Scientific Annals, School of Geology Aristotle University of Thessaloniki (AUTH)	Special volume 98	201-212	Thessaloniki, 2006

HYENA CAVES IN JORDAN

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Abstract: Of 14 lava caves discovered and explored since 2003 in the Jordanian volcanic Al-Shaam Harrat, eight contain traces of usage by the striped hyena (*Hyaena hyaena*). Three caves have a particularly rich record: Al-Fahda, Dabié and Al-Hayya Caves. Hyena cave usage left abundant deposits of camel bones with bones from other animals in the minority (by weight), bones and skulls of the hyena, hyena dens, coprolite deposits, paw traces and polished rocks. Hyenas penetrated caves all the way to their ends, i.e. up to 490 m from the entrance. The habit to carry large bones into caves is similar to that of the extinct European *Crocuta crocuta spelaea*, but unlike the extant African *Crocuta crocuta* and *Hyaena brunnea*. The Jordanian striped hyena may therefore be a good model to use to study the taphonomy of the cave hyena as well as its own cave-related ethology.

Key words: *Hyaena hyaena, Crocuta crocuta spelaea*, caves, lava caves, bone deposits, camel bones, dens, Jordan.

INTRODUCTION

Hyenas account for a large part of the Pleistocene bone deposits in caves in Europe (e.g., Buckland, 1823; Zapfe, 1954; Rosendahl, 1995; Rosendahl *et al.,* 2007). Among the earliest anatomically correct pictures of a bone from an extinct Pleistocene animal was a jaw fragment of a hyena from the Baumann's Cave, Harz Mountains, Germany, collected in 1708 by Johann Christian Kundmann and published in 1737 (Kundmann, 1737; Kempe, 2004). In 1805, Cuvier recognized these teeth as those of a hyena, larger than the living species and finding it more similar to the "hyéne du Cap" than to the "hyéne du Levant". Goldfuss depicted a fossil hyena skull in 1810, and, in 1823, named the fossil species *Hyäna spelaea* (Goldfuss, 1823). It is a distinctly larger subspecies of the extant African spotted hyena (*Crocuta crocuta*) (Rohland *et al.,* 2005). Hyenas can feed on bones; but to consume large bones, it may be of advantage to carry them to a protected den. *C. crocuta spelaea* therefore carried bones, mostly of large Pleistocene herbivores, individually into caves where they were consumed (e.g., Zapfe, 1939). Glacial "hyena den caves" therefore contain a variety of large, partly consumed, individual bones of those animals living nearby, but they never contain complete skeletons. Because cave hyenas are climate indifferent, these bone deposits can represent both glacial and interglacial faunas.

The ethology of *C. crocuta spelaea* (GOLDFUSS, 1823) with respect to caves cannot be studied anymore. It is therefore interesting to look at the recent species of hyenas (spotted hyena *Crocuta crocuta*, ERXLEBEN, 1777; striped hyena *Hyaena hyaena,* LINNAEUS, 1758; and brown hyena *Hyaena (Parahyaena) brunnea,* THUNBERG, 1820) and study their cave usage. This opportunity arose when, during a survey of Jordanian caves, we realized that most

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Table 1
List of currently (May 2006) known and surveyed lava caves in Jordan, sorted by total passage length (after Kempe *et al.,* 2006). H = hyena cave.

Name of Cave	Latitude	Longitude	H	Stations	Length m	Stations	Depth m	Direction	Altitude m	Type
Al-Fahda Cave	32°18′	37°07′	+++	Complex	**923.5**	2 to 54	6.7	SW-NE	832	Lava Tunnel
Al-Badia Cave	32°07′	36°49′	-	32 to 23	**445.0**	1 to 23	17.2	NW-SE		Lava Tunnel
Hashemite University Cave	32°14′	36°34′	++	21 to 35	**231.1**	1 to 23	10.0	NW-SE		Lava Tunnel
Al-Ameed Cave	32°13′	36°33′	++	Complex	**208.0**	2 to 31	4.0	SW-NE		Pressure Ridge
Dabié Cave	32°10′	36°55′	+++	0 to 14	**193.6**	0 1to 13	1.8	NW-SE	893	Lava Tunnel
Abu Al-Kursi East	32°15′	36°39′	++	20 to 34	**153.7**	1 to 34	12.2	W-E		Lava Tunnel
Al-Howa	32°18′	36°37′	-	Complex	**97.1**	2 to 6	10.8	SW-NE		Lava Tunnel
Al-Hayya Cave	32°17′	36°34′	++	1 to 11	**81.3**	1to 9	4.2	NW-SE	911	Pressure Ridge
Abu Al-Kursi West	32°15′	36°39′	++	2 to 18	**77.1**	2 to 18	8.1	N-S		Lava Tunnel
Azzam Cave	32°17′	36°36′	-	13 to 25	**44.1**	1 to 25	4.2	NNW-SSE		Pressure Ridge
Al-Ra'ye Cave	32°17′	36°34′	-	1 to 6	**42.0**	1 to 34	3.5	NW-SE	911	Pressure Ridge
Dahdal Cave	32°17′	36°35′	+	5 to 12	**28.9**	1 to 12	0.0	SW-NE		Pressure Ridge
Beer Al-Wisad	31°46′	37°28′	-	11-3-7	**11.4**	1-2-7	11.5	NE-SW	615	Pit (unknown)
Treasure Pit	30°51′	35°24′	-	Complex	**7.2**	2 to 11	5.8	NE-SW	960	Tunnel ?
Total					**2,544**					

of the caves encountered in Jordan's deserts were hyena caves. This observation is in accordance with findings in Saudi Arabia, where hyena traces are also observed in lava caves of similar settings (Pint, 2006).

LAVA CAVES IN JORDAN

The eastern part of the Hashemite Kingdom of Jordan forms a vast stony desert, partly occupied by volcanic terrain. It is a section of a large intra-continental lava plateau called the Harrat Al-Shaam, stretching from Syria through Jordan into Saudi Arabia, build up by eruptive activity that started in the Oligocene (fig. 1). Its centre is formed by young alkali olivine basaltic lava flows (Al-Malabeh, 1998). The top-most and therefore youngest flows are about 400,000 years old (Tarawneh *et al.,* 2000). They are associated with recognizable eruptive centers such as the Quis Volcano Group (Al-Malabeh *et al.,* 2002), the Al-Bishriyya flow field (Al-Malabeh, 2003) or the Al-Fahda (Jawa) eruption center (Ibrahim & Al-Malabeh, 2006) (from west to east). Their surface is characterized by local playas between ridges that give the terrain a "mottled" appearance. Drainage networks have not yet developed, unlike on the underlying older lavas that feature extensive wadi systems. Younger and older lavas of the Harrat Al-Shaam are covered by a layer of loess, often over one meter thick. In these lavas we explored, surveyed and studied a total of 14 lava caves since September 2003. 2,544 m of passages were surveyed as of May 2006 (tab. 1) (Kempe *et al.,* 2006).

The discovery of so many lava caves in the Jordanian Harrat by A. Al-Malabeh in the period between 1986 and 2006 came as a surprise, first because of the high age of these lavas and second because loess, washed into the caves, could easily seal them in a geologically short period. Al-Fahda Cave, Al-Badia Cave (Beer Al-Hamam), Dabié Cave and the two Abu Al-Kursi Caves are all terminated by sediments. Hashemite University Cave ends with a lava seal. Most of the larger caves are lava tunnels, i.e. former lava conduits in which lava was transported from the volcanic vent towards the flow front (e.g., Hon *et al.,* 1994; Kempe, 2002). Other caves that lack signs of laterally flowing lava are summarized as pressure ridge caves. They seem to be created by upward doming of lava sheets by lateral pressure or by injection and consecutive draining of lava underneath still pliable lava strata. These caves tend to be smaller in extent, but Al-Ameed Cave is a sizeable example of this type of cave formed by two wide but low cavities connected by a 30 m long and 8 m wide crawl passage. Beer Al-Wisad finally is an 11 m deep pit of unknown origin in massive lavas (possibly pillow lavas) of Miocene age. Shifting sand should have filled it a long time ago. An anthropogenic origin of the cave can therefore not be excluded entirely even though the form of the shaft does not at all support such a conclusion.

Upper Cretaceous and lower Tertiary formations underlay the Al-Shaam basalts. These rocks crop out in the southern and eastern part of the Jordanian desert. They contain countless chert beds that form an almost continuous cover of nodules and flakes on top of the calcareous country rock. In these areas we found so far one natural cave (a large overhanging sinkhole) and several artificial cavities that have been used for housing, for stables or to extract flint.

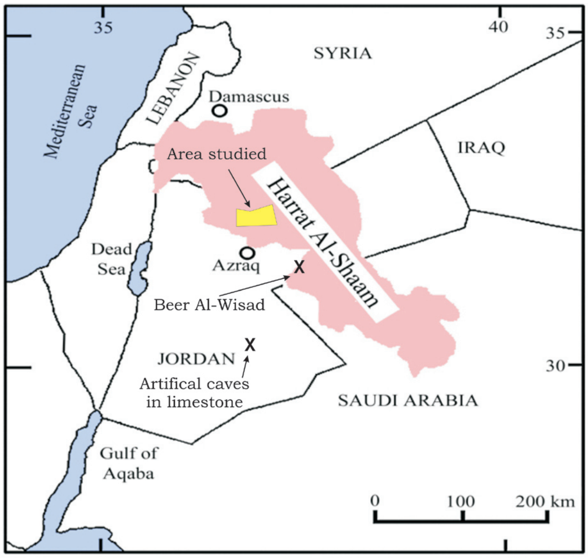

Figure 1. Study area and extent of Harrat Al-Shaam (altered after AL-MALABEH, 1994).

HYENA CAVES

Even more astonishing than the fact that these caves are still accessible are the almost ubiquitous signs that the caves were or are used by hyenas (*Hyaena hyaena*, LINNAEUS, 1758). Specifically Al-Fahda Cave, Hashemite University Cave, Dabié (Arabic for "hyena") Cave, Abu Al-Kursi Caves, Al-Ameed Cave, Al-Hayya Cave, and Dahdal Cave can be classified as hyena caves. Al-Badia Cave and Beer Al-Wisad have overhanging entrance pits unsuitable for hyenas. They are used instead by pigeons. Al-Howa has been opened for us in 2004 and no traces of a former hyena occupation were found. Azzam Cave and Al-Ra'ye Cave are sheep pens, a usage that may have obliterated formerly present hyena traces. Column "H" (tab. 1) classifies the caves so far explored by the intensity of hyena traces. Hyena-transported bones with gnaw marks were also found in one of the artificial caves, making it the ninth hyena cave so far encountered.

Figure 2. Upper jaw and skull of a hyena from Al-Hayya Cave (2005).

Hyenas still live in Jordan, both in the Jordan Valley and in the eastern desert (AL-YOUNIS, 1993; AMR *et al.*, 1996; NISSIM, 1985; QUMSIYEH *et al.*, 1993; SEARIGHT, 1987). In May 2006 the authors saw a hyena from a distance in an area of Wadi Aritain around Jabal Hassan Volcano which lies between Azraq and Al-Safawi. This is in accordance with the ethology of the striped hyena that roams solitarily. Hunting hyenas is not permitted in Syria, so that hyenas can also immigrate from the north in search of food. Overall they do not seem to be plentiful, since we also found carcasses of sheep and camels in the southern desert that did not show evidence of hyena scavenging.

Figure 3. Section of Dabié Cave (2004). The floor is almost continuously covered by bones brought in by hyenas.

Evidence of hyena usage of caves

Hyena usage of caves has left several lines of evidence:

- Skulls and other bones of hyenas (fig. 2), including one mummified hyena (in Dabié Cave) and a few almost complete skeletons,
- large amounts of bones of other animals, mostly of

Figure 4. Hyena coprolite with the typical conical protrusion in a field of decomposed coprolites and camel bones in various stages of consumption (Al-Fahda Cave, 2005).

Figure 5. Hyena den almost at the upslope end of Al-Fahda Cave.

Figure 6. Pit (smaller than den) dug by a hyena or fox at a fissure, possibly in search of water (Al-Fahda upslope section near station 73).

camels, including entire legs and skulls, but also of sheep and/or goats and occasionally antelope with abundant gnaw marks and in all stages of consumption (fig. 3),

- abundant hyena coprolites (fig. 4),
- hyena dens, i.e. shallow pits dug mostly along the sides of the passages and occasionally in the centre of the cave floors (fig. 5),
- excavation pits, dug either in search of water or even in search of cave continuation (fig. 6),
- imprints of feet in soft mud (Al-Ameed Cave), and
- polished corners of rocks ("hyenaschliffe" already mentioned by Nöggerath, 1824; for Kirkdale Cave and Sundwig) at places of regular hyena traffic (Hashemite University Cave).

Caves are also used by fenneks (*Vulpes zerda*, ZIMMERMANN, 1780) (one for example was feeding on the hyena mummy) and possibly by wolves. Bedouins used to close hyena caves with rocks to keep hyenas and wolves out of their area and away from herds.

HYENAS IN AL-FAHDA CAVE

One of the most surprising observations was that hyenas have penetrated the caves all the way to their ends. In Al-Fahda hyenas have visited and lefts dens, coprolites and bones at both ends, 490 and 190 m, respectively, from the entrance (fig. 7). This appears to be the furthest documented penetration of hyenas into caves yet (literature search by the authors). Similar deep ventures of hyenas into caves are reported from Saudi Arabia: 390 m in Kahf Al Shuwaymis and 315 m in Hibashi Cave (pers. com. J. Pint). In reaching those final chambers the animals had to crawl through some tight passages that we had to enlarge to fit through. This suggests that hyenas negotiate spaces as low as 30 cm (fig. 8). At the upslope (western) end of the cave hyenas have dug extensively, moving sediment in the amount of >0.1 m^3. Possibly they tried to follow an air draft. At the downslope end we found a dead, decayed hyena in its den. This suggests that no other hyena or fox had penetrated this far into the cave recently, disturbing the carcass. Interestingly the body is not mummified, but decayed with the bones also mostly disintegrated to a mush (fig. 9). This may be due to the fact that drip water was present even at the end of September.

Al-Fahda cave is very wide (on average 7.51 m) but rather low (tab. 2), unusual proportions for a lava tunnel. It therefore has a very large floor area, about 7000 m^2 (total length times average width). Hyenas did concentrate their feeding places to certain sites not distributing the bones evenly across the floor. Since they could not have

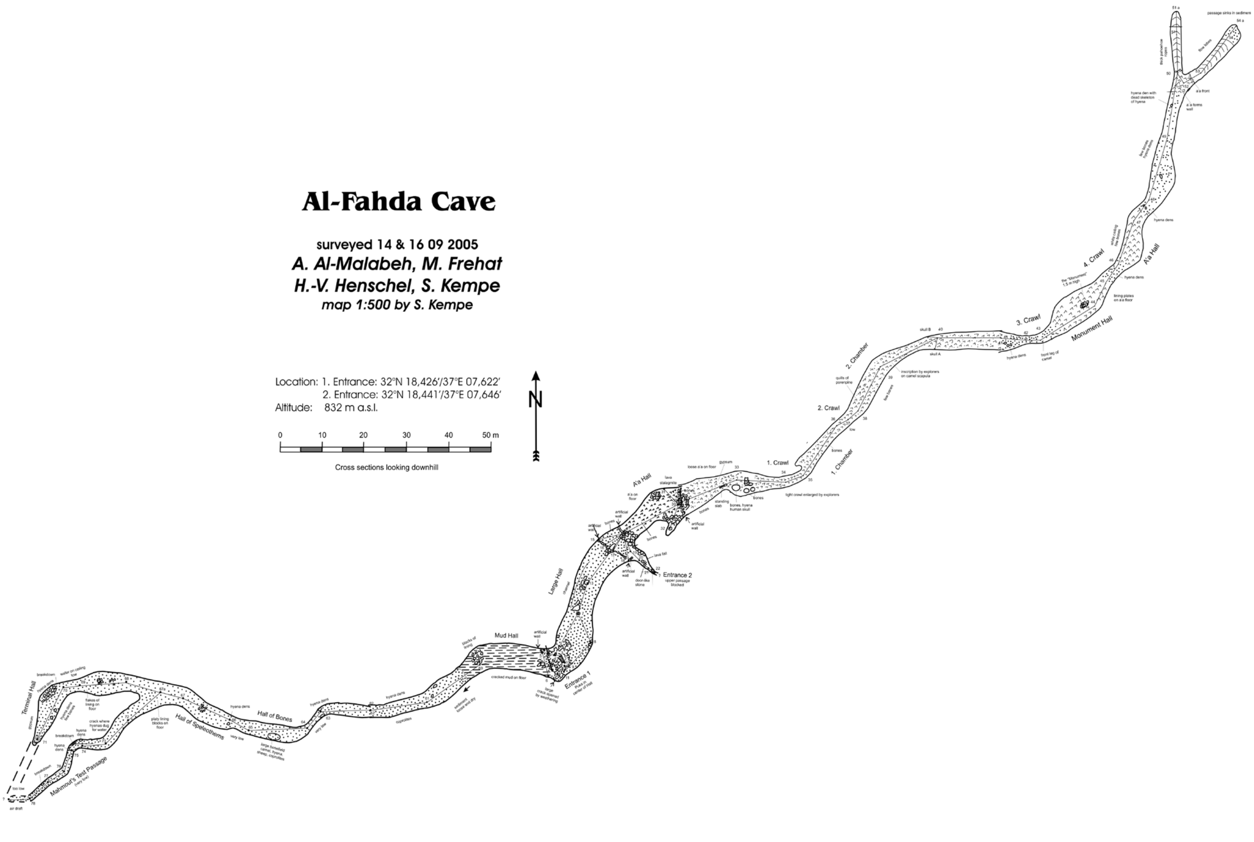

Figure 7. Composite map of the Al-Fahda Cave. It is currently the longest lava cave known on the Arabian Plate.

brought the large amount of camel bones at any single site at one time (fig. 10), these feeding places were repeatedly visited (by the same individual or different ones?). There is no clear link between feeding places and dens, most of the dens do not have bones associated with them. Normally the bones seem to be in no context with each other; at one place however, it can be shown that a hyena dragged in an upper front leg consisting of a humerus

Figure 8. Surveying in one of the low crawls in the lower section (eastern) of Al-Fahda Cave.

Figure 9. A dead hyena in its den very near to the lower end of Al-Fahda Cave.

Figure 10. A typical hyena feeding place with a collection of large camel bones in the downslope section of Al-Fahda Cave.

Figure 11. Human skull cap A near Station 40 in Al-Fahda Cave.

Figure 12. Human skull cap B near Station 40 in Al-Fahda Cave.

and radius/ulna. Entire camel skulls are also found far into the caves.

Table 2
Width and height of Al-Fahda Cave (Kempe *et al.,* 2006).

Width	Maximal at St. 8	17.5 m
	Minimal at St. 64	3.55 m
	Mean width main passage (39 stations)	7.51 m
Height	Maximal St. 14	4.67 m
	Mean height main passage (39 stations)	1.21 m

The cave floor is covered 100 % by sediment upslope of the entrance and to an estimated 30 % downslope of the entrance. These sediments derive from the main entrance (Bedouins once build a channel to feed water into the cave during winter), from a now buried upper entrance or by being transported through ceiling cracks with drip water. In some parts, one can see mud-stalactites at the ceiling: The sediment is re-deposited fine-grained quartz-containing aeolian sediment, probably glacial loess. In these sediments the hyenas have dug many dens, about 20 cm deep and 1 m across. Preferentially these dens are located at the wall and in low passages, sometimes even behind breakdown rocks. Apparently such a situation offers the most protection to the hyena. Often the ceiling height of the passage is lowest in the middle, due to the sediment piled up there from the dens fringing the walls.

Since most of the cave is in total darkness, the question of how the hyenas oriented themselves arises. We have seen a few rocks that seem to be "wet", possibly wetted with urine for markers. Hyaenidae also have an anal gland, the excretion of which is used for frequent territorial marking (e.g., Mills, 1989). Other possibilities are that the hyenas orient themselves by feeling the air-draft in the cave, by echoes and/or by feeling their way with their facial whiskers.

We also found three human skull caps in the cave, two of them at the perimeter of the cave across each other (figs. 11, 12). A first inspection does not suggest that they have been consumed by hyenas. Humans have previously explored the cave beyond the sites of the skull caps and left a stack of rocks (see "the Monument" on fig. 7) in the middle of the passage. There are no traces of burials or any other human bones in the cave. In addition, we found remains of a porcupine.

HYENAS IN DABIÉ CAVE

Dabié Cave is far shorter (194 m) and narrower than (on average 3.6 m of 13 stations) Al-Fahda Cave (fig. 13). The area of the cave is about 700 m^2, one tenth of Al-Fahda. In

Table 3
Bone dimensions measured in Abu Al-Kursi (East) Cave (AAK) compared to the measurements given in Walker (1985) (REF, last column). Letters (A) and (B) refer to the sketches in Walker (1985) for exact placement of measurements.

Bone	Measurement	AAK cm	REF cm
Humerus (right)	Total length	33.2	37.6
(proximal epiphysis loose)	Proximal width (A)	11.15	10.5
	Proximal thickness (B)	8.03	6.05
	Distal width (A)	7.97	8.15
	Distal thickness (B)	4.20	3.85
Humerus (proximal epiphysis missing)	Width of role (A)	7.92	8.15
	Thickness between rolls	4.51	3.85
Ulna & Radius (proximal end missing)	Distal width (A)	7.52	7.9
Ulna & Radius	Proximal gap (A)	4.46	3.80
	Proximal width (B)	9.65	7.65
	Length (without distal end)	51.5	51.2
Ulna & Radius	Overall length	55.5	51.2
	Proximal gap (A)	4.43	3.80
	Proximal width (B)	8.85	7.65
Metacarpal	Overall length	36.6	36.5
	Proximal width (A)	7.25	6.7
	Distal width left roll (B)	4.02	3.85
Tibia & Fibula (left)	Overall length	46.5	44.2
	Proximal width (A)	11.65	11.1
	Proximal thickness (B)	4.7	4.0
	Distal width (A)	8.97	8.35
	Distal thickness (B)	4.90	3.95
	Smallest thickness	4.98	
	Smallest width	3.17	
Tibia & Fibula (right)	Overall length	46.1	44.2
	Proximal width (A)	11.48	11.1
	Proximal thickness (B)	4.15	4.0
	Distal width (A)	8.02	8.35
	Distal thickness (B)	4.33	3.95
	Smallest thickness	4.51	
	Smallest width	2.85	

consequence, the back part of the cave, beginning a few meters inside of Station 11, is covered almost continuously with bones. Hyena dens begin at about 80 m inside. The last ones occur at the very end where bones and sediments almost fill the cave to the ceiling.

When the authors were shown to the cave by a local Bedouin, the entrance was blocked by stones to keep hyenas out of the cave. Formerly, a short channel diverted water into the cave from the wadi that perpendicularly cut the lava flow. When we entered the cave, a strong putrid smell filled the cave. It came from a half-consumed hyena mummy located ca. 40 m from the end of the cave (fig. 14). The hyena is missing its front teeth (fig. 15). We can only speculate how this happened. Either the animal was trapped in the cave when rocks were placed over the entrance and when it tried feverishly to dig its way out, or it lost the teeth in a fight or accident (e.g., with a car) and withdrew to the cave to die. When we returned one and a half years later (fig. 16), we found the mummy split in two. A fennek was in the cave and left it in panic. Apparently it had fed on the remains of the mummy. We collected the remains for further study and as a specimen in the exhibition on mummies planed for 2007 at the Reiss-Engelhorn-Museen at Mannheim, Germany.

In Dabié cave the majority of bones (at least by weight if not necessarily by number) to be camel bones. We also noticed sheep or goat bones, sheep wool and a few hyena bones. Coprolites of both hyenas and foxes occurred as well.

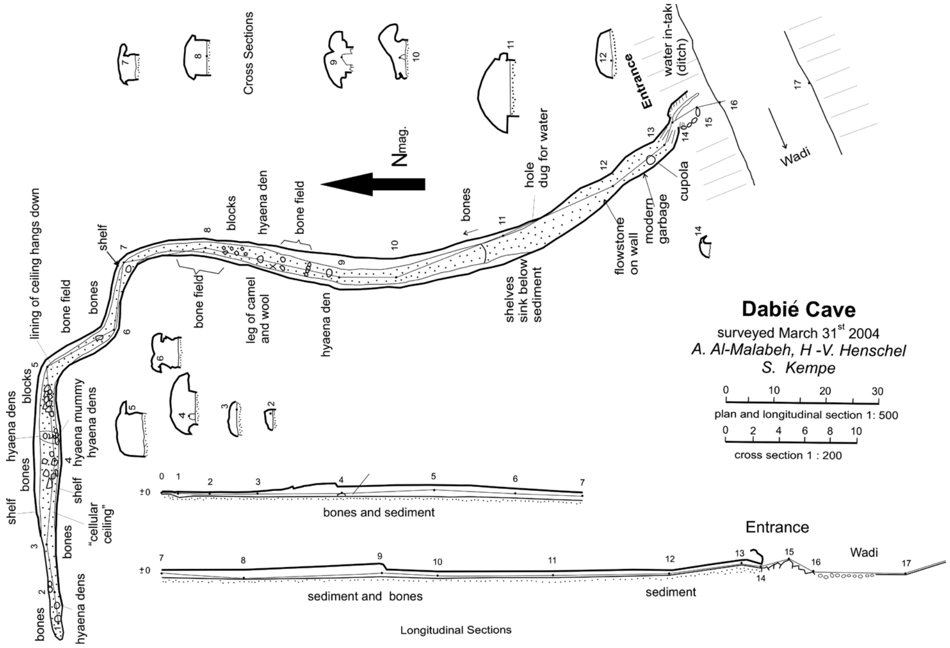

Figure 13. Map of Dabié Cave.

HYENAS IN AL-HAYYA CAVE

Al-Hayya Cave is an 80 m long passage, interrupted by a few blocks of breakdown. It was named after its only live inhabitant, a harmless mouse-eating snake: *Spalerosophis diadema cliffordii,* SCHLEGEL, 1837 (Arab: Bou m'raiat or ar'am (arkam) ahmar, German: Diademnatter, English: Clifford's snake or Diadem snake; pers. comm. Prof. Dr. Wolfgang Böhme of the Museum König in Bonn). The cave floor is covered by dry sediment in which a few hyena dens have been dug. The cave contains quite a lot of bones, among them wolf or dog (fig. 17), hyena, camel, cattle, horse and another human skull cap. We also found a dry mummy of a fennek (fig. 18) that was sent to Mannheim as well for the upcoming exhibition.

FIRST OBSERVATIONS ON HYENA BONE CONSUMPTION

The large amount of bones and coprolites offers the opportunity to study hyena bone consumption. First observations suggest that - at least by weight - camel bones dominate in the cave deposits. In order to be sure of this conclusion (i.e. excluding other large sized animals, like

Figure 14. Dry mummy of a hyena, found in Dabié Cave, March 31st, 2004.

Figure 15. Head of hyena mummy from Dabié Cave; note missing front teeth.

Table 4
Chemical analysis of coprolites (fraction<1 mm); results are weight percentages.

	Ca %	Mg %	PO_4 %	C %	N %	S %	C/N	N/S	Total %
Coprolite 1				10.65	2.20	0.49	4.84	4.49	
4.8 g				10.70	2.23	0.42	4.81	5.31	
				11.48	2.40	0.46	4.79	5.22	
Mean	**22.5**	**0.55**	**30.8**	**10.94**	**2.27**	**0.45**	**4.81**	**5.04**	**67.51**
St. deviation				0.46	0.11	0.036	0.028	-	
Coprolite 2				10.24	1.92	0.31	5.33	6.19	
4.7 g				9.82	1.69	0.17	5.80	9.94	
				10.21	1.88	0.24	5.43	7.83	
Mean	**18.9**	**0.61**	**21.4**	**10.09**	**1.83**	**0.24**	**5.52**	**7.65**	**53.07**
St. deviation				0.24	0.12	0.069	0.25	-	

Figure 16. State of hyena mummy on September 19th, 2005.

Figure 18. Mummy of Fennek from Al-Hayya Cave, September 2005.

Figure 17. Four skulls of wolves or dogs and two of hyenas (to the right) from Al-Hayya Cave, September 2005.

horses or cattle) we measured a few bones in Abu-Al Kursi (eastern section) with a caliper (tab. 3) and compared their dimensions and morphology with published *Camelus* data (Walker, 1985). The measured limb bones are with certainty bones of *Camelus*. Apart from the two humeri which are from subadult individuals, all bones are slightly larger than the respective animal measured by Walker (1985). This applies not so much to the overall length but to the sizes of the epiphyses.

The next observation is that metacarpals and metatarsals seem specifically common and complete. This may be explained by the enormous thickness of the cortical part of the bones, their small joints and their low cancellous bone component, rendering them difficult to gnaw. They are therefore left behind. In contrasts to this the larger (by volume) femuri and humeri are consumed starting with their cancellous epiphyses. These parts of the bone, in spite of their larger diameter, appear easier to get at. In the end, sharply pointed cortical bone fragments, so typical for hyena feeding, remain.

The "end product" of the hyena bone processing is the coprolite. It is typically white in color, indicative of the large percentage of bone-derived apatite. Two coprolites from Dabié Cave, collected in September 2005, were analyzed (tab. 4). Both were similar in weight and contained only a few bone fragments > 1 mm in size (26 fragments with a total of 106.7 mg and 9 fragments with 47.5 mg and a stone with 51.0 mg, for coprolite 1 and 2, respectively). Each sample was analyzed for calcium, magnesium and phosphate with ion chromatography and four times for C, N, S with a Vario-EL Elemental Analyzer. Results show that the coprolites contain high percentages of bone apatite (53.3 and 41.3 %, respectively) and about 25 % (percent C multiplied by an "organic factor" of 2.5) of organic matter. Much of that could be undigested hair that was also macroscopically visible in the samples. Hair may also be responsible for the high sulfur values in the samples (cystine of the hair-protein keratin). The repeated analyses of C, N, S content allow to calculate standard deviations, showing that the composition of the two coprolites is statistically significantly different. Coprolite 1 has a higher C and N content but a lower S content and a lower C/N ratio than Coprolite 2. C/N ratios are quite low, i.e. in the range of proteins, suggesting that not all of the available protein was consumed by the hyena, such as keratin for example. The low N/S values support this conclusion.

DATING THE DEPOSITS

One of questions remaining is that of the age of the bone deposits. At the Reiss-Engelhorn Museen an incisive of one of the collected hyena skulls was dated (sample No. ETH-32026/REM-M18). The age proved to be negative (-185±40 aBP), i.e. bomb-^{14}C contaminated, making the sample younger than AD 1950. Overall, all of the bone deposits appear not very old. Specifically the presence of so many camel-bones is puzzling. Camels have only been present in the Near-East in the last 3000 years (Klingel, 1988, reported that they have been present in Mesopotamia since 1500 BC). Thus, older deposits without camel bones should be found underneath the present layers. For example, one should expect gazelle bones to be dominating in Neolithic times.

Whether these older layers exist or not appears doubtful. In the Hashemite University Cave we found two treasure hunter pits in the cave, less than a meter deep. They contained white layers of disintegrated coprolites but no larger bone fragments. Should the older bones have been dissolved after all? Or should hyena consume all the bones available by and by, specifically if they are not large camel bones?

CONCLUSIONS

The reasons why the desert caves in Jordan have been used so intensively by hyenas may include:

- Use as a cool shelter (the caves have a temperature range from 18 to 24°C) during the hot daytime (maximum temperature may reach up to 45°C);
- To store large bones for later consumption;
- To feed on bones undisturbed;
- To give birth and to raise cubs;
- To die; or
- To search for water (some of the caves still have drip water on the ceiling at the end of September).

Because of the excellent preservation of bones, coprolites, dens and other traces, many additional questions can be studied in these newly discovered and largely undisturbed caves:

- What is the spectrum of animals consumed by hyenas in the caves and what are their proportions;
- What is the role of the few human skull caps found in Al-Fahda and Al-Hayya Caves;
- Which other animals regularly visit the caves;
- What is the stratigraphy of the bone deposits, do older non-camel-dominated strata occur;
- What is the manner of consumption of large bones, does every bone have a different pattern of consumption;
- Which bones are preferentially consumed, which are left over;
- What amount of proteins are extracted from the bone,

(a question answerable by comparing N-Analyses of bones and coprolites);

- How old can bones be and still be consumed by hyenas at a profit (a question answerable by analyzing the bones for collagen);
- Do we find insect or plant remains in the coprolites, since some hyenas regularly consume insects and plants as well (a question answerable by microscopic investigation of the coprolites);
- What is the frequency of visits by males and females, (a question answerable by analyzing coprolites for hormones);
- What is the range in composition in the coprolites and what can they tell us about the animals fed on by the hyenas;
- Can we map out scent trails, marked by urea or anal gland paste?

In comparative studies between brown hyenas and spotted hyenas in the Kalahari, MILLS (1989) pointed out a few differences between the two species: *Crocuta* for example has a small sexual dimorphism (the females being larger and dominant) which is not true for hyena; *Crocuta* hunts large animals (antelopes) in packs for about 50% of its food, while the striped hyena is mostly a solitarily scavenger for carrion, hunting only rarely for small game and supplements its diet with fruits and insects. *Crocuta* is not storing food, hyena does bury excess. Females tend to be territorial in both species (with *Crocuta* using the larger one) while males are more migratory. In *Crocuta* nomadic males mate with clan females while in *Hyaena* the males are immigrants. Both species form female-bonded matrilineal clans. Both species have very long gestation periods and keep the cubs in dens for 15 months, weaning them as late as 12-15 months of age. *Crocuta* does not bring meat to cubs; *Hyaena* does, starting when the cubs are 12 weeks old. *Crocuta* has two cubs on average, *Hyaena* three and mothers may suckle other cubs occasionally. Cubs are raised in both species in dens that are small and narrow, just large enough for the cubs.

This short list of behavioral facts raises several questions with regard to the Jordanian cave-using striped hyena. First of all, their ability to carry large bones into caves makes them similar to the European *C. crocuta spelaea*, but not at all alike either the African extant spotted or the brown hyenas that do not stash large bones. Possibly the hyena had to adapt to a human-dominated desert ecology, where medium-sized (antelopes) and small wild animals are hunted by humans almost to extinction, while humans would leave on the other hand the big bones behind after loosing or slaughtering camels or sheep. Feeding big bones to cubs does not make sense, therefore the question remains, as to if the caves are used for raising cubs at all. Cubs would be protected from most other animals, but not from other hyenas or foxes. Digging pits for sleeping also seems to be an unreported habit (though we did not search the entire literature on the topic yet). Overall the ethology of the striped hyena appears not to be well studied (MILLS, 1989) but seems not to be that much different from the other two species.

We hope to investigate these caves and their hyena-related remains in greater detail and answer some of these questions in order to compare the results with hyena traces of the Upper Pleistocene *C. crocuta spelaea* in Central Europe.

Acknowledgements: The authors gratefully acknowledge the help of the Badia Research Center at Al-Safawi for providing accommodation, The Hashemite University of Zarka for providing a pick-up truck with driver (in 2005 and 2006), and Awaid Al-Nuemat (Al-Safawi) for driving and Abu Ali Al-Odamat (Umm Al-Quteen), who served as a local guide, driver and ever-ready tea cook in 2003 and 2004.

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