2013; Yravedra et al., 2021). Cut marks are relatively short (length range: 1.8–13.0 mm) and are mostly represented by incisions, although scrapes, sawing marks, and chop marks are also documented. They mostly appear on remains of animals of medium-to-large and very large size, and evidence patterns of skinning, defleshing, disarticulation, evisceration, and periosteum removal. Percussion marks include pits, notches, impact flakes, and negative flake scars generated by hammerstone impact during the butchery of bones for marrow processing. There are also tooth-marked bones, most of them gnawed by the giant, short-faced hyena *Pachycrocuta brevirostris*, and some by porcupines (Espigares et al., 2019). This is particularly evident in the case of the Upper Archeological level of FN3, in which hyena coprolites are abundantly preserved (Espigares et al., 2013).

During the last years, a wealth of information on the taphonomy of the Orce sites, the technological features of their tool assemblages and the paleoecology of the faunal community has been published. This makes necessary a review of the paleoenvironments inhabited by the large mammals and the hominins in Guadix-Baza during late Early Pleistocene times, as a way of elucidating the ecological context in which the first hominin arrival in Western Europe took place. In this article, our three main goals are: (i) to review the subsistence strategies of the hominins in the archeological sites of BL and FN3; (ii) to evaluate the roles played by the hominins and carnivores in generating the fossil assemblages preserved at both sites; and (iii) to estimate the size of the hominin population that inhabited the basin.

MATERIALS AND METHODS

Our review of the evidence on hominin subsistence strategies includes: (i) the inferences on the mammalian fauna (**Table 1**) and the paleoenvironments of the basin; (ii) the technological features of the tool assemblages and the anthropogenic marks on the bones of large mammals; (iii) the scavenging opportunities provided by sabertooths to the hominins; and (iv) the inferences on the level of competition among the members of the carnivore guild and their consequences on hominin population density.

We use new data for evaluating the roles of hominins and carnivores as bone collecting and modifying agents in the assemblages of BL and FN3. Specifically, we study the abundance of proximal and distal epiphyses of major limb bones of ungulates and their relationship with the mineral density and marrow yields of these bone portions. For doing so, we use modern analogs (Outram and Rowley-Conwy, 1988; Brink, 1997; Lam et al., 1999) and least-squares regression techniques using SPSS Statistics v. 25. Then, we compare the results obtained with those for VM,

a site conclusively identified as generated in the surroundings of a denning site of the large bone-destroying hyena *P. brevirostris* (Palmqvist et al., 1996, 2011, 2022b; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). Thirdly, we analyze with SPSS Statistics v. 25 the relationship between prey biomass availability and rainfall in a set of African Natural Parks and Game Reserves using data from Hatton et al. (2015) and Fick and Hijmans (2017). Then, we compare these results with the estimates available for BL and FN3 (Rodríguez-Gómez et al., 2016a, 2017a;

Martín-González et al., 2019), to evaluate meat availability in the Orce sites. Finally, we develop a new model of the paleogeography of the Guadix-Baza Depression during the late Early Pleistocene using compiled data on the cartography on the sediments (García-Aguilar et al., 2014). This allows us to estimate with ImageJ v. 1.51 the extent of the paleoenvironments, which provides a reconstruction of the surface area habitable by the large mammals and the hominins. The cartographic surface, which encompasses the area covered by the lake, the outcrop



FIGURE 1 | (A) Geographic location of selected Early Pleistocene to early Middle Pleistocene archeological sites of Europe, North Africa, the Levantine Corridor, and the Caucasus. 1: Barranco León (BL) and Fuente Nueva 3 (FN3), two sites of the Guadix-Baza Depression, Spain (1.5–1.2 Ma; Martínez-Navarro et al., 1997; Orms et al., 2000; Espigares et al., 2013, 2019; Toro-Moyano et al., 2013; Tutton et al., 2021; Yravedra et al., 2021), which have yielded abundant Oldowan assemblages (~3,500 artifacts) and evidence of butchery and marrow processing of large mammal bones, as well as a human deciduous tooth in BL. 2: level TE9 of Sima del Elefante (1.3–1.1 Ma; Carbonell et al., 2008) and level TD6 of Trincheras Dolina (~0.85 Ma, MIS 21; Duval et al., 2018; Parés et al., 2018) in Atapuerca, Spain (a mandibular symphysis and 32 Oldowan artifacts, including four flakes, used for defleshing and marrow extraction have been unearthed in TE9). 3: Alto de las Pícarazas, Spain (1.5–1.4 Ma; Vicente-Gabarda et al., 2016), which preserves >2,000 bone remains (several of them with butchery, percussion, and fracture marks) and seven lithic tools (two shapeless flint fragments and some splinters found during the sieving of sediments). 4: Vallparadis, Level EVT7, Spain (0.98–0.95 Ma, MIS 27; Martínez et al., 2015; but see, for a younger chronology of ~0.85 Ma, Duval et al., 2015), which has yielded small-sized Oldowan tools (notches, becs, scrapers and denticulates on small pebbles, clasts, fragments, and flakes, as well as a large single chopper) elaborated from local raw materials and based on an anvil knapping technique (García et al., 2013). 5: Bois-de-Riquet, Lézignan-la-Cèbe (1.3–1.1 Ma; Bourguignon et al., 2016; but see, for an older chronology, Crochet et al., 2009), which preserves lithic artifacts (177 basalt tools, although anthropically produced artifacts are difficult to differentiate from fragments or blocks detached naturally from the exfoliating surfaces enclosing the sedimentary level). 6: Pont-de-Lavaud (1.1–1.0 Ma; Voinchet et al., 2010), with an Oldowan assemblage that comprises ~8,000 artifacts made exclusively on quartz pebbles and subangular vein quartz fragments, including ~4,000 broken pebbles and 1,321 pieces with percussion marks and evidence of flaking with the bipolar-on-anvil technique (De Lombera-Hermida et al., 2016). 7: Vallonnet Cave (1.2–1.1 Ma; Michel et al., 2017; Cauche, 2022), with percussion tools, shaped pebbles, flakes, cores, and cut-marked bones. 8: Monte Poggiolo, Italy (~0.85 Ma, within the reverse magnetic polarity subchron C1r.1r; Muttoni et al., 2011), which preserves an industry characterized by knapped pebbles and the products derived from their knapping, showing an almost total absence of retouched tools and the presence of some scrapers and denticulates that seem to be incidental and have no distinctive features (Peretto, 2006). 9: Isernia La Pineta, Italy (~0.6 Ma; Coltorti et al., 2005), with flint and cherty limestone artifacts associated with remains of large mammals, characterized by the use of anvils in an opportunistic and rapid way to produce a large number of flakes and residual cores, usually of very small size. 10: Pirro Nord, Italy (1.6–1.3 Ma; Arzarello et al., 2007, 2015; Cheheb et al., 2019), where 5 out of 340 lithic artifacts preserve use-wear traces and are associated with more than one thousand vertebrate fossil remains, several with cut marks or evidence of intentional breakage. 11: Venosa Notarchirico, Italy (0.695–0.670 Ma, MIS 17; Moncel et al., 2020), which Oldowan industry is made on chert and includes flakes (mostly unretouched), broken flakes, debris, retouched nodules, cores, and limestone pebbles, as well as two bifacial tools and a handaxe. 12: Happisburgh 3 and Pakefield, United Kingdom (~0.8 Ma; Lewis et al., 2019), which tool assemblages comprise flint flakes, flake tools, cores, and a handaxe in the case of Happisburgh 1 (~0.5 Ma, MIS 13). 13: Kozarnika Cave, Layers 13a-c, Bulgaria (~0.75 Ma; Muttoni et al., 2017), which has provided an abundant industry (~10,000 artifacts, associated to a rich faunal assemblage) that shows a predominance of fragments from primary flaking (the local flint is very fragile), with the flakes obtained by simple unipolar to bipolar debitage (Sirakov et al., 2010). 14: Denziç, Turkey (1.2–1.1 Ma; Lebatard et al., 2014), which has provided the Kocabaş skull fragment, the only known Turkish fossil of *Homo erectus*. 15: Dursunlu, Turkey (0.99–0.78 Ma; Güleç et al., 2009), where remains of rhino, hippo and horse are found with 135 modified quartz implements. 16: Dmanisi, Georgia (~1.8 Ma; García et al., 2010; Coil et al., 2020), a site that preserves the oldest evidence of human presence out of Africa (see text), with five hominin skulls and several postcranial bones (Gabunia and Vekua, 1995; Lordkipanidze et al., 2005, 2013), a rich assemblage of Late Villafranchian mammals and large numbers of Oldowan artifacts made of basalt, andesite and tuffs; the tool assemblage includes cores (mostly unifacial), flakes and debris, which shows that all stages of flaking activity took place (Continued)

FIGURE 1 | at the site (Mgeladze et al., 2011). 17: Akhalkalaki, Georgia (1.0–0.9 Ma; Vekua, 1986), with thousands of remains of large mammals, including the giant hippo *H. antiquus* (not present in Dmanisi), and artifacts associated to the fauna, which could be not contemporaneous with it (Tappen et al., 2002). 18: Geshar Benot Ya'aqov, Israel (~0.78 Ma, MIS 19; Goren-Inbar et al., 2000), with an Acheulian assemblage composed of bifaces predominantly formed on basalt and core tools mostly made of flint. 19: 'Ubeidiya, Israel (~1.4 Ma; Martínez-Navarro et al., 2009, 2012), with rich core-choppers-flake assemblages and also a small but distinctive group of crude Early Acheulian bifaces, trihedrals, and quadrihedrals. 20: Thomas Quarry I-Unit L at Casablanca, Morocco (1.3–0.5 Ma; Gallotti et al., 2021), which preserves Acheulian assemblages made of quartzite and flint resulting from two production systems, one focused on the production of small to medium-sized flakes, the other devoted to the manufacture of large cutting tools. 21: Tighennif (formerly Ternifine), Argelia (~1.0 Ma; Sahnouni et al., 2018a), with Acheulian tools associated to remains of large mammals accumulated in a primary context. 22: Ain Boucherit (2.4–1.9; Sahnouni et al., 2018b) and Ain Hanech, Argelia (~1.7 Ma; Parés et al., 2014), which preserve Oldowan tools similar to those known at eastern African sites, as well as evidence of cutmarks and use-wear traces that indicate the exploitation by early *Homo* of animal tissues and marrow. 23: Oued Sarrat, Tunisia (~0.7 Ma; Martínez-Navarro et al., 2014b), which has yielded the oldest known cranium of *Bos primigenius*, associated with other small and large vertebrates, and six Acheulian tools. **(B)** Chronostratigraphic chart of Early Pleistocene to early Middle Pleistocene sites with evidence of hominin presence in Europe, North Africa, the Levantine Corridor, and the Caucasus. This chart shows the geochronological units, the land mammals' ages, the magnetostratigraphic units, and the biochronological units (French and Spanish biozones based on micromammals). Marine Isotope Stages (MIS) from Lisiecki and Raymo (2005). Biozones from Palombo (2010) and Minwer-Barakat et al. (2012).

area of alluvial and fluvial deposits as well as the glacia surface, is digitized with ImageJ for calculating the surface habitable by the terrestrial fauna. Based on this estimate, we deliver inferences on the size of the hominin population using the estimates of population density obtained for the hunter-gatherer groups of BL and FN3 (Rodríguez-Gómez et al., 2016a). This in turn leads us to discuss on the long-term viability of this hominin population and the discontinuity of the archeological record in the Guadix-Baza Depression.

RESULTS AND DISCUSSION

Hominin Subsistence Strategies in the Guadix-Baza Depression

The lithic assemblages from BL and FN3 are composed of abundant flakes of small size, cobbles (one third with percussion marks), cores, debris, and flake fragments. The flakes are largely made of flint and, to a lesser extent, of limestones and calcarenites from the surroundings of the sites. Flint was exploited for flake production whereas limestone, although used also for flake production, was mostly employed as percussion instruments (Barsky et al., 2010; Tilton et al., 2018). Recently, Tilton et al. (2021) indicated that BL is the oldest case reported of knapping and percussive activities on an ancient raw material reservoir deposit, because the analysis of the entire lithic collection of the site describes a tool kit composed of cores, flakes, debris, hammerstones, and other macro-tools like heavy-duty scrapers and sub-spheroidal morphologies. Moreover, the positioning of refitting items in the site points to *in situ* knapping (Toro-Moyano et al., 2013), which reaffirms the importance of BL as a raw material repository.

Many primates consume animal resources, but only humans regularly exploit animals the same size or larger than themselves (Butynski, 1982; Pobiner, 2020). Large ungulates represent concentrated packages of fat and protein, which are easily digestible and calorically rich macronutrients, and contribute micronutrients that are scarce in plants, such as heme-iron, folic acid and vitamin B12 (Thompson et al., 2019). Internal bone nutrients (e.g., brains and marrow) provide to humans the precursors to docosahexaenoic fatty acids and oleic acids, key for brain development and female reproductive success in hunter-gatherer societies (Plummer, 2004; Pobiner, 2020).

This explains why the consumption of large ungulates was a fundamental component of the high-quality diet that allowed the evolutionary transformations that led to the genus *Homo* (e.g., reduction of postcanine teeth, brain expansion, enhanced cooperation with non-kin, and shorter interbirth intervals). For this reason, the tool-use/meat-eating package has been considered as inherently linked to the definition of *Homo* (Jiménez-Arenas et al., 2014; Thompson et al., 2019; Pobiner, 2020; however, for a recent criticism of the narrative that links the anatomical and behavioral traits of *H. erectus* to an increase in meat eating, see Barr et al., 2022).

The technological features of the lithic tools from BL and FN3, including the small dimensions of the flakes, allow discussing on carcass acquisition and processing by these hominins. This relates to the classic debate on *Homo* as a hunter or as a scavenger. During the eighties and nineties, most researchers interpreted the cut marks found in the Early Pleistocene sites of East Africa as evidence of defleshing activities by the Oldowan hominins of ungulate carcasses obtained through passive scavenging, which implied a secondary access to these resources (Binford, 1981, 1985; Blumenschine, 1986, 1987, 1991, 1995; Blumenschine and Selvaggio, 1988; Blumenschine et al., 1994; Capaldo, 1997; Selvaggio, 1998; Arribas and Palmqvist, 1999). In contrast, from the nineties onward a new scenario was considered, which envisaged the Oldowan hominins as having primary access to fully fleshed carcasses obtained from hunting or through active, confrontational scavenging (Bunn and Ezzo, 1993; Domínguez-Rodrigo, 1999; Bunn, 2001; Domínguez-Rodrigo and Piqueras, 2003; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2007, 2014; Bunn and Pickering, 2010). The reasoning, based on actualistic studies of predation, was as follows: although the large felids do not consume bone marrow contents, which opened to early *Homo* the opportunity to scavenge these resources, they exploit intensively the prey carcass, which results in a low availability of flesh. The lions of Tarangire National Park (Tanzania) are a good example: they efficiently deflesh small and medium-sized ungulate carcasses and in alluvial environments near water, they even thoroughly deflesh carcasses of prey heavier than 500 kg such as buffalo (Gidna et al., 2014). However, a study on the potential scavenging opportunities in Sweetwaters Game Reserve (Kenya), a conservancy area where lions face a low level of inter-specific

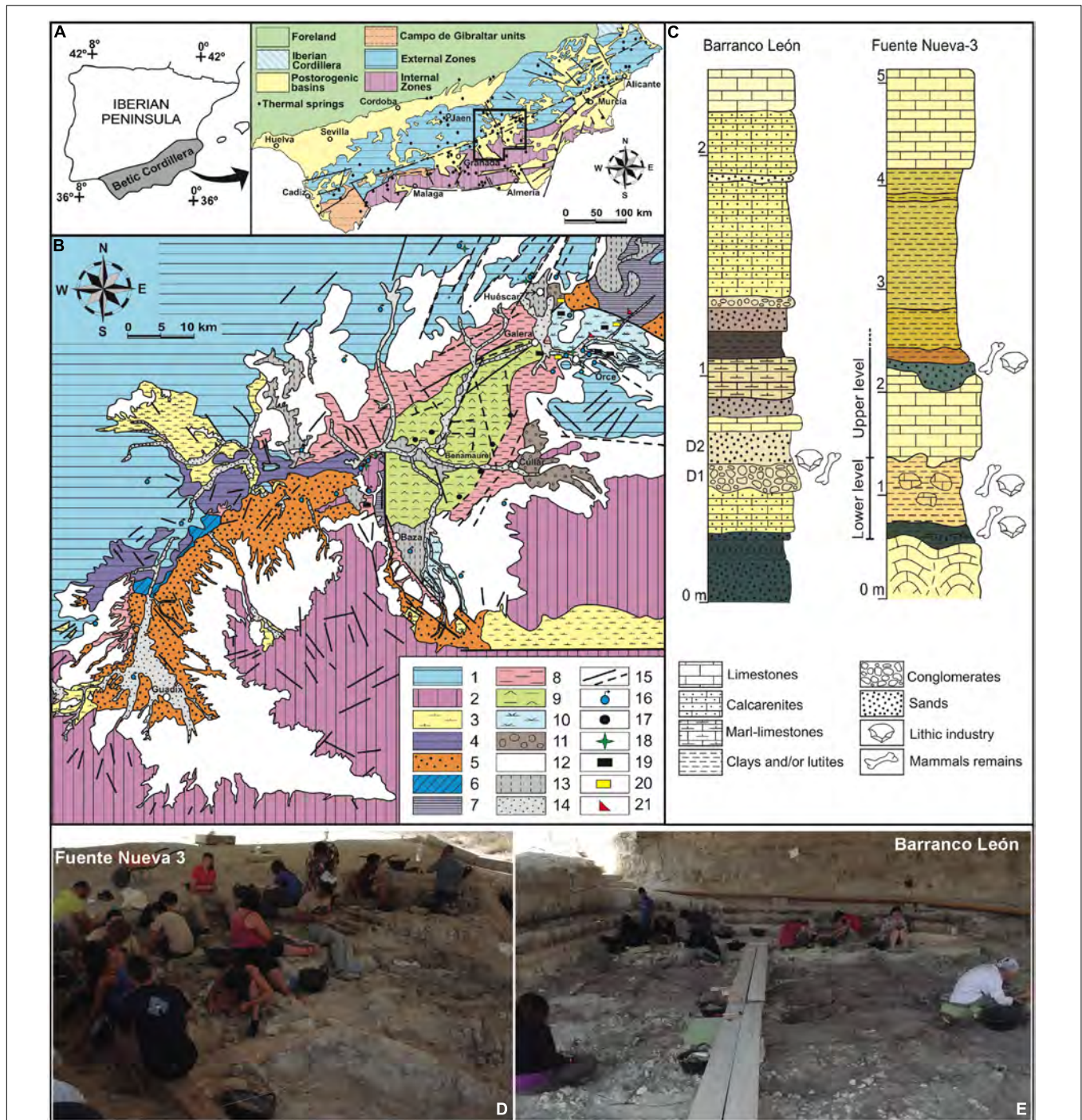


FIGURE 2 | (A) Geological context of the Guadix-Baza Depression in the Betic Cordillera, SE Spain. The box encloses the sedimentary basin. Black dots indicate the thermal springs ($N = 122$) that are nowadays active in the Betic Cordillera, with water output temperatures between 18 and 60°C. **(B)** Tectono-sedimentary map of the Guadix-Baza Depression with indication of those points that preserve geochemical, mineralogical or lithological evidence of thermal activity during the Neogene-Quaternary. Geological cartography updated from García-Aguilar et al. (2014, 2015: **Figure 1**, respectively). 1-External Zones, 2-Internal Zones, 3-Tortonian marine deposits, 4-Turolian alluvial and lacustrine deposits, 5-Plio-Pleistocene alluvial and fluvial deposits, 6-Pliocene lacustrine deposits of the Gorafe-Huélago sector, 7-Late Turolian-Ruscinian lacustrine deposits in the Baza Basin, 8-Middle Villafranchian fluvio-lacustrine deposits, 9-Middle Villafranchian lacustrine marls and evaporites, 10-Late Villafranchian lacustrine deposits, 11-Middle Pleistocene alluvial and lacustrine deposits, 12-Late Pleistocene glacia surface, 13-Holocene fluvial terrace, 14-Modern fluvial sediments, 15-Faults (solid lines; striped lines indicate those faults covered by sediments that have been inferred from aerial photographs), 16-Thermal springs nowadays active, 17-Sulfur deposits, 18-Travertine buildings, 19-Black levels, 20- Magnesium clays, and 21-Silexites. **(C)** Stratigraphic series of Barranco León (BL) and Fuente Nueva 3 (FN3) sites (adapted from Espigares et al. (2019)). **(D)** View of the excavation quarry of FN-3. **(E)** View of the excavation quarry of BL.

competition from hyenas, has shown that lions abandoned 95% of bones of large prey with at least some scavengeable flesh, and over 50% were left with large muscle masses. Moreover, while the scavengeable resources from fresh kills made by lions vary among prey carcasses, a single carcass of a large prey abandoned with only flesh scraps remaining (and all bone marrow contents intact) was usually substantial enough to satisfy the total daily caloric requirements of at least one adult male of *Homo erectus*, as extrapolated from an estimate for anatomically modern humans (Pobiner, 2015, 2020). This provides a solid argument for interpreting the Oldowan hominins as confrontational kleptoparasites or even as marginal, passive scavengers. However, human impact is high in Sweetwaters, and this could modify the behavior of lions, which deflesh their prey more thoroughly in those ecosystems where no modern humans threaten them (Gidna et al., 2014). In any case, Blumenschine and Pobiner (2007) estimated that the marrow that a hominin could extract from twelve long bones of an adult wildebeest carcass would represent 3,000 kcal, a value close to the daily energetic requirements of an adult early *Homo* (Aiello and Wells, 2002). In addition, Bickerton and Szathmáry (2011) suggested that the populations of *H. erectus* would have access to at least one elephant carcass resulting from natural death every month per 1000 km² foraged.

Sabertooths and Scavenging Opportunities for the Hominins

The hunting vs. scavenging debate was largely focused on the sequence of carcass access initially proposed for the bone assemblage from the FLK *Zinjanthropus* site at Olduvai, based on the frequency of tooth-marked and percussion-marked long bones of large mammals (Blumenschine, 1995; Capaldo, 1997; Selvaggio, 1998). The model considered a three-stage sequence of site formation: (i) in stage one, flesh-eating felids partially defleshed long bones, as deduced from the high frequency of tooth-marks on midshaft fragments; (ii) in stage two, hominins processed intact long bones for their marrow contents and left percussion marks, with the presence of cut marks indicating that the bones retained at this stage variable amounts of flesh; finally, (iii) in stage three, bone-cracking hyenas consumed long bone epiphyses for grease, as evidenced by the underrepresentation of these elements in the assemblage and the high percentage of tooth marks on the surviving epiphyses and the distal portions of the diaphyses (see discussion in Arribas and Palmqvist, 1999).

Domínguez-Rodrigo and Barba (2006) suggested that Blumenschine (1995) overestimated the number of long-bone midshafts with tooth marks in the FLK 22 assemblage due to the confusion of these marks with those resulting from microbial bioerosion, which would indicate primary access by the hominins to fully fleshed carcasses (but see criticism of their experimental procedure by Blumenschine et al. (2007)). The most recent analysis of the FLK 22 assemblage, using GIS techniques (Parkinson, 2018), has suggested that hominins had early access to largely fleshed carcasses, particularly those of smaller prey—which they may have primarily acquired through hunting—although patterns of bone damage on

TABLE 1 | Faunal lists (large mammals only) from Venta Micena, Barranco León, and Fuente Nueva-3 (after Alberdi and Ruiz-Bustos, 1985; Moyà-Solà, 1987; Pons-Moyà, 1987; Martínez-Navarro, 1991; Torres Pérez-Hidalgo, 1992; Martínez-Navarro and Palmqvist, 1995; Martínez-Navarro et al., 1997, 2010, 2011, 2021; Cregut-Bonnoire, 1999; Martínez-Navarro and Rook, 2003; Abbazzi, 2010; Alberdi, 2010; Lacombat, 2010; Madurell-Malapeira et al., 2010, 2011; Medin et al., 2017; Bartolini-Lucenti and Madurell-Malapeira, 2020; Ros-Montoya et al., 2021; and references therein).

VENTA MICENA	BARRANCO LEÓN	FUENTE NUEVA-3
	<i>Homo</i> sp.	<i>Homo</i> sp. (only lithics)
<i>Ursus etruscus</i>	<i>Ursus etruscus</i>	<i>Ursus etruscus</i>
<i>Lycaon lycaonoides</i>	<i>Lycaon lycaonoides</i>	<i>Lycaon lycaonoides</i>
<i>Canis orcensis</i>	<i>Canis mosbachensis</i>	<i>Canis mosbachensis</i>
<i>Vulpes alopecoides</i>	<i>Vulpes alopecoides</i>	<i>Vulpes alopecoides</i>
<i>Pachycrocuta brevirostris</i>	<i>Pachycrocuta brevirostris</i>	<i>Pachycrocuta brevirostris</i>
<i>Megantereon whitei</i>	<i>Machairodontinae</i> indet.	<i>Megantereon whitei</i>
<i>Homotherium latidens</i>		Cf. <i>Homotherium</i> sp.
<i>Panthera gombaszoegensis</i>		
<i>Lynx cf. pardinus</i>		<i>Lynx cf. pardinus</i>
<i>Meles meles</i>	<i>Meles meles</i>	<i>Meles meles</i>
	<i>Martellictis ardea</i>	<i>Martellictis ardea</i>
<i>Mammuthus meridionalis</i>	<i>Mammuthus meridionalis</i>	<i>Mammuthus meridionalis</i>
<i>Stephanorhinus</i> cf. <i>hundsheimensis</i>	<i>Stephanorhinus hundsheimensis</i>	<i>Stephanorhinus hundsheimensis</i>
<i>Equus altidens</i>	<i>Equus altidens</i>	<i>Equus altidens</i>
	<i>Equus sussenbornensis</i>	<i>Equus sussenbornensis</i>
<i>Hippopotamus antiquus</i>	<i>Hippopotamus antiquus</i>	<i>Hippopotamus antiquus</i>
<i>Bison</i> sp.	<i>Bison</i> sp.	<i>Bison</i> sp.
<i>Hemibos</i> sp. cf. <i>H. gracilis</i>		
<i>Praeovibos</i> sp.		
<i>Soergelia minor</i>	<i>Ammotragus europaeus</i>	<i>Ammotragus europaeus</i>
<i>Hemitragus albus</i>	<i>Hemitragus albus</i>	<i>Hemitragus albus</i>
Caprini gen. et sp. indet.		
<i>Praemegaceros</i> cf. <i>verticornis</i>	<i>Praemegaceros</i> cf. <i>verticornis</i>	<i>Praemegaceros</i> cf. <i>verticornis</i>
<i>Metacervocerus rhenanus</i>	<i>Metacervocerus rhenanus</i>	<i>Metacervocerus rhenanus</i>
<i>Capreolus</i> sp.		

larger carcasses are consistent with secondary access through aggressive scavenging (Pobiner, 2020). In any case, we must bear in mind that the interpretive context that envisions the Oldowan hominins as primary hunters is based on experimental studies performed on modern felids, which thoroughly exploit the carcasses of their prey. This context does not apply to the Early Pleistocene hominin populations with Oldowan tools of Africa and Europe, where the predator guild was dominated by two sabertooths, *Megantereon whitei* and *Homotherium latidens* (Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1999; Palmqvist et al., 2022a).

Sabertooths have no living analogs and dominated the carnivore guild during most of the Cenozoic, filling the niche now occupied by the pantherine felids (Van Valkenburgh, 2001, 2007). Their long and laterally flattened upper canines were an adaptation for killing quickly megafaunal prey with deep wounds onto the prey throat rather than using the prolonged

suffocating throat bite typical of the extant felines (Gonyea, 1976; Akersten, 1985; Anyonge, 1996a; Antón et al., 2004; McHenry et al., 2007; Christiansen, 2008; Meachen-Samuels and Van Valkenburgh, 2010; Salesa et al., 2010; Andersson et al., 2011; Meachen-Samuels, 2012). However, canine hypertrophy posed a biomechanical constraint on mandibular gape for delivering the killing bite, which involved a major reorganization of the skull to avoid over-stretching of the temporalis muscle during wide gaping (Figure 3) and led to a reduction of the premolar teeth. This is particularly evident in the African sabertooth *M. whitei*, which dispersed out of Africa by ~1.8 Ma (Martínez-Navarro and Palmqvist, 1995, 1996; Palmqvist, 2002): compared to the less specialized *M. cultridens*, the species replaced in Europe by *M. whitei* during the late Early Pleistocene, the third lower premolar is reduced in *M. whitei* to a vestigial peg or even lost, while the fourth premolar and the paraconid of the carnassial are shortened but to a lesser degree, which reflects the greater enlargement of the sabers in the African species (Palmqvist et al., 2007). This resulted in lesser abilities to process the prey carcass and made it available more scavengeable resources for the hyenas and the hominins, which provides the ecological connection between the dispersal of *M. whitei* out of Africa and the first arrival of *Homo* in Europe, a continent where the survival of hominins during the cold season—with lowered plant resources compared to East Africa—depended on the regular scavenging of ungulate carcasses (Turner, 1992; Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1999; Martínez-Navarro, 2004, 2010; Palmqvist et al., 2007, 2022a).

Microwear analyses of canines and carnassials provides additional evidence on the lower ability of sabertooths to process the prey carcass. A comparison of the frequency of pits and scratches in the canines of the North American *Smilodon fatalis* and other living carnivores with disparate feeding and hunting repertoires (e.g., spotted hyenas, lions, cheetahs, and wild dogs) showed that these teeth were used by *S. fatalis* for prey killing and avoided contact with bone during prey consumption (Anyonge, 1996b). In the case of the wear facet of the carnassials, which are employed exclusively in food processing, the bone-cracking pits hyenas exhibit few long scratches and a high proportion of pits to scratches, while the cheetah (which feeds exclusively on soft organs and only consumes bones of small prey; Schaller, 1968; Brain, 1981; Skinner and Smithers, 1990) shows a predominance of narrow scratches with very few pits. Strikingly, the microwear pattern of *S. fatalis* showed relatively narrow and long scratches combined with an extremely low frequency of pits, even lower than in the cheetah (Van Valkenburgh et al., 1990). This suggests that sabertooths probably consumed even less bone than the cheetah to prevent canine breakage, which means that their prey carcasses would retain a significant fraction of scavengeable resources (Van Valkenburgh et al., 1990).

The elongated, laterally flattened canines of sabertooths were optimal for killing large prey, but also were more vulnerable to fracture than the shorter and conical canines of the living felids due to the unpredictable loads generated in prey stabilization during the killing bite (Van Valkenburgh and Hertel, 1993; Van Valkenburgh, 2009). This made the heavily muscled forelimbs of sabertooths imperative for pulling down and immobilizing prey

before positioning the killing bite (Gonyea, 1976; Akersten, 1985; Anyonge, 1996a; Antón et al., 2004; Christiansen, 2008; Salesa et al., 2010; Andersson et al., 2011; Meachen-Samuels, 2012). The latter is reflected in the short and robust forelimb bones of *S. fatalis*, reinforced by cortical thickening, which allowed it to minimize prey struggling, helping to position the killing bite carefully to avoid contact with bone (Meachen-Samuels and Van Valkenburgh, 2010; Martín-Serra et al., 2017). A comparative study of the skulls of *S. fatalis* and the lion based on finite element analysis showed that the sabertooth skull was less equipped to resist the forces generated by a struggling prey, which pointed to rapid slashing bites during prey killing (McHenry et al., 2007). In contrast, the lion uses its stouter canines to hold a suffocating bite in the snout of large prey such as buffalo, which explains that the forelimbs are less important for subduing prey (Salesa et al., 2010; Meachen-Samuels, 2012; Martín-Serra et al., 2017). Moreover, Figueirido et al. (2018) showed that the rostrum of *S. fatalis* was almost entirely composed of cortical bone (which supports better directed loads) while the lion skull had a substantial amount of trabecular bone (which can support unpredicted and multidirectional forces). This indicated that the skull of *S. fatalis* was well-equipped to deliver a quick killing-shear bite, but it could not withstand the unpredictable forces generated when feeding on bones (Figueirido et al., 2018).

The highly derived craniodental and postcranial anatomy of sabertooths suggests that the pantherine felids cannot be considered as their modern functional analogs, because sabertooths: (i) were able to hunt larger ungulate prey relative to their body size, exerting a higher predation pressure on the juveniles of megafauna; and (ii) exploited their prey to a lesser extent, which would have resulted in greater amounts of flesh abandoned in the prey carcass (Binford, 1980, 1981; Marean and Ehrhardt, 1995; Arribas and Palmqvist, 1999; Palmqvist et al., 2003, 2007, 2011, 2022a,b; Ripple and Van Valkenburgh, 2010; Martínez-Navarro et al., 2014a; Van Valkenburgh et al., 2016; Martín-Serra et al., 2017; Martínez-Navarro, 2018). These resources would in turn be available for the scavengers, including the hominins and hyenas, as documented at FN3 (Espigares et al., 2013, 2019; Yravedra et al., 2021). This interpretation makes sense if we consider the lack of an effective weaponry in the Oldowan hominins for subduing large prey with their small flint flakes and cores, or for driving predators from their kills acting as kleptoparasites (Potts, 1991; Blumenshine and Pobiner, 2007; Treves and Palmqvist, 2007). However, throwing stones for driving away carnivores and stealing their prey would be always a possibility, as suggested by Lordkipanidze (2015) for explaining the abundant allochthonous cobbles found in Dmanisi (Coil et al., 2020). Interestingly, manuports of dolomitic limestone are abundantly represented in FN3 (Espigares et al., 2013).

While it has been argued that expanding group sizes prompted Acheulean hominins to become big game hunters (Martínez-Navarro, 2018), perhaps including elephants as their prey (Agam and Barkai, 2018), it is difficult to conceive that the limited technological skills of the Oldowan hominins allowed them to prey on megafauna. Therefore, it is thus more reasonable to consider that Early *Homo* initially expanded its diet from the major reliance on plant foods of australopithecines to scavenging

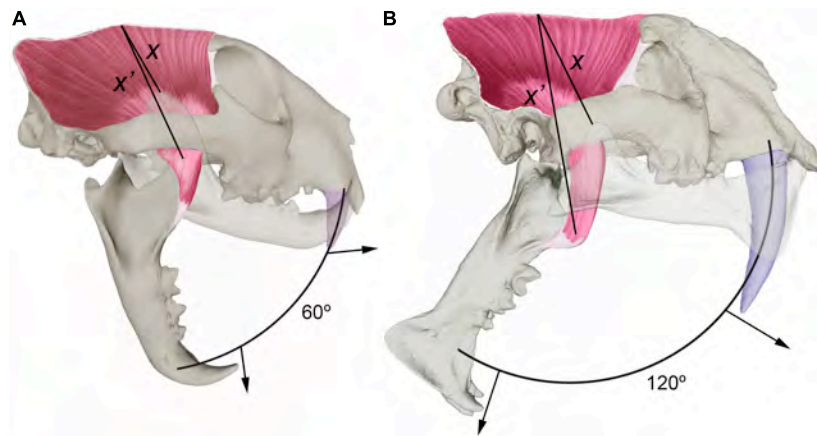


FIGURE 3 | Comparison of the craniodental anatomy of a leopard, *Panthera pardus* (A), with a sabertooth, *Megantereon nihowanensis* (B). The lines X and X' measure the stretching of temporalis muscle from the tip of the coronoid process to the sagittal crest with the jaw closed and open, respectively. The elongation of the upper canines of sabertooths posed a severe biomechanical constraint on mandibular gape for delivering the killing bite, which involved a major reorganization of the temporalis to avoid over-stretching of the muscle fibers during wide gaping. This was achieved by a number of changes in their craniodental anatomy compared to the pantherine felids (Emerson and Radinsky, 1980; Akersten, 1985; Palmqvist et al., 2007; Slater and Van Valkenburgh, 2008; Figueirido et al., 2011; DeSantis et al., 2021): (i) a lowered glenoid fossa; (ii) a shortened coronoid process and a laterally shifted angular process; (iii) a less laterally projected postglenoid process; (iv) an upwardly rotated palate; (v) a shorter and narrower temporal fossa; (vi) a more vertical occiput; and (vii) a protruding incisor arcade, which independized the hypertrophied upper canines from the incisors. Such skull reorganization resulted in a narrowing of the temporalis fibers and their more perpendicular orientation to the tooth row, which allowed to increase jaw gape up to 180° in sabertooths while retaining a degree of muscle stretch like that of pantherine felids. Moreover, the masseter muscle, which exerts its maximum force at smaller gapes, was also reduced. Panel (A) shows that with a jaw gape of 60°, the degree of muscle stretching of the temporalis (measured by the ratio between X' and X) in the leopard (~85%) is like in *Megantereon* (B) with a gape of 120° (~80%). A result of this major skull reorganization in sabertooths was that the point of maximum bite force exerted at the carnassial was positioned more backwardly, which led to a reduction of the post-canine dentition not related to the slicing function of the carnassial. The protruding incisor arcade of sabertooths (B) helped these predators to avoid canine breakage when feeding on the prey carcass because it independized the function of the incisors, used to tear chunks of flesh from the prey carcass (a task performed in modern felids by their stout, conically shaped canines), from the function of the canines, employed to deliver deep wounds during prey dispatch (Biknevicius et al., 1996). Thus, prevention of canine breakage during prey killing and feeding encounters was a strong selective agent in sabertooths and suggests that a non-scavenging behavior was a clear ecological limitation posed by their hypertrophied upper canines.

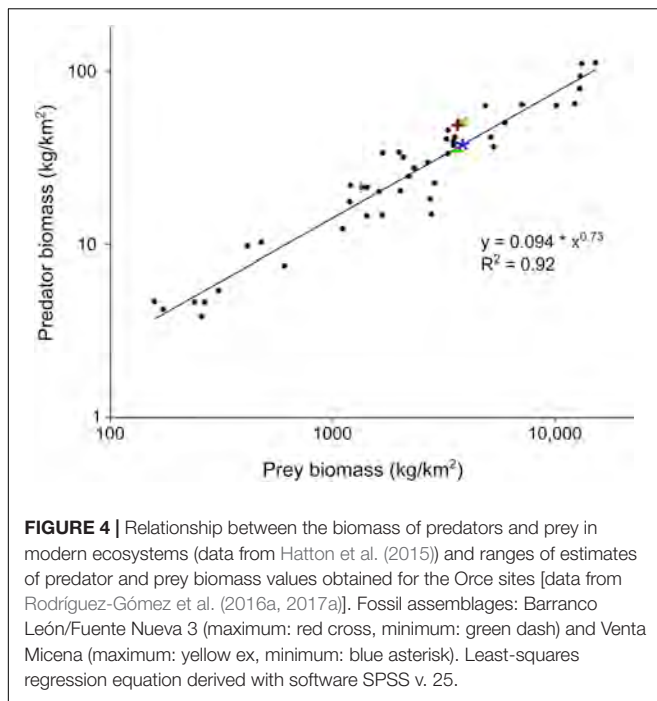
bone marrow, brains and meat (Ben-Dor et al., 2021). Therefore, the trophic level of *Homo* probably evolved from a low base to a high carnivorous position during the Pleistocene, beginning with *H. habilis* as a scavenger and peaking in *H. erectus* as a hunter (Ben-Dor et al., 2021; but see Barr et al. (2022)).

Megaherbivores like adult elephants, hippos and rhinos are often regarded as invulnerable to predation, but it has been suggested that lions regularly hunted such large prey during the Pleistocene (Guthrie, 1990). Lion prides have been documented today hunting elephants, mostly juveniles, in high frequencies in those environments where other ungulates are scarce, like the Savuti area of Chobe National Park, Botswana (Joubert, 2006; Power and Shem-Compion, 2009). However, lions preferentially prey on medium-to-large ungulates when they are abundant (Schaller, 1972), within a weight range of 190–550 kg (Hayward and Kerley, 2005), and only occasionally hunt megafauna (Palmqvist et al., 1996). In fact, elephants are rarely preyed upon by lions (Skinner and Smithers, 1990) and when this does occur it involves yearling calves weakened by drought (Loveridge et al., 2006) or older animals wounded by poaching (Ruggiero, 1991).

Passive scavenging of ungulate carcasses partially defleshed by sabertooths would have enhanced the survival of the hominins of Guadix-Baza during Early Pleistocene times (Martínez-Navarro and Palmqvist, 1996; Arribas and Palmqvist, 1999; Martínez-Navarro, 2004, 2010; Palmqvist et al., 2005,

2007; Espigares et al., 2013, 2019; Martínez-Navarro et al., 2014a; Rodríguez-Gómez et al., 2016a, 2017a). We propose here that they probably exploited a wide repertoire of subsistence strategies, including: (i) the opportunistic hunting of small-sized mammals and other vertebrates (e.g., amphibians and reptiles); (ii) the kleptoparasitism of the prey of primary predators like sabertooths and wild dogs; and (iii) the opportunistic scavenging of carcasses of very large animals not exposed in life to predation that died from other causes, although this is a rather speculative issue. The latter possibility is supported by evidence of competition between *Homo* sp. and *P. brevirostris* for the exploitation of a carcass of an old individual of elephant *Mammuthus meridionalis* in the upper archeological level of FN3: the skeleton of this elephant is dismembered and surrounded in part by flint flakes and coprolites, which suggests a sequential pattern of consumption by the hominins and hyenas (Espigares et al., 2013).

A mathematical model that evaluates the sustainability of the community of secondary consumers, based on the biomass of primary consumers potentially available (Rodríguez-Gómez et al., 2013, 2014a,b, 2016b, 2020), has provided relevant data on the hominin population that inhabited Guadix-Baza (Rodríguez-Gómez et al., 2016a). The model estimates: (i) the age structure and mortality rate that make the population of each primary consumer stable; (ii) the distribution of individuals



among size categories; (iii) the biomass that the secondary consumers can extract from these populations in the long term; and (iv) resource distribution among the members of the carnivore guild. In the case of hominins, the model considered a dietary contribution of 30% of animal resources, in agreement with the diet of modern hunter-gatherer populations at temperate latitudes (Rodríguez-Gómez et al., 2016a). The hunting and scavenging scenarios were both modeled for estimating the population density of *Homo* sp. in Guadix-Baza. This suggested a scavenging behavior as optimal for the population, which would hold 12 individuals per 100 km² during a year, a value close to the mean density of modern hunter-gatherers (Binford, 2001; Marlowe, 2005). The density estimated for a strict hunting behavior was slightly lower, 9.5 individuals/100 km² (Rodríguez-Gómez et al., 2016a). Given that both estimates are similar, to consider a scavenging or a hunting behavior has little effect on the size of the hominin population of the basin, as noted above. The densities estimated for the hominins and carnivores in the Orce sites (Figure 4) agree with the prey/predator biomass ratios derived with the equation of Hatton et al. (2015).

“Meat made us humans” is a recurrent topic in any debate on the subsistence strategies of hominins (Bunn, 1981, 2007; Stanford, 1999; Bunn et al., 2017). This relates to the evolutionary trend toward increasing encephalization in the genus *Homo*, because the high maintenance cost of the nervous system involved a reduction of the digestive tract and a shift toward a more carnivore diet compared to the australopithecines (Leonard and Robertson, 1994, 1996; Aiello and Wheeler, 1995; Jiménez-Arenas et al., 2014). However, the subsistence strategies of early *Homo* probably included a broader spectrum of resources (e.g., small mammals, birds, herpetofauna, invertebrates, eggs, honey, and edible vegetation) that do not leave archeological evidence

(Blasco et al., 2011; Hardy et al., 2017; Prado-Nóvoa et al., 2017; Espigares et al., 2019), as happens in the case of modern hunter-gatherers like the !Kung of the Kalahari Desert and the Hadza of northern Tanzania (Woodburn, 1968; Ho et al., 1972; Lee, 1979; Silberbauer, 1981; O’Connell et al., 1988; Hawkes et al., 1991; Cordain et al., 2000; Binford, 2001; Bunn, 2001; Marlowe, 2005). Lee (1968), Cordain et al. (2000), and Marlowe (2005) have shown a negative correlation between gathering and latitude due to the decrease with latitude in the availability of edible plants. In contrast, gathering is the dominant mode of subsistence in latitudes like those of the Orce sites. In the Baza Basin, freshwater fish could have also been a regular source of long-chain polyunsaturated fatty acids (e.g., omega n-3, n-6 and docosahexaenoic acids) that are essential for the early development of the brain, retina and other neural tissues (Uauy et al., 2001; Kuipers et al., 2010).

There is a lack of knowledge on the vegetal resources available at the Orce sites, as all attempts to extract fossil palynomorphs from the sediment were unsuccessful and even the coprolites of hyena analyzed were palynologically sterile (Carrión, 2002; Carrión et al., 2009). Despite this, inferences on the past vegetation of the basin have been derived from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes in the bone collagen of the herbivores of VM (Palmqvist et al., 2003, 2008a,b), which allowed to infer their feeding habits. Specifically, the species (Table 1) were classified among: (i) browsers (rhino *Stephanorhinus hundsheimensis* and deer *Praemegaceros verticornis*); (ii) mix-feeders (ovibovine *Soergelia minor* and deer *Metacervoceros rhenanus*); and (iii) grazers (horse *Equus altidens*, *Bison* sp., muskox *Praeovibos* sp., goat *Hemitragus albus*, and *M. meridionalis*). The predominance of taxa adapted to grazing in open habitat agrees with: (i) the synecological reconstruction of this paleocommunity as a plain with bush/forest patches (Mendoza et al., 2005; Saarinen et al., 2021); and (ii) the estimate of ~780 mm of annual rainfall derived from the range of $\delta^{15}\text{N}$ values in the ungulates that fed on terrestrial vegetation (García-Aguilar et al., 2014), which is close to the estimate of ~750 mm obtained from the herpetofauna of BL and FN3 (Blain et al., 2016). According to Blain et al. (2021), the first hominin occupations in Western Europe (e.g., BL/FN3 and TE9) would correspond to warm and humid conditions in an open ‘savanna’ environment with 20–25% wood. A study of the herpetofaunal assemblages of BL and FN3 has indicated different conditions for the levels with the highest density of anthropic evidence at these sites: a humid, wooded biotope for BL and a more open and drier biotope for FN3 (Sánchez-Bandera et al., 2020).

Most ungulate species present at VM are also represented in the faunal assemblages of BL and FN3 (Table 1). The exceptions are the mesodont *S. minor*, which is replaced by the hypsodont caprine *Ammotragus europaeus*, and the presence of a second equid species, the large-sized horse *Equus sussenbornensis* (Moullé et al., 2004; Alberdi, 2010; Martínez-Navarro et al., 2010). Hindgut fermenters process a large volume of food in a short time and can feed on low quality grasses too fibrous for a ruminant to subsist on (Janis, 1976; Janis et al., 1984; Duncan et al., 1990). For this reason, the presence of two hypergrazing equids in BL and FN3 suggests more arid conditions and an herbage of lower

quality than in VM (Palmqvist et al., 2008a). This would result in a decrease in the abundance of fruits and other succulent plant stuffs for the hominins, which would make them more dependent on animal resources.

Hominin and Carnivore Involvement in Barranco León and Fuente Nueva 3

Espigares et al. (2019) reported on the cut marks and percussion marks identified in BL and FN3 (see also Yravedra et al. (2021) for FN3). Tooth marks produced by carnivores, particularly the hyena *P. brevirostris*, were also found in the bone assemblages of both sites, but at lower frequencies than in the hyena den of VM (Palmqvist et al., 1996, 2005, 2011, 2022b; Luzón et al., 2021). To evaluate the contribution of hominins and carnivores to the site formation process in BL and FN3, we have performed here a study on the abundance of limb bone epiphyses and compared the results with those for VM.

Figure 5 shows the relationship between the abundance of epiphyses of major limb bones and their estimated marrow yields in the three Orce sites. The regressions for BL and FN3 show an inverse, statistically significant relationship between bone survival and marrow contents ($r = 0.624$, $p = 0.05$ for BL; $r = 0.682$, $p = 0.03$ for FN3), which indicates that the hominins preferentially fractured the anatomical portions with greater nutritional value. However, these regression lines show considerable scatter, as reflected in their wide confidence 95% intervals. There is also a negative relationship in VM, but much closer in statistical terms ($r = 0.885$, $p = 0.001$), which shows a greater selectivity in bone fracturing by the hyenas. **Figure 6** shows the positive relationship between bone survival and mineral density in the three sites. Again, BL and FN3 show lower levels of statistical significance ($r = 0.636$, $p = 0.003$ for BL; $r = 0.548$, $p = 0.015$ for FN3) and more scatter around the regression lines than VM ($r = 0.745$, $p < 0.0001$ for VM).

Marrow determines the interest of the bone collecting and modifying agent on the nutritional contents of the skeletal remains, while mineral density is behind the effort invested in accessing these resources. The hominins fractured the bones in BL and FN3 using stones, a task relatively straightforward that did not represent a major effort, which originated percussion marks (Espigares et al., 2019; Yravedra et al., 2021). Therefore, it is not expected that they were highly selective in their choice of the bones to be fractured, apart from focusing more on the remains that provided more marrow. However, hyenas fractured the bones in VM using their robust premolar teeth assisted by their massive jaws (Palmqvist et al., 2011), which resulted in abundant spiral and longitudinal fractures (Arribas and Palmqvist, 1998). Hyenas were at risk of breaking their teeth or dislocating their jaws while fracturing the densest bones, which forced them to be more selective than the hominins (who risked nothing when fracturing bones with stones). Thus, our results suggest that although BL and FN3 record evidence of hominin and carnivore activity, the main agent involved in the accumulation and modification of the remains preserved at both sites were the hominins.

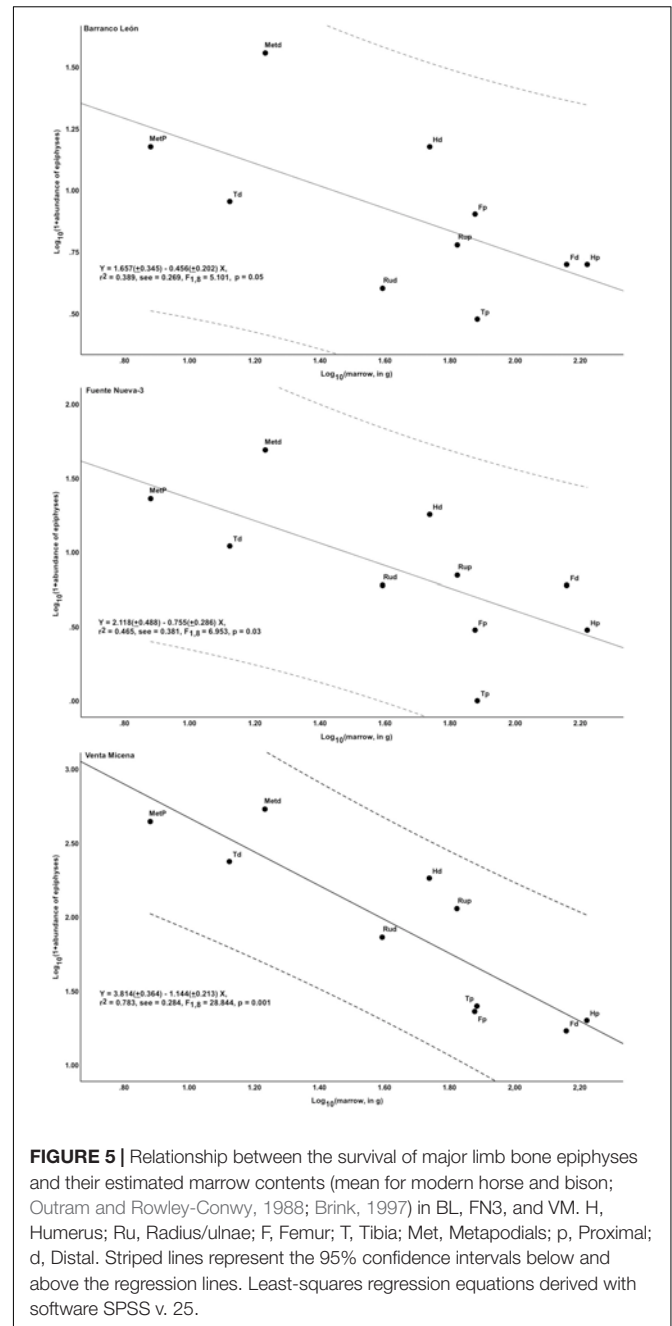
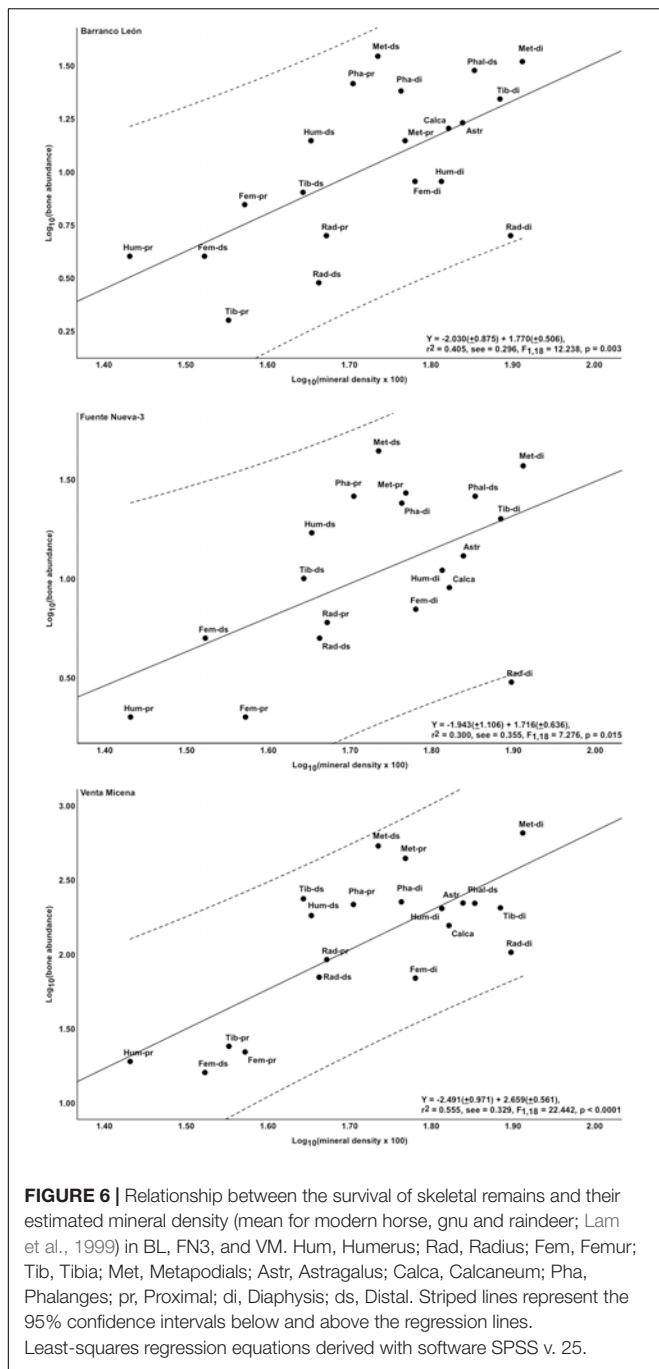


FIGURE 5 | Relationship between the survival of major limb bone epiphyses and their estimated marrow contents (mean for modern horse and bison; Outram and Rowley-Conwy, 1988; Brink, 1997) in BL, FN3, and VM. H, Humerus; Ru, Radius/ulnae; F, Femur; T, Tibia; Met, Metapodials; p, Proximal; d, Distal. Striped lines represent the 95% confidence intervals below and above the regression lines. Least-squares regression equations derived with software SPSS v. 25.

The hyena *P. brevirostris*, the jackal-sized *Canis mosbachensis* and a large-sized crow (unpublished specimen VM-3121, preliminarily classified as *Corvus* sp.; by the moment, this species has not been identified in BL and FN3) were indeed worthy competitors of the hominins for carrion in BL and FN3. Soaring at high altitude is an energetically efficient mode of locomotion, which allows vultures to cover huge distances and discover carcasses by sight or watching the movements of other neighboring birds such as crows (Palmqvist and Vizcaino, 2003). Hyenas and jackals often rely upon visual clues such as circling vultures to identify scavengeable resources, and then run long



distances to secure the carcass (Bramble and Lieberman, 2004). However, they do not perform well running at long distances, as they need to rest after relatively short distances to breathe and cool down. In contrast, humans are comparatively poor sprinters but are well adapted for endurance running (i.e., running many kilometers at relatively low speed over extended time periods using aerobic metabolism) (Bramble and Lieberman, 2004; Lieberman et al., 2007; Pickering and Bunn, 2007; Liebenberg, 2008; Ruxton and Wilkinson, 2012). This results in an advantage for scavenging in open habitats during the

day, particularly during the dry season, when other terrestrial scavengers are prevented from running long distances due to thermoregulatory constraints (Lieberman et al., 2007). Endurance running may have allowed early *Homo* to reach carcasses before other terrestrial scavengers and to exploit them until surrendering them on the arrival of potentially dangerous hyenas. However, the advantages of endurance running are not unanimously accepted. Pickering and Bunn (2007) argued that endurance running: (i) would have required for hunting that in the absence of visual contact, hominins had the ability to track prey; (ii) is not common among modern foragers except for very open and hot habitats, because it is a physically demanding activity; and (iii) scavenging in modern riparian woodland habitats would result in a low competition intensity for carcasses. These arguments are based on two flawed assumptions, the presumptive link between modern human-like cognition and tracking abilities, as well as the notion that the limited (and biased) modern ethnographic record provides an adequate reflection of past behaviors (Lieberman et al., 2007).

Hominins entered the carnivore guild when they became scavengers (and later hunters), which forced them to compete with other carnivores using a combination of strength, speed, stealth, and cooperation. Modern foragers are no exception in this, as a high percentage of scavenging opportunities observed among Hadza and other hunter-gatherers involve power scavenging for driving off lions or hyenas from their kills using simple weapons like sticks and stones (Potts, 1991; Blumenschine and Pobiner, 2007; Lieberman et al., 2007). Given that early *Homo* was neither strong nor powerful, and apparently lacked projectile weapons, it is debatable whether they could engage in competition scavenging with dangerous carnivores (Potts, 1991; Lieberman et al., 2007). Therefore, persistence hunting and scavenging may have been more common before the invention of the bow-and-arrow or the domestication of dogs and horses (Liebenberg, 2008).

Domínguez-Rodrigo and Organista (2007) proposed the use of the following ratios for evaluating the degree of ravaging intensity in an assemblage: (i) axial bones to appendicular ones, which would range from 4.25 for a carcass transported complete or died in a setting devoid of competition among carnivores, to 0 for a completely ravaged skeleton; (ii) femur to tibia, which would range from 1 in a ravaging-free assemblage to 0 in one with maximum ravaging intensity; and (iii) proximal humerus plus distal radius to distal humerus plus proximal radius, which relates to the relative abundance of the least dense bone portions (preferentially consumed by the carnivores) to the densest ones, and takes a value between 1 in an undisturbed carcass and 0 in the situation of highest ravaging. The second ratio is only relevant if carnivores had primary access to complete bones and not to bones already broken by hominins (Domínguez-Rodrigo and Organista, 2007). In the latter case, when taphonomic evidence indicates that the hominins broke long limb bones (as in BL and FN3) and only bone portions instead of whole bones were available for ravaging, they recommend the third ratio as the most informative.

Girdle and limb bones are between three and five times more abundant at the hyena den of VM than vertebrae and ribs,

depending on the excavation quarry analyzed (García-Aguilar et al., 2015; Luzón et al., 2021; Palmqvist et al., 2022b). Ribs are scarcely represented at VM by small fragments and are even less abundant in BL and FN3 (Espigares, 2010). The ratio of ribs, vertebrae and girdle bones to limb bones is 17.9% (52/290) in BL and 11.8% (35/296) in FN3, figures that compare well with VM, 13.5% (532/3,942). In VM, the overrepresentation of the elements of the appendicular skeleton over those of the axial skeleton indicates the dismemberment by hyenas of the ungulate carcasses scavenged and the preferential transport of the limbs to their denning sites (Palmqvist and Arribas, 2001). Our data suggest that the assemblages of BL and FN3 were also biased by the selective transport of remains by the hominins, who were focused to marrow extraction of the remains in a safe place (Espigares et al., 2013). The third ratio shows similar values in the three sites: 0.37 (7/19) in BL, 0.30 (7/23) in FN3 and 0.32 (89/274) in VM. In contrast, there are differences in the values of the ratio of femur to tibia: 0.63 (20/32) in BL, 0.47 (14/30) in FN3 and 0.23 (107/465) in VM. This suggests that the hominins broke the major limb bones in BL and FN3 for exploiting their marrow contents and this led to the loss of the resource that would make them more attractive to the hyenas, thus explaining their better preservation in BL and FN3 than in VM.

Early Pleistocene Environments of the Guadix-Baza Depression

In the Early Pleistocene, the environments of the Baza Basin were dominated by shallow lacustrine systems fed by the precipitation of meteoric waters on the lake surface as well as by the contribution of alluvial waters and thermal springs (García-Aguilar and Palmqvist, 2011; García-Aguilar et al., 2014, 2015). This led to deposits of marls, calcilutites, limestones, evaporites, sands, and dark lutites (Figure 2B). The lacustrine systems were dynamic in both time and space, as evidenced by the lateral wedging of the facies linked to these environments, which resulted in the appearance of non-flooded areas inhabited by the mammalian community and the hominins.

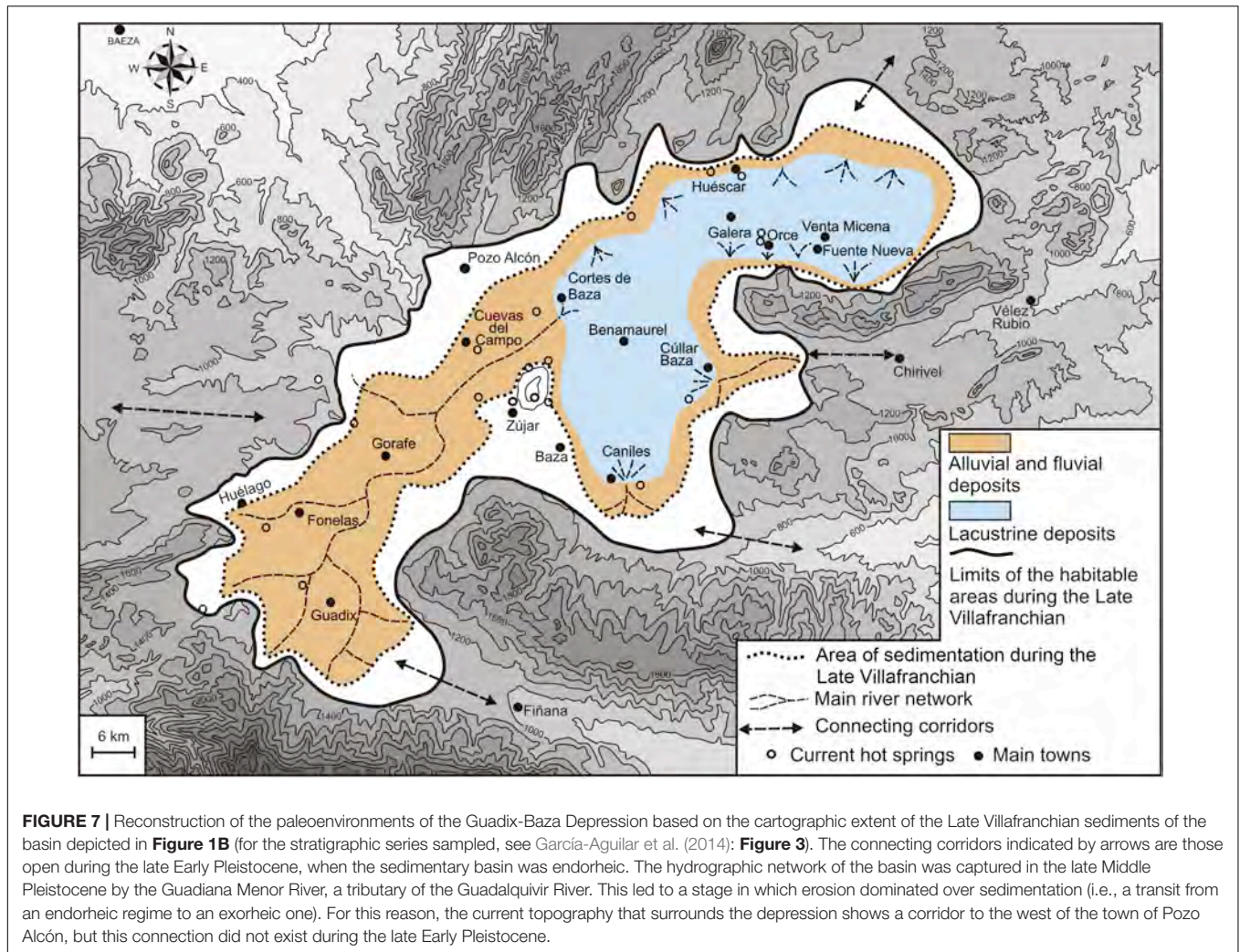
The cartography of the Late Villafranchian deposits that correspond to the archeological levels of BL and FN3 allows reconstructing their paleogeographic context (Figure 7). This was characterized by large flood plains crisscrossed by channels in the Guadix Basin as well as in the W and SW sectors of the Baza Basin, with a lacustrine system that spread through the N and NE sectors of the Baza Basin (Cortes de Baza-Huéscar-Orce sector, Figure 2B). The lacustrine deposits represent a stratigraphic unit with a maximum thickness of 40 m (up to 50–60 m in the lake depocenter), which preserves the main sites of Orce. The unit shows an alternation of levels of marls-calcilutites and limestones, each one meter thick on average, with intercalations of thin levels of dark lutites and detritic facies (conglomerates and sands) to the lake borders (García-Aguilar et al., 2014).

Several mollusks (gastropods *Bithynia tentaculata*, *Hydrobia* aff. *acuta*, *Melanoides tuberculata*, and *Gyraulus* cf. *laevis*; bivalve *Pisidium casertanum*; Figures 8E–I) indicate the presence of an euryhaline environment in BL (Albesa and Robles, 2020). The lacustrine sediments of BL preserve shells of two ostracods,

Candona sp. and *Cyprideis torosa* (Anadón et al., 1994), which live in oligo- to mesosaline conditions (Figures 8A,B). The limits of tolerance to salinity of these species provide clues on the lake waters: *B. tentaculata*, *H. acuta*, and *M. tuberculata* can live with elevated salinities (12–30‰), but their optimum is lower (0.2–3‰ for *M. tuberculata*). In contrast, *P. casertanum* and *G. laevis* tolerate salinities of only up to 3–5‰ (Albesa and Robles, 2020). This indicates a thermophile lacustrine environment with alternating phases of salinity, from freshwater to moderately brackish conditions in the lake waters and higher values of salinity in the surrounding swampy areas. Such inference agrees with (i) the presence in the sediments of microcrystalline gypsum originated by neof ormation (García-Aguilar et al., 2014); (ii) the high $d^{15}N$ values measured in the bone collagen of *Hippopotamus antiquus*, a species that fed on the aquatic macrophytes that grew in the oligosaline waters of the lakes instead of consuming terrestrial grasses, as does the living *H. amphibius* (Palmqvist et al., 2003, 2008a,b, 2022a; García-Aguilar et al., 2014); and (iii) the finding of a common Shelduck (*Tadorna tadorna*) in VM (Figure 8J). This waterfowl dwells in coastal mudflats and lagoons, estuaries, and riverine environments of Europe, generally occurring in salt or brackish water, where it feeds mostly on saltwater snail *H. acuta* (Carboneras and Kirwan, 2018), a species that can survive at salinities of up to 39‰ (Britton, 1985). In the case of VM, the ostracodes *Ilyocypris bradyi* and *I. gibba* (Figures 8C,D) provide additional information on the paleoenvironment: the former lives in high energy streams with abundant underwater vegetation, while the latter evidences shallow lake borders with warm and fresh to oligosaline waters, a sandy substrate and lushy vegetation (Martínez-García et al., 2015, 2017).

The detritic facies of the Baza Basin are composed of sands and silts originated in organic-rich coastal lacustrine environments and emerged plains, although they can also correspond to distal riverine systems (García-Aguilar et al., 2014). Some sandy and silty deposits are associated with conglomerates, which represent flood deposits that penetrated the lakes as highly disorganized deltas (e.g., level D of BL; Arribas and Palmqvist, 2002).

The estimates of prey biomass (kg/km²) for the Orce sites (Figure 9), obtained with the Weibull model following the procedure described by Martín-González et al. (2019) and Rodríguez-Gómez et al. (2022), are lower than those measured in several African Natural Parks and Game Reserves, like Ngorongoro Crater or Amboseli, close to those of Masai Mara, Savuti, Hluhluwe Imfolozi or the Nwaswitshaka River, and higher than in Serengeti, Selous or the Okavango Delta, among many others. This figure shows a direct relationship of prey biomass with annual rainfall (Figure 9A), but not with mean annual temperature (Figure 9B). Prey biomass estimates suggest that meat availability was high in the Orce sites, particularly compared with most sites of Atapuerca. The only exceptions are TD6-1,2 and TD8, in which the estimates are only slightly lower than in BL and FN3. In fact, a comparison of the faunal assemblages of Atapuerca showed that TD6-1,2 and TD8 were the levels with lowest competition intensity among the secondary consumers (Rodríguez-Gómez et al., 2013, 2014a, 2017b), even lower than in VM, BL and FN3. This indicates



that, departing from a similar prey biomass, the Orce ecosystems supported a more diverse predatory guild than those recorded at TD6-1,2 and TD8 (Rodríguez-Gómez et al., 2016a, 2017a). Based on a comparison between these results and those derived with the equations of Rodríguez et al. (2014) to estimate the maximum carrying capacity of the ecosystems of Orce and Atapuerca, Rodríguez-Gómez et al. (2022) proposed that the differences in secondary production between these sites could result from the exceptional geological conditions of Guadix-Baza, particularly the presence of thermal springs that provided a mild and productive paleoenvironment throughout the year (García-Aguilar and Palmqvist, 2011; García-Aguilar et al., 2013, 2014, 2015).

Figure 7 shows the paleogeographic model of Guadix-Baza during the late Early Pleistocene, based on cartographic data of the sedimentary deposits (**Figure 2B**). The outer perimeter of the basin, which corresponds to the limits of the surface emerged and the one covered by the lake waters, encloses an area of 4,050 km². This encompasses the outcrop area of alluvial and fluvial deposits (i.e., flood plains, proximal zones of the alluvial systems and alluvial fans, covered by water only during the rainy

episodes) and the glacia surface, which includes the area with a gentle slope in the foothills situated up to a height of 20 m over this surface. This represents a living area for the terrestrial fauna and the hominins of 2,925 km², while the outcrop area of the lacustrine deposits covers 1,125 km². The extent of the lake would fluctuate between low-stand stages, which correspond to the limestone and marly limestone beds deposited during the drops of the water table, and high-stand stages, which evidence the rising of the water table that resulted in the deposit of marls and calcilutites. The emerged area inhabited by the terrestrial fauna would be greater during the low-stand stages, when the alluvial feeding of the lake originated in the southern and eastern reliefs was scarce and of low energy. Given the limited depth of the lacustrine system (~2 m on average, with large areas on the swampy environments of the lake margins showing a decametric depth), the lowering of the water table would result in wide emerged areas in the lake surroundings. The opposite situation would apply to the high-stand stages, when higher precipitations and a greater recharge of the lake by alluvial waters originated in the perimeter of the basin took place. This would result in a more restricted extent of the terrestrial ecosystems. Low-stand to

high-stand fluctuations would encompass the periodic changes between warm-moist and cold-dry conditions of climatic cycles, which would represent variations in the living area for the terrestrial fauna of 20–25% above (low-stand) and below (high-stand) the cartographic extent of the deposits drawn in **Figure 7**. Moreover, there would be also yearly oscillations in the extent of the water sheet between the winter and summer seasons. Finally, **Figure 7** shows the sedimentary depression during the late Early Pleistocene as a closed, endorheic basin with internal drainage, but with a limited number of connecting corridors for the terrestrial fauna to other surrounding areas, especially to the East. For this reason, the ecological scenario of the Orce sector of the sedimentary depression (a satellite basin of $\sim 170 \text{ km}^2$) resembles the one found in the Ngorongoro Crater, Tanzania, which has a similar extent ($\sim 230 \text{ km}^2$) and hydrothermal context (Deocampo and Ashley, 1999; Deocampo, 2005).

Hominin Population of the Guadix-Baza Depression

The area emerged in the Guadix-Baza Depression ($2,925 \text{ km}^2$) allows calculating the population size of *Homo* sp. that could inhabit it. As noted earlier, the estimate of hominin population density for BL and FN-3 is 0.12 individuals per km^2 considering a scavenging behavior as the optimal scenario for the procurement of ungulate carcasses (Rodríguez-Gómez et al., 2016a). This translates in a population size of ~ 350 individuals, which would result in 7–12 hominin groups based on the estimates of mean local group size for modern hunter-gatherers (Binford, 1980; Marlowe, 2005). If we choose for a strict hunting behavior, which implies that the hominins had not access to the largest prey size classes, the population density would be 0.095 individuals per km^2 (Rodríguez-Gómez et al., 2016a). This would result in a population of ~ 280 individuals distributed among 5–9 foraging groups. Both estimates are very low and clearly below the minimum viable population size for mammals (including primates), which has been estimated in 3,876 individuals, with a 95% confidence interval of 2,261–5,095 individuals (Traill et al., 2007). This suggests that although the prey biomass estimated in the Guadix-Baza was similar or even higher than in many modern African ecosystems, the viability of the hominin population that inhabited the sedimentary basin could be compromised due to random oscillations in population size such as those resulting from fluctuations in resource availability and epidemics. This could eventually lead to bottlenecks, genetic drift, inbreeding depression, and local extinction.

A skull of the hypercarnivorous wild dog *Lycaon lycaonoides* (specimen VM-7000) provides evidence of inbreeding depression in the local population of this species. The skull preserves the cranium and mandible in anatomical connection and corresponds to a relatively old individual with moderately worn permanent dentition (Palmqvist et al., 1999). It displays a high degree of cranial fluctuating asymmetry (FA), which is especially marked in the frontal region, and shows dental anomalies, including agenesis of several teeth like the upper right canine (Bartolini-Lucenti et al., 2021). The incidence of FA in a population must be tested at the population level and not

based on a single individual (Palmqvist et al., 1999). However, the fossil record of *L. lycaonoides* is scarce in Guadix-Baza (a few specimens from VM, see details in Palmqvist et al., 2022b) and VM-7000 is the only complete skull. This limitation on sample size precludes the hypothetico-deductive method and forces to use the 'abductive research method,' which means that the best explanation at hand for interpreting the anomalies of VM-7000 is to consider that they evidence FA resulting from developmental instabilities caused by inbreeding depression (Palmqvist et al., 1999; Bartolini-Lucenti et al., 2021).

Fluctuating asymmetry results from small, random accidents during ontogeny in morphological traits that would otherwise appear as bilaterally symmetric. These perturbations can also emerge from developmental stress (e.g., induced by parasitic infection), but their incidence in a population uses to correlate with the level of genetic inbreeding, which increases the homozygosity of enzyme polymorphisms and results in developmental instabilities (Wayne et al., 1986; Palmqvist et al., 1999; Leamy and Klingenberg, 2005). Inbreeding increasingly becomes a serious threat to local wildlife populations as habitats shrink and fragment (Spiering et al., 2011). This results in bottlenecks and changes in metapopulation structure, which translate in a quite small effective population size and lead to the loss of genetic diversity and inbreeding depression, as documented in the cheetah (Wayne et al., 1986; Menotti-Raymond and O'Brien, 1993; Hedrick, 1996; however, see also Merola (2011)). The expression of the deleterious effects of increased homozygosity and their consequences for individual fitness have been shown in canids (Ellegren, 1999; Fitzpatrick and Evans, 2009; Spiering et al., 2011). Anodontia and cranial asymmetry are documented in small populations of wolves subject to bottlenecks and inbreeding, as happens in Białowieża Forest (Buchalczyk et al., 1981; Vilà et al., 1993). Edwards et al. (2013) showed an increase in fluctuating asymmetry in museum skulls of African painted dogs that span a period of a hundred years, which parallels the decline in the populations of the species in sub-Saharan Africa during the last century. This suggests that the malformations of the fossil skull of VM would reflect developmental instabilities resulting from a high level of genetic homozygosity in the small population of wild dogs that inhabited Guadix-Baza during Early Pleistocene times. Specifically, the population density of *L. lycaonoides* expected for optimal ecological conditions, calculated using the equation of Damuth (1993) for African flesh-eaters in open environments, is 0.23 individuals per km^2 (Rodríguez-Gómez et al., 2017a). However, the value of sustainable density for this predator in VM is lower, 0.13 ind./ km^2 , which translates in a population of only 380 individuals (i.e., like the one estimated for the hominins). Moreover, the effective population size of modern painted dogs is typically reduced to 20–35% of the censused population by reproductive suppression of subordinates and uneven sex ratios (Creel and Creel, 1998). In the case of VM, this would result in an effective population size for *L. lycaonoides* of around one hundred individuals, which would have promoted further inbreeding. However, the dog from VM was able to reach adulthood, as shown by its moderately worn permanent dentition, despite severe developmental handicaps, which suggests that cooperative

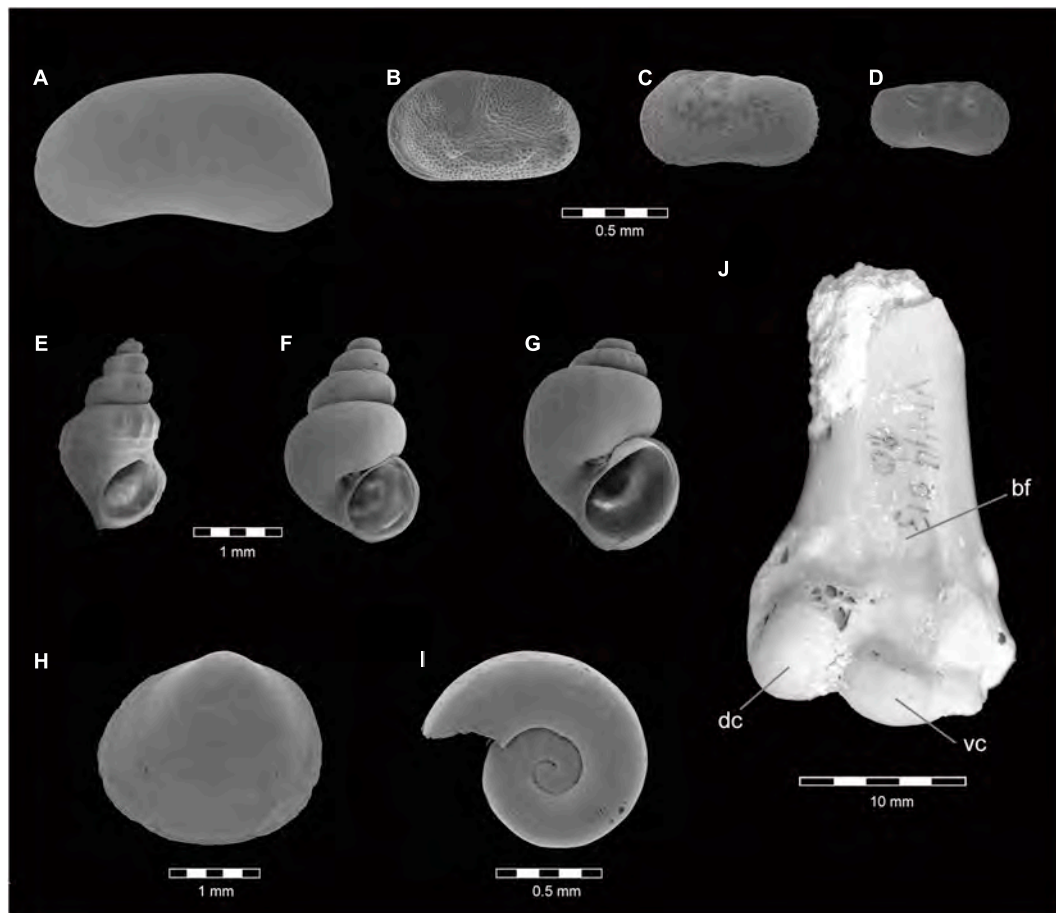


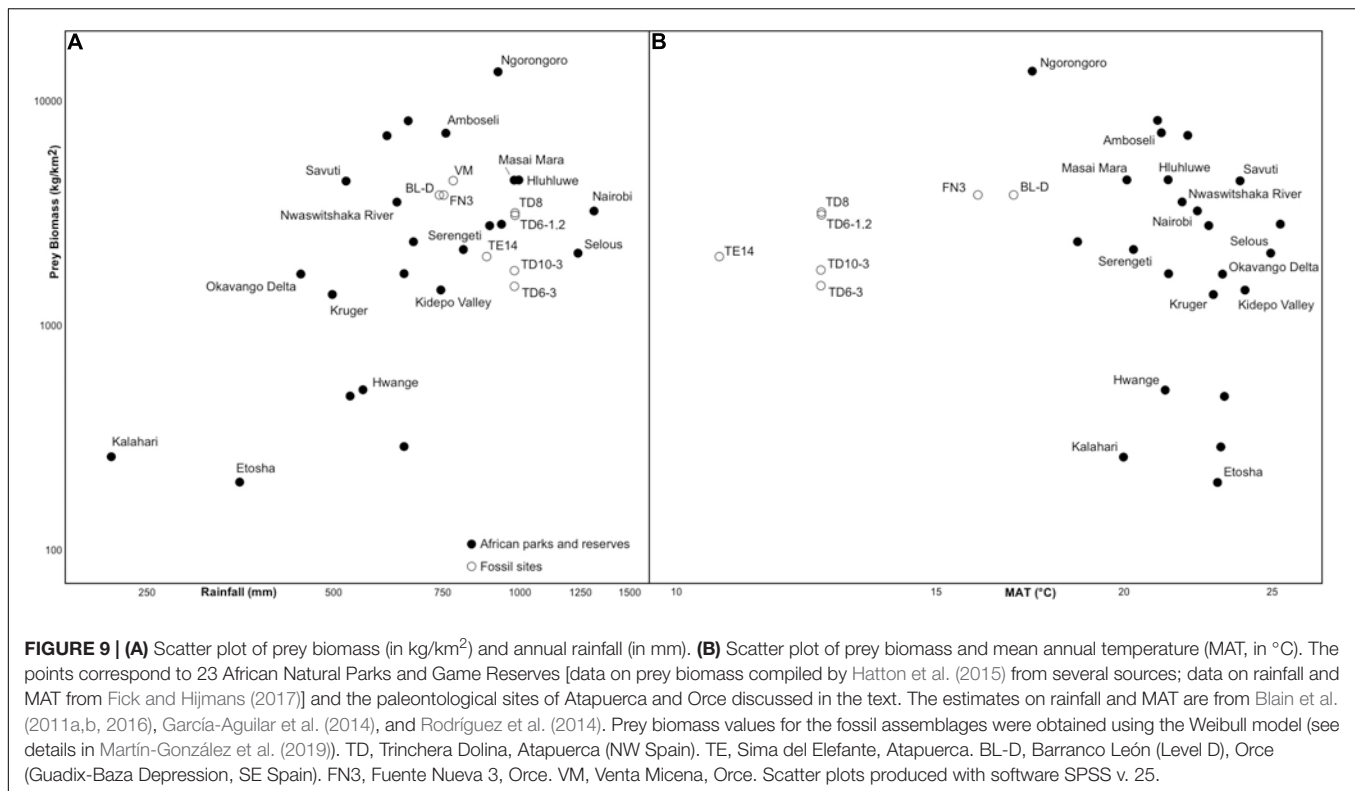
FIGURE 8 | Ostracods, mollusks and avian remains identified in the Late Villafranchian archeological sites of Barranco León (BL) and Fuente Nueva 3 (FN3) in Orce (Guadix-Baza Depression, SE Spain). Scanning electron microscope photographs of ostracod (A–D) and mollusk (E–I) shells. (A) *Candona* sp. (B) *Cyprideis torosa*. (C) *Ilyocypris bradyi*. (D) *Ilyocypris gibba*. (E) *Melanoides tuberculata*. (F) *Hydrobia* aff. *acuta*. (G) *Bithynia tentaculata*. (H) *Pisidium casertanum*. (I) *Gyraulus* cf. *laevis*. (J) Distal humeral portion of an aquatic bird from Venta Micena (specimen VM-D13-10) in cranial view, which has been tentatively attributed to a Common Shelduck (*Tadorna tadorna*), bf-brachial fossa, dc-dorsal condyle, vc-ventral condyle.

behavior from other members of the hunting pack may have helped it to survive (Palmqvist et al., 1999; Bartolini-Lucenti et al., 2021). Similarly, cooperation among hominins has been reported in Dmanisi. This site documents the earliest human presence out of Africa (~1.8 Ma) and preserves a human skull that lost all but one of its teeth several years before the time of death (composite skull D 3444/D 3900), as evidenced by extensive bone loss due to resorption of the alveolar processes. Although the etiology of the absence of teeth differs from that described in the wild dog of VM, the survival of this edentulous individual probably relied also on the assistance (e.g., food chewing) from other members of the group (Lordkipanidze et al., 2005, Lordkipanidze et al., 2006).

The high level of genetic homozygosity deduced for the population of *L. lycaonoides* that inhabited Guadix-Baza — conditions that would presumably apply also to the hominin population — can be explained as resulting from its small size, as this population was geographically isolated from other similar ecosystems in the surrounding areas (Palmqvist et al., 1999). Interestingly, the lion population that inhabits the Ngorongoro

Crater depicts a similar situation: these lions form a small, naturally isolated population of 75–125 individuals, which has been historically subject to severe bottlenecks followed by limited recolonization by lions from the nearby Serengeti ecosystem. This has resulted in high levels of inbreeding and lack of genetic variability in the contemporary Crater lion population compared to the much larger Serengeti population, which correlates with increased levels of sperm abnormality and decreased reproductive performance (Packer et al., 1991).

Any discussion on the level of genetic variability of the population of early *Homo* that inhabited Guadix-Baza makes it necessary to consider the levels of inbreeding depression withstood by modern hunter-gatherers. Genealogical information showed evidence of inbreeding in 165 out of 931 (~18%) individuals of the Hadza population (Stevens et al., 1977). Similarly, the !Kung, Khwe and African Pygmies exhibit low genetic diversity coupled with high frequencies of divergent mtDNA haplotypes not found in the surrounding agricultural groups, which suggests small population sizes and long-term



isolation, respectively (Vigilant et al., 1991; Chen et al., 2000; Oota et al., 2005). Moreover, Trinkaus (2018) showed an unexpectedly high frequency of abnormalities in the fossil record of Pleistocene *Homo*, including from minor but rare dental, vertebral, and carpal variants to exceptional systemic disorders. This suggests ubiquitous stress among the Pleistocene foragers and/or high levels of consanguinity.

Although the hominin population of Guadix-Baza was probably small, it would not remain in strict isolation: there are several connecting corridors in the mountainous reliefs that surround the basin (see arrows in Figure 7). Moreover, some species ecologically and climatically constrained like the hippo probably dispersed by these corridors from the coastal environments, which led to their colonization of the lacustrine environments of this endorheic basin. In the case of the hominins, the corridors would result in some gene flow with other populations from adjacent areas, although the amount of gene introgression was probably limited, as happens in modern hunter-gatherers. Moreover, data from Binford (1980: Table 1) for Equatorial and Subequatorial populations of non-equestrian hunters-gatherers provide a mean number of 24.8 residential moves per group and year, a mean distance of 15.3 km between sites and a mean total circuit distance covered annually of 310.6 km. This suggests that each of the few hominin groups that inhabited the Guadix-Baza Depression would travel each year searching for food a linear distance that would cover the entire basin. These changes in residential moves would presumably follow a random motion, as happens in the case of modern hunter-gatherers (Brown et al., 2007; Raichlen et al., 2014).

For this reason, the probability of intersecting one of the five connecting corridors of the basin perimeter (Figure 7) in any of these foraging random walks would be low, resulting in a limited amount of gene flow with the surrounding populations and long-term isolation.

According to these data, Guadix-Baza was home for a small hominin population during the late Early Pleistocene, which viability in the medium and long term could be compromised by population bottlenecks and inbreeding depression. This explains the sporadic and discontinuous nature of the archeological record in the sedimentary basin. Although such situation cannot be extrapolated to the whole European record of hominin presence for these ancient chronologies, the scarcity of Early Pleistocene archeological sites points to intermittent dispersal events, which probably reflects hominin incursions that failed to establish a more permanent character (Dennell, 2003; MacDonald et al., 2012).

However, we must introduce here a cautionary note: Flores Island, which has an area of 13,540 km² (i.e., ~4.6 times the living area of the Guadix-Baza Depression), has a record of hominin presence since ~0.7 Ma (van den Bergh et al., 2009, 2016). The island allowed the survival of a local population of *H. erectus* during more than half a million years and this happened without any evidence of external gene flow having been detected so far. In their adaptation to the insular environment, these hominins evolved in a short time to a dwarfed form, *H. floresiensis*, which represents a striking case of evolutionary reversal in the trend of body and brain size increase in *Homo* (van den Bergh et al., 2016). This was facilitated

by the relatively small size of the population, although the energy expenditure of the small-bodied *H. floresiensis* could be half that of *H. erectus* (Dennell et al., 2014), which probably resulted in a higher population density. Unlike other hominins, *H. floresiensis* shows a combination of primitive traits in the canine and premolar teeth, which are comparable to those of Early Pleistocene *H. erectus*, together with a molar morphology more progressive than in modern humans (Kaifu et al., 2015). These features make sense in the context of a highly isolated inbred population with small genetic variation (as expected from the founder effect of the island colonizers), a population that was adaptively constrained. It should be noted, however, that a similar combination of primitive and modern characters is also present in *H. luzonensis*, the dwarfed hominin of the larger island of Luzon (Philippines), which probably descended also from an initial population of *H. erectus* (Détroit et al., 2019).

Continuity or Discontinuity in the Earliest Hominin Settlements of Europe?

During the last decades, the discovery of a significant number of Early Pleistocene sites that preserve evidence of hominin presence in Western Europe has renewed the debate on: (i) the chronology of the oldest dispersal of *Homo* out of Africa; (ii) the success of these ancient populations in the colonization of the European landscapes; and (iii) their continuity or discontinuity (Arribas and Palmqvist, 1999; Roebroeks, 2001; Dennell, 2003; MacDonald et al., 2012; Bermúdez de Castro et al., 2013; Rodríguez-Gómez et al., 2014a, 2016a, 2017a,b,c). Although Dmanisi provides conclusive evidence on the presence of hominins at the gates of Europe by ~ 1.8 Ma (García et al., 2010), the overall evidence of hominin settlements in North Africa and Europe is scarce before the Middle Pleistocene and is basically restricted to the circum-Mediterranean realm (Rodríguez-Gómez et al., 2016a, 2017a; Butynski, 1982; Capaldo, 1997; Roebroeks et al., 2018). Muttoni et al. (2010, 2013) proposed that the first occurrence of *Homo* sp. in Southern Europe took place between the Jaramillo subchron and the Brunhes-Matuyama boundary (i.e., in the 0.99–0.78 Ma interval), a time window that encompasses the latest Early Pleistocene global climate transition centered on MIS 22 at ~ 0.9 Ma, the first prominent cold stage of the Pleistocene. Under this view, hominin presence in Southern Europe would have been ephemeral from ~ 1 Ma onward, with occasional short northward expansions along the western coastal areas when temperate conditions allowed it (Roebroeks, 2001; Muttoni et al., 2010). In contrast, Leroy et al. (2011) argued that there were up to 42 possible narrow windows of 41 ka for hominin dispersal in Europe through the Early Pleistocene (2.58–0.78 Ma). In their model of climate and vegetation change, these windows coincided with transitions from glacial to interglacial cycles forced by obliquity, which resulted in the opening of the landscapes with the appearance of grasslands and forested steppes like those of Orce (Mendoza et al., 2005; Saarinen et al., 2021). This landscape was similar to the recent reconstruction of Dmanisi as an open wooded savannah and grassland by Bartolini-Lucenti et al. (2022). Leroy et al. (2011) considered that the presence of hominins was not

possible during the full glacial periods, which would be too cold for them, and neither in the transitions from interglacial to glacial cycles, when the landscapes were densely forested. In any case, the oldest conclusive evidence of human presence in Western Europe is found at BL and FN3 in Orce (~ 1.4 Ma) and TE9 level (~ 1.2 Ma) in Atapuerca (see review in Palmqvist et al., 2016). In addition, the carnivore guild of VM, a site ~ 200 ka older than BL and FN3 that shows no evidence of hominin presence, has a lower level of competition intensity for meat than in the case of BL and FN3 (Rodríguez-Gómez et al., 2016a, 2017a). This suggests that the delay of ~ 0.4 Ma between hominin arrival in the Caucasus and Western Europe was not a matter of ecological opportunity and other factors (climatic or geographic barriers to dispersal) played a role here (Rodríguez-Gómez et al., 2017a).

The scarcity of Early Pleistocene archeological sites in Europe indicates that the colonizing capabilities of early *Homo* outside Africa may have been overestimated, as the dispersals were not automatically followed by permanent settlements (Dennell, 2003). Further fieldwork will undoubtedly fill many gaps in the Early Pleistocene hominin record of Europe, but current evidence is consistent with the view that: (i) the oldest populations outside East Africa were spatially and temporally discontinuous; (ii) hominin expansion was strongly constrained by latitude; and (iii) the occupation of temperate regions north of latitude 40° was largely confined to interglacial periods (Dennell, 2003; Leroy et al., 2011; Rodríguez et al., 2011, 2013; MacDonald et al., 2012; Bermúdez de Castro et al., 2013). However, continuity of hominin settlements in the refuge areas of Southern Europe during the cold periods of the Early Pleistocene cannot be discarded: the presence of hominins at Atapuerca during long time periods suggests that they were well-adapted to the hard and seasonal conditions of the northern hemisphere at a latitude of 42° and an altitude of 1000 m (Bermúdez de Castro et al., 2013). Climate conditions in Guadix-Baza were milder than those of Atapuerca (Figure 9), with the presence of open plains with woodland patches and water-edge areas (Mendoza et al., 2005; Saarinen et al., 2021). This difference between the North and South of the Iberian Peninsula is also seen today (Blain et al., 2009, 2011a,b). Moreover, the thermal springs of Guadix-Baza resulted in a milder and more productive environment in the lacustrine systems of the basin compared to present-day conditions (García-Aguilar et al., 2014, 2015). Therefore, the information available suggests continuity for the human settlements in the Iberian Peninsula during a period of at least 300 ka before the Jaramillo subchron (Agustí et al., 2009; Bermúdez de Castro et al., 2013). According to Agustí et al. (2009), after this phase the hominins would disappear from Western Europe during a long period that included part of the Jaramillo subchron and until MIS 22 (0.88–0.87 Ma). This would be caused by an extreme decrease in mean annual temperature and an increase in mean annual precipitation, as deduced from the herpetofauna (Agustí et al., 2009). However, geochronological and paleomagnetic data for levels of Trinchera Dolina of Atapuerca indicate a continued presence of hominins in northern Spain during the time interval of ~ 1.0 – 0.3 Ma (Bermúdez de Castro et al., 2013).

The archeological record of Sima del Elefante and Gran Dolina cave sites in Atapuerca, which preserves relatively continuous stratigraphic sequences that stretch back from ~1.2 Ma to the Matuyama/Brunhes boundary, suggests that the Iberian Peninsula was occupied by at least two different hominin populations (Bermúdez de Castro et al., 2013). The human remains from level TD6 of Gran Dolina, dated to 0.97–0.79 Ma by a combination of biochronology, magnetostratigraphy and geochronology (Duval et al., 2018; Parés et al., 2018), have been ascribed to *Homo antecessor*, a species considered to represent the most recent common ancestor of Denisovans, Neandertals and modern humans, or at least very close to the cladogenetic event that preceded the divergence of these species (Bermúdez de Castro et al., 2017; Welker et al., 2020). The dental proteome of *H. antecessor* indicates that it represents a close sister lineage to subsequent Middle and Late Pleistocene hominins (Welker et al., 2020). In Sima del Elefante, the few fossils from TE9 do not allow to conclude if *H. antecessor* has deep roots in the Early Pleistocene before the Jaramillo subchron (Bermúdez de Castro et al., 2013, 2017). The hominin population of TE could be different from that recorded at TD6, but the evidence recovered is too scanty to make a strong claim. What seems clear is that the hominins never disappeared from the Atapuerca habitats, as the archeological record at the base of TD4 is of ~1.0 Ma (Carbonell and Rodríguez, 1994). This argues for the continuity of the hominin settlements in the circum-Mediterranean realm, even if we admit the possibility of discontinuity by the local substitution of the original population, its assimilation or crossbreeding.

Finally, Bermúdez de Castro and Martín-Torres (2013) hypothesized the existence of a “source population” of hominins in a central area of dispersal, which they tentatively located in the Levantine Corridor. When climatic and ecological conditions were favorable, hominins would colonize from this area the Eastern and Western territories of Eurasia. Following Carrión et al. (2011); Bermúdez de Castro and Martín-Torres (2013) considered that the key for activating evolutionary change in this hominin population would be the geological instabilities that resulted in an increase in physiographical heterogeneity, biodiversity and ecological interaction. The latter conditions were boosted in the Guadix-Baza Depression by the abundance of thermal springs linked to intense tectonic activity, which was a major determinant in the establishment of biodiversity “hot spots” with high biological productivity (García-Aguilar et al., 2014, 2015; Rodríguez-Gómez et al., 2016a, 2017a, 2022; Palmqvist et al., 2022a).

CONCLUSION

Evidence of anthropogenic action from the archeological levels of BL and FN-3 indicates that the hominin population that inhabited the Guadix-Baza Depression during Early Pleistocene times exploited the prey carcasses left abandoned by saber-tooths, which suggests a subsistence strategy based on passive scavenging rather than on active hunting for obtaining meat, fat, and bone marrow. In addition, other animals of small size available in the environment, including

rodents, leporids, tortoises and birds, were also presumably consumed, together with eggs, invertebrates, honey, and a wide spectrum of edible vegetation. The population size estimated for the hominins of the basin was low, ~350–280 individuals distributed in five to twelve groups of hunter-gatherers. This probably compromised the long-term viability of the population due to the effects of bottlenecks and inbreeding depression, as detected in the coeval population of wild dogs, which probably led them to extinction and helps to explain the scarcity and discontinuous nature of the archeological record in the basin.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

PP wrote the manuscript and all co-authors made contributions. SR-M, BM-N, and PP prepared **Figure 1**. AG-M, JMG-A, AG, and SR-M prepared **Figure 2**. BF prepared **Figure 3**. GR-G prepared **Figure 4**. PP and MPE prepared **Figures 5, 6**. AG-M and JMG-A prepared **Figure 7**. AG and FS prepared **Figure 8**. GR-G and PP prepared **Figure 9**. BM-N, MPE, and SR-M prepared **Table 1**. All authors contributed to the article and approved the submitted version.

FUNDING

This work was supported by four projects from the Spanish Ministry of Science, Innovation and University (Grant Nos. CGL-2016-78577-P, CGL-2016-80975-P, PGC2018-093925-B-C31, and PID2019-111185GB-I00), by two projects from Junta de Andalucía (Grant Nos. UMA18-FEDERJA-18 and P18-FR-3193), by one project from Generalitat de Catalunya (Grant No. GENCAT 2017SGR 859), and by Research Group RNM-146 from Junta de Andalucía.

ACKNOWLEDGMENTS

GR-G was funded by the program IdEx Bordeaux “Investments for the future,” financed by L’Agence Nationale de la Recherche of France (ref. ANR No.-10-IDEX-03-02) with the project *Analysis of Kozarnika food webs and comparison with other Pleistocene sites of Western Europe*. The Program Juan de la Cierva of the Spanish Ministry of Science, Innovation and University funded GR-G (FJCI-2016-28652) and FS (IJCI-2017-32116). GR-G is supported by an “Atracción de Talento” postdoctoral contract (2019-T2/HUM-13370) from the Comunidad de Madrid and Universidad Complutense de Madrid (Spain). FS is supported by a postdoctoral fellowship of Junta de Andalucía. Last but not least, we gratefully acknowledge the insightful comments and helpful criticism from two reviewers and also from the editor, MA.

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