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Mummified cave cheetahs inform rewilding actions in Saudi Arabia

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Cheetahs (*Acinonyx jubatus*) have experienced a steep population decline globally, extirpated from 91% of their historical range, including Saudi Arabia. Information about cheetahs' historic range remains scarce throughout much of its former habitat. A serendipitous discovery of seven naturally mummified cheetahs in several caves along with skeletal remains of 54 cheetahs, and their putative prey, in Saudi Arabia provided a valuable opportunity to elucidate the evolutionary history of cheetahs in their former range. We applied paleochronological dating to establish temporal context, genomic sequencing to infer subspecies present during different time periods, and radiographic analysis to determine age classes. The mummified cheetahs showed ^{14}C calibrated ages dated 4223 ± 40 years BP to 127 ± 40 years BP. Full genome sequences of the mummified cheetahs showed that only the youngest individual clustered with *A. j. venaticus* while the older samples clustered with the West-African cheetah (*A. j. hecki*). We conclude that rewilding of cheetahs in Arabia can be sourced from the closest subspecies of the discovered cheetahs. Our results highlight the important role caves may play as repositories of ancient biodiversity informing, in the absence of benchmarks rewilding efforts.

Most large felid species are highly endangered and continuing to decline, largely due to habitat destruction and overexploitation[1]. Even among felids, cheetahs (*Acinonyx jubatus*) have experienced a particularly severe population decline globally[2], losing nearly 91% of their historical range. They once extended across most of the area of Africa without rainforests and much of Western and Southern Asia, from the Arabian Peninsula to India[2]. Today, five subspecies of cheetah are recognized: *A. j. hecki* (Northwest Africa), *A. j. soemmeringii* (Northeast Africa), *A. j. jubatus* (Southern Africa), *A. j. venaticus* (Asia, now restricted to Iran) and *Acinonyx jubatus raineyi* (East Africa)[3]. More than half (~60%) of all wild cheetahs belong to the southern African subspecies *A. j. jubatus*[2], whereas the Asiatic cheetah (*A. j. venaticus*)—historically the species presumed present in Saudi Arabia—is critically endangered. Only about 50–70 Asiatic cheetahs remain in the wild, comprising a single, small population in Iran[4].

Historic sightings indicate that cheetah occupied the Arabian Peninsula and Levant as late as between 1838 and 1977[5,6] (Fig. 1(A)). The most recent evidence sources from an adult female shot by a local hunter near Jibjat Dhofar, Oman in 1977[7]. Although these records indisputably support the historical presence of the species in Saudi Arabia, Oman, Yemen, Kuwait, Iraq, Jordan, and Palestine, some have contended that the scarcity of evidence fails to adequately represent the true historical distribution of the cheetah[8]. This scarcity owes in part to the species' extremely low densities; Saharan cheetahs reach as few as 0.0002/km^2 [9]. The primary reasons for the disappearance of the cheetah in the Arabian Peninsula are poorly documented, but are thought to be habitat loss and fragmentation, prey depletion, human-wildlife conflict, unregulated hunting, and trade in cheetah as pets or game hunting[2,10–12]. The social and environmental context of these stressors has changed radically since the species' disappearance from Saudi Arabia, with the establishment of > 10 protected areas, species recovery and reintroduction programs of ungulate species, habitat restoration projects, the implementation of community education programs, and the establishment of a government wildlife agency with a wildlife crimes enforcement branch.

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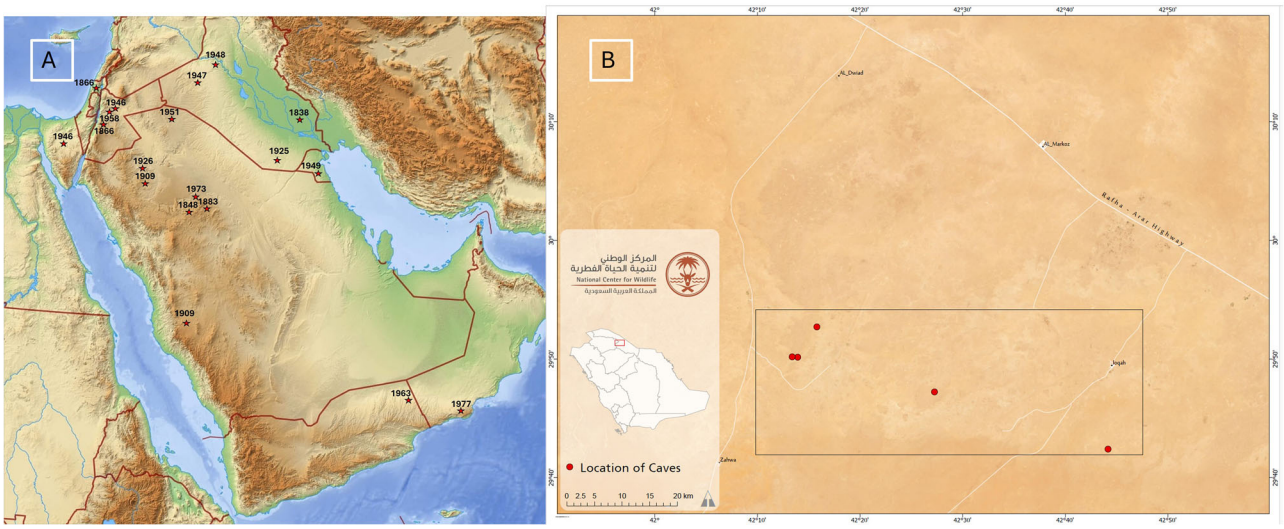

Fig. 1 | Location of the study area in North-Eastern part of Saudi Arabia. A Historical records for cheetah in the Arabian Peninsula and the Levant (represented by asterisk sign). **B** The location of five study caves (represented by red dots).

Changes in wildlife management over the last half-century in Saudi Arabia coincide with renewed interest in meeting global biodiversity goals. Achieving global biodiversity goals requires efforts to re-establish and recover critically endangered species and restore them to their former biogeographic ranges. This is especially crucial for apex predators, whose disappearance can degrade ecosystems by deregulating herbivores[1,13]. Such measures have contributed to resurgent interest in rewilding, which involves reintroducing species into their former ranges[14]. The reintroduction of apex predators has succeeded in restoring function to numerous ecosystems[15–18] and is strongly advocated for by some carnivore experts as a key tool for conservation[18]. In recent decades, Saudi Arabia has successfully restored ungulates to landscapes from which they were extirpated or in which their populations were decreased (*e.g.*, Arabian oryx (*Oryx leucoryx*), Arabian gazelles (*Gazella arabica*), Sand gazelles (*Gazella marica*) and Nubian ibex (*Capra nubiana*))[19]. As populations of long missing ungulates recover, it is timely for the reestablishment of extirpated apex carnivores—among them cheetah.

Here we report on the discovery of seven mummified and 54 skeletal cheetah remains in the Lauga cave network in the Arar area of Northern Saudi Arabia (Figs. 1B, 1S–4S). The discovery of the mummified cheetahs, along with subsequent paleochronological analysis to date the samples, genomic analysis to infer which subspecies was present during different time periods, and radiographic analysis to determine the age class, provides unprecedented insights into the evolutionary history and extinction of cheetahs in Saudi Arabia. We report the first evidence that prehistoric cheetahs in Saudi Arabia are genomically closest to the West-African *A. j. hecki* subspecies. Based on our discoveries, we further discuss recommendations for conservation management with regard to rewilding efforts currently being undertaken in Saudi Arabia.

Results and discussion

In the following, we first describe the characteristics of the environment in which the cheetah mummies were discovered. We then proceed to report findings of three analyses performed on the mummies: (i) radiocarbon dating of the mummies; (ii) paleogenomic analysis of the genomes; (iii) radiographic analysis of skulls to determine the suspected age of the cheetahs found in the caves. Afterwards, we discuss the implication of these findings for future rewilding interests.

Physical environment and general details of the discovery sites

In 2022 and 2023, 134 underground caves were surveyed for wildlife over a 1211 km^2 area of northern Saudi Arabia. Across five caves, 54 skeletal remains and seven mummified cheetahs were discovered. The distance from each cheetah remain to the closest cave entrance averaged 127 m (minimum: 30 m; maximum: 1245 m). Average temperature and relative humidity were 35.5 °C and 22 % at all five cave entrances (29.1 °C and 24 % at the 54 skeletal remains; 26 °C and 28 % at the seven mummified remains).

Cheetahs were highly concentrated in four of the five cheetah containing caves (80%) with only few remains ($n < 3$) of candidate cheetah prey animals found. A large number of gazelle (*Gazella marica*) remains ($n = 164$) were found in only one cave (Cave 2) where cheetah remains ($n = 4$) and a red fox (*Vulpes vulpes*) mummy were also discovered. Sixty-seven percent ($n = 41$) of all cheetah remains were excavated from the only cave accessed through a sinkhole (Cave 1), with one mummified wolf (*Canis lupus*), and two mummified red foxes (*Vulpes vulpes*) and no ungulate remains detected in this same cave.

Radiocarbon dating of cheetah remains

Bone remains extracted from two complete mummies and five skeletal remains were ^{14}C analyzed to ascertain the estimated age of the ancient tissues. Out of seven samples, two cheetah remains showed ^{14}C calibrated ages dated 4223 ± 40 years BP and 127 ± 40 years BP (Table 1).

Radiographic analysis of cheetah skull morphologies

Radiographic analysis of skull morphology (Table 2) classified the 20 evaluated skulls as 14 subadults (18 months to 24 month old) and 6 adults (>24 months). Nine cub (less than 18 months) remains were found in cave 1.

The external morphology and inner structure of the best-preserved mummified remains indicate a high degree of preservation of both osteological and soft tissue (Figs. 2E, S5–S6), compatible with the process of natural mummification. The preservation of the skull, jaw, and foramen magnum (Fig. 2A, B) and well-maintained joint connections, which keep the skull, mandible, cervical structures, thorax and vertebrae in place (Fig. 2C), are evident in 3D virtual reconstructions of mummy 2. A shrunken, but clearly observable encephalon, was evident in the cranium of cheetah mummy 2 (Fig. 2D).

Paleogenetic analysis of cheetah remains

Complete mitochondrial and full genome sequences were obtained for the youngest specimen (mummy 1), the 5th ^{14}C dated specimen in the sequence of age (skeletal remain 3), and the oldest specimen (Skeletal remain 5). The sequences showed relatively low PCR duplication rates (8–11%), typical for ancient DNA sequencing libraries. We obtained around 7000 or 23,000 single nucleotide polymorphisms (SNPs) for phylogeographic analyses after

Table 1 | Conventional radiocarbon ages calibrated in calendar ages and subspecies assignment for the mDNA and genomic analyses

Sample	Subspecies assignment (mDNA analyses)	Subspecies assignment (genomic analyses)	Radiocarbon Age (BP)	$\delta^{13}C$ (‰)[a]	Calibrated Age
Mummy 1	*A. j. venaticus*	*A. j. venaticus*	127 ± 40 BP	−16.9 ± 0.6	279–171 cal BP (35.3%) 153–6 cal BP (60.1%)
Skeletal remain1	not processed	not processed	1410 ± 30 BP	−15.3 ± 0	1352–1286 cal BP (95.4%)
Mummy 2	not enough reads	not enough reads	1871 ± 45 BP	−18.1 ± 0.7	1890–1699 cal BP (93.3%) 1657 –1637 cal BP (2.1%)
Skeletal remain 2	not processed	not processed	2750 ± 30 BP	−15.3 ± 0	2886–2765 cal BP (87.7%) 2928–2896 cal BP (7.7%)
Skeletal remain 3	*A. j. venaticus*	*A. j. hecki*	2904 ± 40 BP	−19 ± 0.4	3170–2929 cal BP (35.3%) 2898–2886 cal BP (60.1%)
Skeletal remain 4	not enough reads	not enough reads	3633 ± 40 BP	−14.3 ± 0.6	4085–4028 cal BP (35.3%) 4014–3840 cal BP (60.1%)
Skeletal remain 5	*A. j. venaticus*	*A. j. hecki*	4223 ± 40 BP	−17.8 ± 0.4	4860–4789 cal BP (35.3%) 4765–4618 cal BP (60.1%)

[a]Listed values of the carbon stable isotopes fractionation term ($\delta^{13}C$) is measured by AMS. These values can differ from the natural fractionation and from those measured by IRMS.

Table 2 | Cheetah age approximations based on measurements for 20 complete skulls retrieved. All measures are provided in mm

Sample ID	Maximum length of Frontal Sinus (mfsl)	Condylobasal length (CBL)	Coronal suture visible 0–3 (cors)	Hard Palate length (hpl)	Upper Canine length	Age approx. (months)
3	26	110.5	2	47	NA	10.8
4	27.5	109.8	2	51	NA	11.8
5	49.28	126.07	3	58.9	NA	26.6
6	43.2	131.1	3	63.6	NA	27.2
7	31.3	108.32	2	54.39	32.71	13.3
8	42.9	136.51	3	65.12	NA	29.1
9	38.13	106.33	2	54.14	26.22	14.8
10	61.83	131.27	3	62.75	NA	35.1
11	38.64	111.76	3	54.33	26.5	18.1
17	42.87	112.28	3	57.92	32.77	20.7
20	51.13	130.97	3	61.15	25.3	29.6
22	34	103.61	2	47.94	19.83	12.1
23	41.74	119.93	3	53.9	19.89	20.5
24	30.75	108.86	2	47.09	29.5	11.8
25	32.37	111.62	3	45.8	NA	14.1
26	35.68	110.01	3	46.64	36.12	14.9
27	29.9	109.29	3	47.96	34.19	13.5
28	45.32	125.4	3	57.34	28.86	24.2
29	44.72	120.1	3	54.61	38.73	21.8
30	38.21	121.7	3	57.23	38.32	20.6

filtering when including just transversions or both transitions and transversions, respectively. The former was used to avoid biases potentially arising from DNA damage in the ancient cheetah data, which commonly affects transversions[20]. Genomic analyses showed similar results for both data sets, so we only show results for the larger data set of 23,000 SNPs.

Genomic analyses indicate a close relationship of mummy 1 with modern samples of *A. j. venaticus* based on both nuclear and mitochondrial DNA, while skeletal remains 3 and 5 show a closer relationship with *A. j. hecki* based on nuclear DNA and *A. j. venaticus* based on mitochondrial DNA (Fig. 3A–D). The Principal Component Analysis (PCA) based on the genome-wide SNPs did not distinguish *A. j. venaticus* and *A. j. hecki* convincingly. However, the two older samples from Saudi Arabia demonstrate clear distinction from the younger sample and are clustering closer to *A. j. hecki*. This finding is supported by the phylogenetic tree and the admixture analyses (Fig. 3B–D).

Conclusions

The results we report here demonstrate seven mummified cheetahs and 54 skeletal remains of cheetah were found preserved in the cave environments of Northern Saudi Arabia, and maintained in good condition for nearly 2,000 years, with some skeletal remains dating back about 4,000 years. Numerous skeletal remains for the modern cheetah have been discovered in Africa[21], and here we report naturally mummified remains of cheetahs from the Arabian Peninsula. Thousands of artificially mummified domestic cats

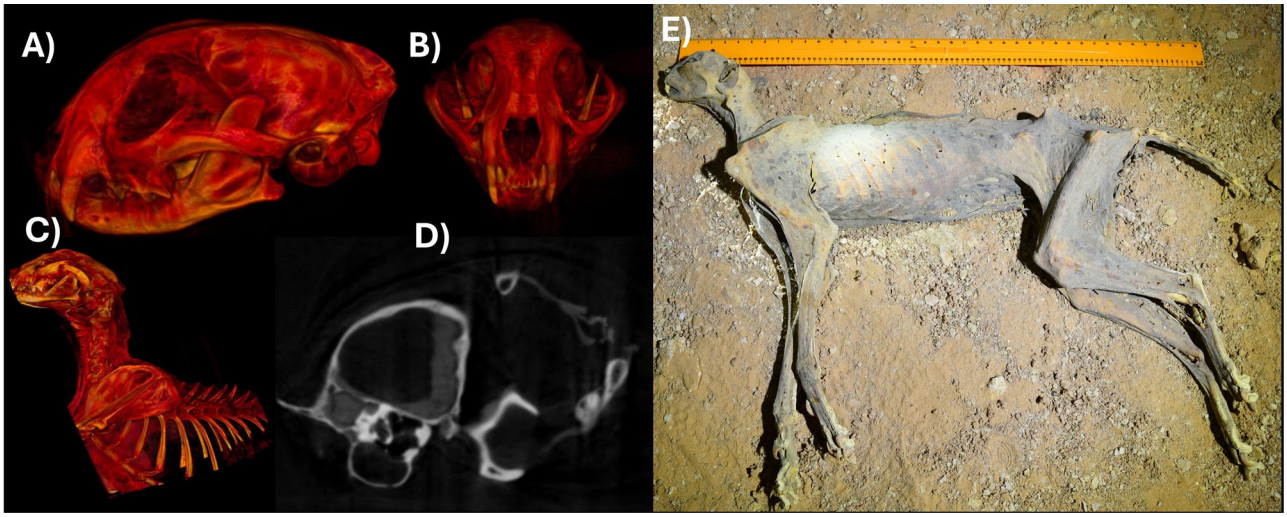

Fig. 2 | Discovered cheetah mummies. A, **B** Radiographic images 3D virtual reconstructions for the skull, **C** Thorax of mummy 2. **D** Soft tissues in the cranium. **E** Mummy 1 at the discovery site inside the cave.

have been retrieved from Egyptian archaeological sites[22], but the findings reported here represent naturally mummified felids within natural cave system.

Natural mummies are created in environments that enable desiccation[23] and are most common in arid soil caves that sustain hot, dry microclimates where bacterial action is inhibited[24,25]. Mummified carnivorous mammals can remain relatively well preserved in dry caves for thousands of years, as has been reported for a Tasmanian tiger (*Thylacinus cynocephalus*) in Western Australia[26,27]. The constant temperature and low humidity of the cave environments is conducive to mummification, which can preserve soft tissues of ancient cheetahs.

The use of caves to fulfil ecological requirements has not been reported for the genus *Acinonyx*[12]. Although the extinct 'American cheetah' (*Miracinonyx trumani)* used caves for denning and storage of carcasses[28]. However, *Miracinonyx trumani* is now considered a sister taxon to the genus *Puma*, with morphological similarities to the cheetah (*Acinonyx jubatus*) arising through convergent evolution[29]. The findings of different age classes of cheetahs suggest that in this region, they may have been using the caves as denning sites. This is evident by the larger proportion of cheetahs found in the caves compared to prey animals.

The use of radiocarbon dating[27,30,31], modern paleogenomic techniques[3,32], and computer tomography (CT)[33,34] provides evidence of the long-term presence of cheetah in Saudi Arabia. Furthermore, the genomic data retrieved from these ancient specimens support the presence of cheetahs clustering with two subspecies, the Asiatic cheetah (*A. j. venaticus*) and the North-western African cheetah (*A.j. hecki*), both now absent from the Arabian Peninsula.

Saudi Arabia has a large network of caves and sinkholes distributed along its Northern border with Iraq[35,36]. Caves are important repositories for animal remains[37], often acting as faunal traps during part of their existence[38,39]. Although there is no evidence for the modern cheetah (*A. jubatus*) using caves for shelter, denning or storage of prey items, they may fall into natural trap caves or enter via steep slopes from which they cannot escape[22,40–42]. Earlier exploration of the cave networks in northern Saudi Arabia yielded numerous animal remains, including wolf (*Canis lupus*) and striped hyena (*Hyaena hyaena*), but failed to detect cheetah presence until the surveys reported here were conducted.

The research presented here provides the first report of naturally mummified big cats enabling ancient DNA analyses. This material opens a window to the past that provides most useful data to inform rewilding efforts, as the extirpation of this species from the Arabian Peninsula took place before information to design rewilding plans was possible. The arid cave environments of Saudi Arabia, and elsewhere, may yet hold further important insights that can inform ecological histories, evolutionary insight, and actionable intelligence for rewilding and conservation. The integration of paleontological and genomic data from the cheetah remains provides a rare opportunity to bridge historical ecology with present-day conservation planning. These findings demonstrate how ancient DNA records can reconstruct lost baseline of species distribution, genetic diversity, and ecological associations which form the critical information for developing evidence-based rewilding and restoration programs. In regions such as the Arabian Peninsula, where historical faunal baselines were erased by millennia of climatic shifts and human pressures, the identification of past cheetah lineages offers valuable reference points for genetic sourcing and feasibility assessments of future reintroduction initiatives.

Materials and methods

Study area and excavation process

At total of 134 caves were investigated in the Saharo Arabian desert biome (480–575 m a.s.l.), in the Phanerozoic limestones of the Arar region in Northern Saudi Arabia (Figs. S7–S10). The Karst topography of this 1211 km^2 survey area is characterised by underground drainage systems with sinkholes and adjoining caves (Figs. S11–S12). Large mammal remains were detected in only 9 caves, among which cheetah remains were detected in five. The first cheetah remains were excavated on 02/08/2022, after the cave was accessed through a sinkhole 16 m in depth. Further excavations during seven subsequent visits (21/08/2022−09/06/2023) extracted a total of 61 cheetah remains, including 7 mummified remains, 32 skeletal remains and 22 skulls from the five caves (Table 3; Fig. 1). Radiographic analysis of 20 complete skulls provided measurements for age determination, according to methodology stipulated in Schmidt et al., 2019 (Table 1).

X-ray and CT scanning

To assess the state of preservation of the mummies, the two best preserved cheetah mummies (Mummy 1 and 2; Table 2) were sent for radiologic 3D virtual reconstructions for examination to evaluate compatibility with the process of mummification.

Radiocarbon dating

Bone remains extracted from two complete mummies and three skeletal remains were placed in sealed plastic bags and sent to Centro di Datazione e Diagnostica dell'Università del Salento, Brindisi, Italy, for ^{14}C data analysis (Table 2). Similarly other two skeletal remains were sent to Beta Analytic, laboratory, Miami, USA for ^{14}C dating. Carbon dating protocols outlined in Quarta et al.[43], which were modified from Longin[44], were followed[43,44]. Macro contaminants were removed by mechanical handpicking under an

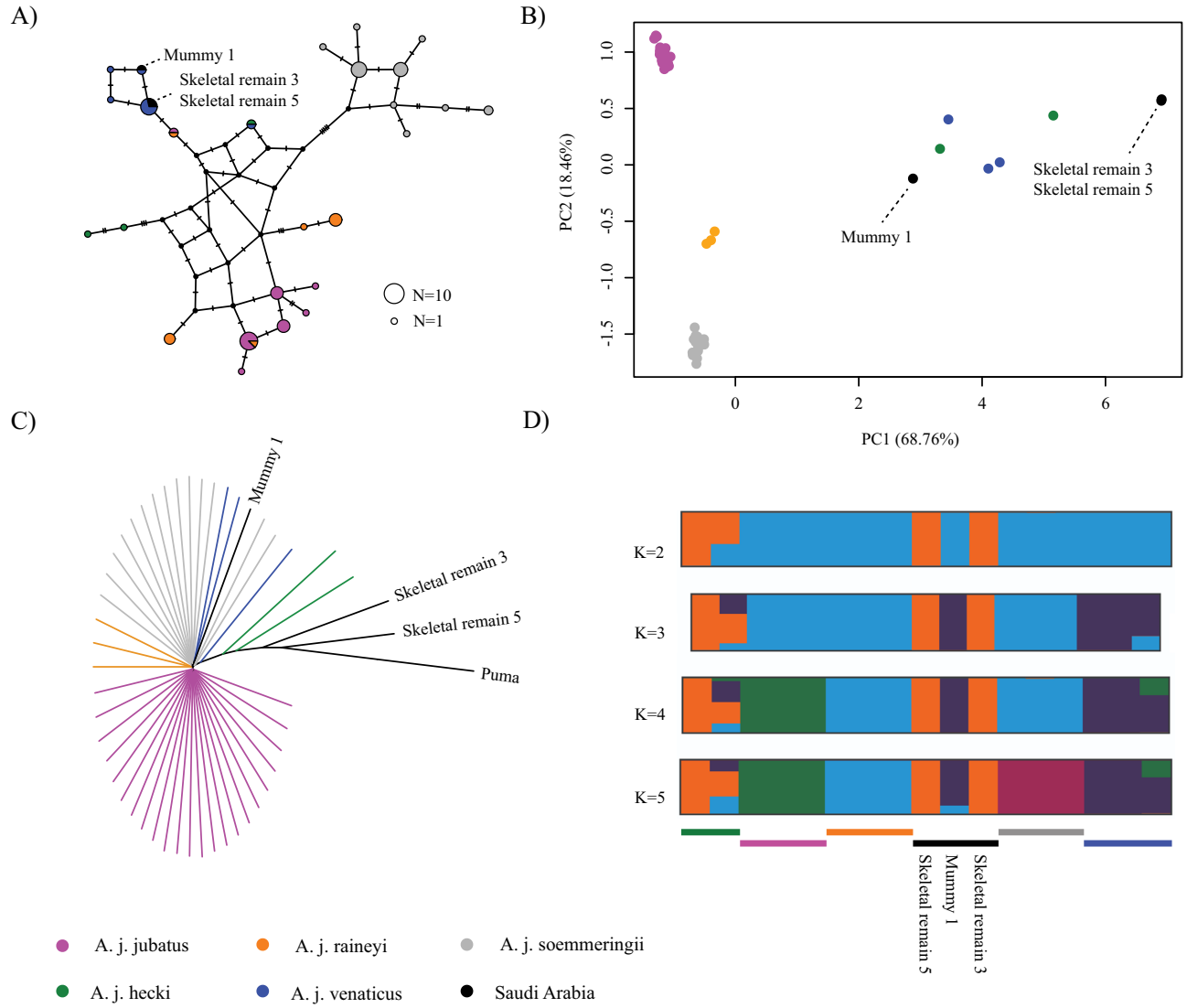

Fig. 3 | Genomic analyses for three cheetah individuals extracted from Cave 1 in Northern Saudi Arabia and mitochondrial and genome-wide data from Prost et al. 2022[3]. A Median-joining network based on a 929 bp of mitochondrial DNA (ND5 and control region) from Prost et al. 2022[3]. All three individuals from Saudi Arabia fall within the *A. j. venaticus* mitochondrial haplogroup; **B** PCA analyses of the genome-wide data show a close relationship of the youngest sample Mummy 1 with individuals from *A. j. venaticus*, and one individual of *A. j. hecki* while the two older samples, Skeletal remain 3 and 5 are clearly distinct from Mummy 1 and clusters closely with an individual of *A. j. hecki*, **C** Phylogenetic tree (based on genetic distances) showing a close relationship of Mummy 1 with *A. j. venaticus* and Skeletal remain 3 and 5 with *A. j. hecki*, and **D** Admixture analysis ranging from two to five ancestral groups (K). The analysis also shows a close relationship of Mummy 1 with *A. j. venaticus* and Skeletal remain 3 and 5 with *A. j. hecki*.

optical microscope. Selected portions of samples were chemically treated to remove possible contamination.

Purified samples were converted to CO_2 by combustion in sealed quartz tubes. The obtained CO_2 was converted into graphite using high purity Hydrogen as a reducing medium and 2 mg Fe powder as a catalyst. All samples yielded sufficient graphite to allow accurate determination of the radiocarbon age by the accelerator mass spectrometer. Radiocarbon concentrations were determined in the accelerator mass spectrometer by comparing the ^{12}C, ^{13}C currents and the ^{14}C counts obtained from the samples with those obtained from standard materials supplied by IAEA (International Atomic Energy Agency) and NIST (National Institute of Standard and Technology).

Conventional radiocarbon age was calculated with a $\delta^{13}C$ correction based on the $^{13}C/^{12}C$ ratio measured directly with the accelerator. Estimation of uncertainty (SD) considered both radioisotope counting statistics and the scattering of the data. Conventional radiocarbon ages were calibrated in calendar ages using internationally accepted calibration curva (IntCal20) for atmospheric data[45]. Conventional radiocarbon ages were converted into calendar years by using the software OxCal Ver. 3.5 based on the last atmospheric dataset[46]. All ages are reported relative to AD 1950 (before present, BP). ^{14}C ages are henceforth referred to as "BP" and calibrated/calendar ages as "cal BP".

Palaeogenomic analyses

Five radiocarbon dated specimens (Table 2) were sequenced for their whole genomic DNA. Four samples were processed at the ancient DNA (aDNA) laboratory at the University of Vienna and one at the aDNA laboratory at the University of Oulu. Single-stranded DNA from the oldest four samples were extracted following the Dabney et al.[47] protocol and sequencing libraries were prepped following the Meyer and Kircher[48] protocol[48,49], DNA for the youngest sample was extracted following Gamba et al.[49] (a modification of the protocol of Yang et al.[50]) and a sequencing library constructed using the NEBNext® Ultra™ II DNA Library Prep Kit (from New England Biolabs, USA)[47,50]. The successfully generated libraries were sent for whole

Table 3 | Individual Cheetah remains collected from 5 underground caves surveyed in North-East Saudi Arabia between 21/08/2022 and 09/06/2023

Taxonomic group	Common name	Nature of remains	Cave 1 (29.7873, 42.4545)	Cave 2 (29.5271, 42.1580)	Cave 3 (29.7167, 42.6265)	Cave 4 (29.7063, 42.7363)	Cave 5 (29.8271, 42.2120)	Total
Acinonyx jubatus	Cheetah	Mummified	4			1		5
Acinonyx jubatus	Cheetah	Partially mummified[a]	2					2
Acinonyx jubatus	Cheetah	Skull only	11	2	7	1	1	22
Acinonyx jubatus	Cheetah	Partial skeleton	23	2	5	1		31
Acinonyx jubatus	Cheetah	Complete skeleton	1					1

[a]Partially mummified denotes a portion of the body remained naturally mummified.

genome sequencing to Novogene (Cambridge, UK). The samples were sequenced at 50x coverage on the Illumina NovoSeq X platform. The raw sequence data were then filtered for quality and the presence of Illumina sequencing adapters using fastp 0.23.4[51]. The processed reads were mapped against the current cheetah chromosome-level reference genome[52] using BWA *mem* version 0.7.17[53]. Next, PCR duplicates were identified using Picard version 2.20.8 (https://broadinstitute.github.io/picard/) and realignment around indels was carried out using GATK 3.8.1.0 (https://gatk.broadinstitute.org/hc/en-us). Lastly, unmapped, secondary, supplementary and duplicate reads were removed from the mapping files using Samtools version 1.18[54]. In order to reconstruct the mitochondrial genomes of the ancient cheetah samples, genomic reads were mapped to the current mitochondrial reference genome[55] using BWA *mem* version 0.7.17 and the mapping files processed with Samtools version 1.18[54]. The obtained genome data were combined with an existing genome-wide SNP dataset of 44 individuals from Prost et al. (2022), generated using ddRAD, and the mitochondrial data with 60 Sanger sequenced mitochondria (929 bp compromising both CytB and ND5) from Prost et al. (2022)[3]. The resulting mapping files, for the genome-wide data, were processed with ANGSD[56], a freely available software which was specifically developed for population genomic analyses. Within ANGSD the bamfiles were filtered for the (1) the presence of no more than 20% of missing data for individual sites and (2) a minimum coverage of 3x for sites for each individual, to account for missing data arising from low coverage data. All ANGSD analyses were run with and without tranisitions (C to T or G to A), respectively, to account for possible DNA damage in the ancient DNA samples[21,57].

To investigate population structuring an unsupervised principal component analysis was carried out using ANGSD (options: *-GL 1 -doGlf 2 -doMajorMinor 1 -doMaf 2 -SNP_pval 1e-6*) and pcangsd (Meisner & Albrechtsen[58]). Signatures of admixture between the populations were investigated using ANGSD (options: *-GL 1 -doGlf 2 -doMajorMinor 1 -SNP_pval 1e-6 -doMaf 1*) and ngsAdmix[58,59]. As admixture analyses are strongly impacted by sample size, three sets of individuals of all subspecies, with three randomly sampled individuals for *A. j. jubatus* and *A. j. soemmeringii*, respectively, were generated. Twenty replicates were performed for all ngsAdmix runs ranging from k = 2 to k = 5, and results were visualised using CLUMPack[60]. A phylogenetic tree based on genetic distances, specifically developed for low-coverage genome data, was reconstructed using ANGSD (options: *-GL 1 -doMaf 2 -doMajorMinor 1 -doGeno 8 -doPost 1 -doSaf 1 -fold 1 -SNP_pval 1e-6*), ngsDist[61] (applied options: *--n_boot_rep 100 --boot_block_size 1*) and FastME[62]. Bootstrap support values were placed on the tree using RaxML[63]. We used the *Puma* as an outgroup[3].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All source data are provided with this paper. Genomic reads for the three cheetah remains can be found on NCBI GenBank under the BioProject PRJNA1301910.

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Author contributions

Boug, Mir, Jbour conceptualized and developed the first draft of the manuscript. Merwe, Amr contributed to data interpretation, Al Salem, Al Beshr, Al Mutairi, Burger, Prost, performed and interpreted the genetic analysis, Galassi, Varotto, performed the palaeoradiological and mummy study, the CEDAD laboratory of the University of Salento (Italy) performed the ^{14}C dating analysis. Angelici, AL A'amri, T. Shamari, Al-Qahtani, K. Shamari contributed to data interpretation, Duarte reviewed the manuscript, provided statistical analysis and contributed to data analysis. All authors commented and contributed to the final draft version.

Competing interests

The authors declare no competing interests.

Additional information

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