Journal Pre-proof


# Pollen analysis of present-day striped hyaena (Hyaena hyaena) scats from central Iran: Implications for dryland paleoecology and animal paleoethology

Morteza Djamali, Marjan Mashkour, Hossein Akhani, Dahvya Belkacem, Belinda Gambin, Michelle Leydet, Nafiseh Samadi, Margareta Tengberg, Emmanuel Gandouin

PII: S0034-6667(20)30162-7

DOI: https://doi.org/10.1016/j.revpalbo.2020.104277

Reference: PALBO 104277

To appear in: *Review of Palaeobotany and Palynology*

Received date: 19 June 2020

Accepted date: 29 June 2020

Please cite this article as: M. Djamali, M. Mashkour, H. Akhani, et al., Pollen analysis of present-day striped hyaena (Hyaena hyaena) scats from central Iran: Implications for dryland paleoecology and animal paleoethology, *Review of Palaeobotany and Palynology* (2020), https://doi.org/10.1016/j.revpalbo.2020.104277

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2020 Published by Elsevier.

# Pollen analysis of present-day striped hyaena (*Hyaena hyaena*) scats from central Iran: implications for dryland palaeoecology and animal palaeoethology

Morteza Djamali[*,1,2], Marjan Mashkour[3], Hossein Akhani[4], Dahvya Belkacem[1], Belinda Gambin[5], Michelle Leydet[1], Nafiseh Samadi[4], Margareta Tengberg[3], Emmanuel Gandouin[1]

[1]Institut Méditerranéen de Biodiversité et d'Ecologie - IMBE (Aix Marseille Univ, Avignon Université, CNRS, IRD), Europôle de l'Arbois, 13545 Aix-en-Provence, France

[2]Iranian National Institute for Oceanography and Atmospheric Sciences (INIOAS), 3 Etemad Zadeh St., Fatemi Ave., 1411813389, Tehran, Iran

[3]UMR7209 AASPE, Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements, CNRS (Centre national de Recherche Scientifique) - MNHN (Muséum national d'Histoire Naturelle) Case postale 56, 55 rue Buffon, 75005 Paris - France

[4]Halophytes and C4 Plants Research Laboratory, Department of Plant Sciences, School of Biology, College of Sciences, University of Tehran, P.O. Box 14155-6455, Tehran, Iran

[5]Institute of Earth Systems, University of Malta, Msida, MSD 2080, Malta

Journal Pre-proof

## ABSTRACT

The striped hyaena is the largest living omnivorous scavenger in SW Asia. It generally lives in semi-arid desert steppe regions, often denning in small caves, rock shelters, and burrows close to human settlements. Bone fragments of wild and domestic animals and desiccated scats are frequently found in the hyaena dens. In this study, eight striped hyaena desiccated scats were subjected to pollen analysis. All scats were rich in pollen and the exine was well-preserved with no visible sign of corrosion. Pollen spectra revealed interesting information on the regional and local vegetation, as well as the foraging behavior and diet of the animal. They reflected an array of different landscapes ranging from natural/semi-natural xerophytic desert steppes, agricultural fields, and grazing pastures. Some scats contained certain pollen taxa very rarely observed in wetland sediments, indicating the high potential of hyaena 'copropalynology' in providing detailed information on the past floristic composition of the landscape. When comparing with archaeobotanical data from the area, the hyaena scat assemblages show that the general physiognomy of the landscape has remained almost unchanged since the 6th millennium B.C., with only minor changes in the composition or density of the woody components of the desert steppe. As most of the Holocene fossil coprolites in archaeological and palaeontological sites of SW Asia would have been left by striped hyaena, the study of the modern analogues of such accumulations in extant hyaena dens is helpful to correctly interpret the fossil faunal assemblages to reconstruct the palaeolandscapes, land-use change, and animal palaeoethology.

**KEYWORDS**

Commensalism; coprolite; feces; palynology; Late Quaternary; SW Asia

## 1. Introduction

In drylands, where wetland systems are hard to find, alternative palaeoenvironmental archives have been explored by palaeoecologists. Among these, the organo-sedimentary structures such as packrat middens, bat guanos, and coprolites have been very informative (Scott, 2000; Pearson and Betancourt, 2002; Carrión et al., 2006). Coprolite remains, originating mainly from carnivores, constitute one of the most attractive materials for Quaternary palaeoecology and have been increasingly analysed by palynologists around the world (Scott et al., 2003; Carrión et al., 2007; Argant and Philippe, 2011; Djamali et al., 2011). Their growing use by palynologists has led some scholars to use the term 'copropalynology' to refer to this new sub-discipline in palynology (Argan, 2014). Most of the well-preserved coprolites found in

Journal Pre-proof

palaeontological and archaeological contexts are of carnivorous origin, mainly belonging to Hyaenidae family (Horwitz and Goldberg, 1989; Argan and Philippe, 2011; Diedrich, 2012a). Due to the absolute dominance of hyaena coprolites in the Pleistocene deposits of Eurasia and Africa, Hunt and Lucas (2019) define a biogeographic/taphonomic province that they name '*Hyaenacoprus* province' as opposed to '*Castrocorpus* province' of N and S America, the latter being dominated by herbivore coprolites. Attribution of coprolites to hyaenas has been based on (i) morphological analogies with modern hyaena droppings, (ii) association with hyaena bones, and more recently (iii) identification of hyaena ancient DNA (Horwitz and Goldberg, 1989; Bon et al., 2012; Diedrich, 2012a; Fourvel and Fosse, 2017). It seems that social and denning behavior of hyaenas defecating on the same latrine sites and the high content of hydroxyapatite in their faeces, facilitating the consolidation and fossilization, are the main factors for their good preservation in Quaternary sediments (Hunt and Lucas, 2019). Bone remains found in hyaena coprolite-bearing Pleistocene deposits of Eurasia and Africa suggest that they probably belong to the extant spotted hyaena i.e. *Crocuta crocuta* (Erxleben, 1777) or its extinct subspecies called the 'cave hyaena' *Crocuta crocuta* subsp. *spelaea* (Goldfuss, 1823) (Yll et al., 2006; Argan and Philippe, 2011; Bon et al., 2012; Diedrich, 2012b). However, the presence of striped hyaena *Hyaena hyaena* (Linnaeus, 1758) coprolites has also been reported in some archaeological sites in the Eastern Mediterranean region (Horwitz and Goldberg, 1989; Mashkour 2003 (Sialk publication). Although no palynological study has been performed on these latter coprolites, their macromorphological, mineralogical, and petrographic examinations have yielded ample paleoenvironmental information. The striped hyaena fossil fecal material can thus be potentially interesting for palaeoecological investigations in semi-arid to arid regions located within the distribution range of the species (Fig. 2a).

Journal Pre-proof

Hyaena coprolites have been reported from Iranian caves (Djamali et al., 2011). In the Wezmeh Cave, located in the Zagros Mountains in western Iran, a copropalynological analysis of hyaena fossil faeces has revealed a lot of information on the regional vegetation as well as the local floristic composition of the landscape, through the detection of some rare endemic plants (Djamali et al., 2011). Archaeozoological identifications of bone remains from the same cave strongly suggest the dominance of the rests of spotted hyaena, although the presence of striped hyaena is not excluded (Mashkour et al., 2008; Monchot, 2008). The latter species has also been documented from other Palaeolithic sites of Zagros (Turnbull, 1975; Marean and Kim, 1998). With the decline of the spotted hyaenas at the onset of the postglacial period (Mashkour et al., 2008), striped hyaenas gradually became the largest dominating scavenger in the dry landscapes of SW Asia. It is thus logical to assume that during the terminal Pleistocene to Holocene, hyaena remains belong to the latter species.

This study is the first copropalynological analysis of modern striped hyaena scats recovered directly from a hyaena den complex in the circum-desert areas of central Iran. The hyaena den of Kaftar Khun (Fig. 1) was surveyed and sampled for its faunal remains, in order to understand the diet and foraging behavior of the animal in present-day dry landscapes of central Iran (Monchot and Mashkour, 2010). The aims of this study are to evaluate the potential of the striped hyaena scats (i) to incorporate and preserve pollen grains, (ii) to reflect their surrounding vegetation and flora, (iii) to reveal their foraging behavior in relation to natural ecosystems and human activities.

## 2. Setting

### *2.1. The site*

Kaftar Khun (also ‘Kaftārkhun’ or ‘Kaftār Khun’ or كفتارخون in Persian) palaeo-travertine is located at about 5 km to the southwest of the city of Kashan in central Iran (33°54’19”N, 51°22’20”E, 1190 m a.s.l.). Geologically, it is one of a series of eroded fossil travertine and tufa deposits formed along a fault system on the eastern foothills of the Karkas Mountains in the west-central Iran (Biglari, 2004; Heydari-Guran et al., 2009). The Kaftar Khun travertine formed along the central segment of the active Kashan fault and no longer has any active spring (Berberian et al., 2012). The site displays several small hollows and rock shelters which have harbored, until very recently, an active striped hyaena den complex (Heydari-Guran et al., 2009; Monchot and Mashkour, 2010). Indeed, etymologically, Kaftar Khun is composed of ‘Kaftar’ (Kaftār) meaning ‘hyaena’ and ‘Khun’ (Khūn) meaning ‘house’ in Persian. The Kaftar Khun hyaena dens were visited in several occasions from 2003 to 2005 and many bone fragments and desiccated scats were collected and identified (Mashkour, 2003a and b; Monchot and Mashkour, 2010). Unfortunately, over the past 15 years the intensive mining activities (to exploit the travertine deposits), along with the construction of a poultry house and a horse stable, have all contributed to the destruction of the site and its surrounding environment, forcing hyaenas to abandon their dens.

Journal Pre-proof

**Figure 1 here**

Kaftar Khun (33°54'18.72"N, 51°22'20.46"E, 1192 m) is located close to the well-known archaeological site of Tepe Sialk in the vicinity of Kashan. This site, composed of two main mounds (‘South Mound’ and ‘North Mound’), displays a succession of cultural phases from Late Neolithic to Classical Antiquity (ca. 6200 BC to 550 BC) (Ghirshman, 1938-1939) interrupted by recurrent abandonments related to palaeo-earthquakes and climatic changes (Berberian et al., 2012). Archaeobotanical and archaeozoological studies of the botanical and

Journal Pre-proof

faunal materials, collected during the 2003-2005 excavation seasons of Sialk, reveal preliminary information on the plant and animal economy during the Neolithic to Iron Age periods (Mashkour, 2003a and b; Tengberg, 2004; Shirazi and Tengberg, 2012; Ilkhani et al., 2019; Mashkour et al., 2019). They show (i) significant cultivation of cereals including both wheat (*Triticum* spp.) and barley (*Hordeum vulgaris*), (ii) intensive exploitation over millennia of woods mainly for fuel (both riparian and desert steppe woody species), (iii) beginning of arboricultural activities during the Iron age, and (iv) presence of steppe animals like gazelles and Persian indicating an arid environment. The availability of these natural plant and animal resources, as well as spring water resources for cereal farming, close to the sites have been two major factors attracting pre-historic human communities to these fringes of the Central Iranian Great Desert (Berberian et al., 2012). The presence of water resources has been also demonstrated in another nearby archaeological site of Shamshirgah, an Iron Age settlement on the outskirt of the central desert (Mashkour and Fahimi, 2019).

*2.2. Climate and vegetation*

Based on data from the meteorological station of Kashan (Fig. 1c), located a few kilometers from the site, the area has an Irano-Turanian pluviseasonal continental climate. This bioclimate, equivalent to Mediterranean pluviseasonal continental in the Mediterranean region, dominating the central part of the Iranian plateau is characterized by high continentality (M-m ≥ 21, where M is the mean of maxima of warmest and m is the mean of minima of coldest months), very scarce precipitation during the growing season (<200 mm/yr) and a long dry season lasting up to eight months (Djamali et al., 2011; Rivas-Martinez et al., 2011). Under the control of such a harsh bioclimate, the vegetation on the eastern foothills of the Karkas mountains falls in the 'xerophytic desert steppe' belt dominating elevations <1500 m in central Iran (Dehghani et al., 2017). Here, the vegetation is composed of a typical Irano-Turanian *Artemisia* steppe (mostly represented by *A. dumosa*, a name which is replaced by *A. sieberi* in the Flora Iranica (Podlech 1986, 2013). The open dwarf-shrub steppe is well developed on the well-drained alluvial plains with numerous xerophytic and tragacanthic herbaceous species and co-dominated by xerophytic shrubs/dwarf shrubs of *Ephedra* spp., *Zygophyllum atriplicoides*, *Pteropyrum aucheri* and subshruby *Astragalus* species. The vegetation is very rich in ephemerals and xerophytic species, mainly belonging to Asteraceae, Brassicaceae, Boraginaceae, Papaveraceae and Poaceae. Further to the east, the vegetation is either psamophytic developed on the vast sand dunes or halophytic developed in the saline depressions both surrounding the city of Kashan or gypsophytic formations on gypsum hills in the east of Kashan. In the vicinity of the Kaftar Khun hyaena den complex, the sparse steppe vegetation is dominated by *Artemisia* sp., *Astragalus* spp., *Acantholimon* spp., *Bromus tectorum*, *Noaea mucronata*, *Cleome coluteoides*, *Peganum harmala*, *Scariola orientalis*, and *Stachys inflata* indicating an overgrazed desert steppe vegetation.

*2.3. Striped hyaena in Iran*

*Hyaena hyaena* (Linnaeus, 1758) is the only extant species of hyaenidae in Iran (Firouz, 2005). The Striped hyaena, a 'near-threatened' species in the IUCN Red List (AbiSaid and Dloniak, 2015), is also considered vulnerable in this country, suffering from the loss of its natural habitats, less availability of carcasses, persecution by local human populations, and vehicle collision (Tourani et al., 2012). Studies of habitat evaluation of the species show that open landscapes dominated by *Artemisia* steppes, with the presence of limestone outcrops providing rock shelters, are the ideal environmental conditions for denning activities (Rezaei et al., 2017). Striped hyaenas are nocturnal foragers, mostly scavenging on remains of other animals left by large carnivores; however, they can occasionally hunt small animals such as lizards, rabbits, rodents and insects (Rieger, 1979; Wagner, 2006; Monchot and Mashkour, 2010). Unlike spotted hyaenas, the striped hyaenas rarely form groups and are mostly solitary animals, occasionally foraging in pairs (Fig. 2). They are adapted to arid and semi-arid conditions but need to regularly drink from water resources located within 10 km of their habitats (Rieger, 1979; Wagner, 2006). Striped hyaenas can be considered as omnivorous scavengers because they also feed on fruits, vegetables and occasionally human refuse (Rieger, 1979; Wagner, 2006). The availability of these plant food resources, as well as the livestock carcasses around human settlements, is increasingly drawing striped hyaenas to peri-urban areas, habitations, and landfills (Monchot and Mashkour, 2010; Shamoon and Shapira, 2019) which is not necessarily beneficial to the survival of this threatened species (Tourani et al., 2012).

**Figure 2 here**

## 3. Materials and methods

Some thirty modern hyaena scats were collected from the Kaftar Khun rock shelter and put into small plastic bags in 2005 by the second author. Eight of the best-preserved scats were selected for pollen analysis (samples KK1 to KK8, Table 1, Fig. 3). After cleaning their surfaces, samples were prepared using the standard extraction technique described by Moore et al. (1991). One *Lycopodium* tracer tablet (Batch 1030, Lund University) was added to each sample before treatment, to calculate the pollen concentrations in grains/g of dry material (Stockmarr, 1973). A minimum of 207 pollen grains were identified and counted under x500 magnification using a Zeiss Axiolab 5 light microscope equipped with Phase Contrast. The Iranian pollen reference collection hosted at the *Institut Méditerranéen de Biodiversité et d'Ecologie* (Aix-en-Provence, France), as well as the pollen atlases of Reille (1992, 1995,

Journal Pre-proof

Journal Pre-proof

1998), Bonnefille and Riollet (1980), and van Zeist and Bottema (1977) were consulted for identification of difficult pollen grains.

**Table 1 here**

A pollen percentage diagram was created in the R package “rioja” (Juggins, 2019). Principal Component Analysis (PCA) was performed on n=8 (number of individuals/observations) by p=74 (number of taxa/variables) pollen matrix of percentages. This analysis allows for the extraction of important information from a multivariate data table (containing individuals/observations described by multiple inter-correlated quantitative variables), it expresses this information as a condensed set of new variables called principal components that can potentially reveal environmental gradients. These new variables correspond to a linear combination of the originals. Thus, PCA reduces the dimensionality of a multivariate data to two or three principal components, that can be visualized graphically, with minimal loss of information. Before PCA analysis, data were square-root transformed to stabilize the variance. Rare taxa, i.e. those present in only one sample (or with a relative abundance consistently <1%), were removed from the analysis. Along with the PCA, a Hierarchical Clustering on Principal Components (HCPC) was also performed. The goal of HCPC is to identify groups (i.e. clusters) of similar objects within the data set (using the Ward's criterion on the selected principal components). PCA analysis was performed using “ade4” R package (Dray et al., 2007) and presented in Fig. 5. The results were then visualized using the R packages “magrittr” (Bache and Wickham, 2014) and “factoextra”. Furthermore, Cluster Analysis was applied to the PCA results using “FactoMineR” package (Husson et al., 2020). Another PCA biplot with more illustrative details was put in the Supplementary Materials.

Journal Pre-proof

The climate diagram, in Fig. 1c, was created in the "climatol" package (Guijarro, 2019). All R packages were run in RStudio version 3.5.3 (RStudio Team, 2015).

**Figure 3 here**

## 4. Results and Discussion

Samples were relatively rich in pollen, with the pollen concentration ranging between 6881 to 70485 pollen/g of dried fecal material (Table 1). Pollen counts varied between 207 and 428 per slide (Table 1), with all pollen grains being included in the total pollen sum to calculate percentages. The pollen percentage diagram is illustrated in Fig. 4 and the PCA biplot of the variables (taxa) *versus* samples is provided in Fig. 5. Overall the samples are generally reflecting an open landscape, with herbaceous pollen dominating the spectra and arboreal pollen comprising very low percentages of the total pollen sum (Fig. 4). A PCA-based non-constrained hierarchical classification helped define clusters of samples based on similarity of their pollen percentages (right side of the pollen diagram, Fig. 4). The PCA biplot in Fig. 5 shows how the eight projected samples are explained by different pollen taxa and along two first PCA Axes.

PCA Axis 1 and Axis 2 together explain 23.1% and 18.6% of variance and indicate that half of the samples (KK1, 2, 4, and 8) present a relatively homogeneous pollen assemblage and group together in the positive side of PCA Axis 1 (KK1, 2, 4, and 8). This is also evident in the HCPC dendrogram lower cluster (Fig. 4). These are dominated by *Artemisia* and Chenopodiaceae *s. str*. Please note that in this paper, we prefer to use the name Chenopodiaceae despite the fact that Angiosperm Phylogeny Group Classification (Byng et

Journal Pre-proof

Journal Pre-proof

al., 2016) suggests a broader sense by using Amaranthaceae. Our argument is that since the pollen structure of Chenopodiaceae represent arid habitat in contrast to Amaranthaceae *s. str*., in which many species are of tropical origin. The whole cluster of KK1, 2, 4, and 8 indicate the hyaenas foraging in the natural dry steppes. The negative side of Axis 1 is more difficult to interpret because the pollen types with highest contributions are of both natural and anthropogenic origin (e.g., Resedaceae and Brassicaceae). PCA Axis 2 opposes sample KK5 and 7 in the negative side and sample KK6 in the positive side. While KK7 is characterized by aquatic plants and riparian trees (*Sparganium*-type, Cyperaceae and *Salix* and *Tamarix*), suggesting hyaenas drinking from a water source (spring, qanat etc.), KK5 appears more characterized by anthropogenic species (e.g., *Plantago maritima*-type, *Vitis* and *Populus*). In contrast, sample KK6 clearly indicates a very anthropic landscape, possibly the abandoned arable lands and/or overgrazed lands in the vicinity of human habitations (e.g. *Tribulus* and *Euphorbia*). Any further interpretation of the other PCA biplot axes may be an overinterpretation of data because according to the scree diagram (top left, Fig. 5), there is little difference between variances explained by axis 3 onwards. We thus propose that the HCPC results provide a better illustration to distinguish the dissimilarities between the different samples.

**Figure 4 here**

4.1. *Regional vegetation*

The pollen spectra of all the examined hyaena scats are largely dominated by pollen taxa characteristic of an open dry landscape covered with an Irano-Turanian *Artemisia* steppes

Journal Pre-proof

containing significant amounts of xerophytic shrubs and dwarf shrubs. *Artemisia* accounts for 50-80% of the total pollen sum except in samples KK2 and KK5 (Fig. 4). Poaceae and Chenopodiaceae (*sensu* Hernández-Ledesma et al., 2015 and not Byng et al., 2016) are the next most abundant pollen types accompanied with many other herbaceous plants with low pollen values. Pollen of desert trees/shrubs dominated by *Calligonum*-type constitute by far the most abundant arboreal pollen in most of the samples (0.8-15%). *Calligonum*-type pollen is produced by two woody genera of Polygonaceae family i.e. *Calligonum* spp. and *Pteropyrum* spp. (excluding *P. naufelum*) (Doostmohammadi et al., 2019). The latter species has its own characteristic morphology. While *Pteropyrum*, as a C3 plant, temporarily dominate seasonal water runnel and alluvial soils near Kashan and the eastern flank of Karkas Mountain, *Calligunum*, a C4 lineage, is a psamophytic genus with several species growing in desert dunes in lower altitudes. Both shrubs are not, however, halophytic and prefer well-drained substrates. *Ephedra distachya*-type pollen is also a background pollen, present in almost all spectra but with very low values (<1%). Nowadays, *Ephedra* spp. are found in the foothills of the Karkas mountains at lower elevations and gypsum hills in the southeastern parts of the region. The presence of *Quercus* pollen is interesting, showing that the values between 0.3 to 4% of oak pollen can highlight long-distant transport, mostly from the Zagros open oak forest located some 200 km to the west and brought by the prevailing westerly winds. Comparison of the pollen spectra of the Kaftar Khun hyaena scats with the modern surface pollen spectra from a mountain-desert transect in north-central Iranian Plateau (Dehghani et al., 2017) indicates a surprisingly high similarity, with those spectra coming from the 'xerophytic desert to semi-desert steppe' dominated by *Artemisia dumosa* on dry soils and *Pteropyrum aucheri* in dry river beds. In both cases *Artemisia* pollen varies between 40-80% and Chenopodiaceae and Poaceae pollen mostly remain around or under 10%. The 'xerophytic desert/semi-desert steppe vegetation belt is found between 800 to 1500 m

(Dehghani et al., 2017), suggesting that the striped hyaena foraging area is limited to this altitudinal range. This vegetation belt also covers vast areas on the southern foothills and alluvial plains of the Alborz Mountains in north-central Iran (Klein, 1994).

Anthracological investigations at the archaeological site of Tape Sialk (8 km northwest of Kaftar Khun) reveal significant prehistoric exploitation of woody components of the xerophytic desert steppes of the region over millennia (Shirazi and Tengberg, 2012). The consumed woody taxa in the Sialk layers are dominated by a mixture of desert trees/shrubs (*Haloxylon* sp., *Lycium* sp.,) and riparian (*Fraxinus* sp., *Elaeagnus angustifolia*, *Salix* sp., *Tamarix* sp.) and montane cliff species (*Celtis* sp.). Absence of the charcoals of *Pteropyrum*/*Calligonum* and *Ephedra*, the main shrub pollen taxa found in the Kaftar Khun scat assemblages is noteworthy. It may be explained by (i) once lower abundance of these taxa or their former extirpation from the landscape by humans, (ii) easier access to riparian species and *Haloxylon* sp., (iii) lower energetic values of *Pteropyrum*/*Calligonum* as fuel compared to other exploited species, and (iv) incomplete sampling of the archaeological layers causing a bias in data. It should also be noted that *Haloxylon* pollen is difficult to distinguish from several other species of Chenopodiaceae and its pollen has certainly been grouped under this family in our pollen diagram.

4.2. *Anthropogenic imprints in pollen spectra*

Pollen types related to human activities are present in all the hyaena scats and include cultivated (ornamental and fruit) trees, cereals and pulses, segetal plants associated with cultivated fields and ruderal plants indicating disturbed soils and pastoral activities (Fig. 4). Diversity and abundance of these pollen types demonstrate that the hyaenas had been living in a mosaic of environments mostly impacted by different human activities. Some of the pollen types (e.g. pastoral indicators *Euphorbia*, *Plantago lanceolata*-type) have been sourced from vast semi-natural ecosystems, such as the grazed/overgrazed xerophytic shrub steppes extended on the mountain slopes and alluvial plains far from the villages and cities. Others (crops and cultivated trees) are however, mostly limited to permanent settlements and urban/peri-urban areas. Some pollen types identified and quantified in the scats provide very specific information on agricultural crop types. Sample KK1, for instance, contains about 1% pollen of pomegranate (*Punica*), a very underrepresented tree in modern pollen rain (van Zeist et al., 2001) and samples KK1 and KK3 display pollen of *Vigna* cf. *unguiculata* or cowpea, a cultivated bean of West and/or East African origin (Xiong et al., 2016) nowadays grown in different parts of Iran including the study area. Cereals are also significantly present in most of the samples, a fact that is largely expected because dry and irrigated cereal farming is commonly practiced in the plain as well as the mountain areas around Kaftar Khun. Among the ruderal and segetal taxa, the presence of the pollen of *Hypecoum* and *Fumaria*, two rarely encountered pollen types in palynological samples is worth mentioning. Both *Hypecoum pendulum* L. and *Fumaria asepala* Boiss. were observed flowering in May 2015 by MD in Kamou village (30 km to southwest of Kaftar Khun). They are ruderal plants growing in abandoned fields, trampled soils, along water courses and roadsides and even in the fissures of paved sidewalks. *Hypecoum pendulum* also occurs in the Artemisia steppes. *Erodium* pollen, present in most of the samples, is produced by species such as *E. cicutarium* (L.) L'Hér., which is common in ruderal and semi-natural steppe soil, it was also observed in Kamou as a weed in the abandoned fields in May 2015. All samples contained the dung-associated fungal spores belonging to *Sporormiella* sp. The values varied from <1% (KK1, KK4, and KK7) to enormous amounts in KK2 (2920% calculated based on the total sum of pollen grains excluding *Sporormiella*), indicating the significant presence of livestock in hyaena foraging areas and the possible consumption of their entrails by hyaenas.

Journal Pre-proof

Archaeobotanical evidence from Sialk suggests that cereal farming (both wheat and barley) was practiced by human communities settled in the area since the Neolithic (6th millennium BCE), with possible grapevine cultivation at least since the Iron Age (Tengberg, 2004). The present-day mixture of diverse landscapes including natural/semi-natural steppes, riparian systems, agricultural lands, orchards, pastures and urban areas have thus been present in the area since the early-mid Holocene, leaving thousands of years for striped hyaenas to adapt to their changing environment by humans.

**Figure 5 here**

4.3. *Palaeoecological and palaeoethological potential*

In general, pollen grains identified and counted in the examined scats were well-preserved and almost no traces of digestion by gastric acids of the animal could be observed, confirming similar observations from Africa (Scott et al., 2003). Pollen data of the eight examined hyaena scats clearly reveal the strong potential of these fecal materials in: (i) reconstructing the natural/semi-natural ecosystems in local and regional scale, (ii) understanding human agro-pastoral activities, (iii) revealing the foraging behavior and diet of the striped hyaenas, and (iv) detecting rare plant taxa.

Both the spotted and striped hyaenas are very mobile animals travelling up to 20 km/24 hours, mainly during the night (Wagner, 2006; Kolowski et al., 2007). The bone accumulation is, however, much more practiced by striped hyaenas compared to spotted hyaenas (Fourvel et al., 2015). The high mobility, combined with the proximity to human settlement areas, allows the striped hyaenas to visit a diverse mosaic of landscapes more or less impacted by human activities. Several studies suggest that the hyaena scat pollen spectra represent the whole area

Journal Pre-proof

foraged by the animal and not only around the den site (Carrion et al., 2001; Scott et al., 2003). Indeed, the pollen can be added to a scat through multiple ways: (i) pollen settled on the food before ingestion, (ii) pollen deposited on the scat after defecation, (iii) pollen found inside the digestive tube of the herbivores, (iv) direct ingestion of flowers, (v) pollen found in drinking water, and (vi) pollen absorbed through cleaning by their rough tongues (Scott et al., 2003; Mohamed Ahmed et al., 2012). The latter process may have been underestimated as a recent study has observed that striped hyaenas take time to clean each other in captivity, on average 1.15 minutes per day (Mohamed Ahmed et al., 2012). These diverse sources and processes of pollen ingestion can explain the abundant and diverse pollen flora encountered in hyaena faeces.

A number of studies indicate that while striped hyaenas avoid direct contact with humans, they remain close to pastoral communities inside or outside the urban/peri-urban areas, which permits them to diversify their food resources (Fourvel and Mwebi, 2011). Osteological identifications of faunal assemblage of the Kaftar Khun den complex by Monchot and Mashkour (2010), shows that 84.6% of the identified specimens belong to domesticated animals with equids (horses, donkeys and mules) comprising 72.1%, followed by domestic cattle (8.1%) and sheep/goat (3.0%). This high percentage of domestic animal bone remains makes the authors suggest that the striped hyaenas have become commensal animals. A recent study of the hyaena population density and distribution in arid NW India also indicates that striped hyaenas not only socially tolerate humans but take advantage of the availability of more food resources in human-dominated landscapes (Singh et al., 2014). In that study, the maximum number of animal detection was recorded at a distance between 1 to 3 km from human settlements. Availability of livestock carcasses and orchards are among the most important factors attracting the animal to habitations (Karami et al., 2006; Singh et al., 2010; Fourvel and Mwebi, 2011; Singh et al., 2014). Consuming the internal organs of domestic

Journal Pre-proof

herbivores may be one of the most important ways of ingestion of pollen of segetal, ruderal and cultivated plants into the hyaena scats. Finding the very rare pollen types in the Kaftar Khun fecal samples (see *Punica*, *Hypecoum*, and *Fumaria*; Fig. 4) has similarly been reported from the Wezmeh Cave in which rare plant taxa such as tulips (*Tulipa* spp.) have been documented (Djamali et al., 2011). Such pollen types are seldom found in sedimentary archives due to the taphonomic history (see e.g. the long pollen records from Lake Urmia, Djamali et al., 2008; pollen data accessible in the European Pollen Database: http://www.europeanpollendatabase.net/index.php). These findings suggest that hyaena fossil scats are an important source of information in relation to the detailed floristic composition of steppe vegetation.

Both spotted and striped hyaenas have played a significant role as omnivorous scavengers in the arid and semi-arid ecosystems of Eurasia and Africa during the Pleistocene. The role of the striped hyaena has become increasingly important in SW Asia after the decline of the spotted hyaenas at the end of the last glacial period (Horwitz and Goldberg, 1989; Mashkour et al., 2008). Although no striped hyaena fossil coprolites have so far been reported from the Iranian Plateau, we believe that some recent coprolites found in the Wezmeh Cave in western Iran correspond to this species, judging from very high morphological similarities (cf. sample KK3 in Fig. 3 of this study to sample WC-2 (405±59 cal. BP) in Fig. 2 in Djamali et al., 2011). The increasing number of archaeological excavations in SW Asian caves and rock shelters are providing abundant faunal remains including hyaena bones and coprolites (Mashkour et al., 2008; Scott et al., 2016). Our results show that the pollen encapsulated in these coprolites can be a major source of information on their environments, their foraging behavior and diet, as well as their interactions with human societies in the far and recent past. Biological investigation of modern hyaena scats collected from different ecosystems across the region can help establish modern analogues for a robust interpretation of the data obtained from fossil fecal materials. Copropalynological investigations are only one of the many different bioarchaeological techniques that can be applied to these precious fossil materials (Horwitz and Goldberg, 1989; Scott et al., 2016). Application of molecular studies of coprolites, further refines the attribution of coprolites to the lowest possible taxonomic levels (Bon et al., 2012; Bennet et al., 2016) and is complementary to their bioarchaeological study.

## 5. Concluding remarks

1. Like their spotted cousins, striped hyaenas also leave faeces that are rich in well-preserved pollen grains with great potential for palaeoecological reconstructions.
2. Pollen grains in all the examined modern hyaena scats were well-preserved and of very different natural and anthropogenic sources.
3. All pollen assemblages revealed the general traits of the regional vegetation composed of a xerophytic desert steppe with sparse desert wood shrubs.
4. Abundance of cultivated, segetal, and ruderal pollen can provide invaluable information on the human agro-pastoral activities and land-use changes.
5. The mixture and diversity of pollen originating from both natural/semi-natural ecosystems and anthroposystems, as well as the diversity of pollen ingestion processes, provides the possibility to obtain a detailed image of the foraging and dietary behavior of striped hyaenas.
6. The studied hyaena faeces pollen assemblages clearly show a commensal behavior of the animal and its use of food resources provided by human activities.
7. Direct and indirect ingestion of flowers adds details to the reconstruction of the floristic composition of the vegetation in the foraging area of striped hyaenas.

Journal Pre-proof

8. Analogy between the examined scats with some Holocene subfossil hyaena scats suggest that striped hyaena coprolites from archaeological/palaeontological sites can be of high potential in bioarchaeological and palaeoenvironmental studies.

**Acknowledgment**

We wish to thank Fereidoun Biglari, Abbas Etemad, Hamid Fahimi, and Saman Heydari-Guran for the organization and valuable assistance during the field works. We are also deeply indebted to Mr. Saeed Davari who kindly provided us with hyaena photographs. Frédéric Guiter is also thanked for preparing photographs from the hyaena scats. This work was funded by UMR 7209 AASPE and the LIA – HAOMA project of Centre National de la Recherche Scientifique (CNRS, France) a four-year grant allocated to the international collaborative project, as well as the French-Iranian joint scientific cooperation "Gundishapur Program 2016" project entitled "KECO?INO" funded by French Ministry of Europe and Foreign Affairs and Ministry of Higher Education, Research and Innovation in partnership with Center for International Scientific Studies and Collaboration (CISSC), Iranian Ministry of Research, Science and Technology.

Journal Pre-proof

## References

AbiSaid, M., Dloniak, S.M.D., 2015. *Hyaena hyaena*. *The IUCN Red List of Threatened Species 2015:* e.T10274A45195080.

Argan, J., 2014. La copropalynologie: coprolithes et paléoenvironnements. Bull. Mus. Anthropol. Monaco 54, 39-44.

Argant, J., Philippe, M., 2011. L'analyse pollinique des coprolithes: Un outil pour la reconstruction du paléoenvironnement. Quaternaire 4, 307-318.

Bache, S.M., Wickham, H., 2014. Package 'magrittr': A Forward-Pipe Operator for R. URL: https://cran.r-project.org/web/packages/magrittr/index.html.

Bennett, E.A., Gorgé, O., Grange, T., 2016. Coprolites, paleogenomics and bone content analysis. In: Fernández-Jalvo, Y., Geigl, E.-M., King, T., Yepiskoposyan, L., Andrews, P. (Eds.), Azokh Cave and the Transcaucasian Corridor. Springer, Dordrecht, pp. 271-286.

Berberian, M., Shahmirzadi, S.M., Nokandeh, J., Djamali, M., 2012. Archaeoseismicity and environmental crises at the Sialk mounds, Central Iranian Plateau, since the Early Neolithic. Journal of Archaeological Science 39, 2845-2858.

Biglari, F., 2004. The Preliminary Survey of Paleolithic Sites in the Kashan region., In: S.M. Shahmirzadi (ed.), The Silversmiths of Sialk (Sialk Reconsideration Project), Report No. 2, Archaeological Research Center, Iranian Cultural Heritage Organization,Tehran, pp. 151-168. (In Farsi)

Bon, C., Berthonaud, V., Maksud, F., Labadie, K., Poulain, J., Artiguenave, F., Wincker, P., Aury, J.-M., Elalouf, J.-M., 2012. Coprolites as a source of information on the genome and diet of the cave hyena. Proc. R. Soc. B 279, 2825-2830.

Bonnefille, R., Riollet, G., 1980. Pollen des savanes d'Afrique Orientale, CNRS Editions, Paris.

Byng, J.W., Chase, M.W., Christenhusz, M.J.M., Fay, M.F., Judd, W.S., Mabberley, D.J., Sennikov, A.N., Soltis, D.E., Soltis, P.S., Stevens, P.F., Briggs, B., Brockington, S., Chautems, A., Clark, J.C., Conran, J., Haston, E., Moller, M., Moore, M., Olmstead, R., Perret, M., Skog, L., Smith, J., Tank, D., Vorontsova, M., Weber, A., Angiosperm Phylogeny G., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181, 1-20.

Carrión, J.S., Riquelme, J.A., Navarro, C., Munuera, M., 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 2705, 1–13.



Journal Pre-proof

Journal Pre-proof

Carrión, J.S., Scott, L., Marais, E., 2006. Environmental implications of pollen spectra in bat droppings from southeastern Spain and potential for palaeoenvironmental reconstructions. Rev. Palaeobot. Palynol. 140, 175-186.

Carrión, J.S., Scott, L., Arribas, A., Fuentes, N., Gil-Romera, G., Montoya, E., 2007. Pleistocene landscapes in central Iberia inferred from pollen analysis of hyena coprolites. J. Quat. Sci. 22, 191-202.

Diedrich, C.G., 2012a. Typology of ice age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) coprolite aggregate pellets from the European late Pleistocene and their significance at dens and scavenging sites. New Mexico Museum of Natural History and Science Bulletin 57, 369-377.

Diedrich, C.G., 2012b. An Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) population, their excrements and prey from the Late Pleistocene hyena den of the Sloup Cave in the Moravian Karst, Czech Republic. Hist. Biol. 24, 161-185.

Djamali, M., de Beaulieu, J.-L., Shah-Hosseini, M., Andrieu-Ponel, V., Amini, A., Akhani, H., Leroy, S.A.G., Stevens, L., Alizadeh, H., Ponel, P., Brewer, S., 2008a. An Upper Pleistocene long pollen record from the Near East, the 100 m-long sequence of Lake Urmia, NW Iran. Quat. Res. 69, 413e420.

Djamali, M., Biglari, F., Abdi, K., Akhani, H., Andrieu-Ponel, V., de Beaulieu, J.-L., Mashkour, M., Ponel, P., 2011. Pollen analysis of coprolites from a late Pleistocene-Holocene cave deposit (Wazmeh Cave, W Iran): A glance at the glacial vegetation and flora of central Zagros Mountains. J. Archaeol. Sci. 38: 3394-3401.

Doostmohammadi, M., Malekmohammadi, M., Djamali, M., Akhani, H., 2019. Is *Pteropyrum* a pathway to $C_4$ evolution in Polygonaceae? An integrative approach to the taxonomy and anatomy of *Pteropyrum* ($C_3$), an immediate relative of *Calligonum* ($C_4$). Botanical Journal of the Linnean Society 192, 369-400.

Dray, S., Dufour, A.-B., Thioulouse, J., 2020. Package 'Ade4': Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences. URL: https://cran.r-project.org/web/packages/ade4/index.html.

Firouz, E., 2005. The Complete Fauna of Iran. I.B. Tauris, New York.

Fourvel, J.-B., Mwebi, O., 2011. Hyenas' level of dependence on livestock in pastoralist areas in the Republic of Djibouti and Kenya: relation between prey availability and bone consumption sequence.

In: Brugal, J.-P. (Ed.), Prédateur dans tous leurs états. Evolution, Biodiversité, Interactions, Mythes, Symboles. XXXI[es] rencontres internationales d'archéologie et d'histoire d'Antibes. APDCA, Antibes, pp. 157-176.

Fourvel, J.-B., Fosse, P., Avery, G., 2015. Spotted, striped or brown? Taphonomic studies at dens of extant hyaenas in eastern and southern Africa. Quat. Int. 369, 38-50.

Fourvel, J.-B., Fosse, P., 2017. Conives (Indre, France): Un nouvel exemple de repaire d'hyènes du pléistocène supérieur. Quaternaire 28, 455-469.

Ghirshman, R. 1938-1939. Fouilles de Sialk près de Kashan 1933,1934,1937, 2 vol.. Librairie Orientaliste Paul Geuthner, Paris.

Guijarro, J.A., 2019. Package 'climatol': climate tools (series homogenization and derived products). URL: "https://cran.r-project.org/web/packages/climatol/index.html

Hernández-Ledesma, P., Berendsohn, W.G., Borsch, T., Mering, S., Akhani, H., Arias, S., Castañeda-Noa, I., Eggli, U., Eriksson, R., Flores-Olvera, H., Fuentes-Bazán, S., Kadereit, G., Klak, C., Korotkova, N., Nyffeler, R., Ocampo, G., Ochoterena, H., Oxelman, B., Rabeler, R.K., Sanchez, A., Schlumpberger, B.O., Uotila, P., 2015. A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. Willdenowia 45, 281-384.

Heydari, S., Ghasidian, E., Conard, N.J., 2009. Iranian Paleolithic sites on travertine and tufa formations. In: Otte, M., Biglari, F., Jaubert, J. (Eds.), Recent Research on Paleolithic of Iran, Proceedings of the XV World Congress UISPP, Lisbon. BAR International series 1968, Vol. 28, Archaeopress, Oxford, pp. 109-124.

Horwitz, L.K., Goldberg, P., 1989. A study of Pleistocene and Holocene Hyaena coprolites. J. Archaeol. Sci. 16, 71-94.

Hunt, A.P., Lucas, S.G., 2019. Hyena hegemony: Biogeography and taphonomy of Pleistocene vertebrate coprolites with description of a new mammoth coprolite ichnotaxon. Ichnos 27, 111-121.

Husson, F., Josse, J., Le, S., Mazet, J., 2020. Package 'FactoMineR': Multivariate exploratory data analysis and data mining. URL: https://cran.r-project.org/web/packages/FactoMineR/index.html.

Journal Pre-proof

Journal Pre-proof

Ilkhani, H. Livarda, A. Fazeli Nashli, H. 2019. Archaeobotanical report about Tappeh Sialk, North Mound. First Impressions. In: Nokandeh, J., Curtis J., Pic, M. (Eds.) Tappeh Sialk the glory of ancient Kashan, Iranian Heritage Foundation, Louvre, Richt, National Museum of Iran., pp. 40-44.

Juggins, S., 2019. Package 'rioja': Analysis of Quaternary science data. URL: https://cran.r-project.org/web/packages/rioja/index.html.

Karami, M., Riazi, B., Kalani, N., 2006. Habitat evaluation of the striped hyena (*Hyaena hyaena hyaena*) in Khojir National Park. Environmental Science 11, 77-86. (In Persian with English abstract)

Kassambara, A., 2020. Package 'factoextra': Extract and visualize the results of multivariate data analyses. URL: https://cran.r-project.org/web/packages/factoextra/index.html.

Klein, J.-C., 1994. La végétation altitudinale de l'Alborz Centrale (Iran). Institut Français de Recherche en Iran, Tehran.

Kolowski, J.M., Katan, D., Theis, K.R., Holekamp, K.E., 2007. Daily patterns of activity in the spotted hyena. J Mammal. 88, 1017-1028.

Marean, C.W., Kim, S.Y., 1998. Mousterian large mammal remains from Kobeh cave. Behavioral implications for Neanderthals and early modern Humans. Current Anthropology 39, 79–113.

Mashkour, M., 2004a. Paleo-environmental studies in Sialk (Kashan). In: Malek Shahmirzadi (Ed.), The Silver Smith of Sialk, Report No. 2, Iranian Cultural Heritage and Handicraft and Tourism Organization, Tehran, pp.189-194. (In Persian).

Mashkour, M. 2004b. Preliminary report of archaeozoological studies of the third season of the Sialk Reconsideration Project. In: Malek Shahmirzadi (Ed.), The potters of Sialk, Report No. 3. Iranian Cultural Heritage and Handicraft and Tourism Organization, Tehran, pp. 95-108. (In Persian).

Mashkour, M., Bon, C., Demeter, F., Friess, M. Sheikhi, S., Huet, L., Thomas, L., 2019. Tappeh Sialk Human and Animal Osteological Collections at the National Museum of Natural History, In: Nokandeh J., Curtis J., Pic M. (Eds) Tappeh Sialk the Glory of Ancient Kashan. Iranian Heritage Foundation, Louvre, Richt, National Museum of Iran, 45-55p

Mashkour, M., Fahimi, H., 2019. Iron Age animal exploitation at the edge of the Dasht-e Kavir, central desert of Iran. The case of Shamshirgah (Qom-Iran). In: Hassanzadeh, Y., Vahdati, A., Karimi, Z., Proceedings of the international conference on The Iron Age in Western Iran and Neighbouring Regions, vol 1. Iranian Cultural Heritage and Handicraft and Tourism Organization, Tehran. pp. 191-200.

Mashkour, M., Monchot, H., Trinkhaus, E., Reyss, J.-L., Biglari, F., Bailon, S., Heydari, S., Abdi, K., 2008. Carnivores and their prey in the Wezmeh Cave (Kermanshah, Iran): A late Pleistocene refuge in the Zagros. Int. J. Osteoarchaeol. 19, 678-694.

Monchot, H., 2008. Des hyènes tachetées au Pléistocène supérieur dans le Zagros (grotte Wezmeh, Iran). Archaeozoology of the Near East VIII, TMO 49, Maison de l'Orient et de la Méditerranée, Lyon, pp. 65-78.

Monchot, H., Mashkour, M., 2010. Hyenas around the city (Kashan, Iran). J. Taphonomy 8, 17-32.

Moore, P.D., Webb, J.A., Collinson, M.E., 1991. Pollen Analysis, 2nd ed., Blackwell, Oxford.

Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.M., Szoecs, E., Wagner, H., 2019. Ordination methods, diversity analysis and other functions for community and vegetation ecologists. URL: https://cran.r-project.org/web/packages/vegan/index.html

Pearson, S., Betancourt, J.L., 2002. Understanding arid environments using fossil rodent middens. J. Arid Env. 50, 499–511.

Podlech, D., 1986. *Artemisia*. [Compositae VI – Anthemideae]. In: Rechinger K.-H. (Ed.) Flora Iranica, Vol. 158, Graz. pp. 159-223.

Podlech, D., 2013. Some remarks on Artemisia subgenus Serephidium (Asteraceae) mostly from Afghanistan. Rostaniha 14, 48-58.

Reille, M., 1992. Pollen et spores d'Europe et d'Afrique du Nord, Laboratoire de botanique historique et de palynologie, Marseille.

Journal Pre-proof

Journal Pre-proof

Reille, M., 1995. Pollen et spores d'Europe et d'Afrique du Nord, Supplément 1, Laboratoire de botanique historique et de palynologie, Marseille.

Reille, M., 1998. Pollen et spores d'Europe et d'Afrique du Nord, Supplément 2, Laboratoire de botanique historique et de palynologie, Marseille.

Rezaei, S., Naderi, S., Karami, P., 2017. The ecological study of striped hyaena (Hyaena hyaena) denning areas in the Haftad Qolleh protected Area, Arak, Iran. Natural Environment, 70, 351-362.

Rieger, I., 1979. A review of the biology of the striped hyaenas, *Hyaena hyaena* (Linne, 1758). Saugetierkundliche Mitteilungen 27, 81-95.

RStudio Team, 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Scott, L., 2000. Pollen. In: Partridge, T.C., Maud, R.R. (Eds.), The Cainozoic of Southern Africa. Oxford Monographs on Geology and Geophysics No. 40, Oxford Univ. Press, Oxford, pp. 339-350.

Scott, L., Fernández-Jalvo, Y., Carrión, J., Brink, J., 2003. Preservation and interpretation of pollen in hyaena coprolites: taphonomic observations from Spain and southern Africa. Palaeont. Afr. 39, 83-91.

Scott, L., Rossouw, L., Cordova, C., Risberg, J., 2016. Palaeoenvironmental context of coprolites and plant microfossils from Unit II. Azokh 1. In: Fernández-Jalvo, Y., King, T., Yepiskoposyan, L., Andrews, P. (Eds.), Azokh Cave and the Transcaucasian Corridor. Springer, Dordrecht, pp. 287-295.

Shamoon, H., Shapira, I., 2019. Limiting factors of Striped Hyaena, *Hyaena hyaena*, distribution and densities across climatic and geographical gradients (Mammalia: Carnivora). Zoology in the Middle East 65, 189-200.

Shirazi, Z., Tengberg, M., 2012. Vegetation and wood exploitation at Tape Sialk from the Neolithic to the Iron Age. In: Shahmirzadi, S.M. (Ed.), The villagers of Sialk. Research Center of Iranian Cultural Heritage, Handicrafts and Tourism Organization, Tehran, pp. 17-26.

Singh, P., Gopalaswamy, A.M., Karanth, K.U., 2010. Factors influencing densities of striped hyenas (*Hyaena hyaena*) in arid regions of India. Journal of Mammalogy 91, 1152–1159.

Singh, R., Qureshi, Q., Sankar, K., Krausman, P.R., Goyal, S.P., Nicholson, K.L.? 2012. Population density of striped hyenas in relation to habitat in a semi-arid landscape, western India. Acta Theriol. 59, 521-527.

Stockmarr, J. 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 615–621.

Tengberg, M., 2004. Archaeobotanical analysis at Tepe Sialk. Results from the 2003/04 season. In: Shahmirzadi, M.S. (Ed.), The potters of Sialk. Sialk Reconsideration Project No. 3, 25-32.

Tourani, M., Moqanaki, E.M., Kiabi, B.H., 2012. Vulnerability of striped hyaena, *Hyaena hyaena*, in a human-dominated landscape of central Iran. Zool. Middle East 56, 133-136.

Turnbull, P.F., 1975. The mammalian fauna of Warwasi Rock Shelter, West-central Iran. Fieldiana Geology 33, 141–155.

van Zeist, W., Bottema, S., 1977. Palynological investigations in western Iran. Palaeohistoria 19, 19–85.

van Zeist, W., Bottema, S., van der Veen, M., 2001. Diet vegetation at Ancient Carthage, the archaeobotanical evidence. Groningen Institute of Archaeology, Groningen.

Wagner, A.P., 2006. Behavioral ecology of the striped hyena (*Hyaena hyaena*). Unpublished Ph.D. Thesis, Montana State University, Bozeman, U.S.A.

Xiong, H., Shi, A, Mou, B., Qin, J., Motes, D., Lu, W., Ma, J., Weng, Y., Yang, W., Wu, D., 2016. Genetic Diversity and Population Structure of Cowpea (*Vigna unguiculata* L. Walp). PLoS ONE 11, e0160941. doi:10.1371/journal. pone.0160941.

Yll, R., Carrión, J.S., Marra, A.C., Bonfiglio, L., 2006. Vegetation reconstruction on the basis of pollen in Late Pleistocene hyena coprolites from San Teodoro Cave (Sicily, Italy). Palaeogeogr. Palaeoclimatol. Palaeoecol. 237, 32-39.

## Figure and Table captions :

Journal Pre-proof

Figure 1. a. Geographical position of the study site (Kaftar Khun) at the edge of central Iranian Plateau. b. The IUCN map for worldwide distribution of *Hyaena hyaena* (in dark brown) in Eurasia and Africa. c. Climate diagram based on Iran Meteorological Organization data from the city of Kashan.

Figure 2. a. Two striped hyaenas recently photographed in central Iran (not Kaftar Khun). b. Den complexes are mostly found in rock shelters formed in limestone outcrops. c. The position of the den complex in a travertine outcrop, photo looking north. d. Photo looking northwest: foreground shows xerophytic desert *Artemisia* steppe and background shows the suburbs of the city of Kashan and the central Iranian desert. Photo a is courtesy of wildlife photographer M. Saeed Davari. Photos, b, c, and d by MM.

Figure 3. Pictures of six of the hyaena scats studied in this paper.

Figure 4. Pollen percentage diagram of the eight hyaena scats. *Sporormiella* percentage in sample KK2 is >2900% calculated based on total pollen sum.

Figure 5. PCA biplot comprising the main pollen types (variables) found in hyaena scats K1 to K8 (samples).

Figure S1. PCA Biplot (samples/variables) of the Principal Component Analysis (PCA). The quality of representation (cos2) of samples (K1 to K8) is illustrated by the relative size of the circles. Contrib: contribution of variables. 42.2% of the variation is explained by the first two axes.

Table 1. Size and some pollen measurements of the studied desiccated hyaena scats of Kaftar Khun.

Table 1. Size measurements and some pollen values of the studied desiccated hyaena scats of Kaftar Khun.

| Sample | Size | | No. pollen types | Total Pollen counts | Weight of treated sample (g) | Pollen concentration No. /g |
|---|---|---|---|---|---|---|
| | Length (mm) | Breadth (mm) | | | | |
| KK1 | N/A | N/A | 16 | 428 | 0.5 | 31982 |
| KK2 | 26 | 23 | 20 | 377 | 1.1 | 52538 |
| KK3 | 39 | 20 | 25 | 207 | 1.1 | 14694 |
| KK4 | 70 | 21 | 27 | 380 | 1.5 | 10845 |
| KK5 | 28 | 31 | 29 | 283 | 1.3 | 55345 |
| KK6 | 87 | 26 | 33 | 428 | 1.8 | 17896 |
| KK7 | 31 | 28 | 27 | 344 | 2.7 | 6881 |
| KK8 | 53 | 34 | 16 | 379 | 1.9 | 70485 |

Highlights

- We studied modern scats of striped hyaenas in Iran with pollen analysis
- All scats were rich in pollen and displayed good pollen preservation
- Hyaena scat pollen data provided information on palaeoenvironment and human activities
- Holocene hyaena scat pollen can provide information on animal behaviour

Journal Pre-proof