



# Sharing food with hyenas: a latrine of *Pachycrocuta brevirostris* in the Early Pleistocene assemblage of Fuente Nueva-3 (Orce, Baza Basin, SE Spain)

M. P. Espigares<sup>1</sup> · P. Palmqvist<sup>1</sup> · M. D. Rodríguez-Ruiz<sup>2</sup> · S. Ros-Montoya<sup>1</sup> · A. Pérez-Ramos<sup>1</sup> · G. Rodríguez-Gómez<sup>3,4</sup> · A. Guerra-Merchán<sup>1</sup> · J. M. García-Aguilar<sup>1</sup> · A. Granados<sup>1</sup> · I. Campaña<sup>1</sup> · B. Martínez-Navarro<sup>5,6,7</sup>

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## Abstract

The Early Pleistocene archeological site of Fuente Nueva-3 (FN3) preserves some of the oldest evidence of hominin presence in Western Europe, including a huge assemblage of Oldowan tools and evidence of butchering and marrow processing of large mammal bones. Moreover, there is also evidence of the regular presence of carnivores at the site, including a small proportion of bones that show tooth marks, the majority of which can be attributed to the giant, short-faced hyena *Pachycrocuta brevirostris*, and there are 220 coprolites, most of them from the Upper Archeological Level. In order to identify the defecating agent, we analyze here the coprolites and compare them with other specimens from the literature and with scats from zoo spotted hyenas (*Crocuta crocuta*). The morphology, color, size, and chemical composition of the FN3 coprolites allow us to attribute them to the hyena *P. brevirostris*, which is also represented at the site by fossil specimens. In addition, we evaluate the origin of the accumulation of coprolites and discuss on the role played by the scavenging hyenas in the accumulation and modification of the bone remains unearthed at the site, which allows evaluating the contribution of the giant hyena to this Early Pleistocene site. Finally, based on the lithology of layer 5 of the Upper Archeological Level, fine sands and clays deposited in a salt-lake environment, we hypothesize that this layer may have acted as a quicksand where large-sized animals like elephants were trapped and their carcasses lured scavenging carnivores.

**Keywords** Coprolites · Early Pleistocene · Hyaenidae · Western Europe · Hominin-carnivore interactions

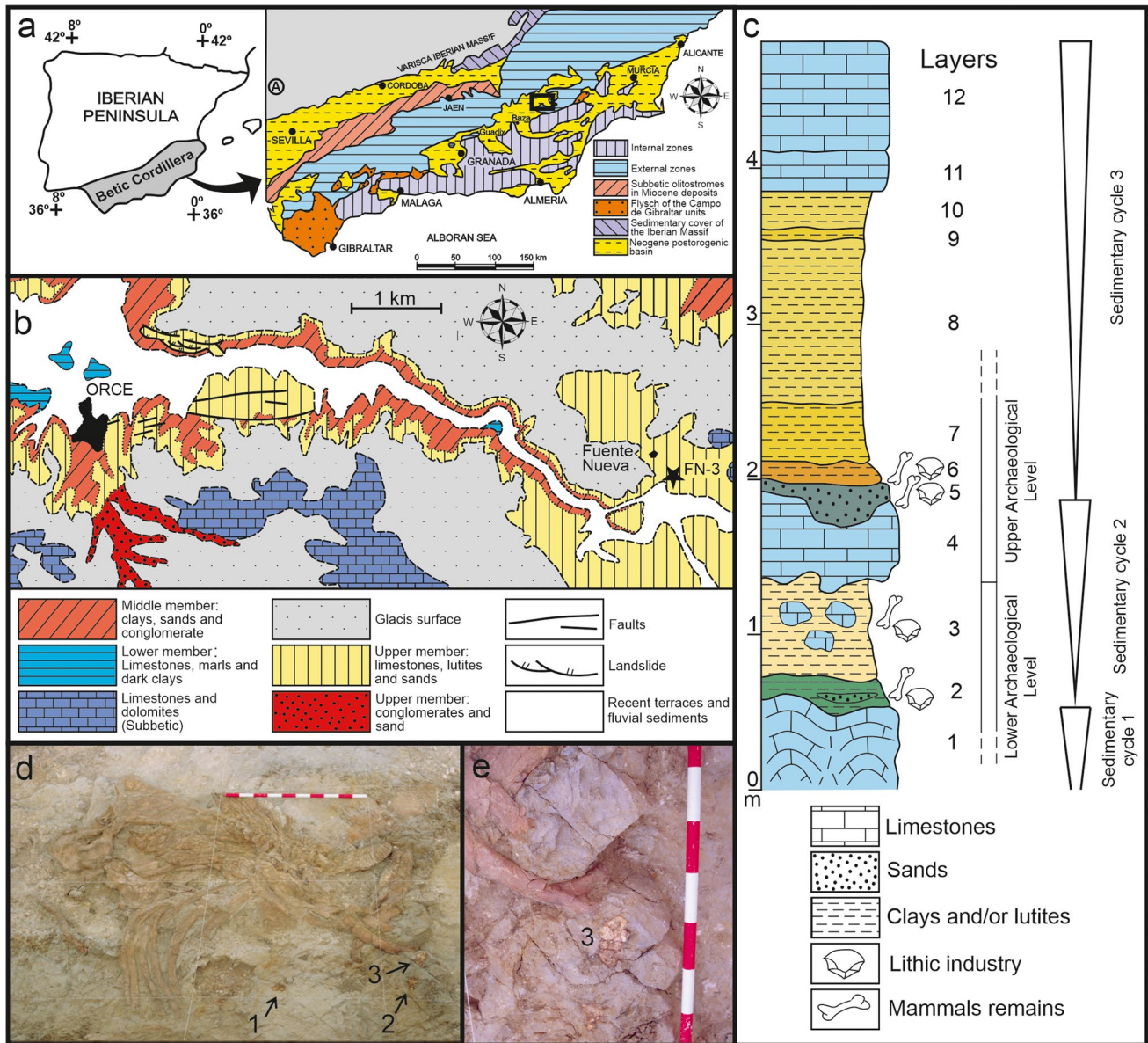
✉ M. P. Espigares  
mpespigares@uma.es

✉ B. Martínez-Navarro  
bienvenido.martinez@icrea.cat

- <sup>1</sup> Departamento de Ecología Y Geología, Universidad de Málaga, Málaga, Spain
- <sup>2</sup> Departamento de Química Inorgánica, Cristalografía Y Mineralogía, Universidad de Málaga, Málaga, Spain
- <sup>3</sup> Departamento de Geodinámica, Estratigrafía Y Paleontología, Universidad Complutense de Madrid, Madrid, Spain
- <sup>4</sup> Centro UCM-ISCIH de Evolución Y Comportamiento Humanos, Madrid, Spain
- <sup>5</sup> Institut Català de Paleoecologia Humana I Evolució Social, IPHES-CERCA, Tarragona, Spain
- <sup>6</sup> Area de Prehistoria, Universitat Rovira I Virgili, Tarragona, Spain
- <sup>7</sup> ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain

## Introduction

The late Early Pleistocene of the Orce area (Baza Basin, SE Spain; Fig. 1) is mainly represented by the paleontological site of Venta Micena (VM), which is dated to 1.5–1.6 Ma (Palmqvist et al. 2022a), and by the archeological sites of Fuente Nueva-3 (FN3) and Barranco León (BL). The latter two localities, with a chronology close to 1.4 Ma (Duval et al 2012; Toro-Moyano et al. 2013; Palmqvist et al. 2016), preserve one of the oldest records of hominin presence in the European subcontinent, based on the finding of huge assemblages of Oldowan tools and skeletal remains of large mammals that preserve evidence of butchering and marrow processing. The tools, which represent the whole reduction sequence, are composed of abundant small flakes, blocks and cobbles, cores, and debitage made of flint, limestones, and calcarenites from the surroundings of the sites. Flint was largely exploited for flake production while limestone, although also used for flake production, was mostly employed for percussion



**Fig. 1** **a** Geological context of the Guadix-Baza Depression in the Betic Cordillera, SE Spain. The box encloses the Orce-Fuente Nueva sector of the Baza Basin; **b** geological map of the Orce-Fuente Nueva

sector showing the location of the FN3 site; **c** stratigraphic series of the FN3 site; **d** photographs of three in situ coprolites (1, 2, 3) that surround an elephant carcass; **e** detailed view of one of them (3).

tasks (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, 2015a, 2015b; Toro-Moyano et al. 2011, 2013; Tittton et al. 2018, 2021). The tools are associated with abundant remains of large mammals, some of which show cut and percussion marks related to defleshing, butchering, and marrow processing (Espigares et al. 2013, 2019; Yravedra et al. 2021, 2022a; Palmqvist et al. 2023 and references therein). Moreover, a deciduous tooth of *Homo* sp. has been unearthed from BL, which represents the oldest hominin fossil from Western Europe (Toro-Moyano et al. 2013).

Espigares et al. (2019) analyzed the evidence of anthropogenic activity in both sites, where carnivore modifications are also present but at low frequencies (see also Yravedra et al. 2021, 2022a; Courtenay et al. 2023). However, the Upper Archeological Level (UAL) of FN3 shows a high accumulation of hyena coprolites, which suggests that carnivore activity was particularly high at this level. In contrast, there are a low number of coprolites in the Lower Archeological Level (LAL) of FN3 and a high density of non-flaked, allochthonous blocks and cobbles from the Jurassic limestones of the site surroundings. Nearly half of these blocks display percussion

marks (Barsky et al. 2015b, 2022), which suggests that hominin activity was important at this level.

Coprolites are mineralized or desiccated feces preserved in caves, shelters, and open-air sites (Reinhard and Byant 1992). The term coprolite was first used by Buckland to describe rounded black phosphatic structures, which corresponded to mineralized ichthyosaur feces of Early Jurassic (Lias) age that contained fish scales and bones (Buckland 1829; Pemberton 2012). However, the first fossil scats recognized as hyena coprolites came from Late Pleistocene deposits of Kirkdale Cave (Buckland 1822, 1824).

Coprolites are an excellent source of information, because they can provide insights on the taphonomic history of an assemblage. As ichnofossils (i.e., trace fossils), coprolites are key to understanding aspects of the behavior of the defecating agent related to food processing, consumption, digestion, or excretion, which result in differences in the morphology and composition of coprolites (Hunt et al. 2012; Marinova et al. 2013).

The high preservational quality of the coprolites, sometimes considered as a *Konservat Lagerstätten*, provides a unique information on the diet and digestive system of the producing agent, which is not found elsewhere (Seilacher et al. 2001; Bull et al. 2002; Hollocher and Hollocher 2012; Qvarnström et al. 2016). The feces of certain types of organisms are more durable than others, thus being more prone to fossilization. In particular, the coprolites excreted by carnivores, and especially by those like hyenas, whose diet includes a large amount of bones, have a preservation advantage due to their phosphatic composition and bone fragments content, which facilitates their fossilization. This explains why the coprolites of carnivores are much better preserved and largely outnumber those of herbivores (Chin 2002; Hollocher and Hollocher 2012; Linseele et al. 2013).

Coprolite size is also very indicative, as fecal volumes roughly scale with the body mass of the animal. By this reason, modern feces allow to infer, approximately, the size of the organism that produced them (Chin 2002; Farlow et al. 2010; Fig. 11). In addition, inclusions within coprolites provide information on the prey consumed by carnivores and omnivores, including humans (Reinhard et al. 2007): different species of mammals, birds, reptiles, fish, mollusks, and crustaceans have been identified in coprolites (Zangerl and Richardson 1963; Speden 1969; Waldman 1970; Bishop 1977; Parris and Holman 1978; Sohn and Chatterjee 1979; Martin 1981; Stewart and Carpenter 1990; Coy 1995; Meng and Wyss 1997; Meng et al. 1998; Chin 2002; Rhode 2003; Harrison 2011; Qvarnström et al. 2019; Bellusci et al. 2021). Coprolites can also provide evidence on predator–prey relationships, digestive efficiency, parasitism, or for identifying fauna not represented in the fossil record, e.g., through the identification of hairs included in coprolites (Chin 2002; Taru and Backwell 2013; Qvarnström et al. 2016).

Another interesting aspect of the study of coprolites is the floristic characterization of the environment through the study of pollen and spores, which are usually preserved within them. Many studies have reported on the presence of fossil pollen in coprolites (Scott 1987; Carrión et al. 2001; Scott et al. 2003; Diedrich 2012; Pineda et al. 2017). Unfortunately, pollen and palynomorphs are scarce and poorly preserved in the sediments of FN3 (Jiménez-Moreno 2003) and only one recent study has reported on them (Ochando et al. 2022). In the case of the coprolites from the Orce sites, efforts to locate pollen have not yielded positive results (Carrión, 2002; Carrión et al. 2009). In addition to pollen, others components not directly related to the diet that can be present in the coprolites are parasites, minerals, or phytoliths (Reinhard and Bryant 1992; Lewis 2011).

Hyena coprolites are easily distinguishable from the excrements of other carnivores because they contain a high proportion of CaO and P<sub>2</sub>O<sub>5</sub>, which results from the consumption and digestion of bones (Kruuk 1972, 1976; Larkin et al. 2000). Hyena coprolites consist of aggregates that show a predominance of spheroidal and globular forms, with a whitish color and gritty texture (Horwitz and Goldberg 1989; Saunders and Dawson 1998; Larkin et al. 2000). Diedrich (2012) characterized the morphology of the feces and coprolites attributed to recent (*Crocuta crocuta*) and Late Pleistocene spotted hyenas (*Crocuta spelaea*) from Central Europe found in caves and open-air sites. He found that these coprolites are composed of aggregates of various individual elements (pellets), which he classified in seven shape types (see Diedrich 2012).

As noted above, coprolite size is very informative, because it usually correlates with the size of the defecating agent. However, other factors may also play an important role in the final morphology, size, and composition of the coprolite, including season of year, health and age of the individual, or type and amount of food ingested. As result, carnivore species of different sizes produce scats that overlap metrically (Farrell et al. 2000; Harrison 2011; Linseele et al. 2013; Taglioretti et al. 2014; Shillito et al. 2020), although the low dietary variability in the bone-cracking hyenas favors less variability in fecal morphology than in other carnivores with more varied diets (Stuart and Stuart 1998; Chin 2002; Chame 2003; Diedrich 2012). In their analysis of spotted hyena droppings, Larkin et al. (2000) concluded that they are hard and durable, sink rapidly in water, and withstand considerable trampling in the sediment while retaining a consistent shape, thus being recognizable for a long time.

In addition to shape and consistency, color is one of the most characteristic features of hyena feces, which turn white when dried, constituting the classic “album graecum” (Buckland 1824).

Finally, given that hyenas are bone-cracking carnivores, their feces contain small bone fragments and/or teeth that show evidence of digestion, pollen (mainly from the

stomach and intestines of their prey), and sometimes also hairs, which can be present as inclusions in the coprolites (González-Sampériz et al. 2003; Backwell et al. 2009). The droppings of extant spotted hyenas use to preserve small bone fragments with evidence of digestion and very small amounts of organic matter (Kruuk 1972; Larkin et al. 2000). In the case of the striped hyena (*Hyaena hyaena*), which has a more varied diet, the drops generated have more organic contents (Horwitz and Goldberg 1989).

Fossil coprolites are common in many paleontological sites. Their earliest record, attributed to an invertebrate, dates back to the Cambrian (Chen et al. 2007; Hunt et al. 2012), and vertebrate coprolites are frequently reported through the Phanerozoic Era (Northwood 2005; Backwell et al. 2009; Owociki et al. 2012; Vajda et al. 2016). Hunt and Lucas (2019) provided a list of more than 230 sites that preserve Pleistocene sloth and hyena coprolites. Pineda et al. (2017) published the presence of two latrines in the Early Pleistocene deposits of the Iberian Peninsula, at La Mina (Unit II, Barranc de la Boella, Tarragona) and TD6.1 (Sierra de Atapuerca, Burgos). In the case of FN3, Espigares et al. (2013) identified 34 hyena coprolites, attributed to *P. brevirostris*, which surrounded an elephant (*Mammuthus meridionalis*) carcass unearthed in the year 2002. Since this finding, the number of coprolites recovered in the site until the year 2015 has increased to 220, 3 in the LAL and 217 in the UAL.

The giant, short-faced hyena *Pachycrocuta brevirostris* is commonly recorded in the Early Pleistocene sites of the Orce area (Palmqvist et al. 2011). This species is considered by some authors as more closely related (and in all probability also as ethologically closer) to the extant brown hyena (*Parahyaena brunnea*) and striped hyena, which both behave more as a scavenger than as a hunter and have a more omnivorous diet than the spotted hyena (Kruuk 1972, 1976; Stuart 1982; Turner 1990, 1992). A study of jaw biomechanics of *P. brevirostris* has shown that this extinct hyena was able of exerting a substantially greater bite force during bone fracturing compared to the living hyenas (Palmqvist et al. 2011). The Venta Micena site in Orce has been interpreted as a number of bone accumulations originated by *P. brevirostris* around their breeding dens. Taphonomic studies have shown a high degree of bone modification, as many of the remains accumulated by the hyenas are fractured and important anatomical portions are missing (Arribas and Palmqvist 1998; Arribas 1999; Palmqvist and Arribas 2001; Espigares 2010; Palmqvist et al. 2022a; Yravedra et al. 2022b), and there are some bones with evidence of digestion (Espigares 2010; Palmqvist et al. 2022a). These data, together with the enormous size estimated for *P. brevirostris* (~ 110 kg; Palmqvist et al. 2011), suggest that the coprolites of this species should resemble more closely the ones

of the extant *C. crocuta* than those of the other two living bone-cracking hyenas.

In this paper, we analyze the accumulation of coprolites in FN3 with the goal of characterizing their mode of accumulation and obtaining paleoecological and ethological inferences about the putative defecating agent, the giant hyena *P. brevirostris*.

## Scent marking and latrines in hyenas

Latrines, which have been reported in numerous animal species, are generated by the repetitive use of the same place for defecation. This usually results in the accumulation of between two and several hundred of feces (Buesching and Jordan 2019). Latrines are used not only for defecation and urination, but also for the deposition of glandular secretions useful for scent marking of the territory (Macdonald 1980; Gorman and Mills 1984; Mills and Gorman 1987; Buesching and Jordan 2019). Several hypotheses have been suggested for explaining the use of latrines in different species, including protection of food resources, information center, reproductive advertisement, predator–prey interactions, and landmarks that facilitate orientation (Buesching and Jordan 2019).

Hyena latrines are frequent in open-air settings and use to be associated with environmental features, including dry pools, tracks or roads, on top of a dune, at a tree, at a kill, in the open, or at tall thick vegetation (Gorman and Mills 1984; Mills and Gorman 1987). However, latrines can also be found in other contexts, such as caves (Brain 1981; Berger et al. 2009; Pineda et al. 2017). Differences have been observed in the proportions in which these environmental features are chosen depending on the hyaenid species. For example, a high percentage of latrines of brown hyenas are located near a tree or shrub, while spotted hyenas prefer a track or road, a dry pool, or on top of a dune (Gorman and Mills 1984; Mills and Gorman 1987). However, intraspecific variation resulting from different ecological pressures is also observed, as shown by two populations of *C. crocuta* in the southern Kalahari Desert and Ngorongoro Crater, respectively (Mills and Gorman 1987).

Latrines play an important role for hyaenids, as all living species (including *C. crocuta*, *H. hyaena*, and *P. brunnea*, but also the aardwolf *Proteles cristata*) scent mark their territories depositing feces at latrines and secretions produced by their anal pouch onto the grass (Gorman and Mills, 1984).

Bearder and Randall (1978) distinguished between “temporary latrines” and “long-term latrines.” The formers tend to develop in the short-term around sites of interest, such as the surroundings of large ungulate carcasses (as in the case of the elephant carcass of FN3; Espigares et al. 2013), whereas the latter relate to prominent environmental features scattered throughout the territory, which the hyenas visit regularly

during long periods of time. In a study on the spatial use and seasonal patterns of *C. crocuta* communal latrines, Vitale et al. (2020) documented several latrines used during two or three consecutive years and observed an annual cycle of latrine use related to seasonal rainfall: the scats were mainly accumulated during the dry season, while they largely disappeared due to rainfall during the wet season.

Despite the use of latrines by all extant hyaenids, some interspecific variations can be noted. Skinner and Van Aarde (1981) documented differences between *P. brunnea* and *C. crocuta* latrines: the ones of *P. brunnea* are smaller and clearly demarcated, being probably used by single individuals; in contrast, the latrines of *C. crocuta* spread over an area of about 100 m<sup>2</sup> and the feces are deposited communally by all clan members, with the individuals defecating or emitting glandular secretions (paste) on top of other preexisting feces or pastes. The result is a mixture of scents produced by different individuals, which can be detected from at least 2 km downwind (Mills and Gorman 1987).

### The site of Fuente Nueva-3

FN3 is an open-air site that lies in the NE sector of the Guadix-Baza Depression (Orce, SE Spain) (Fig. 1a–b), a postorogenic Neogene-Quaternary intramontane basin that extends over an area of ~4000 km<sup>2</sup> and preserves a thick sedimentary record composed of lacustrine and fluvial deposits (García-Aguilar and Palmqvist 2011; García-Aguilar et al. 2014, 2015; Palmqvist et al. 2022b). The depression was subject to intense hydrothermal activity, which provided mild and productive environments for the terrestrial fauna during the Early Pleistocene (García-Aguilar et al. 2014, 2015), the remains of which were preserved in abundant paleontological localities in the vicinities of the town of Orce (Martínez-Navarro 1991; Arribas and Palmqvist 1998; Palmqvist et al. 2011, 2022a, 2022b; Martínez-Navarro et al. 2018; Granados et al. 2021).

### Chronology

The age of the fertile levels of FN3 has been estimated in  $1.19 \pm 0.21$  Ma using a combined approach based on biostratigraphy, magnetostratigraphy, and electron spin resonance (ESR) (Duval et al. 2012; Toro-Moyano et al. 2013). In addition, an age of  $1.50 \pm 0.31$  Ma has been derived for FN3 based on cosmogenic nuclides (Álvarez et al. 2015). Moreover, suids are absent from Europe in the biochronological range comprised between the post Tasso Faunal Unit, which marks the base of the Late Villafranchian (~1.8 Ma), and their arrival in Western Europe at layer TE9 from Sima del Elefante (1.22 Ma) (Martínez-Navarro et al. 2015). Therefore, their absence from FN3 suggests an age

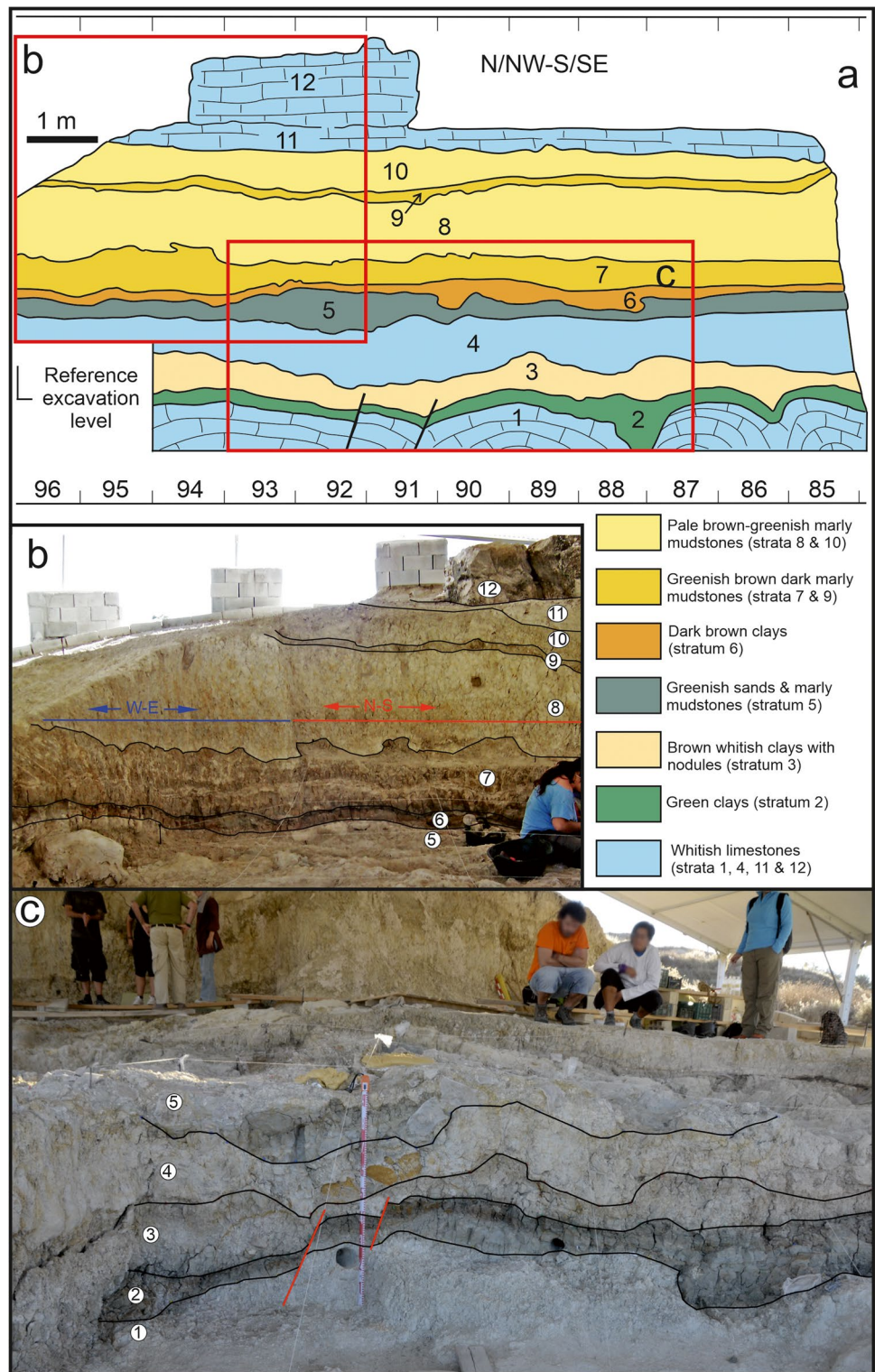
older than 1.22 Ma for this site. According to all these lines of evidence, the most parsimonious age estimate for FN3 is ~1.4 Ma (Palmqvist et al. 2016).

### Stratigraphy

Twelve layers, numbered from bottom to top, have been described in the slightly sub-horizontal stratigraphy of the FN3 site (Oms et al. 2011). This stratigraphy consists of a succession of layers constituted by nodular whitish limestones (layers 1, 4, 11, and 12), irregular layers of yellowish marly lutites (layers 2, 3, 6, 7, 8, 9, and 10), and a layer of dark greenish sands in intermediate position (layer 5) (Figs. 1c and 2). These layers can be grouped into three sedimentary cycles (Fig. 1c). Each cycle shows a lower part constituted by levels of colored marly lutites and clays, as well as levels of sands with frequent iron oxides and carbonate nodules, and an upper part characterized by limestones with evidence of microkarstification, together with intraclasts and diagenetic markers. Subaerial pedogenesis is evident in all stratigraphic levels. Therefore, the first cycle is only represented by its upper part, layer 1; the second cycle comprises layers 2 to 4, and the third cycle is formed by layers 5 to 12 (Figs. 1c and 2). These cycles were deposited in a lutitic-carbonate, shallow lacustrine to swampy environment, which was variable in depth and facies type, and sporadically subject to fluvial influence.

Most of the layers of the FN3 site have a variable thickness, showing irregular boundaries between them due to soft-sediment deformation structures and erosive processes. Layers 1, 2, and 3 show plastic deformation, specially in the case of layer 1, which has a rounded surface, similar to pillows (Fig. 2). These layers are also affected by two small syn-sedimentary normal faults, with a vertical throw of a few centimeters (Fig. 2). These soft-sediment deformation structures are generally explained as the result of earthquakes (Oms et al. 2011) and have been described in other parts of the Baza Basin (Alfaro et al. 1997, 2010). Layer 4 appears to have been less affected by these deformations and its deposition fits the paleosurface, while its top is irregular and eroded by layer 5. Layer 5 consists of sands with lenticular shapes that can be interpreted as the result of low-energy fluvial flows. These flows may have eroded the unconsolidated top of layer 4 and, then, by decreasing the energy of the flows, the channels would be filled, flattening the surface. Very low energy flows would deposit silts and fine sands in level 5, where most of the fossil remains are found. Later, a succession of marly lutites and clays were deposited, forming layers 6 to 10. The boundary between layers 7 and 8 shows an important irregularity, which can be indicative of an erosive process and, therefore, a subaerial event in the lake margin. Finally, the stratigraphic section of FN3 ends with the

**Fig. 2** **a** Stratigraphic scheme of the layers of the FN3 site (modified from Oms et al. 2011). **b** Image showing the morphology of the upper layers (5 to 12). **c** Image showing the morphology of the lower layers (1 to 5). Red lines indicate faulting.



deposition of horizontal limestones (layers 11 and 12). It is worth noting that the layers with mammal bones and lithic tools do not show evidence of noticeable transport by traction currents (Oms et al. 2011).

From an archeological point of view, the fertile stratum of FN3 has a thickness of about 1.5–2 m and comprises layers 1 to 7, which have been grouped in two main archeological levels (Fig. 1c): the Lower Archeological Level (LAL,

layers 1–3) and the Upper Archeological Level (UAL, layers 4–7) (Turq et al. 1996; Martínez-Navarro et al. 1997; Oms et al. 2010, 2011; Espigares et al. 2013, 2019; Reinoso et al., 2020; Palmqvist et al. 2023). Although bone remains and lithic tools have been recovered from six different layers, most of them come from layers 2, 3, and 5 (Table 1).

Ancient anthropic presence is documented in FN3 by the presence of huge tool assemblages (up to the 2015 excavation season, 1367 Mode 1 lithic artifacts + 375 stones, most of which were probably intentionally brought to the site by the hominins). The tools are mainly composed of flakes and debris made on flint and limestone, lithologies that outcrop in the site surroundings (Barsky et al. 2010, 2015a, 2015b; Toro-Moyano et al. 2011), and are associated to a rich fossil assemblage with remains ( $n=9041$ ) of 19 species of large mammals. The taxonomic spectrum includes a proboscidean (*M. meridionalis*), three perissodactyls (rhino *Stephanorhinus hundsheimensis* and horses *Equus altidens* and *Equus suessenbornensis*), seven artiodactyls (hippo *Hippopotamus antiquus*, bison *Bison* sp., water buffalo *Hemibos* sp. cf. *gracilis*, goat *Hemitragus albus*, sheep *Ammotragus europaeus*, megacerine deer *Praemegaceros* cf. *verticornis*, and fallow deer *Metacervocerus rhenanus*), and eight carnivores (lynx *Lynx* cf. *pardinus*, hyena *P. brevirostris*, painted dog *Lycaon lycaonoides*, jackal *Canis mosbachensis*, fox *Vulpes alopecoides*, bear *Ursus etruscus*, weasel *Martellictis ardea*, and badger *Meles meles*) and some remains of probably two sabertooth cats. In addition, remains of small mammals (15 spp., including a porcupine), herpetofauna (23 taxa), and some avian fossils are also preserved (Martínez-Navarro et al. 1997, 2003, 2010; Espigares et al. 2019; Bartolini-Lucenti and Madurell-Malapeira 2020; Ros-Montoya et al. 2021; Martínez-Monzón et al. 2022; Palmqvist et al. 2023 and references therein).

Taphonomic analyses concluded that the subsistence strategies of the FN3 hominins included the exploitation of carcasses of medium-to-large sized animals for obtaining

meat, fat, and bone marrow. These activities are evidenced by the preservation of cut marks resulting from defleshing, evisceration, disarticulation, and skinning, as well as from periosteum removal. Intentional breakage of bones is based on evidence of percussion marks, pits, notches, impact flakes, and negative flake scars produced during bone fracturing to access the medullary cavities (for details, see Espigares et al. 2019; Palmqvist et al. 2023). Some bones (~3%; Yravedra et al. 2021) preserve tooth marks, although modification by carnivores is less frequent than that of anthropogenic origin (Espigares et al. 2019; Yravedra et al. 2021; Palmqvist et al. 2023). Size and morphology of most tooth marks suggest that they are the result of a large carnivore, probably the hyena *P. brevirostris*, although some marks of a small carnivore have been also identified (Espigares et al. 2013, 2019), probably the medium-sized canid *C. mosbachensis*, which tooth marks have been identified in the bone assemblage from BL (Courtenay et al. 2023). Moreover, there are some marks made by porcupines (Espigares et al. 2019). In addition to the tooth marks, carnivore activity is manifested by the presence of abundant coprolites tentatively attributed to *P. brevirostris*, which are especially abundant in the UAL (Espigares et al. 2013, 2019; Yravedra et al. 2021).

The rich lithic assemblage from FN3 and the inferences on resource availability and competition intensity among the members of the carnivore guild provide interesting data on the subsistence strategies of the earliest hominin population of Western Europe (Rodríguez-Gómez et al. 2016; Espigares et al. 2019; Palmqvist et al. 2022b).

## Materials and methods

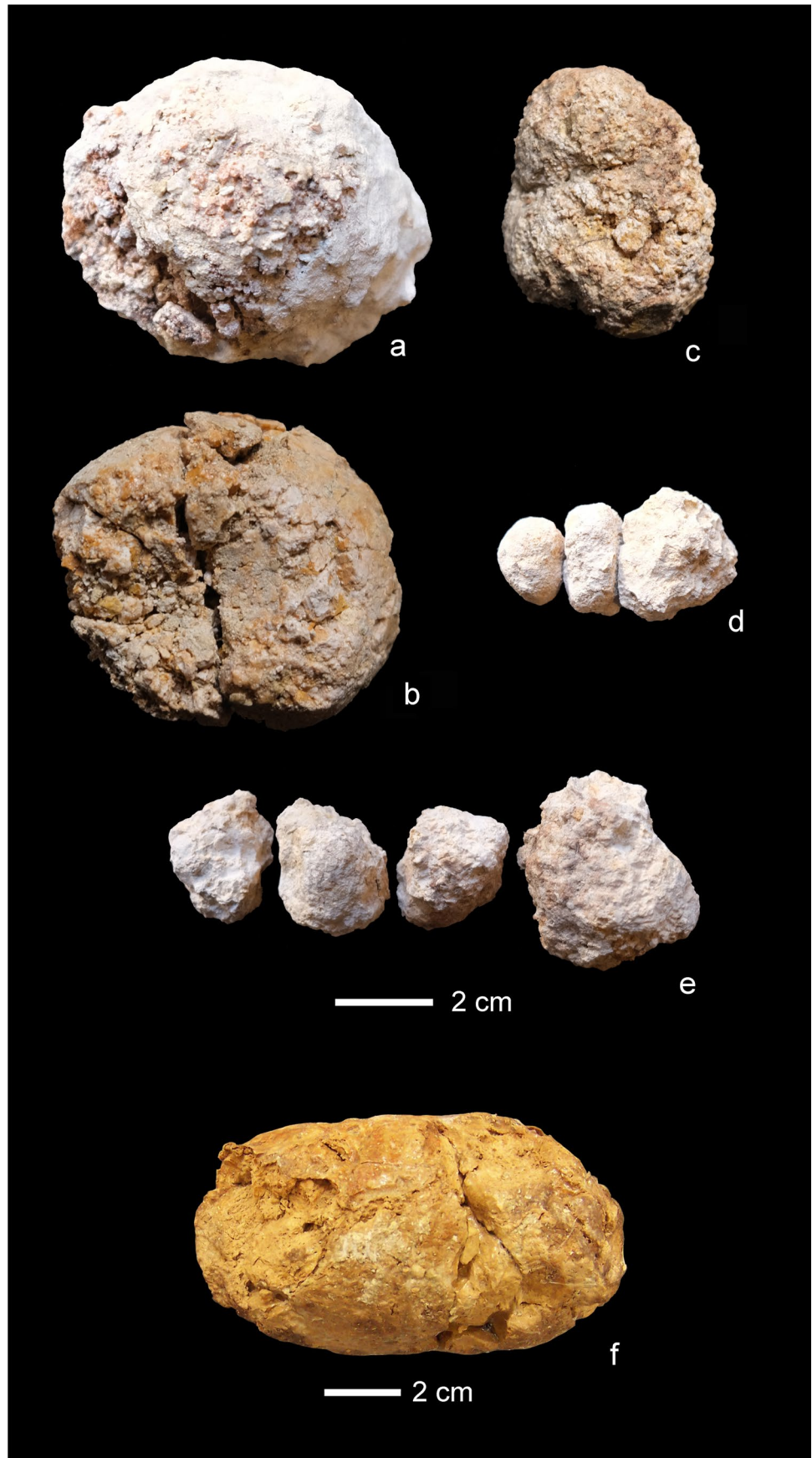
The coprolites analyzed in this study mainly belong to layer 5 of the UAL ( $n=216$ ) although one coprolite was found in layer 7 and three coprolites are from LAL

**Table 1** Number of bones, remains of *M. meridionalis*, coprolites, lithic tools, and stones from FN3 grouped by layers. Category 2–3 corresponds to materials recovered during the excavation campaigns up to the year 2003, in which the remains from both stratigraphic

	Layer	<i>M. meridionalis</i>	Bones*	Coprolites	Lithic tools	Stones	Total
LAL	1 (top)	–	27	–	9	–	36
	2	–	330	1	43	–	374
	3	–	434	2	140	8	584
	2–3	41	1443	–	315	321	2120
	LAL total	41	2234	3	507	329	3114
UAL	4	–	–	–	–	–	–
	5	315	5466	216	468	46	6511
	6	22	203	–	6	–	231
	7	7	111	1	8	–	127
	UAL total	344	5780	217	482	46	6869

levels were collected together. Those records that could not be confidently ascribed to one layer have not been included in this table. \* includes the remains of *M. meridionalis*

**Fig. 3** Examples of coprolites analyzed. **a, b** Isolated pellets from FN3; **c, d, e** fussed pellets from FN3; **f** coprolite from BL





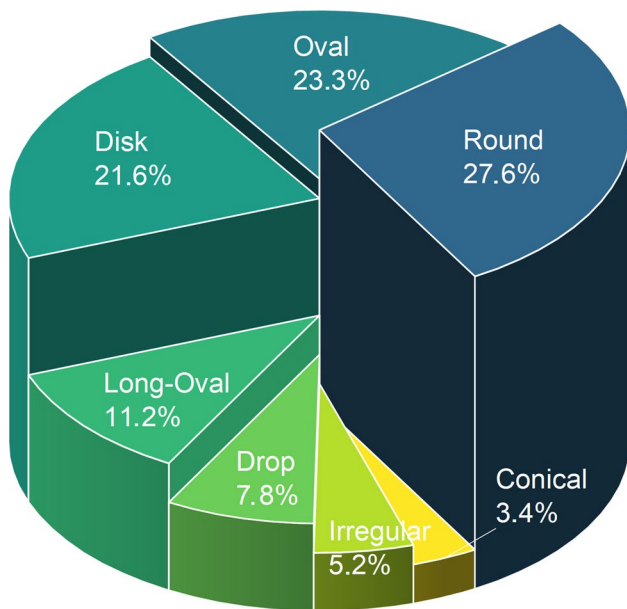


Fig. 4 Frequency of pellet morphologies in FN3

(Table 1). In addition, coprolites from the site of BL ( $n = 31$ ) have also been included in the study (Fig. 3). The coprolites were unearthed during systematic excavations and fieldwork at FN3 between the years 2001 and 2015. The preservational state of coprolites from open-air sites

is frequently worse than those recovered from caves. In the case of FN3, some specimens were recovered in good state of preservation at the time of excavation, but most of them presented a variable state of disintegration. This made it necessary to use an acrylic resin, Paraloid B 72, dissolved in acetone during the extraction of the coprolites for preserving them. Other coprolites were severely disaggregated at the time of excavation and it was only possible to recover the fragmented material in plastic bags. Moreover, feces of extant individuals of *C. crocuta* provided by the Research Department of OASYS Parque Temático del Desierto de Tabernas (OASYS-PTDT, Almería, Spain) have been analyzed using different techniques to compare them with the results obtained for the FN3 and BL coprolites.

In this study, the dimensions, morphology, and composition of the coprolites were analyzed. Due to the preservational state of coprolites, their length, width, and thickness was measured in 101 of them; in other 25 coprolites, only their length and width could be measured. Morphological analysis was performed following Diedrich (2012), who differentiated seven pellet morphotypes (conical, disk, oval, long-oval, round, irregular, and drop) (Fig. 4). Following Chin (2002), coprolite color was determined with the Munsell Soil-Color Charts (Munsell Color 1975).

The spatial distribution (x, y, z) of bones, coprolites, lithic artifacts, and stones was recorded using a Cartesian coordinate

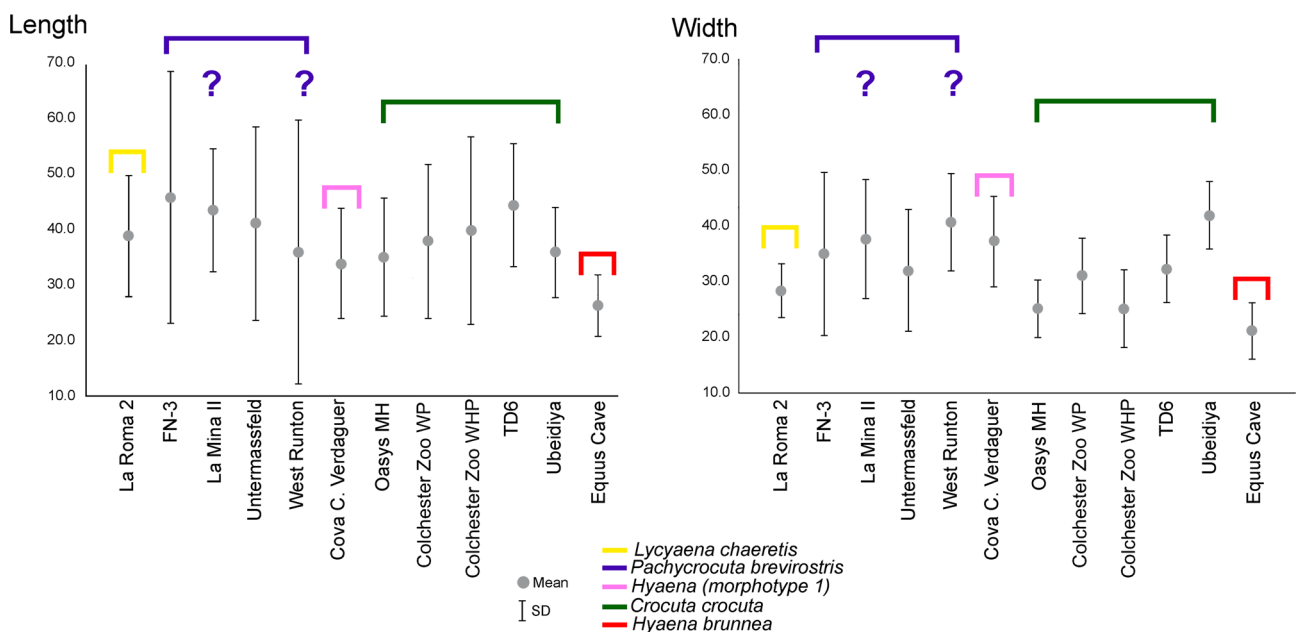


Fig. 5 Comparison of the length and width of the FN3 coprolites with the scats of modern *Crocuta crocuta* and the hyena coprolites from Europe and Africa. 1: La Roma 2 (Pesquero et al. 2011); 2: FN3 (original data); 3: La Mina II (Pineda et al. 2017); 4: Untermassfeld (Keiler 2001); 5: West Runton (Larkin et al. 2000); 6: Cova del Coll

Verdaguer (Sanz et al. 2016); 7 OASYS-PTDT (original data); 8: Colchester Zoo (with pellets) (Larkin et al. 2000); 9: Colchester Zoo (without pellets) (Larkin et al. 2000); 10: TD6 (Pineda et al. 2017); 11: Ubeidiya (Gaudzinski 2004); 12: Equus Cave (Fernández-Jalvo et al. 2010)

system. Scatter diagrams of the remains in both the vertical section (X–Z) and plant (X–Y) of the excavated surface of FN3 were created using Origin2021b software. In order to analyze the orientation of the elements, these data were represented in rose diagrams using the Stereonet software.

For components determination and coprolite mineralogical and chemical composition, ten samples of coprolites from FN3 and one from BL were selected. They were studied by X-ray diffraction (XRD), X-ray fluorescence (XRF), X-ray microscopic computed tomography (X- $\mu$ CT), and scanning electron microscopy (SEM).

XRD patterns were recorded using a Philips X'Pert PRO MPD at the Servicio Centralizado de Apoyo a la Investigación (SCAI) of the University of Málaga (UMA), with  $\text{CuK}\alpha_1$  radiation and Ge monochromator, operated at 45 mA and 35 kV, with  $0.01^\circ$   $2\theta$  step size and 2 s counting time. Randomly oriented samples were used to determine the semi-quantitative principal mineral composition, using the X'Pert High Score Software, based on Rietveld analysis, and the PDF2-2003 database (International Center for Diffraction Data).

Whole-rock analyses of the major elements of some samples were carried out using XRF in an ARL PERFORM<sup>X</sup> (Thermo Fisher) spectrometer (SCAI, UMA). Glass beads with lithium tetraborate were employed to minimize the preferential orientation of phyllosilicates. The detection limit for major elements was 0.4 wt.%. Ignition loss (LOI) was determined from 0.65 g of powdered sample, first dried at 105 °C and then heated at 950 °C for 2 h.

Sample 7 was analyzed with SKYSCAN 2214 (Bruker) X-ray computed microtomography (X- $\mu$ CT; SCAI, UMA).

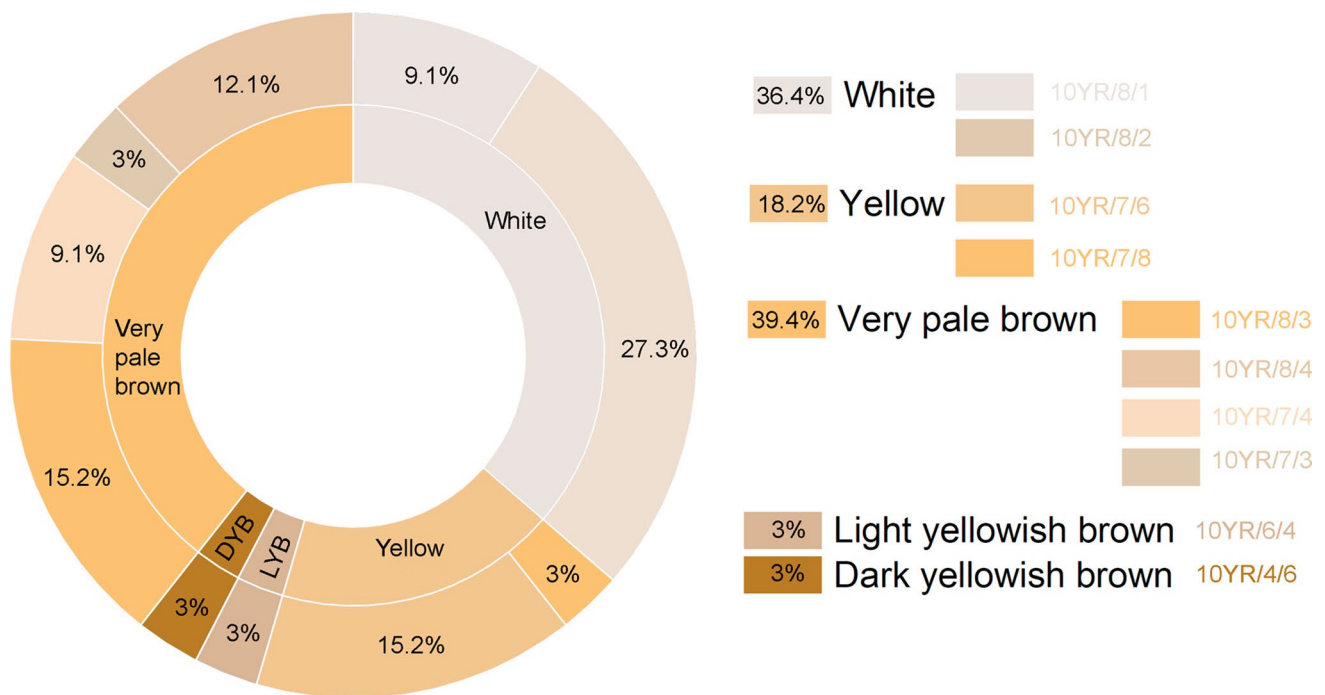
Images were obtained with an X-ray tube using a W filament (operated at 130 kV and 66  $\mu$ A) and employing a 1-mm Cu foil. The geometrical settings included a source to object distance of 37.696 mm and an object to detector distance of 313.309 mm. A set of 1276 images was acquired over a 360° rotation at 0.3° rotation steps, with an exposure time of 2.8 s and a resolution of 2276  $\times$  2880. Voxel size at the end of the image cleaning and enhancement process was 0.0748 isometric voxels (same value on the x-, y-, and z-axes).

The resulting image stacks were enhanced, removing background noise and potential artifacts resulting from data acquisition. For doing this, different algorithms and digital filters were implemented in specific virtual reconstruction and image processing software such as 3D Slicer v 4.9.0 (Kikinis et al. 2014) and ImageJ (Rueden et al. 2017). Subsequently, the enhanced images were segmented by thresholding the histogram of gray values (Pertusa 2010). This process is very sensitive and depends on material properties such as bone density and mineralization (Pérez-Ramos and Figueirido 2020).

Some selected coprolite samples were studied with a scanning electron microscope (SEM) to obtain textural feature images and punctual chemical composition of coprolites. These observations were carried out using a JEOL JSM-6490 LV SEM equipped with an X-ray energy-dispersive (EDX) system (OXFORD INCA Energy 350) at an accelerating voltage of 20 kV, 70 nA beam current, and counting time of 100 s per step, using internal available standards in microanalyses system. Samples were gold sputter coated (220 nm thick) to obtain secondary electron (SE)

**Table 2** Dimensions (in mm) of the pellets from FN3

		Number	Max	Min	Mean	SD
General dimensions	<i>Length</i>	126	120	1	43.7	20.3
	<i>Width</i>	126	80	1	34.0	14.2
	<i>Thickness</i>	101	50	1	21.0	12
Fused pellets	<i>Length</i>	4	180	30	89.8	66.8
	<i>Width</i>	4	70	20	47.8	21.1
Conical	<i>Length</i>	2	85	70	77.5	10.6
	<i>Width</i>	2	60	50	55.0	7.1
Disk	<i>Length</i>	24	35	3	13.7	9.1
	<i>Width</i>	44	75	20	49.0	14.6
Oval	<i>Length</i>	26	75	27	50.3	12.1
	<i>Width</i>	26	60	17	37.7	12.1
Long-oval	<i>Length</i>	12	120	30	81.7	27.7
	<i>Width</i>	12	80	15	47.9	17
Rounded	<i>Length</i>	30	52	15	33.9	10.5
	<i>Width</i>	30	50	15	30.5	10.2
Irregular	<i>Length</i>	3	33	30	31.7	1.5
	<i>Width</i>	3	28	18	22.0	5.3
Drop	<i>Length</i>	7	30	1	12.7	10
	<i>Width</i>	7	30	1	10.4	10.2



**Fig. 6** Proportions of matrix colors of the coprolites from FN3 using the Munsell Soil-Color Chart

images at 100 $\times$ , 500 $\times$ , 1500 $\times$ , 2000 $\times$ , 3000 $\times$ , 3500 $\times$ , 5000 $\times$ , and 10,000 $\times$  magnification.

Coprolite surfaces were analyzed with a digital microscope (DINO-LITE Model AM4115TL) for detecting and photographing small fragments of digested bones included in them.

The dimensions, morphology, and composition of the coprolites were compared with modern spotted hyena scats from Colchester Zoo (Larkin et al. 2000), OASYS-PTDT (original data), as well as with other modern and fossil scats of spotted hyenas (*C. crocuta*) and brown hyenas (*P. brunnea*) (Fernández-Jalvo et al. 2010) and hyena coprolites from European and African sites with a similar chronology, including BL (Larkin et al. 2000; Keiler 2001; Harrison 2011; Pesquero et al. 2011; Bennet et al. 2016; Sanz et al. 2016; Pineda et al. 2017; Espigares et al. 2019).

Coprolites were not intentionally disaggregated during the taphonomic analysis. The high disaggregation state of most of them allowed the observation of internal features, the identification of inclusions, and the sampling for mineralogical and chemical analysis.

## Results

### Morphological analysis

Almost all coprolites from FN3 are composed of isolated pellets (Fig. 3a–b), but at least six are formed by several

associated pellets (Fig. 3c–e), one of them linked to the carcass of *M. meridionalis* (Figs. 1d–e, 3). Three coprolites formed by several pellets (two composed of four irregular or drop-shaped pellets and one composed of two pellets with a rounded and irregular morphology) correspond to the posterior region of the coprolite. Two coprolites, composed of two pellets with long-oval and rounded morphologies, correspond to the central part of a coprolite. One coprolite, composed of two pellets with conical and disk-shaped morphologies, is from the anterior part of a coprolite (see Diedrich 2012: Fig. 5). Isolated pellets present a predominance of rounded, oval, and disk-shaped morphologies (Figs. 3 and 4). Coprolites are scarce at BL ( $N=31$ ), but their morphology is consistent with the characteristics described in FN3 (Fig. 3f).

### Dimensions

The pellets from FN3 are very variable in size. These differences can be attributed to the dissimilarities between the seven pellet-shape types defined by Diedrich (2012): pellets with conical, disk, oval, and long-oval shapes are larger than those with rounded, irregular, and drop shapes. In addition, the presence of some fussed pellets can mask their size (see Fig. 3). Size values from FN3 pellets are provided in Table 2.

The size of the FN3 coprolites is similar to those from the late Early Pleistocene (Jaramillo) site of Untermassfeld, where *P. brevirostris* has been conclusively identified (Keiler



**Fig. 7** Fragments of digested bones preserved in the FN3 coprolites

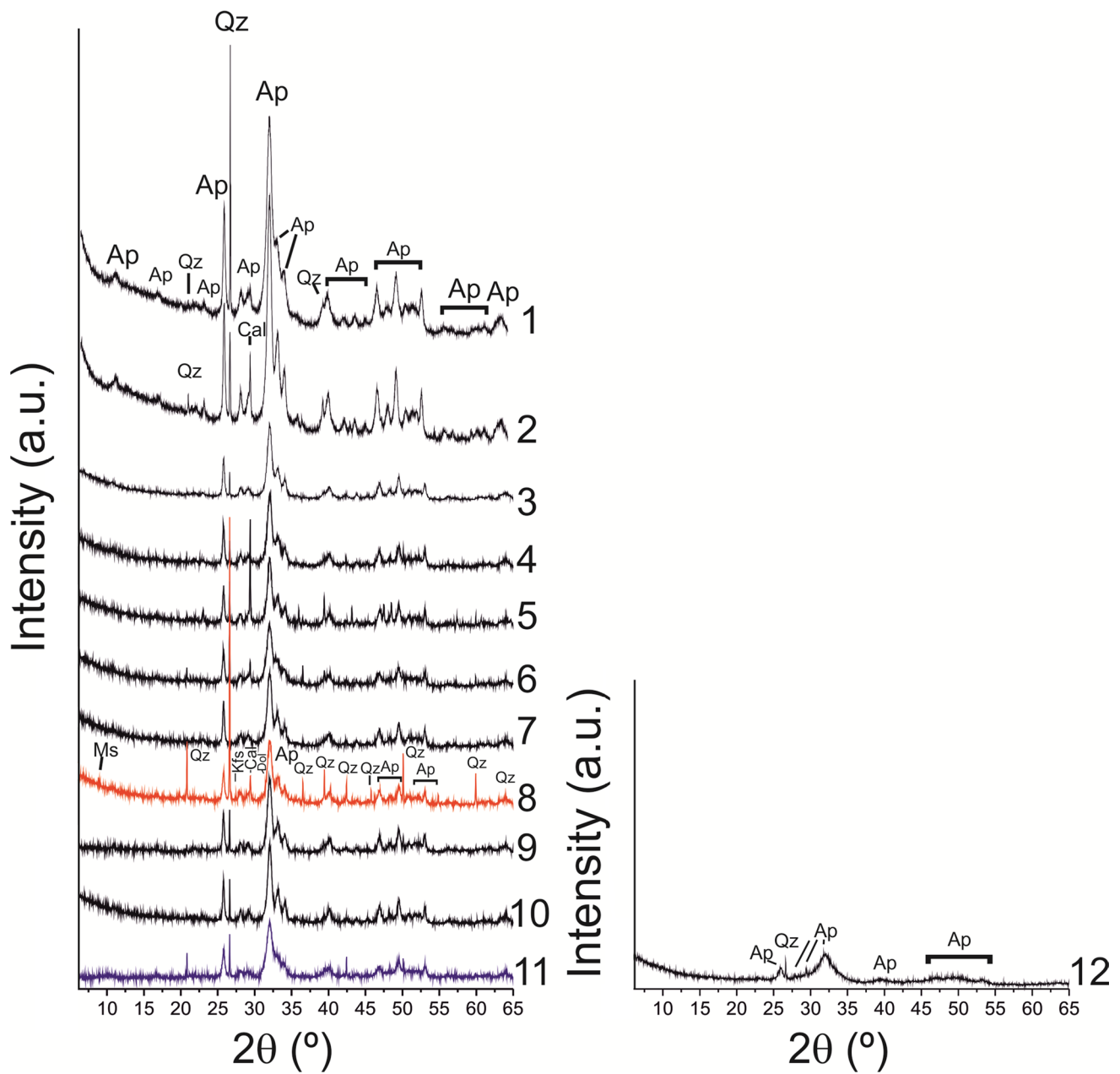
2001), and also to the coprolites from la Mina II and West Runton, sites in which it has been suggested that this hyena was probably present (Larkin et al. 2000; Pineda et al. 2017). These coprolites are clearly larger than those produced by spotted hyenas (*C. crocuta*) and especially by brown hyenas (*P. brunnea*) (Fig. 5). Given that there is a rough correlation between feces size and the body size of the defecating agent, the larger dimensions of the FN3 coprolites can be attributed to the huge body mass of *P. brevirostris*, which was a large and extremely powerful hyaena with a body mass in excess of 100 kg (Turner and Antón, 1996) compared to the living *C. crocuta* and *P. brunnea*, which have a mass of 55 kg and 42 kg, respectively (Palmqvist et al. 2011).

### Color

The color of hyena feces is a distinctive feature that facilitates their recognition. As noted before, the lower part

of the hyena's intestine contains the album graecum, a green paste which mixture with the mineral component of bone (calcium hydroxyapatite) results in the typical whitish color of the coprolites when they are in contact with the atmosphere (Buckland 1824; Matthews 1939).

According to the Munsell Color Chart for Soils, the FN3 coprolites show mostly white and very pale brown tonalities (Fig. 6). Sometimes the coprolites may be of darker colors. This evidences an abundance of organic matter inclusions, which are produced when the hyenas eat large quantities of flesh and grease (Matthews 1939), for example, when they find the carcass of a large-bodied ungulate (Bearder 1977). The 34 coprolites that surround a carcass of *M. meridionalis* at FN3 evidence this, showing darker tones than others found in the same stratigraphic level and more distantly placed from the elephant carcass, which tend to be lighter (Espigares et al. 2013).



**Fig. 8** X-ray diffraction diagrams of the studied coprolites. The numbers are the laboratory references of each sample. Abbreviations for minerals following Warr (2021). 1–10: Samples from FN3; 11: sample from BL; 12: sample of modern *Crocota crocuta* provided by

the Research Department of Oasys Parque Temático del Desierto de Tabernas (Almería, Spain). Ap, apatite; Qz, quartz; Cal, calcite; Ms, muscovite; Kfs, K-feldspar; Dol, dolomite; Pl, plagioclase

**Inclusions**

Coprolite contents can have different origins (animal, plant, mineral, or fungal) and can range broadly in size (Shillito et al. 2020). Macroscopic and digital magnification observation allowed to identify bone fragments of large mammals

inside many FN3 coprolites (Fig. 7). These fragments show diagnostic features, such as polishing, rounding, or thinning of the cortical surfaces, which evidence digestion. Bone fragments range between 1.1 and 19.2 mm. As previously mentioned, no fossil palynomorphs have been found in the coprolites from FN3.

**Table 3** Techniques used for the study of samples from FN3 and BL. Semi-quantitative mineral estimation from XRD of FN3 (samples 1 to 10) and BL (sample 11) outcrops. *XRD*, X-ray diffraction; *XRF*, X-ray fluorescence; *SEM*, scanning electron microscopy; *X-μCT*, X-ray microscopic computed tomography; *Tr*, trace. *Ap*, apatite; *Qz*, quartz; *Cal*, calcite; *Ms*, muscovite; *Kfs*, K-feldspar; *Dol*, dolomite; *Pl*, plagioclase

Site	Sample	XRD	XRF	SEM	X-μCT	Mineralogy						
						Qz	Kfs	Pl	Cal	Dol	Ap	Ms
FN3	1	x		x		13			2		85	
	2	x		x		6			3		91	
	3	x	x			6					94	
	4	x				6					94	
	5	x				8	Tr		20		72	
	6	x	x			15			2		83	
	7	x	x		x	2					98	
	8	x	x			36	9	6	3	Tr	42	4
	9	x	x			9					91	
	10	x				10			6		84	
BL	11	x	x	x		14					86	

## Analytcs data

### X-ray data and chemical bulk-rock composition

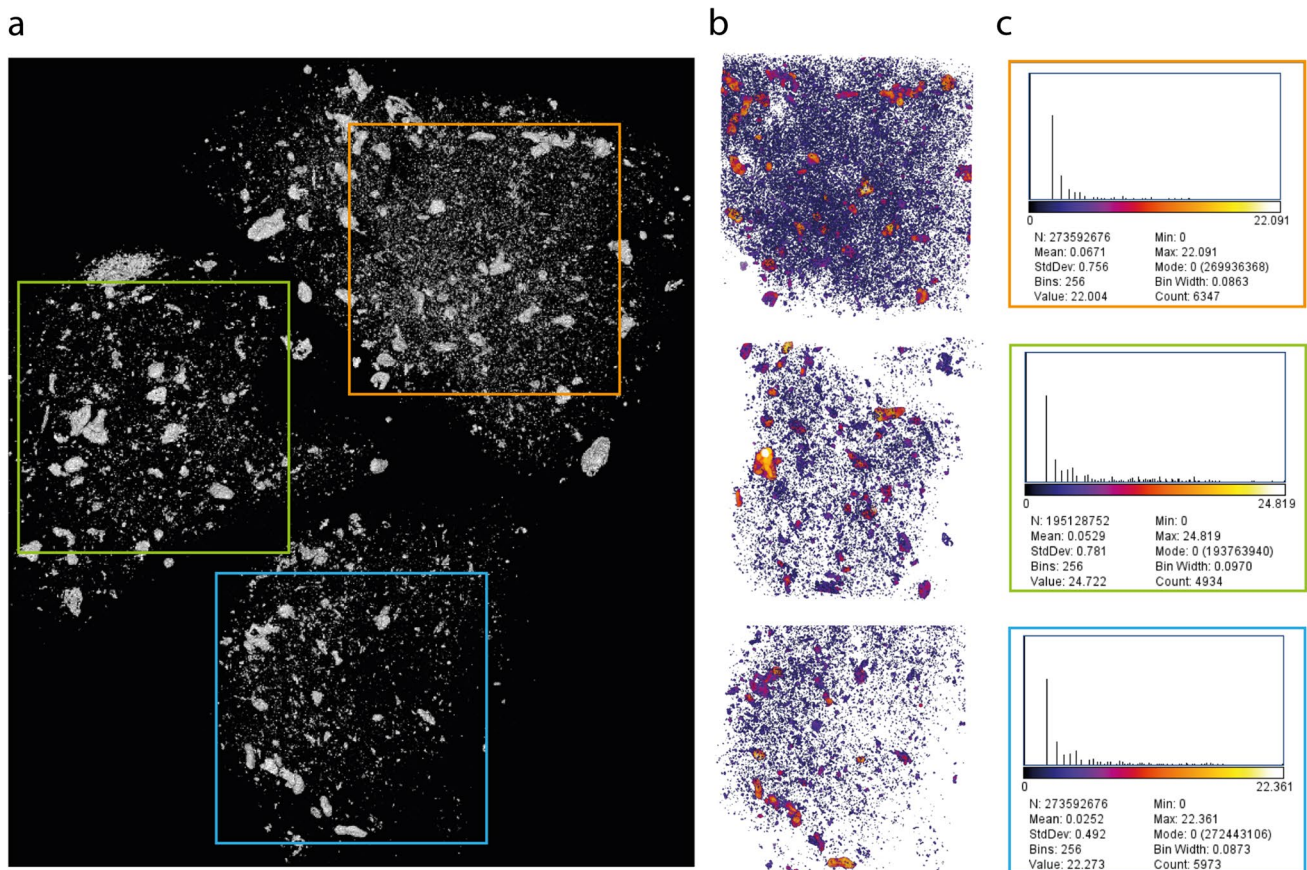
According to the XRD patterns, the studied coprolites mainly consist of calcium phosphate (> 80%; mostly fluorapatite and hydroxyapatite, and minor contents of carbonate-apatite) and quartz (~ 10%), accompanied occasionally by calcite [Fig. 8 (1–11) and Table 3]. The very high quartz contents (36%) and the existence of muscovite, feldspars, and dolomite in sample 8 (Fig. 8) suggest the contamination of this coprolite by the surrounding sediment. The

mineralogical composition of the studied coprolites is the same than in the feces of living hyenas from OASYS Parque Temático del Desierto de Tabernas (XRD diagram 12 of Fig. 8). Nevertheless, an increase of the high of the baseline and a bad signal/noise ratio are observed in the XRD diagrams from the hyenas' feces, due to the presence of amorphous material as organic matter.

Chemical analyses of major elements in some samples are given in Table 4. The most obvious difference is observed in the SiO<sub>2</sub> contents, which depend on the quartz content of the sample. Sample 8 shows the highest quartz contents (Table 4; Fig. 8, XRD diagram 8).

**Table 4** XRF whole-rock analyses of major elements (oxide weight, in %) of coprolites from FN3 (samples 3, 6, 7, 8, and 9) and BL (sample 11). (1) Normalized content of SiO<sub>2</sub>, Al<sub>2</sub>O<sub>3</sub>, CaO, K<sub>2</sub>O, and P<sub>2</sub>O<sub>5</sub> (oxide weight, in %). < BDL, below detection limit; LOI, loss on ignition

Oxide (wt. in %)	Sample 3	Sample 6	Sample 7	Sample 8	Sample 9	Sample 11
SiO <sub>2</sub>	2.59	7.25	0.48	22.44	2.74	4.36
Al <sub>2</sub> O <sub>3</sub>	0.60	1.21	0.22	2.26	0.34	0.29
Fe <sub>2</sub> O <sub>3</sub>	0.90	0.93	0.64	1.09	0.24	1.99
MnO	0.008	0.004	0.004	0.004	0.000	0.003
MgO	0.32	0.38	0.31	0.54	0.39	0.42
CaO	50.62	46.76	52.28	35.27	46.45	47.13
Na <sub>2</sub> O	0.52	0.53	0.82	0.79	0.65	0.63
K <sub>2</sub> O	0.17	0.31	0.06	0.83	0.09	0.06
TiO <sub>2</sub>	0.04	0.09	0.01	0.26	0.04	0.04
P <sub>2</sub> O <sub>5</sub>	34.87	31.19	36.03	23.18	31.85	31.73
Zr (ppm)	<BDL	105	<BDL	173	<BDL	<BDL
LOI (wt.%)	9.34	11.33	9.13	13.33	17.21	13.71
Total	99.98	99.99	99.99	99.98	99.99	100.32
<sup>(1)</sup> SiO <sub>2</sub> (wt.%)	2.92	8.36	0.54	26.72	3.36	5.22
<sup>(1)</sup> Al <sub>2</sub> O <sub>3</sub>	0.68	1.40	0.25	2.69	0.42	0.34
<sup>(1)</sup> CaO	56.97	53.91	58.70	42.00	57.02	56.39
<sup>(1)</sup> K <sub>2</sub> O	0.19	0.36	0.06	0.99	0.11	0.08
<sup>(1)</sup> P <sub>2</sub> O <sub>5</sub>	39.25	35.97	40.45	27.60	39.10	37.97
CaO/P <sub>2</sub> O <sub>5</sub>	1.45	1.50	1.45	1.52	1.46	1.49



**Fig. 9** Bone densitometric analysis and bone thickness distribution of a coprolite from FN3. **a** Bone densitometry: the three regions marked by squares show distinctive patterns. **b** Analysis of the distribution

of bone thickness in each region depicted in **a**. Cold colors (thickness  $\leq 1$  mm); warm colors (thickness  $\geq 1$  mm). **c** Plots of the distribution frequencies of bone thickness by region

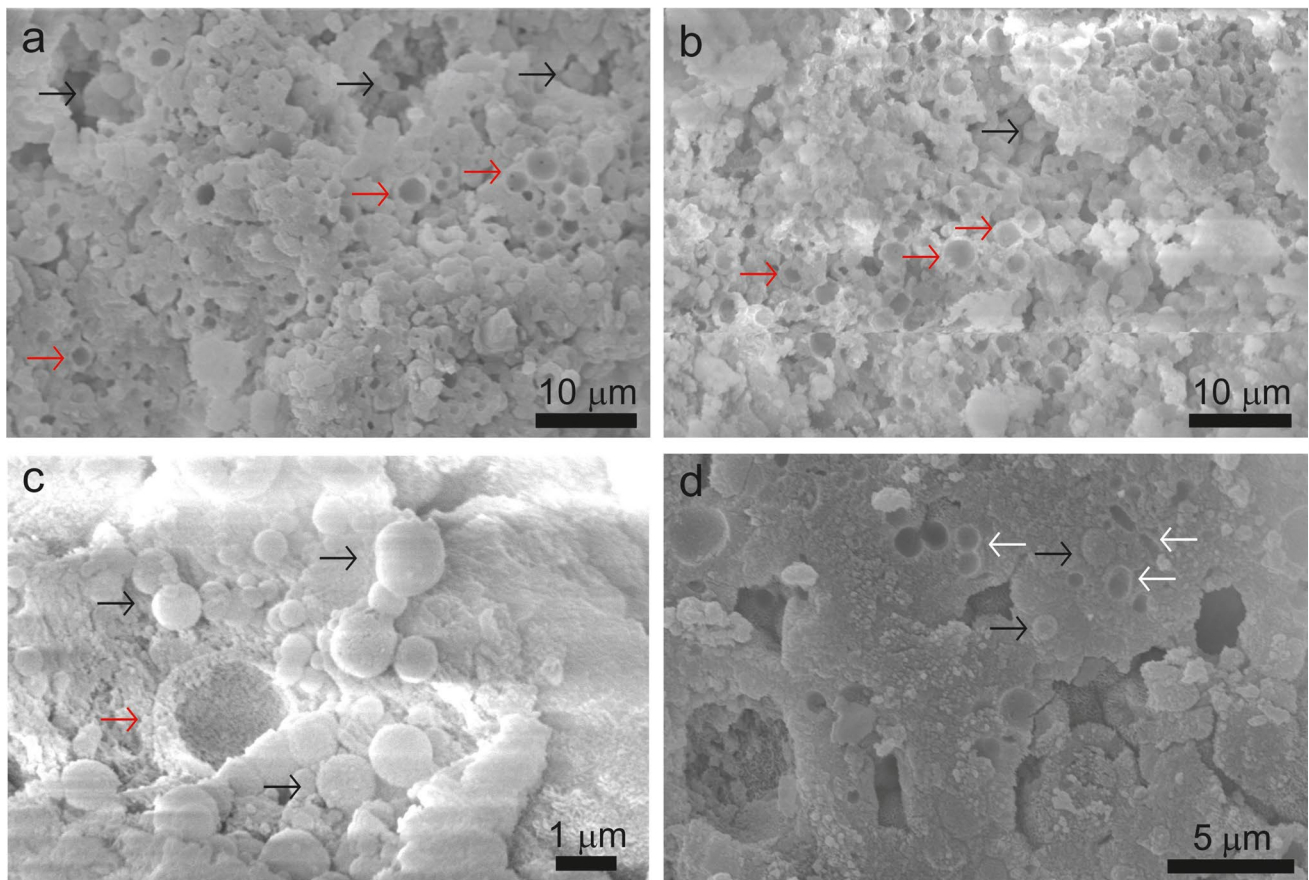
Furthermore,  $\text{Al}_2\text{O}_3$  and  $\text{K}_2\text{O}$  contents relate with the presence of K-feldspars and muscovite in sample 8 (Tables 3 and 4), which is due to the contamination of this sample by the surrounding sediment. Likewise, sample 6 shows high  $\text{Al}_2\text{O}_3$  and  $\text{K}_2\text{O}$  contents (Table 4), which are also suggestive of the presence of sediment remains, even though the index minerals do not appear in the XRD diagram (they probably appear as trace contents). Also, there is a positive correlation between the amounts of CaO and  $\text{P}_2\text{O}_5$  and the fluor- and hydroxyapatite contents of the samples (Tables 3 and 4), with the CaO to  $\text{P}_2\text{O}_5$  ratio being higher in those samples containing carbonate minerals (samples 6 and 8, Table 4). A high abundance of  $\text{P}_2\text{O}_5$  in the coprolites reflects the carnivorous diet of the defecating animal (Chin et al. 2003; Hollocher et al. 2010). In the FN3 coprolites, their high  $\text{P}_2\text{O}_5$  contents were probably derived from dissolved bone, microorganisms, and animal soft tissues.

### X- $\mu$ CT study

Figure 9 shows that many bone particles of small ( $< 10$  mm thick, cold colors) and large size (22 to 24 mm thick, warm colors) can be observed in the three coprolite fragments analyzed in the study by X- $\mu$ CT. The abundance of bone particles of  $\leq 24$  mm indicates the efficiency in bone chewing and bone cracking of the agent that produced the coprolites, and correlates with the composition of hyena coprolites observed in previous studies (Kruuk 1972; Holekamp et al. 1997; Van Valkenburgh and Binder 2021).

### SEM study

The secondary electrons (SE) images of coprolites from FN3 and BL show the presence of spherical or globular structures (Fig. 10a–d, black arrows) of 1 to 3  $\mu\text{m}$ , which sometimes reach up 5 or 6  $\mu\text{m}$  (Fig. 10a). Moreover, a porous



**Fig. 10** Secondary electrons (SE) images of coprolites from FN3 (**a–c**) and BL (**d**). **a–b** Typical aspect of coprolites from the archeological site of Fuente Nueva-3 (FN3), which are composed of microspherulites (black arrows) and spherical cavities (red arrows). **c** Details of microspherulitic structures and spherical cavities in the

FN3 coprolites. **d** Typical aspect of coprolites from the site of Baranco León (BL), which are composed of microspherulites (black arrows), small voids that resemble bacteria (white arrows), and large cavities

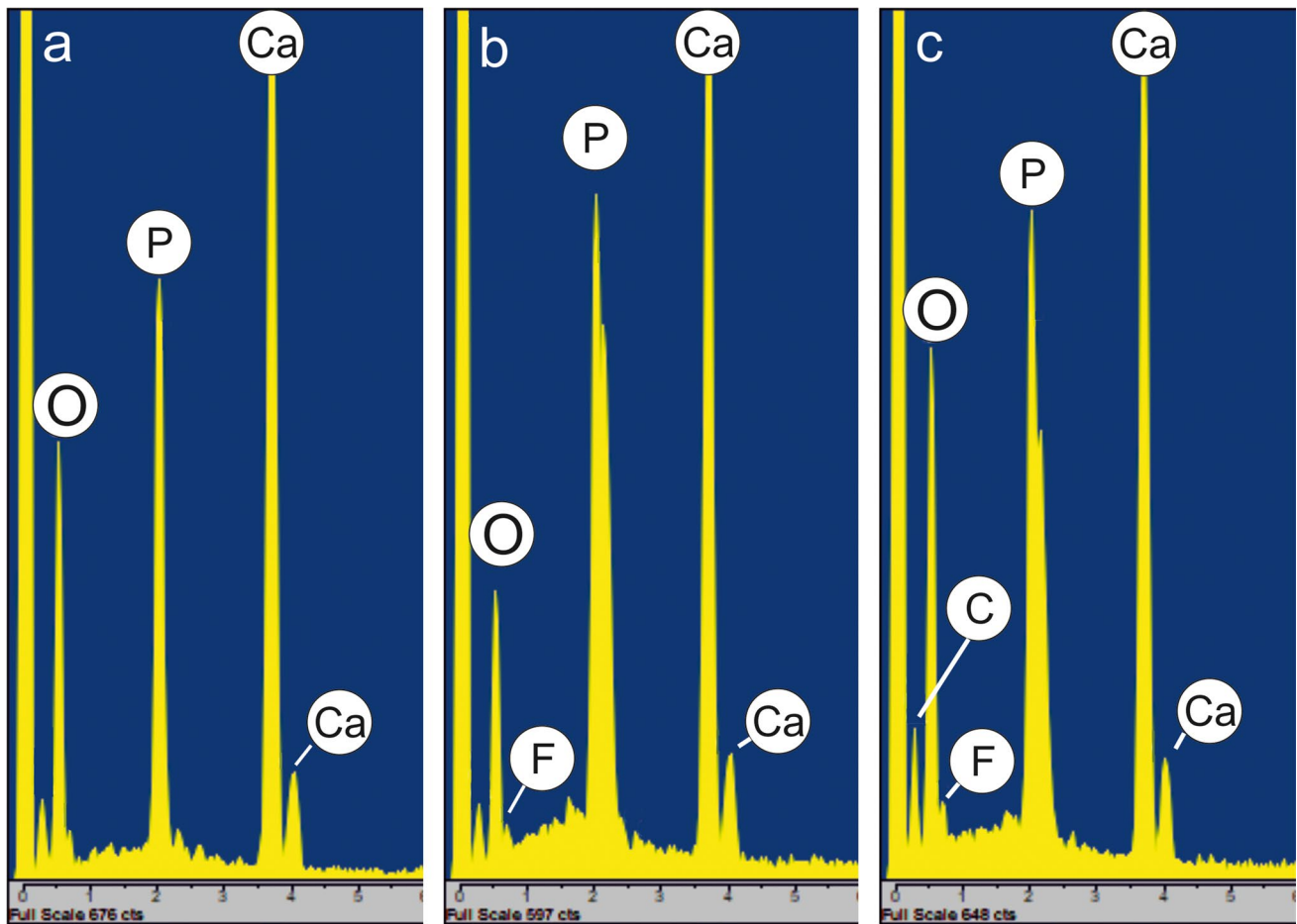
fabric or spherical cavities is also frequent (Fig. 10a–d, red arrows). These spherical or globular structures, which have been named in many studies as microspherulites (e.g., Canti 1999; Hollocher et al. 2010; Owocki et al. 2012; Pesquero et al. 2014; Pineda et al. 2017), are commonly found in hyena feces and coprolites. The BL coprolite shows abundant large cavities (Fig. 10d) and small elongated and circular voids (Fig. 10d, white arrows). The circular voids are microspherulites and the elongated ones resemble rod-shaped bacteria (Owocki et al. 2012; Pesquero et al. 2014; Pineda et al. 2017).

Some EDX spectra show high calcium and phosphorus peaks, which are indicative of the presence of hydroxyapatite, the major mineral phase of bone (Fig. 11a). Some of them also show a fluorine peak, which evidences the presence of fluorine apatite (Fig. 11b), a mineral phase that replaces in part hydroxyapatite in many fossils from the Orce sites (Arribas and Palmqvist 1998). Nevertheless, most spectra display a variable percentage of carbon (Fig. 11c). The chemical

analyses of the coprolites, obtained by SEM study, agrees with the presence of mineral contents of the higher apatite-group obtained from XRD data (Fig. 8, 1 to 11; Table 3) and with the high CaO and P<sub>2</sub>O<sub>5</sub> percentages detected in the XRF analyses (Table 4).

The composition of the FN3 coprolites was compared with extant and fossil feces attributed to different hyena species (Table 5) among which the values of a coprolite from BL was also included. The coprolites from FN3 and BL show similar Ca and P contents, with the exception of sample number 8, which is contaminated by sediment. These values are very similar to those of La Roma II site, where *Lycyaena chaeretis* is documented (Pesquero et al. 2011), and to one of the two coprolites published by Larkin et al. (2000) from Boxgrove, which are attributed to *C. crocuta*. The values in this table show Ca and P contents that are overall lower in the coprolites and feces of *C. crocuta* and especially in those of *H. hyaena*, which is by far the species with the lowest Ca contents compared to the coprolites attributed to *P. brevirostris*.





**Fig. 11** Profiles of the EDS analysis from different isolated points in the coprolites from Fuente Nueva-3. **a** Hydroxyapatite profile. **b** Fluorine-apatite profile with carbon. **c** Carbonate-apatite profile

### Spatial distribution

Figures 12 and 13 show separate longitudinal (X–Z) and plant (X–Y) sections, respectively, of the spatial distribution of skeletal remains, lithic tools, stones (i.e., limestone blocks that were presumably brought to the site by the hominins, half of which show evidence of impact; Espigares et al. 2013; Barsky et al. 2015b, 2022), hyena coprolites, and remains of *M. meridionalis*. As mentioned above, two main archeological levels can be distinguished in FN3, the Lower Archeological Level (LAL) and the Upper Archeological Level (UAL). In both levels, bones and lithic tools are frequently recorded. Stones predominate in the LAL. In contrast, coprolites and remains of *M. meridionalis* are mainly documented in the UAL. As a result, there is a band without skeletal remains in the X–Z projection (Fig. 12), which allows a visual differentiation between the LAL and UAL. It must be noted that the partial carcass of elephant that appears in Fig. 1d was unearthed within a block of sediment; for this reason, the Z-coordinates of these skeletal

remains were not recorded and they are not included in Fig. 12. The orientation of the bones has also been analyzed. Three rose diagrams have been produced, one for all bones for which orientation data are available, including the two archeological levels (Fig. 14a), and two others for the UAL and LAL considered independently (Fig. 14b, c). The rose diagram for all bones and that of the UAL show no preferred orientation of the skeletal remains, which allows to discard their allochthonous deposition and resedimentation. In contrast, the directions N–S, E–W, and to a lesser extent NE–SW and NW–SE are more represented in the LAL. However, it must be noted that these orientations are somewhat over-represented. The reason is that in the excavation seasons prior to the year 2005, from which most of the records of layers 2 and 3 come from, direction measurements were not taken with a compass. In any case, no preferential directions of accumulation related to bone transport by currents are evident, an interpretation also reinforced by the absence of polishing and rounding on the bone surfaces (Espigares 2010; Oms et al. 2011).

**Table 5** Results of calcium (Ca) and phosphorous (P) determination and loss on ignition (LOI) (expressed as percentages) from FN3, BL and modern and fossil fecal remains from different hyena species

	Ca	P	LOI	Method	Species	Reference	Nature
Col 01	26.93	11.34	18.59	Wet chemistry	<i>C. crocuta</i>	Larkin et al. 2000	Modern
Col 02	26.56	11.95	23.84	Wet chemistry	<i>C. crocuta</i>	Larkin et al. 2000	Modern
QEP	21.75	7.40	31.21	Wet chemistry	<i>C. crocuta</i>	Larkin et al. 2000	Modern
F5661 (box)	24.46	8.83	5.38	Wet chemistry	<i>C. crocuta</i>	Larkin et al. 2000	Fossil
F5662 (box)	35.08	14.31	6.16	Wet chemistry	<i>C. crocuta</i>	Larkin et al. 2000	Fossil
TN 01	28.41	13.36		Wet chemistry	<i>C. crocuta</i>	Lewis 2011	Fossil
<i>C. crocuta</i>	25.54 ± 10.76			Unknown	<i>C. crocuta</i>	Kruuk (1976; N=20)	Modern
<i>H. hyaena</i>	12.07 ± 7.2			Unknown	<i>H. hyaena</i>	Kruuk (1976; N=20)	Modern
FN3-S3	35.8	15.06	9.34	XRF	<i>P. brevirostris</i>	Original data	Fossil
FN3-S6	32.92	13.41	11.33	XRF	<i>P. brevirostris</i>	Original data	Fossil
FN3-S7	36.62	15.41	9.13	XRF	<i>P. brevirostris</i>	Original data	Fossil
FN3-S8	24.92	10.00	13.33	XRF	<i>P. brevirostris</i>	Original data	Fossil
FN3-S9	32.96	13.80	17.21	XRF	<i>P. brevirostris</i>	Original data	Fossil
BL-S11	33.20	13.65	13.71	XRF	<i>P. brevirostris</i>	Original data	Fossil
WR 01	28.71	10.94	13.32	Wet chemistry	<i>P. brevirostris?</i>	Larkin et al. 2000	Fossil
WR 04	26.17	11.91		Wet chemistry	<i>P. brevirostris?</i>	Lewis 2011; Parffit and Larkin et al. 2000	Fossil
RO-2007–26	32.23	16.54	15.2	XRF	<i>L. chaeritis</i>	Pesquero et al. 2011	Fossil
RO-2008–3	33.59	13.91	17.6	XRF	<i>L. chaeritis</i>	Pesquero et al. 2011	Fossil

## Discussion

This paper reports on the finding of a huge accumulation of coprolites in the UAL of FN3. These coprolites have been previously attributed to the giant hyena *P. brevirostris*, the only species of hyena documented in the Early Pleistocene sites of Orce (Espigares et al. 2013, 2019), of which several isolated teeth have also been recovered at the FN3 site.

Our results show that the morphology, size, color, mineralogical, and chemical composition (presence of apatite-group minerals, main inorganic constituent of bones, and high CaO and P<sub>2</sub>O<sub>5</sub> contents) of the coprolites, as well as the inclusions of bone fragments and the presence of microspherulites in them, match with those expected in the coprolites produced by a large hyena, which confirms their previous ascription to *P. brevirostris*.

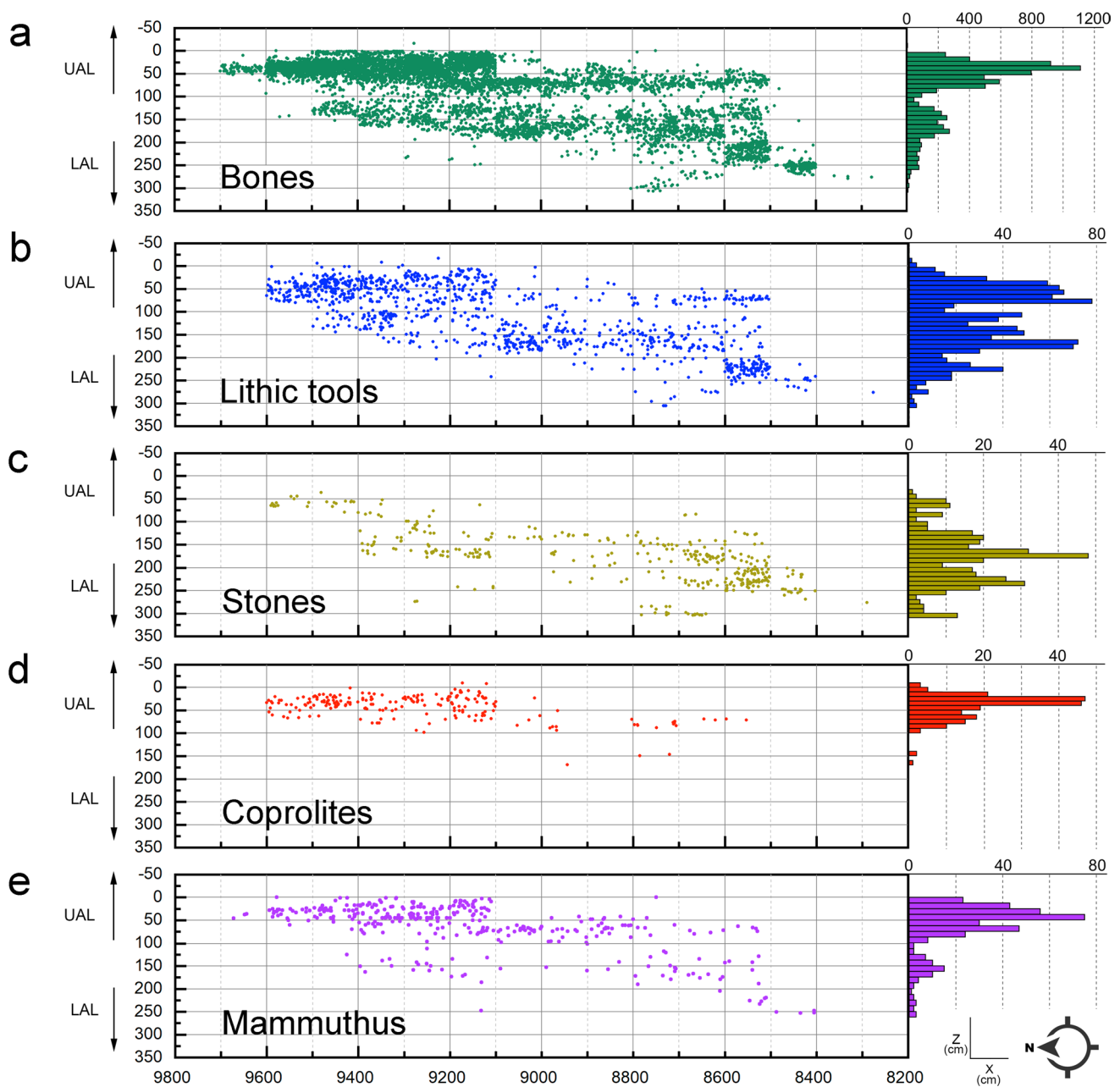
Why are the coprolites recorded mainly in the UAL? The more plausible interpretation for this accumulation is that it corresponds to a *P. brevirostris* latrine.

Other latrines have been published at the latest Early Pleistocene sites of La Mina II (Barranc de La Boella) and TD6 (Atapuerca) (Pineda et al. 2017), both in Spain. In addition, abundant coprolites attributed to *P. brevirostris* have also been recovered from the Epivillafranchian site of Untermasfeld (Germany), probably representing the remains of latrines with a territorial marking function (Keiler 2001). Similarly, Coil (2016) published in the early Late Villafranchian site of Dmanisi (Georgia,

Caucasus) (Block 2) a concentration of 93 coprolites of *P. brevirostris* in 4 m<sup>2</sup>, surrounded by a high number of bones with tooth marks, which probably represents also a latrine. Other Late Villafranchian and Epivillafranchian sites with coprolites attributed to *P. brevirostris* are West Runton (Parffit and Larkin 2010), Cueva Victoria (Carrión et al. 2007), Trlica Cave (Argant and Dimitrejevic 2007), Vallparadis (Madurell-Malapeira et al. 2017), Ceyssaguet (Argant and Bonifay 2011), Taurida Cave (Lavrov et al. 2021), Poggio Rosso (Mazza et al. 2004), Pirro Nord (Arzarello et al. 2007), Venta Micena (Palmqvist et al. 2022a), and Zhoukoudian (Boaz et al. 2000).

The latrine identified at FN3 corresponds to an open-air setting. This type of setting is frequently used by extant hyenas (Kruuk 1972; Gorman and Mills 1984; Mills and Gorman 1987; Vinuesa 2018) and is also documented in the fossil record (Pesquero et al. 2011; Pineda et al. 2017). Figure 15, based on data from Mills and Gorman (1987), shows the percentage of different settings in which modern open-air latrines of *C. crocuta* are placed. As previously mentioned, environmental characteristics are key to choosing the latrine position and ecological pressures can determine differences between populations of the same species (Gorman and Mills 1984; Mills and Gorman 1987).

Among the different locations shown in Fig. 15, latrines situated at a kill site are relatively frequent (7.2%) and can be classified in the category of “temporary latrines” described by Bearder and Randall (1978), which develop near short-term sites of interest, such as carcasses. In contrast,



**Fig. 12** Spatial distribution in a longitudinal section (X–Z) of bones, lithic tools, stones, coprolites, and remains of elephant *M. meridionalis* in FN3. The Z-axis is represented vertically and the X-axis horizontally. The histogram for bone frequencies marks the approximate

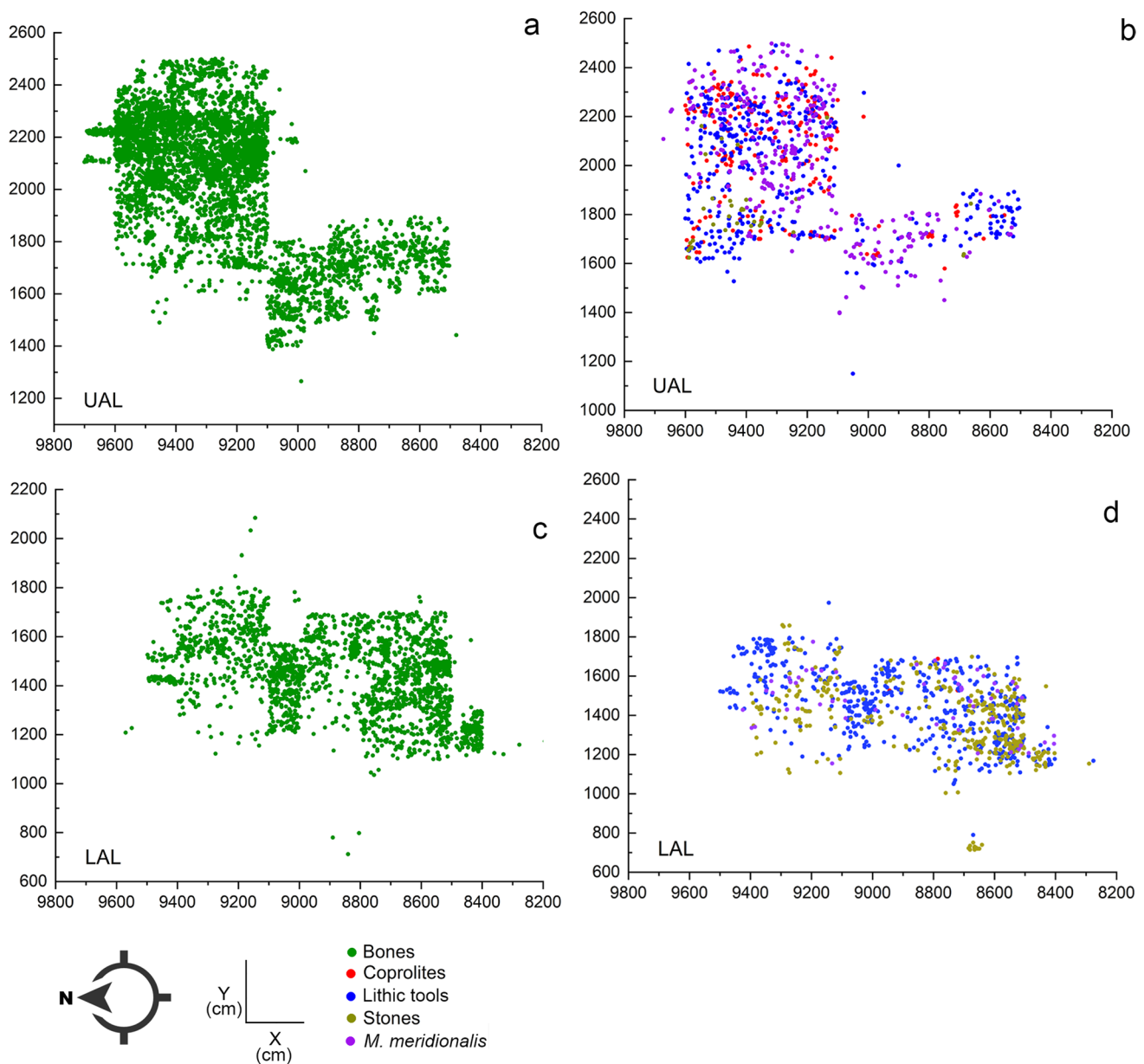
boundary between the UAL and LAL. Points represent the central position of bones, and their dimensions have not been considering in this representation

“long-term latrines” are associated to environmental landmarks and are visited repeatedly over a long period of time, including drinking places (Macdonald 1980).

The discussion that follows focuses on the type of latrine represented by the FN3 coprolites, as deduced from the spatial distribution of fossils.

Bones are the elements most frequently documented at the FN3 site and their abundance is similar in both archeological levels (UAL and LAL), which indicates an intense occupation

of the region by many species, especially ungulates. As in the case of bones, lithic tools are frequently preserved in both levels and appear associated with bones bearing cut marks and evidence of marrow processing (Espigares et al. 2013, 2019; Yravedra et al. 2021; Palmqvist et al. 2023). This suggests that the hominins were present in the area during the formation of both archeological levels, especially during the deposition of layers 2–3 and 5. However, there is a marked difference if we look at the spatial distribution of stones and

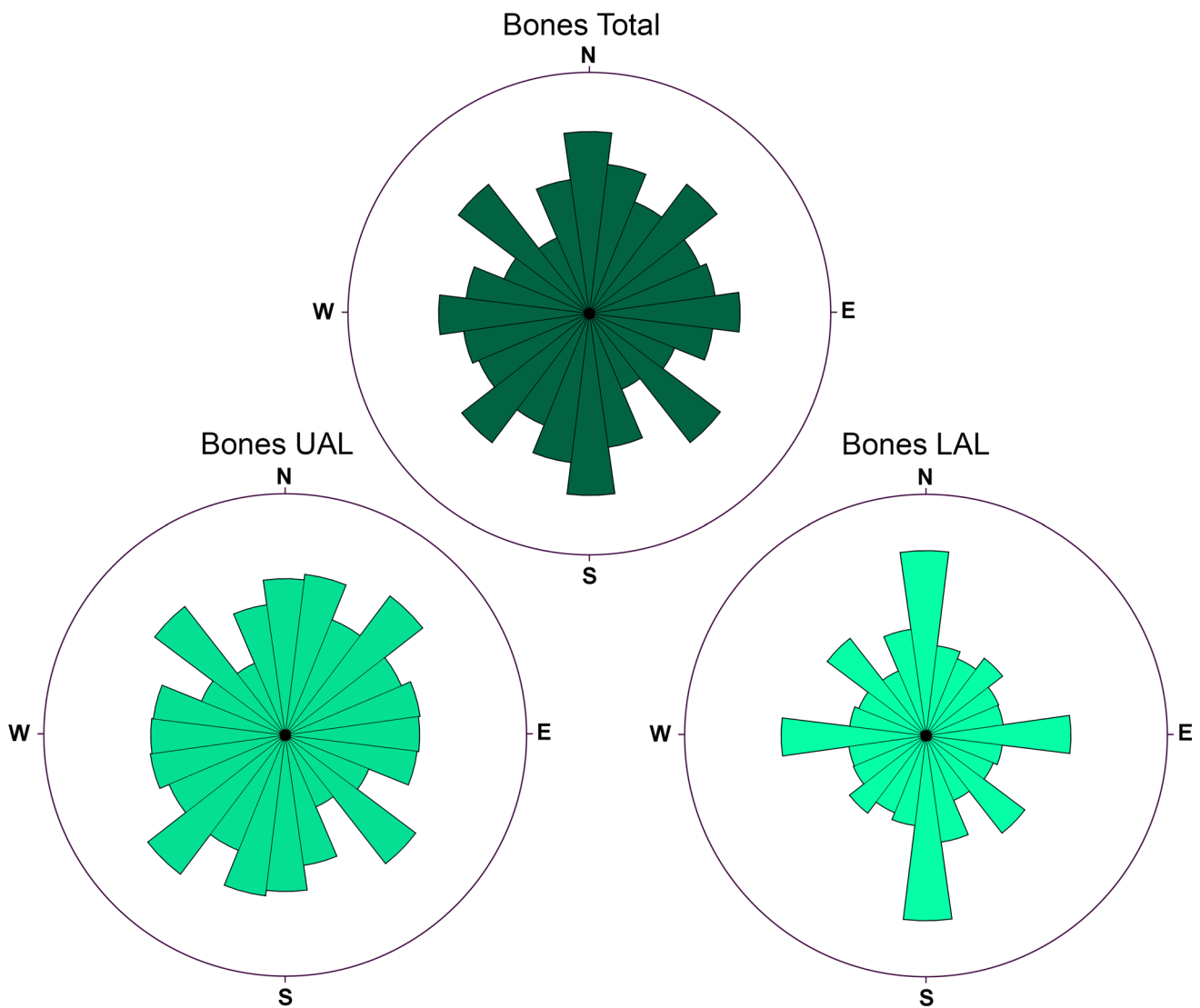


**Fig. 13** Spatial distribution in plant view (X–Y) of bones (**a**, **c**) and coprolites, lithic tools, stones, and remains of elephant *M. meridionalis* (**b**, **d**) in the UAL and LAL of FN3. Points represent the central position of bones, which dimensions have not been considered in this representation

coprolites (Fig. 12c–d). Most stones appear in the LAL and the scarce ones found in the UAL are mostly associated with the partial carcass of *M. meridionalis* (Espigares et al. 2013). Some of these stones have been interpreted as manuports and were presumably brought to the site by the hominins (Barsky et al. 2015a, 2015b; 2022). In contrast, the coprolites are almost entirely located in the UAL (Figs. 12d and 13b). This marks two distinctive scenarios from the point of view of territory use by hyenas: during the period of time in which the LAL was formed the region was not regularly frequented by hyenas, while the high frequency of coprolites in the UAL

evidences an area frequently occupied by hyenas. As a result, during the UAL there was a spatial (and probably also temporal) coexistence of hyenas (more nocturnal) and hominins (predominantly diurnal), whose presence is recorded by abundant lithic tools and the finding of anthropogenic marks on the skeletal remains of large mammals (Espigares et al. 2019; Yravedra et al. 2021).

Another significant aspect of the spatial distribution of fossils is the abundance of proboscidean remains, which are much more frequently represented in the UAL than in the LAL, including a partial carcass of elephant which belonged



**Fig. 14** Rose diagrams for the spatial orientation of the skeletal remains in FN3. Separate projections are also provided for the UAL and LAL

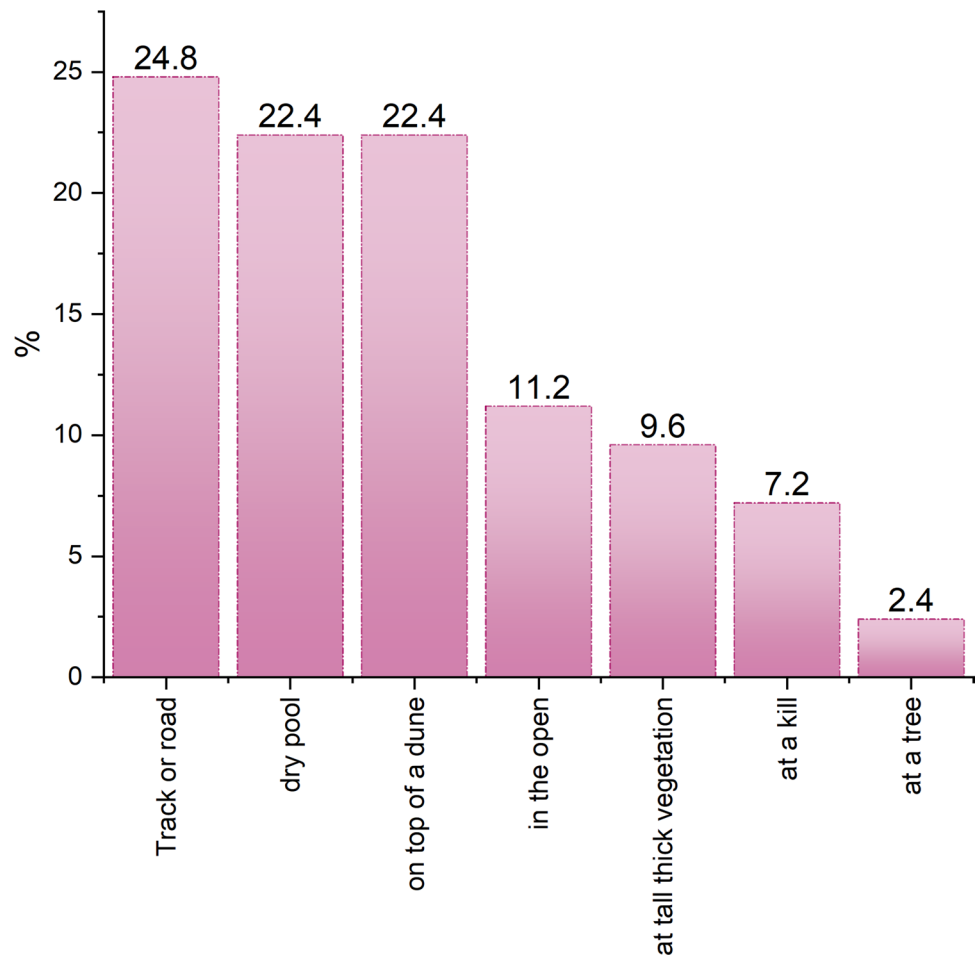
to an old female (as deduced by the morphology of the jaw symphysis and the advanced degree of wearing of the third lower molar, respectively) and two very large tusks, probably of a male individual, measuring > 4 m in length and with a diameter at its widest part of > 30 cm. The proboscidean remains found in FN3 until the year 2015 correspond to, at least, ten individuals of all ages, from newborns to old adults (Ros-Montoya 2010; Espigares et al. 2019). Most of these remains appear in the UAL and seem to have been accumulated in a small space, within a surface area of 40 m<sup>2</sup> and a depth of only 1 m.

The data presented above can help to establish whether the coprolites recovered at the UAL of FN3 represent a temporary or a stable latrine. Coprolites, as well as elephant bones and teeth, are concentrated in the UAL. In addition, one event with 34 coprolites surrounding the elephant carcass has been

identified (Espigares et al. 2013). However, despite the large number of skeletal remains of proboscideans at the UAL of FN3 and with the only exception of this carcass, no accumulations of coprolites associated with elephant remains have been located at the site. This could be due to the fact that teeth are the most frequently recovered anatomical elements of *M. meridionalis*. According to Haynes (1988), an accumulation of more than one elephant carcass is invariably not the result of serial predation but of die-offs at water sources during seasonal droughts in the course of several decades. Elephants were therefore a relatively frequent resource in the UAL, which could be exploited by both the hominins and hyenas (Espigares et al. 2013).

This situation allows us to speculate on a more permanent use of this area by the hyenas as a latrine, linked to the relatively frequent presence of elephant carcasses. It

**Fig. 15** Frequencies of settings in which modern open-air latrines of *Crocota crocuta* appear, based on data from Mills and Gorman (1987) (total number of latrines = 116)

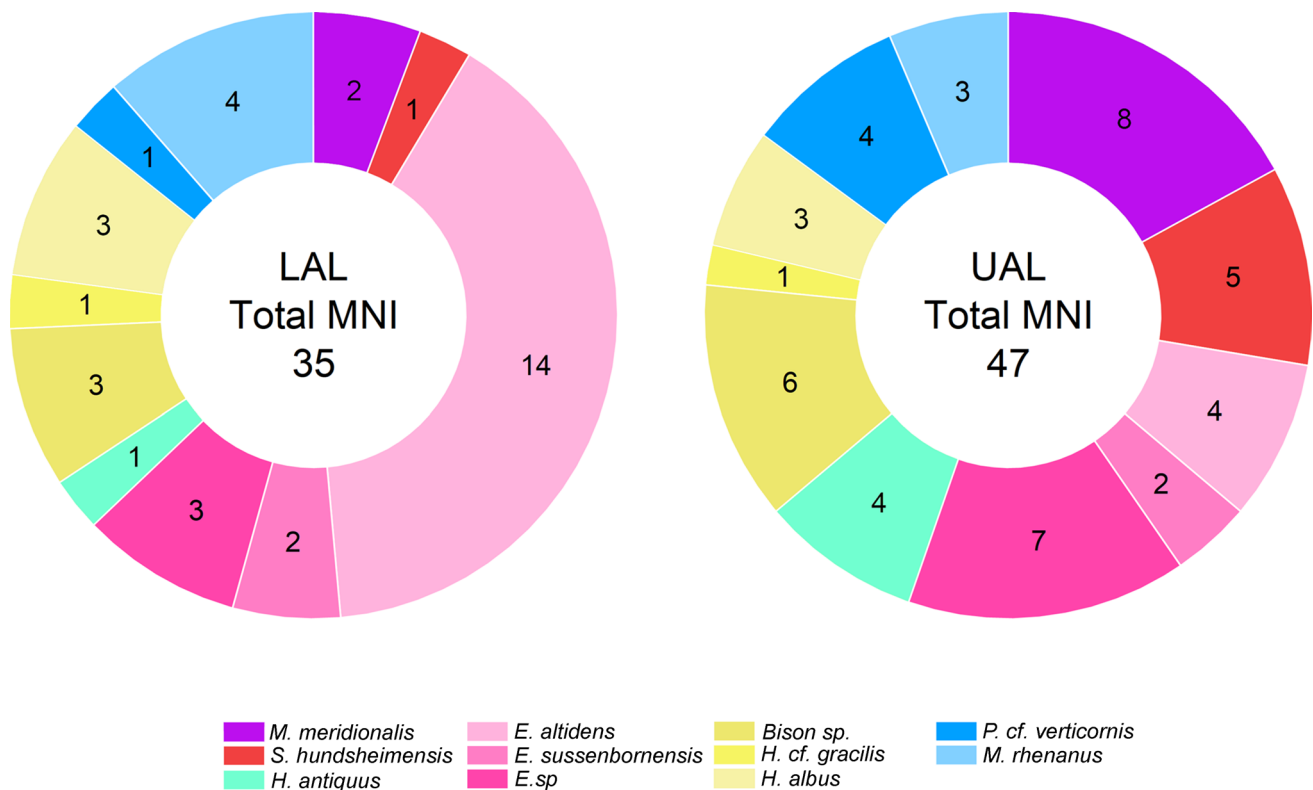


is noteworthy the association in the fossil record of hyena coprolites and proboscidean remains, as in the case of Untermaassfeld (Keiler 2001), West Runton (Larkin et al. 2000), or La Mina II (Pineda et al. 2017). Cozzi et al. (2015) showed that the presence of an elephant carcass influences the ranging and feeding behavior of *C. crocuta* for at least 10–14 days, although carcass consumption may take up to 50 days after the proboscidean death, constituting a point of attraction and contact for multiple species of scavengers and for individuals of neighboring hyena clans. However, the coprolites of FN3 are not exclusively related to elephant remains, being associated with other skeletal remains of large mammals very variable in size, in a region with a permanent source of water (Espigares et al. 2019; Palmqvist et al. 2023).

Given the differences between the two archeological levels of FN3, the relative abundance of herbivore species in them can be used to infer further behavioral aspects of *P. brevirostris*. If these relative abundances are calculated from the NMIs (data from Espigares et al. 2019), the species abundances are more balanced in the UAL than in the LAL, where there is a high frequency of *Equus* (Fig. 16). In addition, there is another interesting difference between both

levels: the UAL shows a clear predominance of megaherbivores, which represent 36.1% of the ungulate individuals identified compared to 11.4% recorded in the LAL (Fig. 16). Although these differences are probably a consequence of the agents involved in the modification and accumulation of the skeletal remains in both archeological levels, they can also emerge from differences in the sedimentary context, which need to be analyzed in greater depth.

More specifically, there are lithological differences between the LAL and UAL of FN3 (Oms et al. 2011). The fertile levels of the LAL (layers 2–3; Figs. 1 and 2) are composed of green clays (layer 2) and brown whitish clays with nodules (layer 3). In contrast, the fertile levels of the UAL (mainly layer 5, and to a lesser extent layers 6 and 7; Figs. 1 and 2) are composed of greenish sands and marly mudstones (layer 5), dark brown clays (layer 6), and greenish-brown dark marly mudstones (layer 7). Given their composition, fine sands and clays, the layer 5 of the UAL could have behaved as quicksand that became unstable when it was forced to move by the pressure exerted by large-sized animals like proboscideans: experimental data on quicksand from salt-lake environments composed of fine sand, clay, and salt water, similar to those found in



**Fig. 16** Relative abundance of ungulate species recorded in the UAL and LAL of FN3 according to the minimum number of individuals (MNI) (data from Espigares et al. 2019)

Orce (García-Aguilar et al. 2014, 2015; Palmqvist et al. 2022b), show that the quicksand acts as a trap for the animals caught, which find it very hard to escape (Khaldoun et al. 2005). This quicksand shows extreme sensitivity to small variations in stress due to liquefaction of the materials. The higher the stress, the more liquid and viscous the quicksand becomes, so movement by a trapped body causes it to sink (Khaldoun et al. 2005). However, the objects with a density of  $1 \text{ g ml}^{-1}$  (i.e., the average density of mammal tissues) are not completely sucked beneath the surface but sink halfway into the quicksand (Khaldoun et al. 2005). This scenario would explain the abundance of skeletal remains of megafauna in the UAL, particularly elephants, which halfway sunk carcasses would regularly attract the scavenging hyenas (Espigares et al. 2013).

The increased exposure of elephants to the risk of entrapment in a quicksand results from the high weight per unit area supported by their limbs. Specifically, data from Pasenko (2017) on body mass and footprint diameters of the manus and pes of a number of African and Indian elephants allows estimating the weight supported per unit area by their feet:  $0.93 \text{ kg/cm}^2$  in both an adult male and an adult female of 4899 kg and 3962 kg, respectively;  $0.77 \text{ kg/cm}^2$  in a young adult female of 2386 kg;  $0.57 \text{ kg/cm}^2$  in a 5 years old male of 1515 kg; and  $0.35 \text{ kg/cm}^2$  in a

1.5 years old male elephant of 726 kg. In the case of the black rhino (~ 1500 kg), the diameters of the fore- and hindfeet measured in the footprints from Laetoli (data from Leakey and Hay 1979) provide an estimate of  $0.80 \text{ kg/cm}^2$ . In contrast, the weight per unit area supported by the feet of the Laetoli hyena (probably *Hyaena bellax*, a synonym of *P. brevirostris*; Palmqvist et al. 2011) is lower,  $0.32 \text{ kg/cm}^2$ , and is even more so in the case of *Australopithecus afarensis*,  $0.17 \text{ kg/cm}^2$ . These data suggest that while adult elephants could occasionally become trapped in the quicksand of layer 5 of FN3, the hyenas and hominins would have been much less exposed to this risk, thus being able to scavenge on these carcasses. In the case of the very young elephants, which remains are also represented in the UAL of FN3, their lower ratios of weight to foot area may tentatively suggest that these animals would not entrap themselves, but would stay in the vicinity of their mother's trapped carcass, where they would also eventually die.

## Conclusions

The Upper Archeological Level (UAL) of the Early Pleistocene site of FN3 preserves 217 coprolites. The morphology, color, mineralogical, and chemical composition of these

coprolites, as well as the presence of inclusions in them, agree with those produced by hyenas. Their average size is larger than in the case of those coprolites produced by the extant *C. crocuta*. The features of the coprolites and the faunal remains from the site allow to ascribe these coprolites to *P. brevirostris*. As a result, the UAL of FN3 represents a fossil latrine probably related to the frequent presence of proboscidean carcasses at the site, with at least one event in which the coprolites are clearly associated with a carcass of megafauna, as there is a partial elephant skeleton surrounded by 34 coprolites. However, the coprolites are also associated with other ungulate remains, mainly equids, bovinds, and large-sized cervids.

The data presented here allow to establish differences between the two occupation levels of FN3. In the Lower Archeological Level (LAL), the presence of hyenas is scarce. In contrast, they are well represented in the UAL by some dental remains, tooth marks, and coprolites. The lithology of layer 5 of the UAL, fine sands and clays deposited in a salt-lake environment, suggests that this level could have acted as a quicksand in which large-sized animals, particularly elephants, were trapped and halfway sunk, thus attracting the scavengers.

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**Author contribution** MPE, PP, MDRG, and BMN wrote the main manuscript text and all co-authors made contributions. MPE prepared Figs. 4, 5, 6, 12, 13, 14, and 15 and Tables 1, 2, and 5; SRM prepared Figs. 3 and 7; MDRG prepared Figs. 8, 10, and 11 and Tables 3 and 4. AGM, JMGA, AG, and IC prepared Figs. 1 and 2, APR prepared Fig. 9, and GRG prepared Fig. 16. All authors read and approved the final manuscript.

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**Data availability** Data are available on request to the corresponding author.

**Code availability** Not applicable.

## Declarations

**Ethics approval** Not applicable.

**Consent to participate** All authors agree to participate.

**Consent for publication** All authors agree to publish the paper.

**Competing interests** The authors declare no competing interests.

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