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The Lost Large Mammals of Arabia

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ABSTRACT

Aim: If successful, plans to restore the vegetation of the Arabian Peninsula (AP) as announced by the Middle East and Saudi Green Initiatives will see the greatest increase in vegetation cover since the beginning of the Holocene Humid Phase (HHP), roughly 9–10,000 years ago. This marked an expansion in human population that was followed by animal extinctions and extirpations that have been accelerating to the present day. The re-greening of Arabia presents a major opportunity to reverse much of this species decline; yet no complete list of the large mammal fauna of the AP during the Holocene has ever been published.

Location: Arabian Peninsula.

Time Period: Holocene.

Major Taxa Studied: Large mammals.

Materials and Methods: This paper tackles the problem by drawing on a database of archaeological and historical reports, as well as examination of thousands of published and unpublished rock images, complemented by analysis of over 30,000 toponyms.

Results: Evidence that 15 large mammal species became extinct or extirpated in the Arabian Peninsula since the beginning of the Holocene; previous published historical distribution maps of lions and aurochs shown to be incomplete; historic ranges of cheetah, Syrian wild ass, African wild ass, wild dromedary, lesser kudu, Arabian oryx, wild sheep and bezoar/wild goat distributions expanded; first published evidence of greater kudu, and Somali wild ass in the AP during the Holocene; most complete list of large mammals of the AP from the early Holocene; list of species that made it across the Sahara or recorded in the Levant during historical times that could also have colonised the AP, but for which evidence is yet to be conclusive; support for the Holocene and not the start of the modern era to be the conservation benchmark for re-wilding; and description of key features on how to identify lost species in rock art.

Main Conclusions: This study shows that the Holocene large mammal fauna of the Arabian Peninsula consisted of many African species previously thought to have become extinct much earlier or not known to have colonised this part of western Asia. Moreover, some Levantine/Asian species were also present providing a unique fauna with affinities from both Afrotropical and Palearctic realms.

1 | Introduction

In Arabia, there has been much interest in land restoration since 2021, thanks to the launching of the Saudi Green Initiative (SGI), and the Middle East Green Initiative (MGI) with their respective goals of establishing 10 and 50 billion trees over the coming decades[1]. The expected areas to be restored will be 0.75 million km^2 in Saudi Arabia[2] and 2 million km^2 across the Middle East.

This is in addition to the Bonn Challenge's worldwide aim to restore 350 million hectares of degraded and deforested land by 2030[3].

Such potentially substantial increases in new habitat can have a positive impact on wild animals, particularly species that have declined due to habitat fragmentation, degradation and loss. Numbers and diversity of species would be expected to increase even without any human intervention as animals move in to colonise restored land. However, some species, particularly large mammals (> 5 kg: as per Faith 2014), need to be reintroduced as their size makes them less able to cross natural and artificial barriers. They are also the group of animals most threatened by extinction or extirpation, as extinction risk is correlated with mammals' body size (Nowak 1999).

There are examples of successful large mammal introductions around the world that have resulted in regionally extirpated species being re-established. In Arabia, the most well known is the Arabian oryx (*Oryx leucoryx* Pallas, 1777) that was declared by the IUCN to be extinct in the wild in 1972 (Price 2011), with the last remaining individuals confined to zoos and private collections. In 1982, the oryx were reintroduced to the wild in the Sultanate of Oman (Mallon et al. 2023). Subsequent introductions in Saudi Arabia, Israel, Jordan and the UAE have resulted in the IUCN changing the oryx's status from Extinct in the Wild to Endangered in 1986 (IUCN SSC Antelope Specialist Group 2017). Further increases in population led to an additional reduction in threat status from Endangered to Vulnerable in 2011.

In some cases, animal introductions have surprised ecologists. The reintroduction of wolves to Yellowstone National Park, USA, had a profound impact on the population of elk (*Cervus elaphus* Linnaeus, 1758) by reducing the numbers of this overabundant species (White and Garrott 2005). This led to an increase in quaking aspen (*Populus tremuloides* Michx.) according to Ripple and Larsen (2000) plus a knock-on increase in small mammal populations as wolves deterred coyotes, their main predators (Miller et al. 2012). In Costa Rica, Spanish settlers introduced cattle and horses during the colonial period. These animals acted as a substitute for extinct megafauna, dispersing large tree seeds (Janzen and Martin 1982). This had a positive effect on native guanacaste (*Enterolobium cyclocarpum* (Jacq.) Griseb.) and jicaro (*Crescentia alata* Kunth) tree species, that began to spread after the arrival of the introduced animals. The implication from this is that animal grazing was positive by promoting the spread of the native species.

The loss of large mammals has affected ecosystem balance that continues to this day. Consequently, an ecosystem cannot be considered as fully restored unless lost species or their proxies are brought back. Carnivorous large mammals influence ecosystem processes by preventing overgrazing, while large herbivores act as dispersers of large seeds, open up the understorey and indirectly regulate fire (Pedrono et al. 2013). Re-wilding is not just about bringing back single species, but rather about re-establishing functioning communities, through restoration of ecosystem processes and connections (Price 2011). The implication here is that land restoration on a scale proposed by the SGI and MGI should include the reintroduction of lost species as one of its key pillars. Failure to do so will cause ecosystem recovery to go in a different direction to the original ecosystem, with some native species becoming invasive as has been observed in examples of island restoration (Kawakami and Horikoshi 2022; White and Garrott 2005).

1.1 | Establishing a Conservation Benchmark

When it comes to replacing lost species, the question that follows is when to set the historical baseline or conservation benchmark. These human constructs are not usually clear-cut but provide a helpful way of delineating a conservation-focused timeline, normally related to anthropogenically induced species extinctions. In the New World, the arrival of European settlers in 1492 with their advanced technology caused a sudden jump in the extinction rate, and provides a logical conservation benchmark (Caro 2007), that some call the modern era (Monsarrat and Svenning 2022).

To determine a conservation benchmark, it is necessary to consider the extent to which the climate has changed and what have been the main drivers of extinction. Clearly there is no point in bringing back species that existed when the climate was so different to the present that the animal would now be unable to survive. On the other hand, if humans have caused a species' extinction, then that species should survive if reintroduced so long as the anthropogenic cause has been dealt with. The most important drivers of extinction are human influence and climate (Lima-Ribeiro and Diniz-Filho 2013); the latter impacting on vegetation cover, with variations in rainfall resulting in cycles of colonisation and extinction (Stewart et al. 2019). Humans have not been immune to these effects which explains sparse anthropogenic evidence in the Arabian Peninsula (AP) during Marine Isotope Stage (MIS) 2 hyper arid phase (Rose and Usik 2010) that lasted between 19,000 BP and 9000 years BP (Parker and Rose 2008). Only the edges of the AP were colonised by humans at this very arid time, the environment being too severe in the interior for them (Uerpmann et al. 2009). This was followed by a period of relatively high wetness known as the Holocene[4] humid phase (HHP: 9000–6000 years BP[5]), when rainfall was higher than it is today, allowing wild animals to colonise from Africa, Asia and the Levant.

The HHP coincides with the Neolithic period, a time of major expansion of human settlement into the Arabian interior (Dinies et al. 2015) plus technological development. One of the earliest technologies to have impacted animals was the use of dogs, that date back to the 7th and maybe even the 8th millennium BC (Guagnin, Perri, et al. 2018). It was during this period that 'desert kites' first appeared which were used, often with dogs, as mass killing traps for wild game, especially gazelle (Crassard et al. 2022, 2023). The advent of domestic herbivores occurred around the same time (Scerri et al. 2018), and while they could have taken pressure off hunting wild game (Guagnin, Perri, et al. 2018), there may have been an impact on grasslands (Dinies et al. 2015). Worldwide, the colonisation of humans into any area has always been followed by megafaunal extinction events (Burney and Flannery 2005), as has been noted for Australia (Saltré et al. 2016), Tasmania (Turney et al. 2008) and New Zealand (Collins et al. 2014). The early Holocene is also the last period of natural mammal colonisation, with the arrival of dorcas gazelle (*Gazella dorcas* Linnaeus 1758) estimated to have occurred between 8000 and 6000 years BP (Harrison and Bates 1991; Tchernov et al. 1986).

The duration and magnitude of the HHP is the matter of some debate and disagreement. On the one hand, Neugebauer et al. (2022) consider it to have been short lived in the Tayma area of northern Arabia, lasting between 8800 and 7900 cal years BP. Dinies et al. (2016), who also studied the Tayma area, found not only grasslands occurring between 9000 and 8000 cal years BP, but also the presence of the heather *Erica arborea* L. between 8800 and 4800 cal years BP; a plant currently only found at tops of high mountains in southwestern Arabia. On the other hand, lake formation in the Jubbah area may have started as early as 12,200 cal years BP and swamps were still present by 7500 cal years BP (Crassard et al. 2013). Engel et al. (2012) bring the HHP later to between 9500 and 5800 cal years BP. In the Empty Quarter, lakes date to between 8800 and 6100 years BP (Edgell 2006). Models show a peak increase in rainfall of 300% (150 ± 25 mm compared to the present average of 45 mm in the Tayma region [Dinies et al. 2015]). In Shuwaymis, the modelled peak of 177 mm is 536% greater than the current average of 33 mm (Guagnin et al. 2016).

Those who accept a longer HHP claim that it came to an end around 5500–6000 years BP (Delany 1989; Drechsler 2007; Macholdt et al. 2019). It was followed by a drier period that continues to this day. Some animals were extirpated during the transition from humid to dry phase (such as the aurochs in the Empty Quarter: Edgell 2006), though it is not certain if the cause of extinction would have been due to climatic or anthropogenic factors, or a combination of both. In the USA, the importance of climate, human influences or a mix of both varied according to extinct taxa and region (Broughton and Weitzel 2018). On the other hand, if animals persisted well beyond the HHP before becoming extinct, then those extinctions are more likely to be anthropogenically induced, as the climate has not changed since. In contrast to climate, human impacts have increased throughout the Holocene, notably with the domestication of camels and horses around 3400 years BP (Uerpmann and Uerpmann 2012; Schiettecatte and Zouache 2017), allowing hunters to chase prey. These impacts were exacerbated during the modern era with the arrival of firearms (post 1500: Robin 2018) and motorised vehicles (post 1940: Al-Nafie 1989; Foster-Vesey-Fitzgerald 1952; Mallon et al. 2023). In the 20th century alone, Arabia lost seven large mammal species (Al-Nafie 1989; Harrison and Bates 1991) including Saudi gazelle (*Gazella saudiya* Carruthers & Schwarz, 1935), wild goat (*Capra aegagrus* Erxleben, 1777), wild sheep (*Ovis ammon* Linnaeus, 1758), Yemen gazelle (*Gazella bilkis* Groves and Lay 1985), lesser kudu (*Tragelaphus imberbis* Blyth, 1869), Arabian oryx (*Oryx leucoryx* Pallas, 1777) and cheetah (*Acinonyx jubatus venaticus* Griffith, 1821).

It is not enough to replace only species that became extinct during the modern era (Al-Nafie 1989), as human-induced extinctions may go back to the beginning of the Holocene, as is the case for Africa (Faith 2014). Instead, we suggest that the Middle Holocene (6000–5000 years BP) should be used as the benchmark for conservation (Figure 1), as this is the earliest date when the climate was the same as it is now. In addition, the Early Holocene should also be considered as a secondary benchmark as this is the era before humans started to wipe out animal populations, and any species that became extinct due to hunting (rather than climate change) should also be included in the list of potential species to be brought back. This would restore the

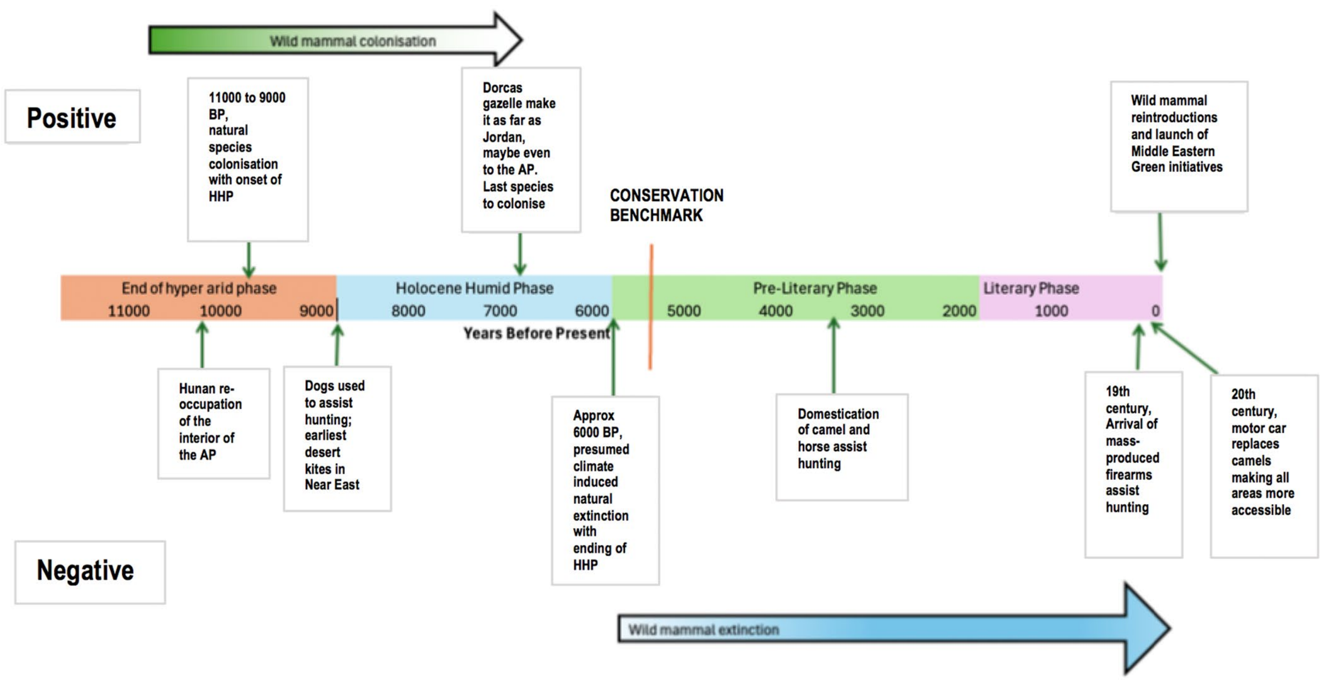


FIGURE 1 | Positive and negative influences on wild animals and the proposed Conservation Benchmark. Note that some processes were very gradual and spread over a long period of time, even millennia, but for sake of clarity, thin arrows have been used to suggest an approximate time for a positive or negative influence.

land to its original condition before human intervention shaped it, resulting in the most robust ecosystem possible.

The conservation benchmark varies between countries. In Israel, the Holocene is considered the start of dramatically increasing human impact on the environment (Tsahar et al. 2009). Despite a relative stable climate, declines in wild species ranges are apparent during this era based on examination of bone and teeth assemblages. While declines started during the Holocene, complete extirpation first occurred during the Iron Age. In the United Kingdom, the pre-Neolithic mid Holocene (8000–5000 years BP) is considered the most recent pristine state (Hodder et al. 2009). The same is true of central and western Europe (Vera 2000).

Such long time frames suggested above contrast with Price's (2011) recommendation to only go back 200 years in Arabia. While it is true that this would preserve some regionally restricted species, it would not be a true representation of wild Arabia and would omit many large mammals.

To date, no complete list of the Holocene large mammals of the AP exists. Even the most up to date list of large mammals (Harrison and Bates 1991) is over 30 years old and does not reflect taxonomic changes that have taken place since its publication. The purpose of this article was to respond to this gap in knowledge by updating the current list of large mammals of Arabia as well as to document the distribution of species within the AP during the Holocene, with the aim of further informing the discussion around species reintroductions as an important component of habitat restoration.

2 | Methods

An inventory of the large mammals of the AP was taken from Harrison and Bates' (1991) book *The Mammals of Arabia*. Despite its age, the book still remains the most complete work on mammalian biodiversity for the Peninsula (Mallon et al. 2023). Large mammals (above 5 kg average weight) were taken from this publication. Small and medium-sized mammals like hyraxes, squirrels, hares, hedgehogs, rodents, shrews, bats, small cats, genets, mongooses and hares were therefore excluded. Large mammals that occur outside the territories of Saudi Arabia, Yemen, Oman, the UAE, Qatar and Kuwait were also excluded as this study is only concerned with the AP. Additional reference sources include Mallon and Budd (2011) who provide a list of carnivores of Arabia. Domestic species such as camels, dogs, horses, donkeys, cattle, goats and sheep were not added to the list. However, wild ancestors of these species were included if they occurred in the past such as aurochs, the wild camel, wild ass, wild goat and wild sheep.

A variety of sources were used to uncover species that have become extirpated or extinct from the AP. These included rock inscriptions (e.g., Maraqten 2015; Robin and Gajda 1994; Robin 2018) archaeological excavations (e.g., Cattani and Bökönyi 2002; Drechsler 2007; Kallweit 1996; Kennedy et al. 2023), osteological finds (e.g., Stewart 2021) and historical literary accounts of travellers (e.g., Niebuhr 2017). Rock art was also examined from published sources, especially volumes such as Anati (1970, 1972, 1974), Khan (1993, 2007, 2013), Nayeem (2000), Olsen (2013) and Robin (2018). Searches for publications were made using Google Scholar. Also unpublished sources were used including the Bradshaw Foundation's Rock Art of Saudi Arabia[6] website and the Arabian Rock Art Heritage Project's website[7] that provides lists of large mammal rock imagery and their locations. These collections are not exclusive, and some images are found across the sources but together the number of animal rock art images examined run into the thousands.

Unpublished rock art sources were provided by the authors' own expeditions, the archives of the Philby-Ryckmans-Lippens Expedition[8] (Ryckmans 1954), personal contacts' photographic collections and the social media website X (formerly known as Twitter). Users of X publish photographs and include keywords as hashtags. The user self-selects what images to publish and determines what keywords to use. There is bias in what they publish so X cannot be used to get relative importance of one species over another but is a very good tool for quickly sifting through a large number of petroglyph images to search for a particular species. The other advantage of X is that many of the images posted are not found in any published sources. Petroglyphs of large mammals have the benefit of being impressive or even unusual (such as lion or cheetah), so are likely to be posted where found. On the other hand, one downside of X is that only 800 of the most recent posts are displayed, meaning that older posts are continually being withdrawn. Also, accounts can be suspended due to inactivity or even because of a complaint. Both mean that the links given for some of the rock art may no longer work, although at the time of writing of this report they were active. For this reason, a screenshot of every image in X was taken including author's details and comment to create a permanent record. For copyright reasons, these screenshots have not been reproduced in this article but can be posted on request. Another downside with X is that authors can use a pseudonym, making it very difficult to know who they are. Also, they can protect a location by posting a vague location, such as 'west of Tabuk', or even provide an incorrect site name. Our attempts to obtain location information was met with few answers, though the people we did contact were able to provide an exact location, and we were able to find the petroglyph they posted.

Keywords used in internet searches were based on the hypothesis that large animals that historically occurred north of the Sahara potentially may have been found in the AP during the Holocene. Given that the climate was wet enough to allow animals to cross the Sahara, it is likely conditions would have been equally suitable to make the crossing from North Africa to Arabia via the Sinai. A list of these species was taken from Drake and Blench (2017) with the list narrowed down to those that can easily be speciated in rock art. Additional species currently found in the Levant were included as it is possible that during previous humid periods they could have spread south. Searches within X were both in English and Arabic in both singular and plural with all plural forms of the Arabic provided by Cowan (1979) and shown in Table 1.

While rock engravings vary in their level of detail, it is still possible to speciate many large mammals (Al-Nafie 1989; Garcia et al. 1991). Yet it is important to note that these windows into the biogeography of this time are selective (Robin 2018),

TABLE 1 | Search keywords.

English name	Arabic names	Transliterated Arabic names
Lion/lions	أسد/ أسود	asad, asūd
Cheetah/cheetahs	فهد/ فهود	fahd, fuhūd
Elephant/elephants	فيل/ فيلة/ أفيال	feil, fiyalah, afyal
Giraffe/giraffes	زرافة / زرافات	zarafa, zarā'if
Buffalo/buffalos	جاموس / جواميس	Jamus, jawamis
Rhinoceros/rhinos	كركدن / كركدنيات	karkaddan, karkadanniyāt
Rhinoceros/rhinos	وحيد القرن / وحيدي القرن	waḥīd al-qurn, waḥīdi al-gurn
Bear/bears	دب / دببة	dub, debabah
Wild boar	خنزير بري / خنازير برية	khanzīr barrī/khanazir barrīeah
Antelopes/gazelles	ظبي / ظباء	Daby, iba

focusing on animals that are impressive in size, or good for hunting (Judd 2011). Small mammals, reptiles, insects and birds (except ostriches) are rarely engraved even if they may have been common in the locality, though this limitation was not an issue for our study that only focused on large mammals. Also, rock engravings are constrained by geology (Judd 2009) and to some extent climate. They are found in areas where rock is available and exposed (Johnston 1991), thereby excluding heavily forested areas or areas of floodplain, plateaus and sandy deserts. Even where exposed rock faces occur, not all rock is easy to inscribe. Petroglyphs are favoured in areas where rock is soft and bears a weathered varnish that shows a contrasting background colour when engraved (Macholdt et al. 2019). For this reason, rock engravings should indicate definite presence rather than proven absence.

Dating of petroglyphs is a problematic subject, though the consensus among rock art experts is that engravings in the AP do not pre-date the Holocene. On exposed cliff faces, sandstone petroglyphs rarely survive beyond 5000 years extending to 10,000 years for sheltered conditions (Bednarik and Khan 2017). On granite and other resistant rocks, they may extend longer but this must be balanced against the general depopulation of the AP before the Holocene (Stewart et al. 2019). Despite the limitation of difficulty of dating, the engravings are able to reveal a number of animals that have now disappeared in part or entirely from Arabia (Al-Nafie 1989; Guagnin, Shipton, et al. 2018).

Toponyms were obtained from two unpublished gazetteers: A Saudi database of 73,000 place names from the Saudi Geonames App and a publicly available Omani and Yemeni gazetteer (https://oman.places-in-the-world.com/ & https://yemen.places-in-the-world.com/) plus an unpublished gazeeter from the Omani Supreme Committee for Town Planning, produced in 2011. These were scanned using the same keywords as the Twitter search. Another source of toponyms was Google Maps, and the same keywords were used as for the gazetteers. An animal toponym does not provide full certainty the animal existed in that location, as some places are named after topographical resemblance to an animal, such as Elephant Rock, Al Ula, KSA. In such cases, the toponym was rejected. The location of toponyms was determined by using Google Maps or satellites.pro websites for gazetteers that did not provide co-ordinates.

Where information was available on the location of petroglyphs (e.g., Guagnin et al. 2015) and archaeological finds (e.g., Abu-Azizeh et al. 2022), their location was mapped in order to determine their historic distribution. Once the maps of large mammals' distribution had been compiled, they were compared with maps of current and historic ranges (e.g., Harrison and Bates 1991; IUCN 2022).

3 | Results

Table 2 presents the biodiversity of the large and medium-sized mammals of the AP, with dates of extinction or extirpation from Arabia where known. It is the most complete list of large mammals from the Holocene to the Anthropocene in the AP, as well as correcting deficiencies in previous lists due to incomplete data, taxonomic revisions, discovery of new species and species that have been overlooked due to their having become extirpated or extinct. Taxonomic order follows Kingdon (2015).

The sections below provide detail for each species that has become extinct or extirpated from the AP, with justifications as to why they are thought to have existed in the past. Photographs are only given where permission for publication has been granted.

3.1 | Globally Extinct Species

3.1.1 | Syrian or Asiatic Wild Ass/Onager

Macdonald (2019) provides some guidelines on how to separate horses (*Equus ferus* subsp. *caballus* Linnaeus, 1758) from asses in rock art. Horses have a relatively small head, flowing mane and tail made of stiff hairs joined at the base. Asses have a heavier head, stiff upright manes and stalk-like tails with a tassel at the end. These conventions are generalities, and of course, there are exceptions, for example, a groomed horse can have a tasselled tail (Olsen 2017). Other aids to speciation are inscriptions that can accompany rock engravings, for horses and asses are given their own names. Also, the context of the image can help, as only horses are depicted with riders in heroic hunting or

TABLE 2 | Large and medium-sized mammals of Arabia (> 5 kg).

Taxonomic order and family	Species name	Common name	Former distribution in Arabia	Last record	Current distribution in Arabia	References
Order Primates						
Cercopithecinae	*Papio hamadryas* (Linnaeus, 1758)	Hamadryas baboon	SW Saudi Arabia to S. Yemen	Extant	W Saudi Arabia to S. Yemen	Harrison and Bates (1991)
Order Rodentia						
Hystericidae	*Hystrix indica* (Kerr, 1792)	Indian crested porcupine	Mountainous areas of the AP	Extant	Oman and Yemen, UAE and KSA	Chreiki et al. (2018)
Order Carnivora						
Canidae	*Canis aureus* (Linnaeus, 1758)	Golden jackal	All Arabia except for the interior	Extant	E Saudi Arabia	Mallon and Budd (2011), Silva (2015), Stoyanov (2020)
Canidae	*Canis lupus* subsp. *arabs* (Pocock, 1934)	Arabian wolf	All Arabia, apart from sandy deserts	Extant	SE and E Oman, extinct from UAE, non-sandy Saudi Arabia, S. Yemen	Cunningham and Wronski (2010), Mallon and Budd (2011)
Canidae	*Vulpes vulpes* subsp. *arabica* (Thomas, 1902)	Arabian red fox	All Arabia except centre of great deserts	Extant	All Arabia except centre of great deserts	Mallon and Budd (2011)
Canidae	*Vulpes rueppellii* (Schinz, 1825)	Ruppell's sand fox	Arid steppes of Arabia	Extant	Arid steppes of Arabia	Mallon and Budd (2011)
Canidae	*Vulpes cana* (Blanford, 1877)	Blanford's fox	All mountain and rock areas of Arabia	Extant	W Arabia, S & N Oman	Aloufi and Eid (2019)
Canidae	*Vulpes zerda* (Zimmerman, 1780)	Fennec fox	Kuwait	Extant	Extirpated	Abu Baker et al. (2022), Mallon and Budd (2011)
Mustelidae	*Mellivora capensis* (Schreber, 1776)	Honey badger	All Arabia	Extant	All Arabia	Harrison and Bates (1991)
Felidae	*Panthera leo* subsp. *leo* (Linnaeus, 1758)	Lion	All Arabia	Late 1800s	Extirpated	See text in this article
Felidae	*Panthera pardus* subsp. *nimr* (Linnaeus, 1758)	Arabian leopard	N & S Oman, Arabian Shield area of Saudi Arabia, Yemen	Extant	S. Oman, Yemen, SW Saudi Arabia	Mallon and Budd (2011), Jacobson et al. (2016), A. Spalton pers. comm (2023)
Felidae	*Caracal caracal* (Grey, 1843)	Caracal	NW, W, SW Saudi Arabia, Yemen, N & SE Oman	Extant	NW, W, SW Saudi Arabia, Yemen, N & SE Oman	Mallon and Budd (2011)
Felidae	*Acinonyx jubatus* subsp. *venaticus* (Schreber, 1775)	Asiatic cheetah	All Arabia	1977	Extirpated	Durant et al. (2017)

(Continues)

Taxonomic order and family	Species name	Common name	Former distribution in Arabia	Last record	Current distribution in Arabia	References
Felidae	*Felis silvestris* subsp. *lybica* (Forster, 1780)	Wild cat	All	Extant	All non-sandy parts of Arabia	Mallon et al. (2023)
Hyaenidae	*Hyaena hyaena* (Linnaeus, 1758)	Striped hyaena	All Arabia, apart from sandy deserts	Extant	N and S Oman, extinct from UAE, non-sandy Saudi Arabia, Yemen	Mallon and Budd (2011)
Order Perissodactyla						
Equidae	*Equus hemippus* (Geoffroy Saint-Hilaire, 1855), formerly *Equus hemionus hemippus*	Onager/Syrian wild ass	Northern areas of the AP, in what is now southern Syria, north-eastern Jordan and Israel	1929 in a German zoo; extinct from Saudi early 1900s	Extinct	Macdonald (2019), NCWCD (2004), Olsen (2013, 203, 207)
Equidae	*Equus africanus* (Heuglin & Fitzinger, 1866)	African wild ass	Central and NW AP	Undated petroglyph	Extirpated	Al-Nafie (1989), Guagnin, Shipton, et al. (2018)
Equidae	*Equus africanus somaliensis* (Noack, 1884)	Somali wild ass	Not known	Undated petroglyph	Extirpated	See text in this article
Order Artiodactyla						
Bovidae	*Syncerus antiquus* (Duvernoy, 1851)	African Giant Buffalo	Yemen	7000 BP	Extirpated	Drechsler (2007)
Bovidae	*Bos primigenius* (Bojanus, 1827)	Aurochs	N. Saudi Arabia, C., E. and S. Arabia	Undated petroglyph	Extinct	Guagnin et al. (2015), Guagnin, Shipton, et al. (2018), Nayeem (2000)
Bovidae	*Tragelaphus imberbis* (Blythe, 1869)	Lesser kudu	N. Saudi Arabia (Shuwaymis, Hail) and Yemen	1968	Extirpated	Guagnin, Shipton, et al. (2018), Harrison and Bates (1991), Khan (2007)
Bovidae	*Tragelaphus strepsiceros* (Pallas, 1766)	Greater kudu	Only known from two locations	Undated petroglyph	Extirpated	See text in this article
Bovidae	*Gazella arabica* (Lichtenstein, 1827) formerly *Gazella gazella*	Arabian gazelle	Mountains and foothills of Saudi Arabia, Oman and Yemen	Extant	Mountains and foothills of Saudi Arabia, Oman and Yemen	IUCN (2017a, 2017b), Harrison and Bates (1991) as *Gazella gazella*
Bovidae	*Gazella bilkis* (Groves and Lay 1985)	Queen of Sheba's gazelle	N. Yemen	1953	Extinct	Greth et al. (1993)
Bovidae	*Gazella marica*, formerly *Gazella subgutturosa* (Thomas, 1897)	Arabian sand gazelle	Gravel plains of W Saudi Arabia and Yemen	Extant	Central and east Arabia	Hemami et al. (2020)

(Continues)

Taxonomic order and family	Species name	Common name	Former distribution in Arabia	Last record	Current distribution in Arabia	References
Bovidae	*Gazella saudiya* (Carruthers & Schwarz, 1935), formerly *Gazella dorcas saudiya*	Saudi gazelle	Kuwait, Saudi Arabia and Yemen.	1970	Extinct	Hammond et al. (2001), IUCN (2016a, 2016b)
Bovidae	*Oryx leucoryx* (Pallas, 1777)	Arabian oryx	All desert regions of Arabia	1972 (extinct in the wild)	Reintroduced to Oman and parts of Saudi Arabia	Al-Nafie (1989), Harrison and Bates (1991)
Bovidae	*Ovis ammon* (Linnaeus, 1758)	Wild sheep	N. Oman	1981	Extirpated	Harrison and Bates (1991)
Bovidae	*Capra aegragus aegagrus* (Erxleben, 1777)	Wild goat/ bezoar goat	Western Hajr, UAE	1968	Extirpated	Drew et al. (2005), Olsen (2013, 200)
Bovidae	*Capra nubiana* (F. Cuvier, 1825)	Nubian ibex	Mountains and escarpment areas of Arabia	Extant	C and S Oman, Yemen, Arabian shield areas	Ross et al. (2020)
Bovidae	*Arabitragus jayakari* formerly *Hemitragus jayakari* (Thomas, 1894)	Arabian tahr	N. Mountains of Oman and UAE	Extant	N. Mountains of Oman and UAE	Harrison and Bates (1991), Ropiquet and Hassanin (2005)
Camelidae	*Camelus arabs, Camelus concordiae* or unnamed species	Wild camel	All of Arabia	Bronze Age, approximately 3000 BP	Extinct by late iron age, replaced by *Camelus dromedarius*	Guagnin, Shipton, et al. (2018), Martini (2019)

battle images. Ancient hunting images of an equid surrounded by dogs will be of asses not horses as the wild horse did not occur in Arabia.

The Syrian or Asian wild ass (*Equus hemippus* Groves & Grubb, 2011) was formerly known by the scientific name *Equus hemionus* subsp. *hemippus* I. Geoffroy Saint-Hilaire, 1855 or *Equus hemionus*[9] by Davies (1980) and Olsen (2013). Mediaeval and early modern reports of this wild ass are from northern Arabia, the Nejd in northern Saudi Arabia and the Hijaz of the western AP (Macdonald 2019). The IUCN SSC Equid Specialist Group (2018) state that it extended through the AP as far south as central Saudi Arabia (Figure 2). The last recorded sighting from Saudi Arabia dates back to the early 1900s (NCWCD 2004) while the last wild specimen was shot near Azraq oasis in Jordan in 1927 (Day 1981).

The few black and white photographs illustrate that this ass does not have any morphological features to distinguish it from other equid species, apart from being smaller in size and having a smaller head, more similar to a horse than a donkey. Olsen (2013) describes it as being intermediate between horse and donkey. Lack of diagnostic features therefore make rock art speciation difficult. Even archaeological investigations of equids mostly only narrow speciation to genus, meaning that bones can either be *Equus hemippus, Equus asinus, Equus africanus* or *Equus ferus*. Davies (1980) notes that *Equus asinus* and *Equus hemippus* dentition is indistinguishable.

Uerpmann (1987) considered the African wild ass (*Equus africanus* Heuglin & Fitzinger, 1866) to be the only species of wild ass that inhabited Arabia during the Holocene, but the fact that the Syrian wild ass existed until recent times (Macdonald 2019) plus petroglyphs of this species provide ample evidence that both species were found there during the Holocene, though they may not have occurred at the same place.

Comparisons of engravings (Schinz 1835), old photographs of *Equus hemippus* and its near relative the Persian onager (*Equus hemionus subsp. onager* Boddaert, 1785) shows that onagers can have colour variation in their coats. Added to this are light patches on the stomach that sometimes extend upwards at the joint of belly and hind legs, and even forelegs. These features can combine to make the flanks look like a series of squares of different colours. We propose that where rock art depicts ancient equids with squares or a piebald pattern, these would be the Syrian wild ass. Examples of these can be seen in Khan (2007, 172) from Wadi Damm (NW KSA: Olsen (2013, 206) from Jubbah, KSA; and panel 105A of Guagnin (2015, 11)[10] from Shuwaymis, KSA Figure 3). Interestingly, the two latter examples show the ass surrounded by dogs, an indicator that these are wild rather than domesticated asses, as nomads would never

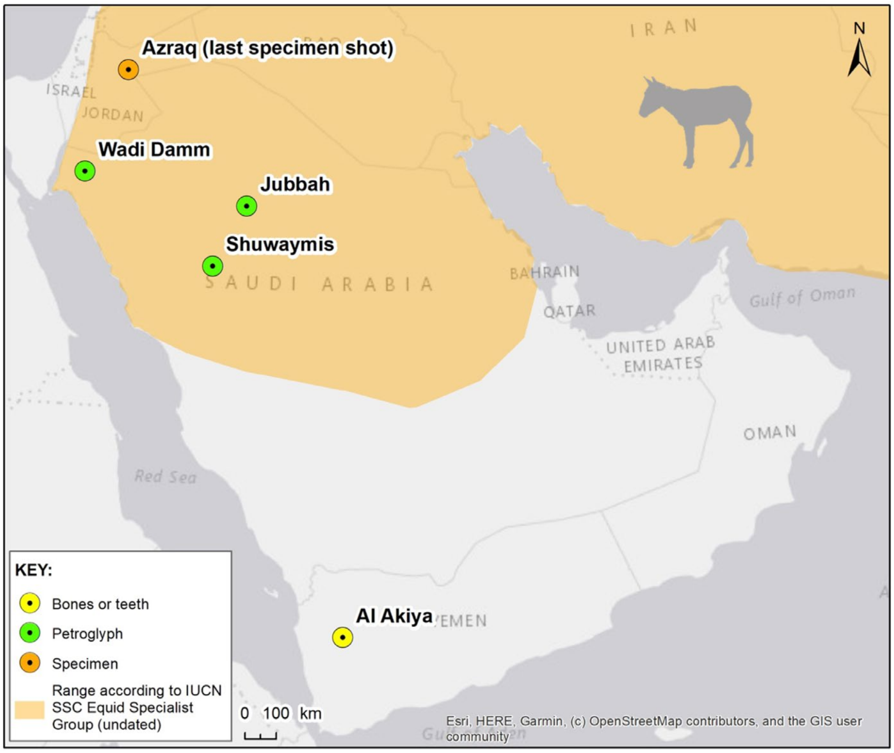


FIGURE 2 | Anthropocene and Holocene distribution of onager in the AP. *Sources*: Azraq, Jordan, (Day 1981); Wadi Damm, KSA, Khan (2007, 172); Jubbah, KSA, Olsen (2013, 206); Shuwaymis, KSA, Guagnin (2015, 11); Al Akiya, Yemen, Kallweit (1996). Mallon et al. (2023) place a population around Taif, KSA but the basis of this record is not known.

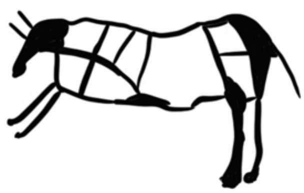
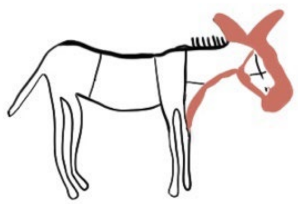
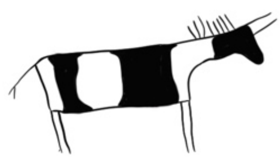
		
Wadi Damm Khan (2007: 172)	Shuwaymis West http://saudi-archaeology.com/subjects/onager-or-african-wild-ass/attachment/wild-ass-at-shuwaymis-west_/ Brown areas are later additions and change speciation	Jubbah Olsen (2013: 206)

FIGURE 3 | Onager petroglyphs.

need to use a pack of dogs to bring down a domestic animal. This is confirmed by the fact that all equid scenes in Shuwaymis show developed patination, thereby indicating advanced age. The petroglyph from Wadi Damm has been estimated to date to the Chalcolithic (5500–4500 years BP) based on nearby archaeological finds (Khan 2007, 172).

Unusually, the image from Shuwaymis depicted in Guagnin (2015, 11) has had a later change in head shape, with a considerably larger head added. Her interpretation is that this originally was a Syrian wild ass that then was re-drawn to show an African wild ass being hunted by a pack of dogs. When dogs hunt an animal, they will usually select a weak individual from a herd and surround it, which is why hunting scenes rarely depict dogs surrounding a herd of animals. So although only an individual ass is shown in the scene, it can be inferred that it was part of a herd before being separated out for the kill. One can only wonder why an artist decided to change the engraving to indicate change in speciation, and it is unlikely to have been because an individual Syrian ass was intended, then an individual African ass appeared later. Instead, it is more likely that originally the Syrian ass herds predominated in this region and then as the climate dried or human activity induced a decrease in vegetation, they came to be replaced by herds of the more drought tolerant African wild assess. This change must have been significant enough to impress the rock artist to alter the image. Another interpretation is that changing a depiction from onager to African wild ass could have been symbolic rather than reflecting environmental change.

An *Equus hemippus* tooth has been found at Al-Akiya (AK4) near Sanaa in the Yemen, dating from the 5th to 4th millennium BC (Kallweit 1996). This is the only record where experts have been definitive about speciation to onager. Its location far from all other records is surprising (Figure 2), and we would advise treating this record with caution. Also in Yemen is a rock inscription of a hunting expedition in Wadi Abadan, dated to 355 AD, in which onagers are mentioned as being hunted (Maraqten 2015). This is based on the interpretation of the word *fr'* in the ancient South Arabian script that sounds similar to the Arabic word for onager (Robin and Gajda 1994). Another South Arabian inscription from Wadi Ayan in Yemen uses the word *hmr* that has also been interpreted as onager (Maraqten 2015), while the Arabic for donkey is *hmr*. The usual word for domestic donkey in Safaitic is *hmr* in contrast to *'rd* which is onager (M. Macdonald pers. comm). We therefore are not convinced that the Yemeni inscriptions refer to onager. Historical evidence for wild asses increases as one travels north of the AP, or by going back in times to eras predating the Holocene. Macdonald (2019) provides many rock engravings of wild asses from southern Syria, north-eastern Jordan and Israel. He considers them to have been relatively common there in the past, but there is no way of determining if they are *E. hemippus* or *E. africanus*. During the Late Pleistocene, the equid fauna was dominated by *Equus hemippus*, which was also one of the most common taxa in the AP (Stewart et al. 2019).

3.1.2 | African Giant Buffalo

Drechsler (2007), Garcia et al. (1991) and Kallweit (2001) record osteological remains of African giant buffalo (*Syncerus antiquus* Duvernoy, 1851; 2017 formerly *Bubalus antiquus*, or *Pelerovis antiquus*) found in Sa'adah, Yemen, dating to 6250 ± 90 years BP. McCorriston & Martin et al. (2009) claim that engravings of the same species have been found in rock shelters within the same area of Yemen, though we have not been able to confirm speciation as the images are not publicly available. The Yemen location is the only Holocene record for this species in the AP (Figure 4).

Besides Arabia, North Africa is the only other region where this species survived into the Holocene extending as far east as SW Egypt (di Lernia 2021). During the late Pleistocene (35,000–17,000 years BP), the Rub al Khali (Empty Quarter) supported *Bubalus* when the current dunes were steppe and savannah (Delany 1989; McClure 1984; Stewart et al. 2019). The African giant buffalo was also present in Al Wusta, KSA, during the earlier humid phase of 92.2 ± 2.6 ka to 90.4 ± 3.9 ka (Groucutt et al. 2018).

The animal went globally extinct in North Africa during Roman times (Klein 1994), though Faith (2014) considers its disappearance to have been earlier, during the Middle Holocene. This extinction would have coincided with an abrupt climatic shift

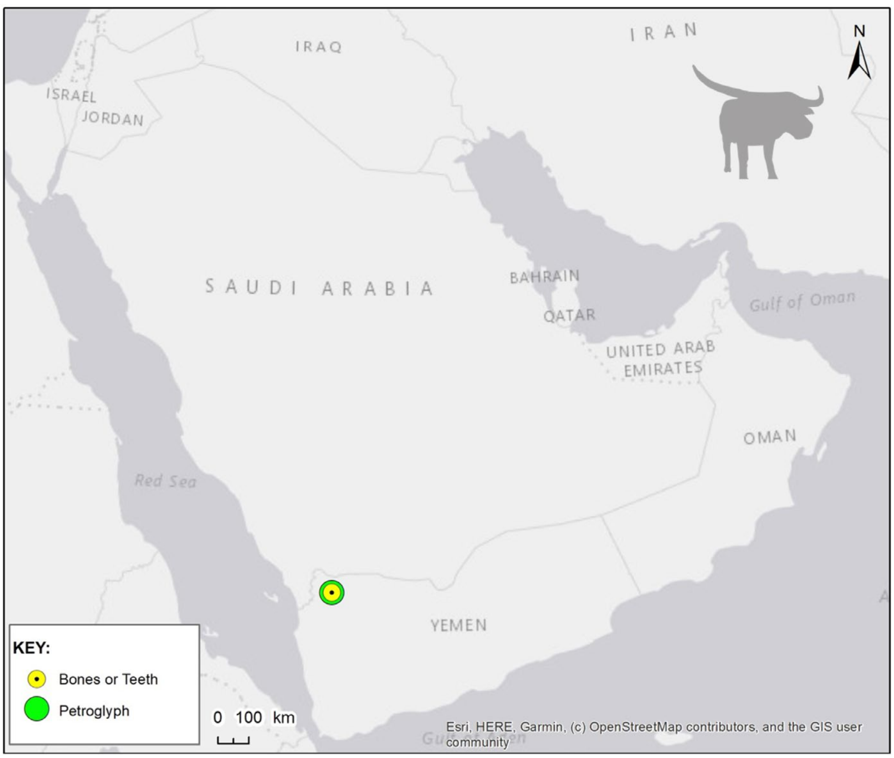


FIGURE 4 | Distribution of African giant buffalo in the Holocene AP. *Sources*: Drechsler (2007), Garcia et al. (1991), Kallweit (2001), McCorriston and Martin (2009). Known from osteological remains and petroglyphs (unverified by us) at one location only. Icon by Zimices, https://creativecommons.org/licenses/by/3.0/.

towards extreme aridity. While the climate is certainly to blame, hunting and competition with pastoralists and livestock for scarce water may also have played their part.

3.1.3 | Aurochs

The aurochs (*Bos primigenius* Bojanus, 1825) is the ancestor of taurine cattle (*Bos taurus* Linnaeus, 1758), formerly *Bos taurus* subsp. *primigenius* (Bojanus, 1827) and zebu cattle (*Bos indicus* Linnaeus, 1758) or *Bos taurus* subsp. *indicus* (Linnaeus, 1758), the major domestic extant cattle taxa (Park et al. 2015). The domestication of *Bos taurus* can be traced to the Near East, between 10,800 years BP and 10,300 years BP (Ajmone-Marsan et al. 2010), which roughly coincides with the start of the HHP. Domestic cattle are likely to have been brought into the AP from the Levant following domestication, and for millennia, domestic cattle and aurochs would have coexisted. Accounts of hunting expeditions from Shabwah, and Abadan (Nisab), in Yemen (Robin 2018) talk of captures of cows (*bqr*) and bulls (*ḥwry*) between 3rd and 5th centuries AD. As the account lists wild animals and is clearly meant to impress, it is more likely that it refers to aurochs than domestic cattle.

Although domestic cattle are much smaller than their wild ancestors, this does not aid in speciation of rock engravings. Guagnin et al. (2015) suggest ways of separating aurochs from domestic cattle depicted in petroglyphs. It is worth noting here that there is no uniform way of illustrating domesticated cattle, though some distinct styles are apparent. Animals with small round heads, ears protruding behind the horns and eyes, and eyes represented by small circles drawn outside the head are speciated as cattle, as animals with these traits have never been depicted in rock art as being hunted, though they may be superimposed on hunting scenes. Another style for depicting cattle is a small head with the horns forward and out like bicycle handlebars, the head smaller than natural size and the horns larger for emphasis. Or the small head and thin neck are fused with horns protruding forwards then backwards like a stretched letter 'm'.

Aurochs speciation on the other hand is based on horn shape, that point forward close to the forehead such that the tips of the horns are visible to the animal, even close to the eyes (McCorriston and Martin 2009). Other indications of an aurochs (or wild ox) is that it is hunted, with trapping stones or surrounded by hunters pointing their bows at their victim. To date, the only aurochs petroglyphs found within the AP have been recorded at Kilwa in Saudi Arabia, 30 km from the Jordanian border at a latitude north of Aqaba (Guagnin et al. 2015), at Jubbah, KSA (Guagnin, Shipton, et al. 2018) and Hima, KSA (Robin 2018): illustrated in Figure 5.

Excavations below a 7000-year old man-made structure called a *mustatil* near Al Ula in Saudi Arabia have revealed 36% of bones are *Bos taurus* and 52% are recorded as *Bos sp.* since aurochs could not be excluded (Kennedy et al. 2023) though the authors consider domestic cattle to be more likely given the relatively recent age of the bones. Likewise, the few *Bos* remains in Umm Jirsan cave (near Khaybar, KSA) could potentially be aurochs, though the late date (2824 ± 31 cal years BP) is more suggestive of domestic cattle (Stewart 2019). Another mustatil, also near Al Ula, yielded aurochs, though at extremely low quantities, dated to between 5300 and 500 cal BC (Abu-Azizeh et al. 2022).

Bos bones or teeth from the Holocene have been positively identified as *B. primigenius* in north and west Yemen (Drechsler 2007; Garcia et al. 1991; Kallweit 2001), the Saudi

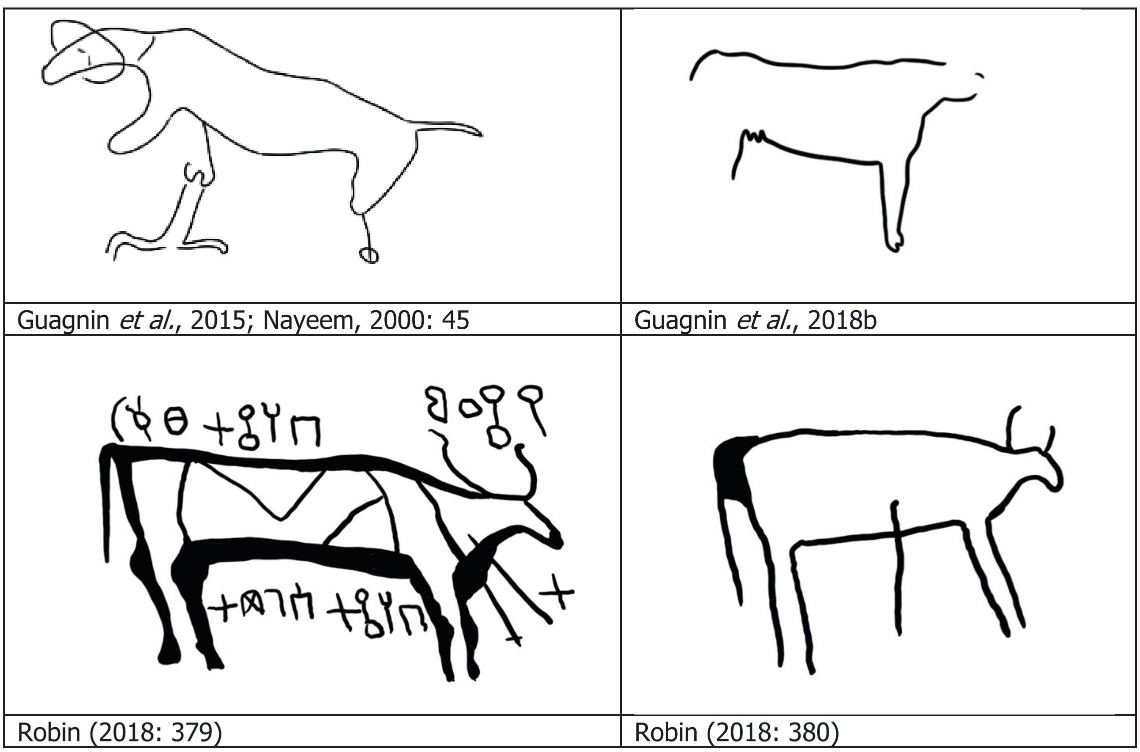


FIGURE 5 | Aurochs petroglyphs.

Empty Quarter, (Delany 1989; Edgell 2006) specifically Mundafin (McClure 1988; Robin 2018), and Jebal Buhais, Sharjah (McCorriston and Martin 2009; Uerpmann and Uerpmann 2008a, 2008b, 2008c). The five locations in Yemen that have yielded aurochs bones are Sa'ada, Wadi Tayyilah[11] (WTH: 6th millennium BC), Ash Shumah (6684–6675 BC: Cattani and Bökönyi 2002), Durayhimi and Gabel Qutran (Drechsler 2007). A sixth site; Wadi Dahr (also known as Wadi Zahr), contains bones of very large cattle that could also be aurochs (Kallweit 1996). Uerpmann et al. (2009) suggest these animals were the dominant fauna in Yemen. Finds of aurochs from the Empty Quarter date to the Early Holocene, 8800–6100 years BP (Edgell 2006), but the animals would have become extinct following the change towards a hyper-arid climate. The change occurred at the end of the HHP due to the lack of standing water following the onset of the dry period. Those from Jebal Buhais in Sharjah date to the late sixth to early fifth millennium BC (McCorriston and Martin 2009).

Aurochs remains in the Empty Quarter have also been found from an earlier humid phase (Late Pleistocene: 26,660–21,090 years BP: Delany 1989; Edgell 2006). The above records illustrate that aurochs were found across the AP (Figure 6), though it is not known if these were isolated populations or if they were widespread. Nevertheless, they challenge the idea that aurochs were absent from all but the far north of the AP as depicted in some maps (van Vuure 2002, 2014). On the contrary, McCorriston and Martin (2009) expected aurochs to have been widely distributed in the AP during the HHP due to the favourable habitat that would have existed at that time. They certainly were present in Holocene era Israel and Jordan, becoming extinct as recently as 1200–586 BC during the local Iron Age (Tsahar et al. 2009).

3.1.4 | Yemen/Bilkis/Queen of Sheba's Gazelle

The Yemen, Bilkis or Queen of Sheba's gazelle (*Gazella bilkis* Groves and Lay 1985) was first described in 1985 based on skins collected in 1951 (Al-Safadi 2000; Groves and Lay 1985; Greth et al. 1993). When the skins were collected the gazelle had been common in the Taiz province of Yemen, but no records were found after 1953, so it had already become extinct by the time it was described. As a species endemic to Yemen, with a very small range (Figure 7), it was particularly vulnerable to extinction.

Petroglyphs do not help in speciation of gazelles as different species can occur in the same area and there are no morphological features that help to separate them. Also, the often highly fragmented nature of bone samples, where found, renders speciation difficult (Martin et al. 2009). Whatever the species, gazelles are thought to have been abundant in the past, since vast structures called 'desert kites' were built to hunt them (Groucutt and Carleton 2021; Crassard et al. 2022).

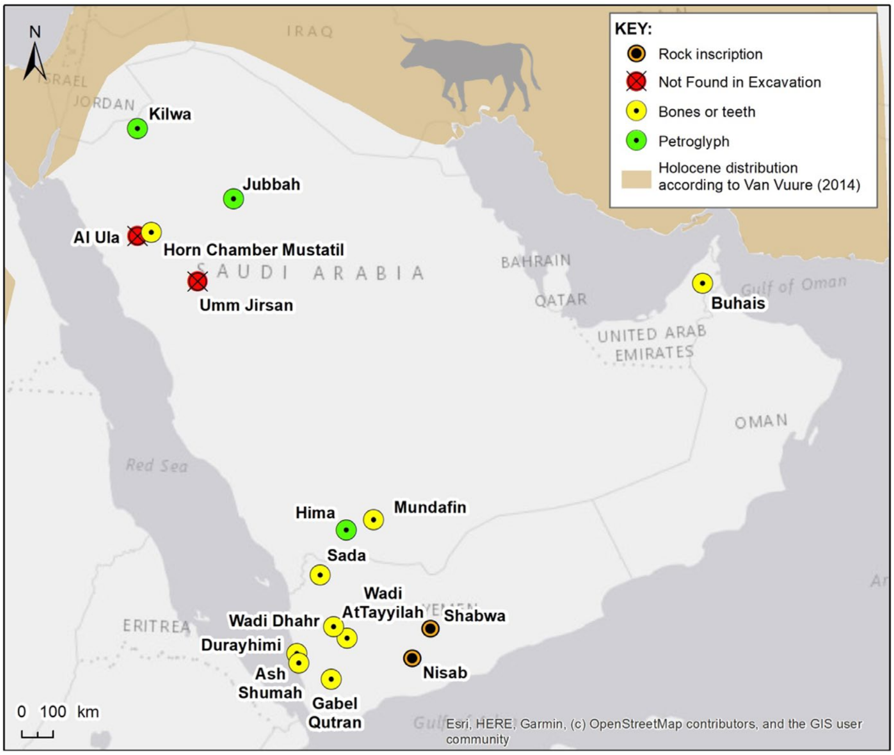


FIGURE 6 | Distribution of aurochs in the Holocene AP. *Sources*: Kilwa, KSA, (Guagnin et al. 2015); Jubbah, KSA, (Guagnin, Shipton, et al. 2018); Al Ula, KSA, (Kennedy et al. 2023); Umm Jirsan, KSA, (Stewart et al. 2019); Jebal Buhais, Sharjah, (McCorriston and Martin 2009); Sa'ada, Yemen, (Cattani and Bökönyi 2002); Wadi Tayyilah, Yemen, (Cattani and Bökönyi 2002); Ash Shumah, Yemen, (Cattani and Bökönyi 2002); Durayhimi, Yemen, (Drechsler 2007); Gabal Qutran, Yemen, (Drechsler 2007); Mundafin, KSA, (McClure 1988); Hima, KSA, (Robin 2018). Aurochs image from DFoidl (modified by T. Michael Keesey), https://creativecommons.org/licenses/by/3.0/.

FIGURE 7 | Distribution of Bilkis gazelle in the AP prior to extinction. *Source:* Harrison and Bates (1991). Gazelle icon from Rebecca Groom, https://www.phylopic.org/images/3b2e5f7d-58a3-49ea-b367-d6fac1f7beab/gazella-gazella.

3.1.5 | Saudi Gazelle

This gazelle was originally thought to be a subspecies of mountain gazelle (*Gazella gazella* Pallas, 1776; Hammond et al., 2002) but was given full species status in 1935 as Saudi gazelle (*Gazella saudiya* Carruthers & Schwarz, 1935). In 1951, it was downgraded to a subspecies of the dorcas gazelle (*Gazella dorcas* subsp. *saudiya* Carruthers & Schwarz, 1935) according to Rebholz et al. (1991). It not only returned to full species status in 1988 but also declared extinct in the wild (Thouless et al. 1991). Since then, there was hope that it might be found in private collections, but to date, all efforts have been in vain, and in 2008, it was given full extinction status (IUCN SSC Antelope Specialist Group 2017). The records of Saudi gazelle are shown in Figure 8.

3.1.6 | Wild Dromedary

Despite the ubiquity of the domestic dromedary (*Camelus dromedarius* Linnaeus, 1758), its origins remain the source of speculation and debate. Osteological investigations in Syria reveal that two different camel species existed between 150,000 and 45,000 years BP. One of these, the giant Syrian camel (*Camelus moreli* Martini, 2019), was the largest Old World camelid known, while the other camelid (*Camelus concordiae* Martini, 2019) was slightly smaller than existing dromedaries (Martini 2019). Morphological differences and size make *Camelus moreli* an unlikely ancestor to the wild dromedary. On the contrary, *Camelus concordiae* is morphologically close to *C. dromedarius*, making it a plausible direct ancestor or close relative. It has been found as far south as the Sea of Galilee in Israel from Pleistocene deposits (Martini 2019). Whichever *Camelus* was the ancestor, its absence from the African continent since the Late Pleistocene would suggest dromedaries originated from Arabia (Almathen et al. 2016).

The earliest date of dromedary domestication has been assumed to be 3400 years BP (Uerpmann and Uerpmann 2012), while Burger et al. (2019) and Grigson (2014) provide a range of 3800–3100 years BP, and others are open to domestication going back to 5000 years BP (Cherifi et al. 2017; Hoch 1979; Spassov and Stoytchev 2004). This would put it on a parallel date to Bactrian camel domestication (Almathen et al. 2016). After domestication, there was a period of < 2000 years when wild and domesticated dromedaries coexisted, until the wild dromedary became extinct (Almathen et al. 2016). This is thought to have occurred during the end of the iron age (Guagnin, Shipton, et al. 2018; Guagnin et al. 2020) and certainly before the Christian era (Almathen et al. 2016), though problems with osteological speciation between the wild and domesticated species make it difficult to be certain exactly when this happened. The decrease in bone size visible from the Late Bronze to the Early Iron Age is considered to be an indicator of the shift from wild to domestic dromedary, with the domestic being slightly smaller on average (Uerpmann and Uerpmann 2008c). This interpretation would suggest that wild dromedaries were still common in the Late Bronze Age, as evidenced by the findings of bones at Umm an Nar in the UAE (Hoch 1979). On the other hand, other authors disagree with the size reduction on domestication hypothesis (Curci et al. 2014) which would mean that dromedaries considered wild may actually have been domesticated, and would imply an earlier domestication. Support for the anti-size reduction on domestication hypothesis comes from the fact that if the

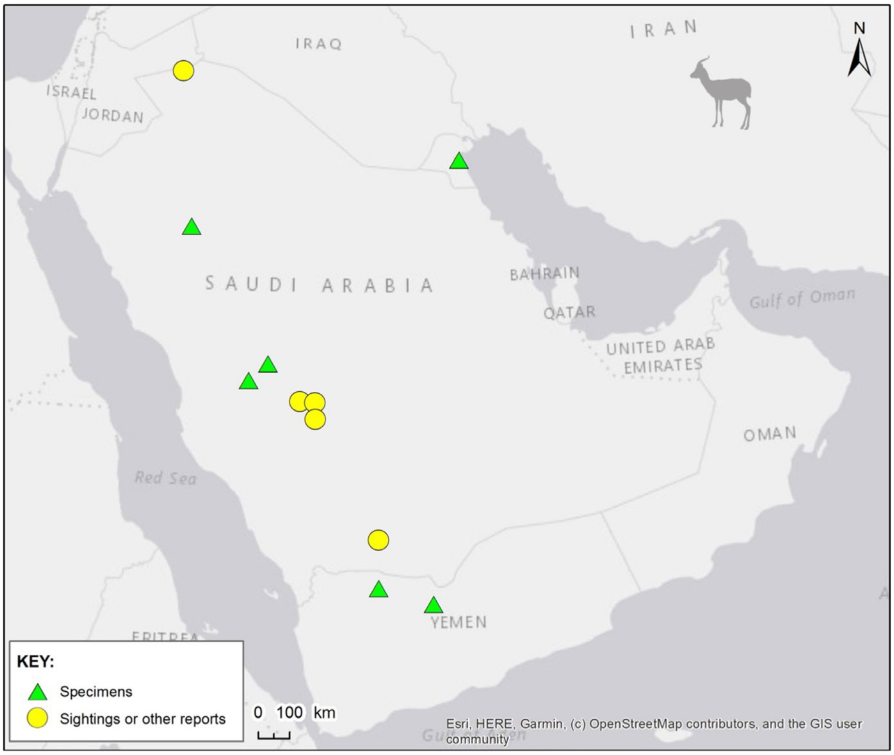


FIGURE 8 | Records of Saudi gazelle in the Arabian Peninsula. Geographical location is not precise. Information from Thouless et al. (1991). Gazelle icon from Rebecca Groom, https://www.phylopic.org/images/3b2e5f7d-58a3-49ea-b367-d6fac1f7beab/gazella-gazella.

wild ancestor was *Camelus concordiae*, it was actually smaller than current domestic camels (Martini 2019).

Either way, dromedary remains or engravings from the Neolithic era can only be of the wild dromedary. The oldest wild dromedary remains have been found in the Levant (Azraq in Jordan), dating between 9000 and 8000 years BP. In the AP, wild dromedary skeletons are known only from the east (modern UAE and northern Oman), and absent from excavations in Yemen, leading to the interpretation that they were limited to the south east coast of Arabia (Almathen et al. 2016). The absence of dromedary bones in a number of Late Stone Age digs corroborates this opinion.

Morphological differences between wild and domesticated dromedaries are not distinct enough to enable speciation in rock art, though experts theorise that if a dromedary is shown as being hunted, then it is most likely to be wild[12]. Based on this assumption and using other methods for determining chronology of rock engravings such as analyses of overlays and image context and content (Guagnin et al. 2022) makes it possible to separate wild dromedaries among the corpus of rock engravings, albeit conservatively. When the locations of these engravings are plotted on a map alongside skeletal remains (Figure 9, Tables 3 and 4), a different interpretation of their distribution emerges. Contrary to previous interpretations, wild dromedaries appear to have been widespread across Arabia (Figure 10), but a rare animal with the sporadic presence of small wild herds (Compagnoni and Tosi 1978). Also, there are indications that they may have experienced a sudden population decline around 8000–6000 years BP (Almathen et al. 2016). This would explain why they are absent from so many Late Stone Age excavations. In addition, dromedaries are most common in the most recent rock engraving era (Nayeem 2000), at a time when domesticated animals were present. It would be reasonable to conclude that dromedary populations expanded after domestication, and Curci et al. (2014) note an increase towards the end of the second millennium BC, though even at this time kitchen waste is dominated by other domestic and wild animals.

3.2 | Extirpated Species/Extinct From Wild

3.2.1 | Lion

Outside Africa lions are currently only found in a small part of India in Gujarat state (de Manuel et al. 2020). The lions that used to live in the Middle East and those remaining in India are called Asiatic lions (*Panthera leo* subsp. *leo* Linnaeus, 1758; formerly *Panthera leo* subsp. *persica* Meyer, 1826) and are smaller than their African counterparts.

Lions were described as being numerous in NW Saudi Arabia in 168 BC (Burstein 1989). In Yemen, they are known from pre-Islamic inscriptions (Robin 2018). During the early Islamic period, lions were recorded in southern Saudi Arabia (Bisha, Haly, Itwad, Tabalah and Tarj) and in Yemen (Hamil, As Sahul and Zabid) by the 10th century Yemeni scholar Hamdani (Robin 2018; Schnitzler 2011). The abundance of localities where lions were present suggests they were not rare at this time (Robin 2018). Ludovico di Varthema came across 'certain animals like lions' in 1503 on his route between Dahmar and Aden (Badger 1863, 85), though these could be a reference to

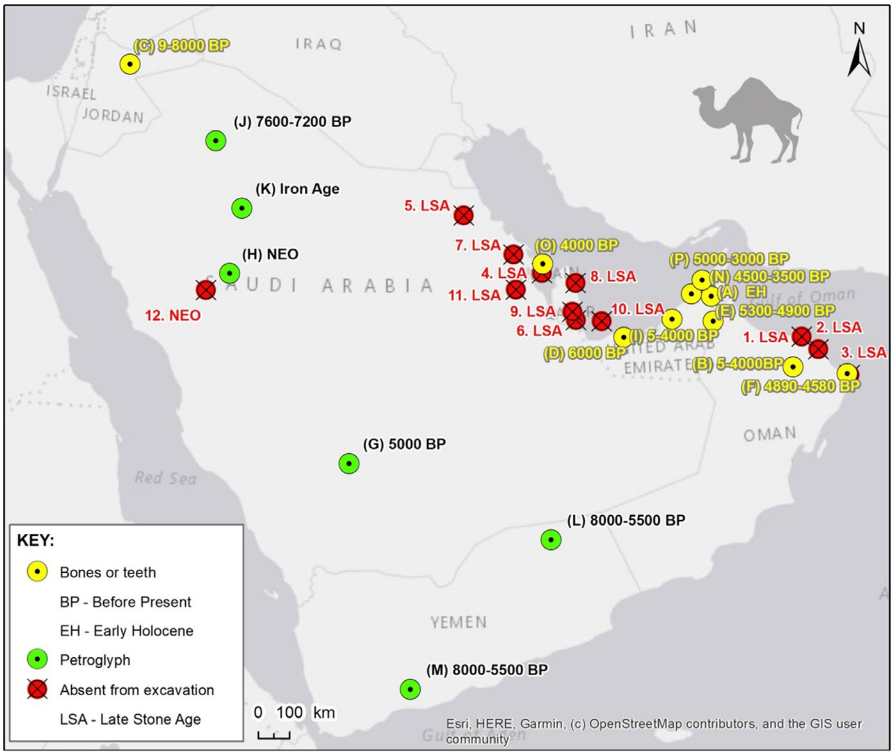


FIGURE 9 | Locations where wild dromedary were present or absent during the Holocene. Adapted from Yule (2022). For sources, see Tables 3 and 4. Numbers according to Tables 3 and 4. Dates in years BP or according to eras: NEO—Neolithic; EH—Early Holocene; LSA—Late Stone Age. Dromedary icon from public domain, created by Steven Traver.

hyaenas. Niebuhr states in his account of a 6-year expedition to 'Arabia' between the years 1761 and 1767 that lions were found there but does not provide more details on the location (Niebuhr 2017, 188). As his travels included Iraq, he could have been referring to the lions there rather than in the AP. Charles Doughty never came across lions in his travels in Arabia in the 1870s, but was told that the Sherif of Taif kept a lion in a cage (Doughty 1888b, 190), and travellers he met from southern Arabia said they still occurred in Yemen (Doughty 1888a, 459). Lions were also noted by travellers to the Nisab and Djof (Al Jawf) regions of Yemen in 1928 (Schnitzler 2011).

Maps showing the historical distribution of lion in Arabia fall into two categories. Some maps show lion occurring in north Jordan, Syria and Iraq but not the AP (e.g., Antunes et al. 2008; Bertola et al. 2016; de Manuel et al. 2020). Other maps show the same distribution as above but with lion occurring around coastal areas of Arabia (Black 2016). An alternative lion range map has been produced by Cooper et al. (2021) who modelled theoretical current distribution based on areas with a similar climate to lion country in Africa. He also produced theoretical distribution maps of suitable habitat for lion for the Holocene (6000 years BP) and Last Glacial Maximum (LGM: 21,000 years BP) based on the lions' present range climatic data from Africa extrapolated to current and historic climate conditions in the AP. This shows parts of Yemen and SW Saudi Arabia to be suitable lion habitat at the present climate. Cooper et al.'s (2021) current theoretically suitable areas for lion are smaller than the theoretical Holocene distribution while the LGM model distribution covers more extensive areas than the Holocene but by no means the entire AP (Figure 11).

Mapping the distribution of lion petroglyphs from this study (Figure 11) shows that lion were more widespread across the AP than indicated by any previous maps. Also, the number of petroglyphs depicting lion (examples of which are shown in Figure 12) and literary sources would indicate that they were not uncommon. The reason that lion are more widespread than indicated by Cooper et al. (2021) illustrates that care must be taken in assuming current lion distribution to be limited to climate when the reality is that anthropogenic factors rather than climate change have caused lion to retreat from the most arid regions (Faurby and Araújo 2018). Actually, lion do occur in very dry parts of Africa, such as the Skeleton Coast National Park (Stander 2019), where they have become uniquely adapted to the desert environment with rainfall of < 100 mm per year. By 1990, they were completely extirpated from the park, but subsequent favourable conservation practices allowed them to recolonise after 2002. By 2012, there were five prides living entirely within the park (Stander et al. 2023). Each pride occupies an area averaging 4726 km^2 (Stander 2019), the largest recorded home range for the species and a response to low prey availability. Guagnin et al. (2016) state that lions need prey with a body mass of between 92 and 632 kg, but the adaptability of these large carnivores is evident in Namibia, where they fed on prey as small as ducks weighing only 1 kg. Indeed, of the eight species taken, only seals exceeded 65 kg (Stander et al. 2023). The authors note that the Skeleton Coast is not typical lion habitat, with environmental constraints forcing them to select prey outside their normal prey range. Further evidence of the resilience of lions comes from the recovery of the last Asian lions in Gujarat, India. From a population of < 50 individuals covering an area

TABLE 3 | Wild camel finds in the AP.

	Site	Kind	Country	Date	Source
A	al-Buhais 18	Skeletal	Sharjah	5100–4700 cal. BC	Curci et al. (2014, 210), Uerpmann and Uerpmann (1999, 2002, 249), Uerpmann and Uerpmann (2008a, 2008b, 2008c, 101–4)
B	al-Muyassar M22	Skeletal	Oman	3rd mill. BC	Uerpmann (1989, 165), Uerpmann and Uerpmann (2002, 247–8), Curci et al. (2014, 209)
C	ʾAzraq	Skeletal	Jorden	7th mill. BC	Sima 2000, 19
D	Baynunah	Skeletal	Abu Zabi	Late stone age 5th Mill BC	Curci et al. (2014, 210), Beech et al. (2009)
E	Hili 8	Diverse skel parts	al-Ayn	3300–2900 BC	Curci et al. (2014, 209)
F	Ra's al-Ḥadd HD6	Skeletal	Oman	2890–2580 BC	Curci et al. (2014, 210)
G	Sha'ib. Musamma	Pecked	KSA	3000 BC	Curci et al. (2014, 217), Spassov and Stoytchev (2004)
H	Jubbah	Engraving	KSA	Neolithic	Guagnin, Shipton, et al. (2018)
I	Umm an-Nar	Skeletal	Abu Zabi	3rd Mill. BC	Hoch (1979)
J	Dumat Al Jandal	Relief	KSA	5600–5200 BC	Guagnin et al. (2022)
K	Jebal Oraf	Engraving	KSA	Iron Age 800 BC to 400 AD	Guagnin et al. (2020)
L	Bir Hima	Relief	KSA	6000–3500 BC	Anati (1968b), 58, figs 6–15, Curci et al. (2014, 217)
M	Jebel Kawkab	Engraving	Yemen	6000–3500 BC	Curci et al. (2014, 217), Anati (1968a, 1968b), Anati (1972)
N	Al Sufouh2	Skeletal	UAE	3rd to 2nd Mill. BC	Curci et al. (2014)
O	Qala'at al-Bahrain	Skeletal	Bahrain	2000 BC	Curci et al. (2014)
P	Tell Abraq	Skeletal	UAE	3rd to 1st Mill. BC	Curci et al. (2014)

Note: Adapted from Yule (2022) and Beech et al. (2009).

of a few hundred square kilometres at the onset of the 19th century, they have expanded tenfold to over 500, spread across 13,000 km^2 (Jhala et al. 2019).

3.2.2 | Cheetah

Wall paintings in Saudi Arabia are extremely rare, but a fragment has survived from Qaryat Al Faw[13] that depicts a cheetah (*Acinonyx jubatus venaticus* Griffith, 1821). The long slender body and particularly the narrowing at the groin compared to the chest make cheetah more likely than leopard. Also, the large closed spots are more similar to the cheetah, though the distinct tear line that is unique to this species (Stuart and Stuart 2017) is absent (see Figure 13A). Qaryat al Faw and its wall paintings date from the first centuries of the Christian era. The painting style is reminiscent of Qasr Al Hamra in the Jordanian desert that dates to the 8th century AD Ummayad period (Masseti 2015), with a strong emphasis on depicting local animals.

Cheetah are more difficult to separate from leopard in rock art than in paintings, and there are very few cheetah petroglyphs (Olsen 2013). However, the way these cats attack their prey differs, and this can help in speciation. Cheetah use speed while

TABLE 4 | Stone age finds without definite wild dromedary remains.

#	Site	Country	Source
1	Khor Milih	Oman	Uerpmann and Uerpmann (2002, 248–9)
2	Ras al-Hamra	Oman	Uerpmann and Uerpmann (2002, 248–9)
3	Ras al-Jins	Oman	Uerpmann and Uerpmann (2002, 248–9)
4	al-Markh	Bahrain	Roaf (1976, 149), Uerpmann and Uerpmann (2002, 249)
5	Dosariya	KSA	Uerpmann and Uerpmann (2002, 249)
6	Abu Khamis	KSA	Uerpmann and Uerpmann (2002, 249)
7	ʻAyn Qannas	KSA	Uerpmann and Uerpmann (2002, 249)
8	Khawr	Qatar	Uerpmann and Uerpmann (2002, 249)
9	Shagrah	Qatar	Uerpmann and Uerpmann (2002, 249)
10	Dalma	Abu Zabi	Uerpmann and Uerpmann (2002, 249)
11	Umm al-Qaiwain lagoon	Umm al-Qaiwain	Uerpmann and Uerpmann (2002, 249)
12	Umm Jirsan	KSA	Stewart et al. (2019)

Note: From Yule (2022).

leopard go for stealth (e.g., see petroglyph in Olsen 2013, 208), with a final rush at close quarters, or even pounce on their victim (Kingdon 1991). Therefore, images of spotted animals with long slender bodies and legs (Olsen 2013) running after prey are more likely to be cheetah, whereas heavier bodied animals are interpreted as leopard. This is especially if they have their arms outstretched (e.g., see Olsen 2013, 209), as leopard sometimes use their powerful forearms prior to biting their victim (Kingdon 1991). The habitat also differs, with cheetah found in savannas, steppes and semi deserts, whereas leopard are distributed more widely from near deserts to forest (Kingdon 1991). Petroglyphs of spotted animals in rocky, forested country are therefore more likely to be leopard. Prey species characteristic of rocky areas such as ibex would also steer speciation in favour of leopard (Figure 13B). On the other hand, cheetahs have a small head relative to their bodies (Figure 13C).

In some cases, it may be hard to separate cheetahs from dogs when spots are absent in the rock art. Cheetah and leopard have long bodies and legs, and long stiff tails that can curve upwards and inwards (Figure 13C), while dogs are often depicted with short tails curling upwards and inwards towards the head, like an inverted question mark. An animal hunting an ostrich from Jabu (Tayma) is most likely to be a dog due to the short, inwardly curving tail (see Olsen 2013; Figure 13D).

Only one toponym in the AP was found with the name cheetah: Fahud in Oman, taken from the Arabic for cheetah which is *fhd*. Robin (2018, 329) describes four inscriptions from Shabwah, Abadan (Nisab) and Shihr in Yemen where he translates the South Arabian word *fhd* as 'lynx', but given that lynx are not found in the AP and given the similarity of *fhd* with Arabic, we consider cheetah to be a better translation. The inscriptions date from the 3rd to 6th centuries.

The last record of cheetah in the AP comes from Dhofar in Oman, where an individual was shot in 1977 (Harrison and Bates 1991). In Yemen, the last sighting dates from 1963 east of Sanaw (Harrison and Bates 1991; Mensoor 2023), and the last report from Saudi Arabia goes back to 1954 (Al-Nafie 1989). But cheetahs will soon be back, for the National Center for Wildlife (NCW) in Saudi Arabia has launched a national Cheetah Conservation Strategy aimed at reintroducing the animals[14]. Harrison and Bates' (1991) map of cheetah sightings, specimens and tracks is complemented by Kingdon (1991), toponyms, rock engravings and mummified remains to provide a more comprehensive picture of their distribution in Figure 14.

In Egypt, cheetahs were last recorded between 1950 and 1555 years BP. The eastern Egyptian cheetahs may have been the same subspecies as the extinct population that used to occur in the AP (Charruau et al. 2011), while cheetah from western Egypt shared the same haplotype with cheetah from Libya, Algeria and Western Sahara. This will be further verified once recently discovered mummified cheetahs from Rafha caves in KSA[15] have been genetically tested.

3.2.3 | African or Nubian Wild Ass

The African wild ass (*Equus africanus* von Heuglin & Fitzinger, 1866), specifically the Nubian ass subspecies (*Equus africanus subsp. africanus* von Heuglin & Fitzinger, 1866) is the ancestor of the domestic donkey. Lydekker (1904) called this *Equus asinus* subsp. *africanus*, while Groves and Smeenk (2007) carried out an exhaustive review of taxonomy and proposed *Equus (Asinus) africanus africanus*. Confusingly, some authors refer to the African wild ass as the 'wild *Equus asinus*', using the scientific name of the domestic donkey. This has been criticised by Gentry (2005) who states that wild ancestors of domestic species should not share the same scientific name. The African wild ass is currently classified by the IUCN as Critically Endangered (Moehlman et al. 2015).

The domestic donkey is considered a subspecies of the African wild ass (*Equus africanus* subsp. *asinus* Linnaeus, 1758) or a separate species (*Equus asinus* Linnaeus, 1758). Sometimes the wild ancestor of the domestic donkey is called *Equus asinus* subsp. *africanus* (Schiettecatte and Zouache 2017). In accordance with Gentry (2005), the correct name for the domestic donkey should

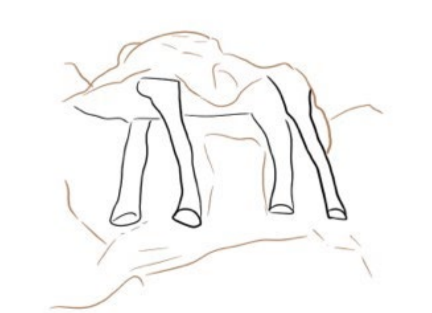
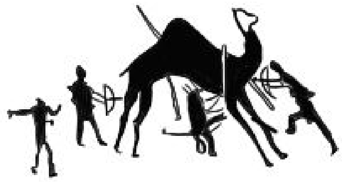
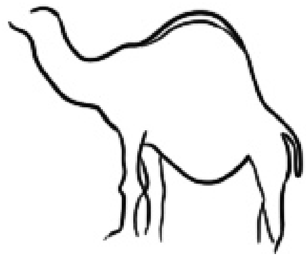
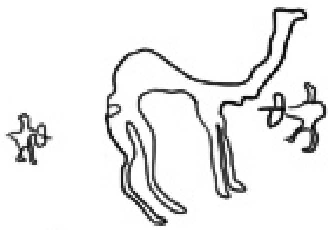
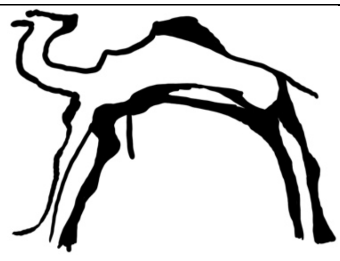
		
Dumat Al Jandal, KSA Guagnin *et al.*, 2022. Black lines are hand carved, brown are natural erosion lines, top of camel missing.	Sha'ib Musamma, KSA Curci *et al.*, 2014:217; Spassov & Stoytchev, 2004	Umm Sanman, Jubbah, KSA Guagnin *et al.*, 2018b
		
Jabal Oraf, KSA Guagnin *et al.*, 2020	Hima, KSA Robin 2018: 361	Hima, KSA Robin 2018: 379.
	← Beige areas are retouches to the original design and significantly later than the original. The writing may or may not be contemporary with the image. Unclear letters are not shown. Note the animal is tethered so this may be a trapped wild camel or a domesticate.	↑ Spears shown in beige for emphasis. They are drawn on top of the engraving, and it is not known if they are contemporary or added later.
Hima, Robin 2018: 381		

FIGURE 10 | Wild dromedary petroglyphs or rock reliefs.

be *Equus asinus*, noting that publications may use any of the above names.

Both domestic and wild species have a distinctive black vertical stripe at shoulder when seen in profile. van Bemmel (1972) separates the true wild *E. africanus* from *E. asinus* or hybrids by the patch of colour at the base of the ear and the colour of the belly. *E. africanus* has no dark patch at the base of ear but does have countershading of the belly. These observations aside, the morphological similarity between domestic donkey and its wild ancestor make it difficult to distinguish between the two species on rock engravings, unless the animal is hunted, in which case it is likely to be the non-domesticated African wild ass. Where no shoulder stripe is apparent, speciation becomes impossible as the aforementioned species do not always bear a stripe, and other equines also coexisted in the AP such as the Syrian or Asiatic Wild Ass (see below) and domestic horse (*Equus caballus*[16]).

Guagnin, Shipton, et al. (2018) provides possible evidence of this species from Jubbah, KSA (see Figure 15). An equine with the characteristic shoulder stripe is shown beneath human figures that have been dated to the Chalcolithic or Bronze Age thanks to their full patination. This would date the equine from the 6th millennium to early 4th millennium BC, which predates domestication (5000 years ago, according to Kimura et al. (2011)). A further 17 engravings of African wild ass were recorded at Jebal Oraf in NW Saudi Arabia (Guagnin et al. 2020).

Professor Abdulaziz Alghazzi posted an engraving on his X account that shows this animal being hunted by an oversized man with a bow and arrow[17] and surrounded by other hunters (Figure 15). The shoulder stripe is clearly evident, and the hunting scene rules out this being a domesticated donkey. The location of the rock engraving is not given.

Separating the domestic donkey bones from its wild ancestor is not easy but may be differentiated on the morphology of their metapodials (Stewart 2021). Skeletal remains of putative African wild ass found at Ash Shumah in Yemen have been dated to 6385–5980 cal. BC (Drechsler 2007), and may even have been in

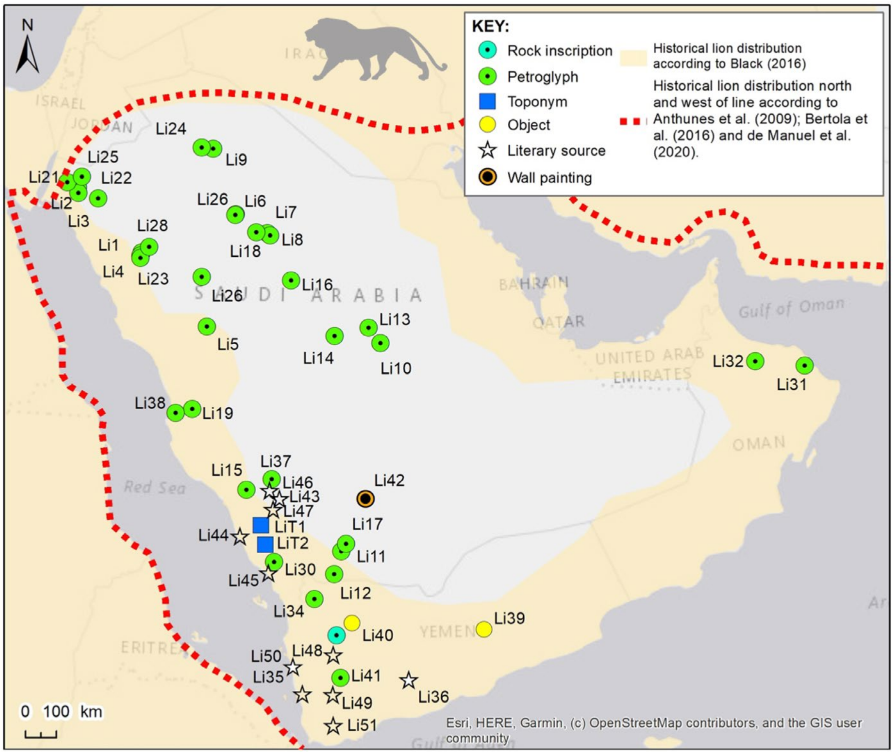
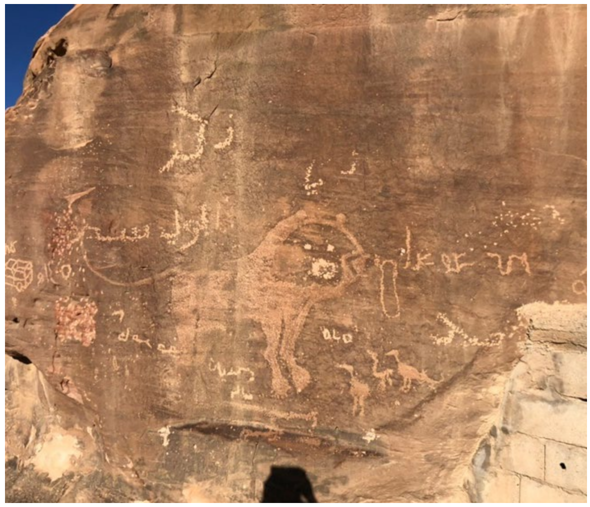


FIGURE 11 | Lion distribution from published literature compared to rock engravings. Locations and sources: Li1: Jabal al-Khraymāt (Incorrectly identified as Hassou Aba Mafir, Jabal Al Brar-SE of Tayma, KSA according to Nayeem (2000, 101) but corrected by Díez (2017)). KSA; Li2: Wadi Damm, KSA (Nayeem 2000, 84; Khan 1993, Plate 54, no. 402). Li3: Bajdah, KSA (authors observation). Li4: Wadi Ekma (probably Wadi Ikmah), Al Ula, KSA (Nayeem 2000, 103). Li5: Suweidra, 55 km from Madinah half way between Hanakiya and Madinah, KSA (Nayeem 2000, 128; Khan 2007, 203). Li6: Jubbah, KSA (Nayeem 2000, 155; Khan 2007, 207; Olsen 2013, 54). Li7: Jabal Yatib, 25 km SE of Hail, KSA (Nayeem 2000, 179; Khan 2007, 286; Olsen 2013, 39), https://www.wafyapp.com/article/popular-lion-themed-rock-art-sites. Li8: Milihiya, 40 km SW of Hail, 10 km from Jabal Yatib, KSA (Nayeem 2000, 186). Li9: Sakaka, KSA (Nayeem 2000, 202). Li10: Al Musaiqrah, near Al Quwayiyah, 88 km SW of Riyadh, KSA (Nayeem 2000, 221). Li11: Jabal Qarah, Hima, KSA (Nayeem 2000, 243; Khan 1993). Li12: Najran, KSA (Khan 2007, 211). 2500–300 BP. Li13: Qariyat Al Asba, near Qawiyah on Riyadh to Mecca highway, KSA (Khan 2007, 191; Olsen 2013, 46; https://1.bp.blogspot.com/-YqybzTIOuS0/X9RUJBgF0UI/AAAAAAAAjso/JW0KbSoUp2UuU-tbZUfqNufIe8Kx7r0mACLcBGAsYHQ/s900/Qaryat%2Bal-Asba%2BB%2528Grafitti%2BRock%2B1%25291.jpg). Li14: Hibl Thahlan, KSA, https://twitter.com/olem3tsh/status/1642479807983124482. Li15: Baha, KSA (Khan 2007: 206). Li16: Al Qassim, KSA (https://twitter.com/iAF305i/status/1517598071718400000). Li17: Jabal Kawkab, Najaran (https://twitter.com/alnjrani_r/status/1291422769926864898/photo/1), https://www.wafyapp.com/article/popular-lion-themed-rock-art-sites. Li18: Hail, KSA (Khan 2007, 209). Li19: Jabal Amdaan, Makkah Province, KSA (Wes Hopwood). Li20: Wadi Al Mutaiwi, KSA, https://www.arabnews.com/node/1647596/ajax/jserrors/aggregate. Li21: Jibal Al Lawz, KSA (Khan 2007, 291). Li22: Tabuk, KSA (Khan 2007, 330). Li23: Al Ula, KSA (McDonald et al. 2017). Li24: Dumat al Jandal, KSA, https://twitter.com/salamah1120/status/1186609409411207168. Li 25: Al-Suwaylimiyyah, KSA (author's observation); Li26: Shuwaymis, KSA (Guagnin, Perri, et al. 2018; Olsen 2013, 78). Li27: Jabbal Umm Senman, KSA. https://www.wafyapp.com/article/popular-lion-themed-rock-art-sites. Li28: Al Sinya, Al Ula, KSA (Olsen 2013, 42, 133), 45 km from Al Ula to Tayma. Li29: Jabu, KSA (Olsen 2013, 99). Li30: Abha, KSA (Christopher Clarke). Li31: Wadi Daiqa, Oman, (Nayeem 2000, 429). Li32: Wadi Sahtan, Oman, (Nayeem 2000, 425). Li33: Location name not given (Schnitzler 2011). Li34: Jabal Sama, Yemen, (Nayeem 2000, 467). Li35: Tihama Plain, Yemen (Schnitzler 2011). Li 36: Djof, Nisab, Yemen, (Schnitzler 2011). Li37: Dahthami Wells, KSA (Christopher Clarke); Li38: Khulais, KSA (Christopher Clarke). Li39: Seiyun, Yemen, https://fitzmuseum.cam.ac.uk/explore-our-collection/highlights/ANE101979. Li40, Nashshan, Yemen, https://www.flickr.com/photos/101561334@N08/42314715035. Li41, Umayma, Dhamar, Yemen, (Maraqten 2015). Li42, Qaryat Al Faw, KSA, https://destinationksa.com/qaryat-al-faw-arabias-forgotten-city/. Li43, Bisha, KSA (Robin 2018). Li44, Haly, KSA (Robin 2018). Li45, Itwad, KSA (Robin 2018). Li46, Tabalah, KSA (Robin 2018). Li47, Tarj, KSA (Robin 2018). Li48, Hamel, Yemen (Robin 2018). Li49, As Sahul, Yemen (Robin 2018). Li50, Zabid, Yemen (Robin 2018). Li51, AlMaqidi, Yemen (Robin 2018). Li51, Jabal Riyām, Yemen (Robin 2018; https://dasi.cnr.it/index.php?id=37&prjId=1&corId=0&colId=0&navId=402857628&recId=3912&mark=03912%2C005%2C004). LiT1: Sha'B Al-Asad, KSA (Al-Zahwah), toponym | LiT2: Al-Asad, KSA, toponym.

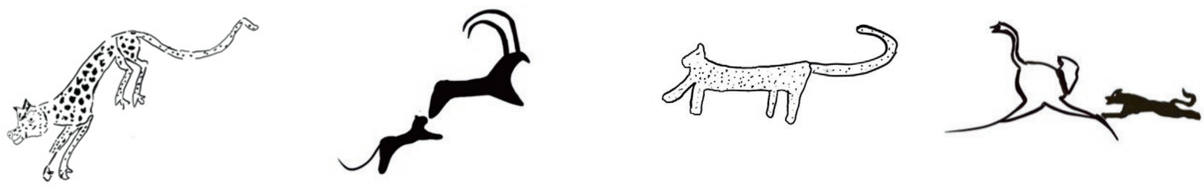
the process of domestication based on morphological variability (Cattani and Bökönyi 2002). In the Tihama coast of Yemen, wild ass remains have been found in Wadi Rima (Khalidi 2005), and Jahaba (Tosi 1986). Also, archaeological investigations at Jebal Buhais in Sharjah dated between 5100 and 4300 BC have uncovered bones of *Equus africanus* (Uerpmann et al. 2000). They have also been found at Ras Al Hamra in Oman, dated to between 3638 and 5207 cal BC (Drechsler 2007; Uerpmann 2003). Other African wild ass finds in Oman are at Khor Milh (Uerpmann 1991), dated to between the 5th and 4th millennium BC. At Ain Qanas, Saudi Arabia, remains of the African wild ass have been dated to 5500 BC (Uerpmann 1991). Our knowledge

Jabal Yatib, Hail, KSA
(Christopher Clarke)



Wadi Damm, Tabuk, KSA. Note eyes and mouth are a later addition.
(Christopher Clarke)

FIGURE 12 | Lion petroglyph examples.



A. Cheetah: Qaryat Al Faw, https://destinationksa.com/qaryat-al-faw-arabias-forgotten-city/

B. Leopard: Mecca, https://twitter.com/bgbg2013/status/1293951239412162562/photo/1

C. Cheetah; Shuwaymis, KSA, Khan, 2007:204; Guagnin *et al.*, 2018b, http://saudi-archaeology.com/subjects/cheetah.

D. Dog; Jabu, Tayma, KSA, Olsen, 2013:103

FIGURE 13 | Petroglyphs/painting of cheetah and other easily confused species.

of the Holocene distribution of *Equus africanus* is mainly from these skeletal remains (Figure 16). Outside the AP, and going back further in time, *Equus africanus* has been found in the Natufian site of Ra's al-Naqab in southern Jordan, which predates the Holocene (Macdonald 2019).

3.2.4 | Somali Wild Ass

The other African wild ass subspecies is the Somali wild ass (*Equus africanus somaliensis* Noack, 1884), also known as *Equus (Asinus) africanus somaliensis* according to Groves and Smeenk (2007). This animal has no vertical shoulder stripe but bears horizontal stripes across its legs. Only one example of a petroglyph of this species has been found so far in the AP, at Jabal Fardat Shamous, KSA (see Bednarik and Khan 2017, 186; Figure 17)[18]; the banded leg stripes and lack of shoulder strip make speciation easy (Figure 18).

3.2.5 | Lesser Kudu

Until the last decade, the presence of lesser kudu (*Tragelaphus imberbis* Blyth, 1869; previously *Strepsiceros imberbis* Blyth, 1869) being native to the AP was based on two sets of horns recovered from animals that had been shot in the 1960s. One was from Nuqrah in Saudi Arabia, and the other from Jabal Halmayn in Yemen (Harrison and Bates 1991; see Figure 19). No written records, sightings nor skeletal remains could back up the assertation that they were native, leaving the possibility they were of introduced individuals. Martin et al. (2009) thought it debatable if kudu ever existed in Arabia. Nor was there any evidence that they managed to cross the Sahara during the African Humid Phase (Drake and Blench 2017).

The matter was laid to rest by the discovery of 91 lesser kudu rock engravings by Guagnin, Shipton, et al. (2018) in the vicinity of Jubbah in KSA. Other examples of lesser kudu can be found in the literature that was published prior to the findings of Guagnin, Shipton, et al. (2018), but the authors did not speciate to lesser kudu. These include Jabal Yatib near Hail (Khan 2007, 182) and Milihiya, also near Hail (Nayeem 2000, 188), illustrated in Figures 19, 20 and 21. A further lesser kudu has been found near Madinah by Sultan Alsharif together widening the extent of occurrence map of Guagnin, Shipton et al. (2018). An engraving of a lesser kudu with emphasised vertical stripes from Saudi Arabia has been posted on the

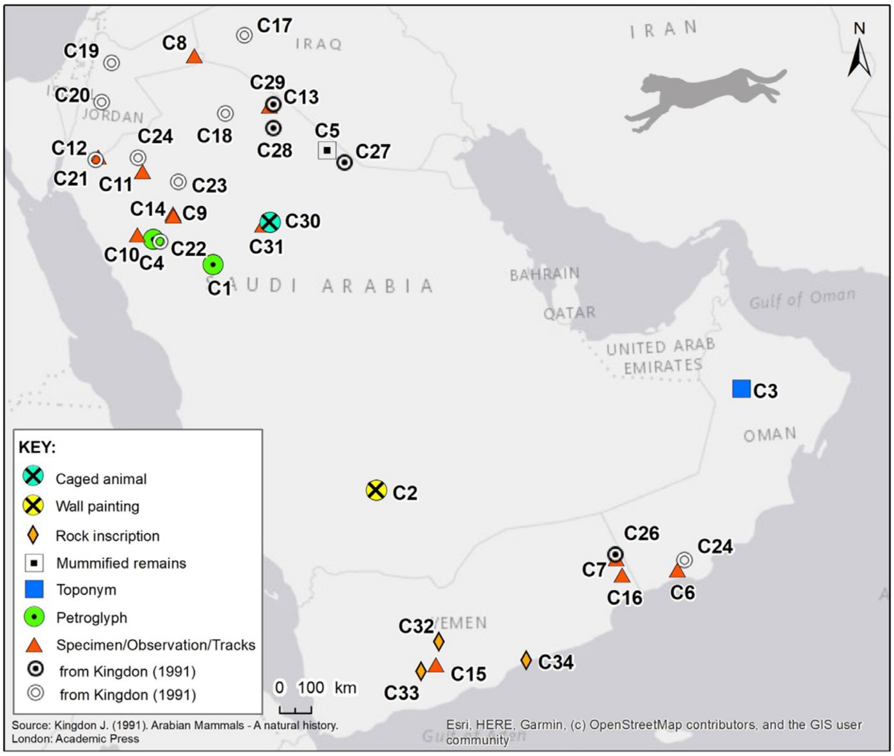
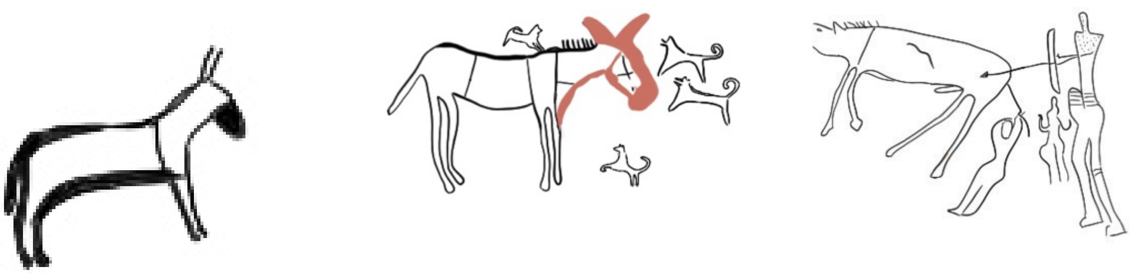


FIGURE 14 | Cheetah records in the AP, Holocene to the present. *Sources*: C1: Shuwaymis, KSA, (Khan 2007, 204; Guagnin, Shipton, et al. 2018, http://saudi-archaeology.com/subjects/cheetah). C2: Qaryat Al Faw, KSA, https://destinationksa.com/qaryat-al-faw-arabias-forgotten-city/. C3: Fahud, Oman, Toponym. C4: Sharaan, Al Ula (Christopher Clarke). C5: Rafha cave, KSA, https://www.arabnews.com/node/2144896/saudi-arabia. C6: Jibjat, Dhofar, Oman, (Harrison and Bates 1991). C7: Wadi Mitan, Yemen, (Harrison and Bates 1991; Mensoor 2023). C8: Near Jordan and Iraq border, (Harrison and Bates 1991). C9: Jabu, Tayma, KSA, (Olsen 2013, 103). C10: Al Ula, KSA, (Harrison and Bates 1991). C11: Mughayra, KSA, (Harrison and Bates 1991). C12: Halat Ammar, KSA, (Harrison and Bates 1991). C13: Near Arar, KSA, (Harrison and Bates 1991). C14: Tayma, KSA, (Harrison and Bates 1991). C15: Ataq, Yemen, (Mensoor 2023). C16: Wadi Mitan, Yemen, (Mensoor 2023; Harrison and Bates 1991). C17–C29: Unnamed locations from map in Kingdon (1991). C30: Hail, captive cheetahs in the gardens of the emir in 1878–1879 recorded by Lady Anne and Sir Wilfred Blunt, Olsen (2013). C31: Hali, KSA (Harrison and Bates 1991). C32: Shabwah, Yemen, 3rd century (Robin 2018). C33: Nisab, Yemen, 4th century (Robin 2018). C34: Shihr, Yemen, 6th century (Robin 2018). Geographical locations not precise. Icon from public domain created by Margot Michaud.



Jabal Oraf, Jubbah
Guagnin *et al.*, 2018b

Shuwaymis West
http://saudi-archaeology.com/subjects/onager-or-african-wild-ass/attachment/wild-ass-at-shuwaymis-west_/
Brown areas are later additions and change speciation.

Unknown location
https://twitter.com/ProfAlghazzi/status/1712092326451974501

FIGURE 15 | African wild ass petroglyphs.

social media website X (Twitter). The finder used the pseudonym Lazzam_mawan06[19], but does not provide the actual location within KSA (Figure 21).

Delany (1989) notes that lesser kudu have never been found in Pleistocene deposits in Israel. On the basis of this, he suggests they spread from southern Arabia northwards during times of low sea

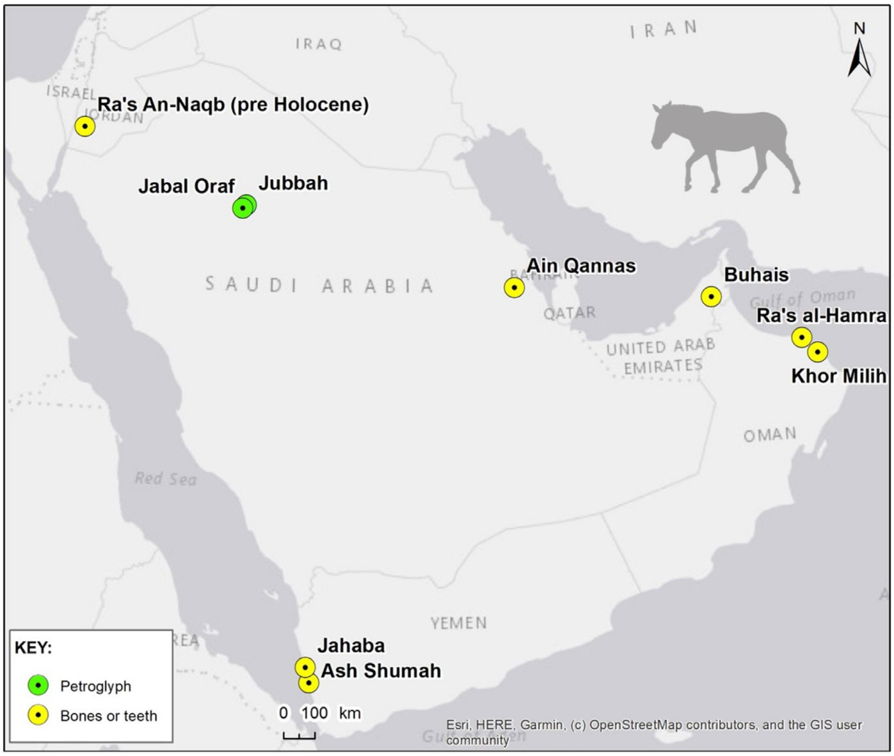


FIGURE 16 | Anthropocene and Holocene distribution of African wild ass in the AP. *Sources*: Ra's An-Naqb, Jordan; (Macdonald 2019). Jubbah, KSA (Guagnin, Shipton et al. 2018). Jabal Oraf, KSA (Guagnin et al. 2020). Ain Qannas, KSA (Uerpmann 1991). Jebal Buhais, Sharjah (Uerpmann et al. 2000). Ra's al-Hamra, Oman (Drechsler 2007; Uerpmann 2003). Khor Milih, Oman (Uerpmann 1991). Wadi Rimah (Khalidi 2005). Jahaba, Yemen (Tosi 1986). Ash Shumah, Yemen (Drechsler 2007). Public Domain icon from Steven Traver.

FIGURE 17 | Holocene distribution of Somali wild ass in the AP.

level, either 35,000–30,000 years BP or 18,000–17,000 years BP. On the other hand, Stewart et al. (2019) report that Tragelaphines were restricted to Africa during the Late Pleistocene, which would suggest a Holocene era colonisation of the AP.

3.2.6 | Greater Kudu

An image posted by Badr Albaqaawi on Twitter[20] from Baqa'a Governorate in Saudi Arabia shows an antelope with twisted horns (Figure 22). Key features include a prominent neck, spirally twisted corkscrew horns with five half turns, a beard, a

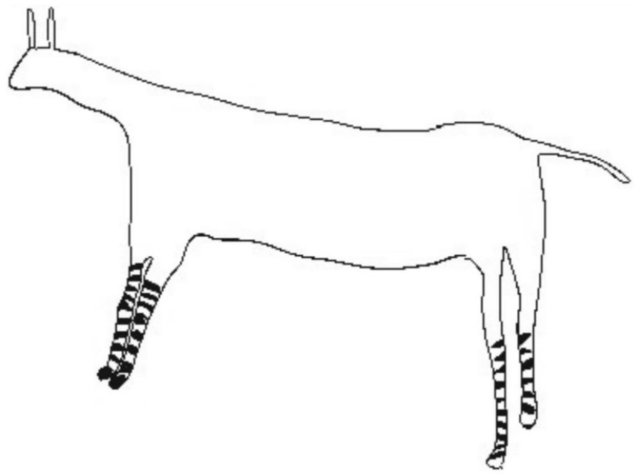


FIGURE 18 | Somali wild ass petroglyph. https://twitter.com/mash10000/status/1064529484802596866/photo/1

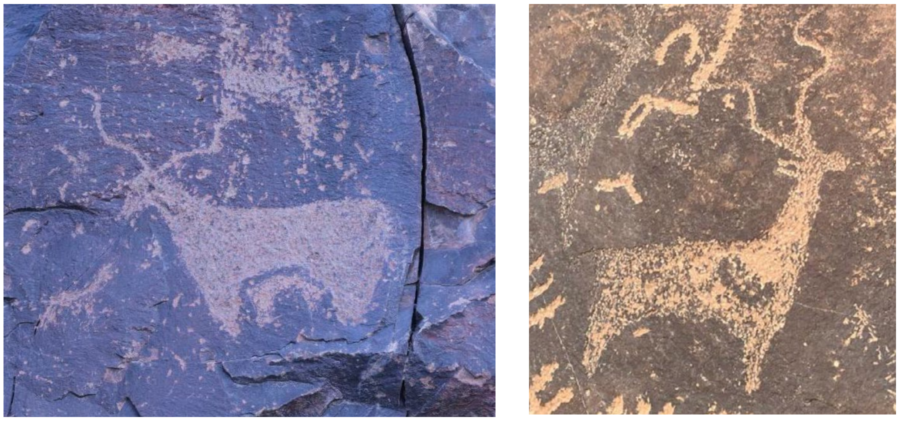
thick central vertical stripe and stippling on the body as if to suggest colour. The image is larger than that of other animals (caprines) and this may have been to emphasise size or importance.

Several alternative antelope species are possible for this image, the first being lesser kudu (*Tragelaphus imberbis*), mentioned in the previous section. The second alternative is the Addax antelope (*Addax nasomaculatus* Blainville, 1816) that used to live across the entire Sahara up to the Egyptian Nile (Hempel et al. 2021). It is mainly white with a dark patch on the forehead and light brown patches around the face. By contrast, the lesser kudu is dark brown with numerous white stripes on the body and two thick white bands on the upper and lower neck (Harrison and Bates 1991). While the two species are easily speciated from photographs, this is more difficult with rock art unless stripes are shown, as the body shape and horns are very similar.

The third alternative is greater kudu (*Tragelaphus strepsiceros* Pallas, 1766). Colour markings for this animal are similar to the lesser kudu, and the much greater body size does not help in speciation of rock art images. Other differences are the more prominent tail, lack of white neck patches, fewer stripes and more distinctive mane extending beyond the shoulders and beneath the neck as well as a prominent beard (Harrison and Bates 1991). Also, the horns are more outspread.

Of the three alternatives, greater kudu is the closest to the image. The stippling and stripe rule out addax, while the beard, neck mane (absent from lesser kudu: Harrison and Bates 1991) and outstretched horns more closely fit greater than lesser kudu

FIGURE 19 | Anthropocene and Holocene evidence of lesser kudu in the AP. Icon by Kai Caspar, https://creativecommons.org/licenses/by-sa/3.0/. *Sources*: 1—Jubbah, Guagnin, Shipton, et al. (2018). 2—Jabal Yatib, Khan (2007,182). 3—Milihiya, Nayeem (2000, 188). 4—Nuqrah, Harrison and Bates (1991). 5—Jebal Halmayn, Harrison and Bates (1991).



Madinah
(Sultan Alsharif)

Jabal Yatib near Hail
(Christopher Clarke)

FIGURE 20 | Photographs of lesser kudu petroglyphs not published before or published but not speciated as kudu.

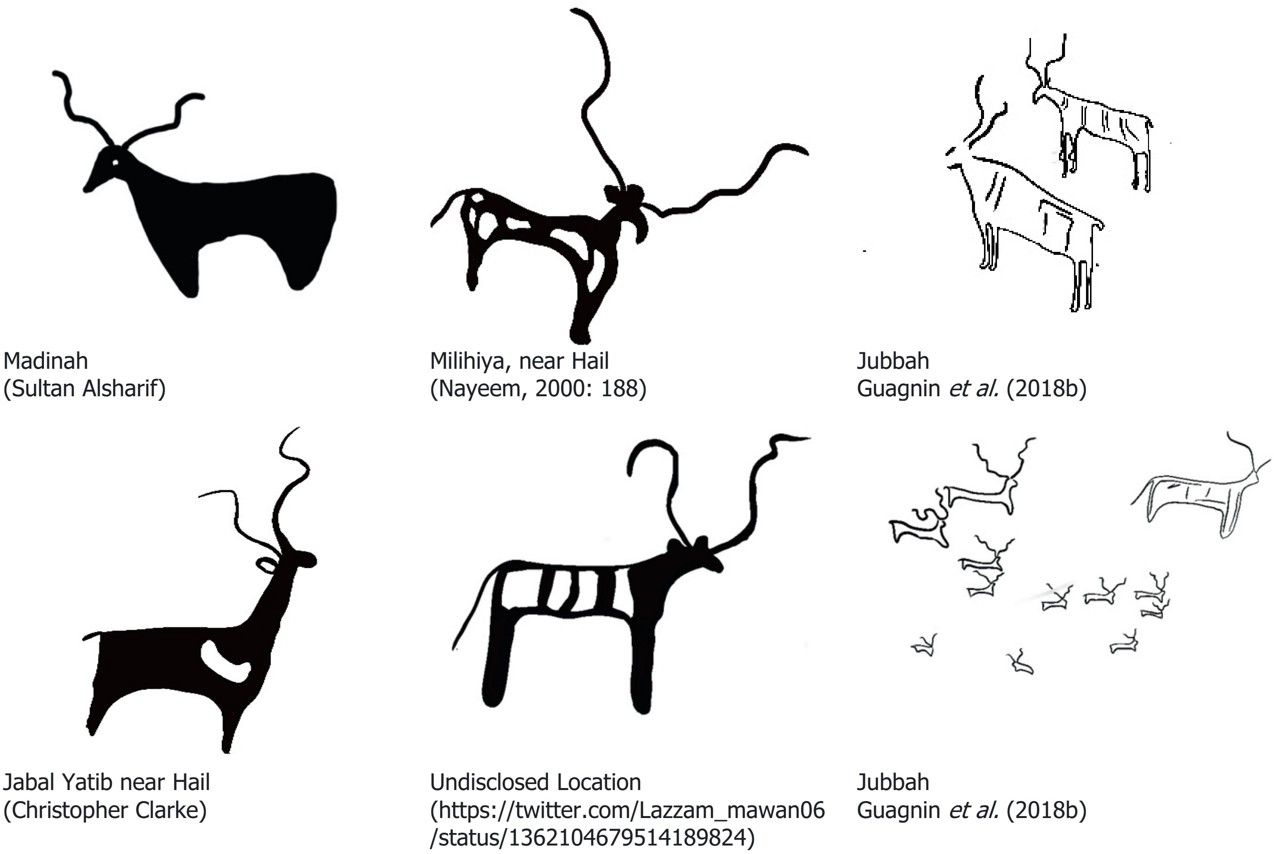
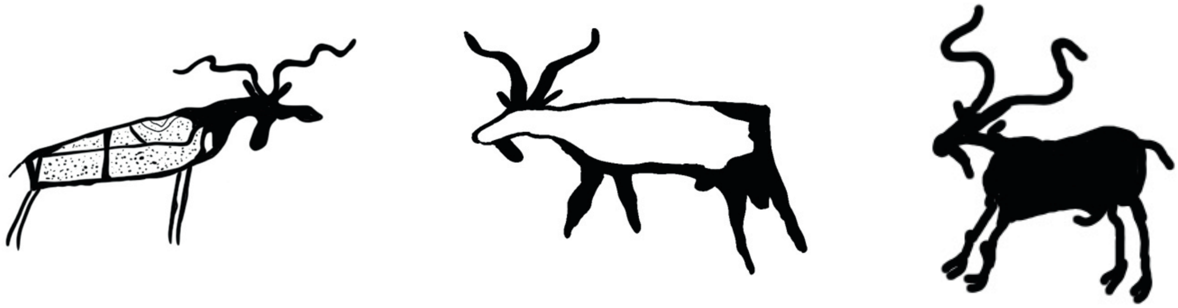


FIGURE 21 | Lesser kudu petroglyphs.

(the Latin species name of lesser kudu *imberbis* actually means 'without mane' according to Furstenburg (2016)). Another engraving of a greater kudu has also been found from Twitter[21]. This one from Tayma region was identified by the finder as greater kudu. The beard is well delineated. This animal only has three half turns on the horns. No stripes are marked, but the engraver appears to indicate colour patches on the body as well as the mane on the underside of the neck, another diagnostic feature. It closely resembles another petroglyph in Arar[22], KSA which we identify as greater kudu. No coat markings are shown but the exaggerated beard are common to all three petroglyphs.

The kudu petroglyphs are only found in the northern AP (Figure 23). In Africa, both kudu species are found in the east, with the current distribution of greater kudu occurring as far north as Sudan near the Egyptian border (Furstenburg 2016; IUCN 2020). The lesser kudu is less widely distributed with its current northern limit close to Djibouti. No evidence has



Baqaa, KSA
https://twitter.com/bm0167/status/1190913321316290560

Tabuk, KSA,
https://twitter.com/Meshari_0000/status/1526601100916400130/photo/1

Arar, KSA
https://twitter.com/SAldhmshy50207/status/1746661405938298992/photo/2

FIGURE 22 | Greater kudu petroglyphs.

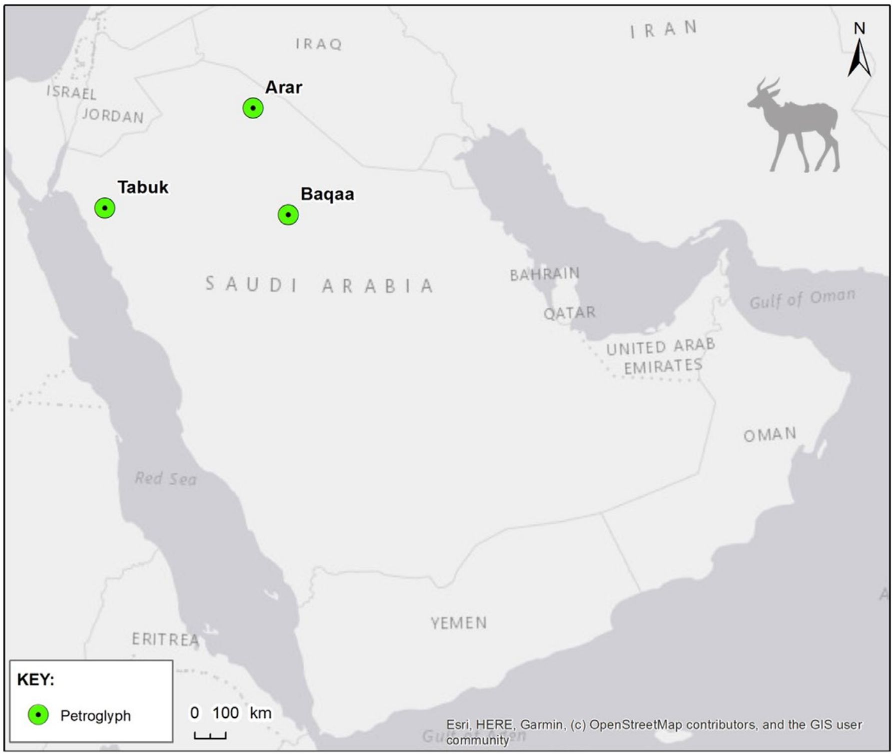


FIGURE 23 | Holocene distribution of greater kudu in the AP. Greater kudu only known from petroglyphs. Icon by Charles J. Sharp and T. Michael Keesey, https://creativecommons.org/licenses/by-sa/3.0/. *Sources*: 1—Tabuk, KSA, https://twitter.com/Meshari_0000/status/1526601100916400130/photo/1. 2—Baqaa, KSA, https://twitter.com/bm0167/status/1190913321316290560.

been found of greater or lesser kudu having crossed the Sahara from archaeological or North African rock engravings (Drake and Blench 2017). While these antelopes are currently unique to Africa, they actually originated in Eurasia as evidenced by Pliocene and Pleistocene deposits, and only recently spread to Africa (Furstenburg 2016).

3.2.7 | Arabian Oryx

Arabian oryx (*Oryx leucoryx* Pallas, 1766) are endemic to Arabia (NCWCD 2004) and were once widespread in the sandy areas of the AP (Harrison and Bates 1991, fig. 280; see Figure 24) according to accounts from the 1800s and early 1900s, yet there are no toponyms bearing their name. However, relentless overhunting resulted in extinctions and fragmentation of the population, and the last remaining animals were shot in the Jiddat Al Harasis, Oman, in 1972 (Fisher 2016). After this, the animals were extinct from the wild, though captive specimens remained in zoos and wildlife collections. These animals were then used to reintroduce the oryx back into the wild. Several countries across the AP now have at least one oryx herd across a number of protected areas (Figure 24) in what is hailed as a conservation success story and an inspiration that the lost animals of Arabia can be

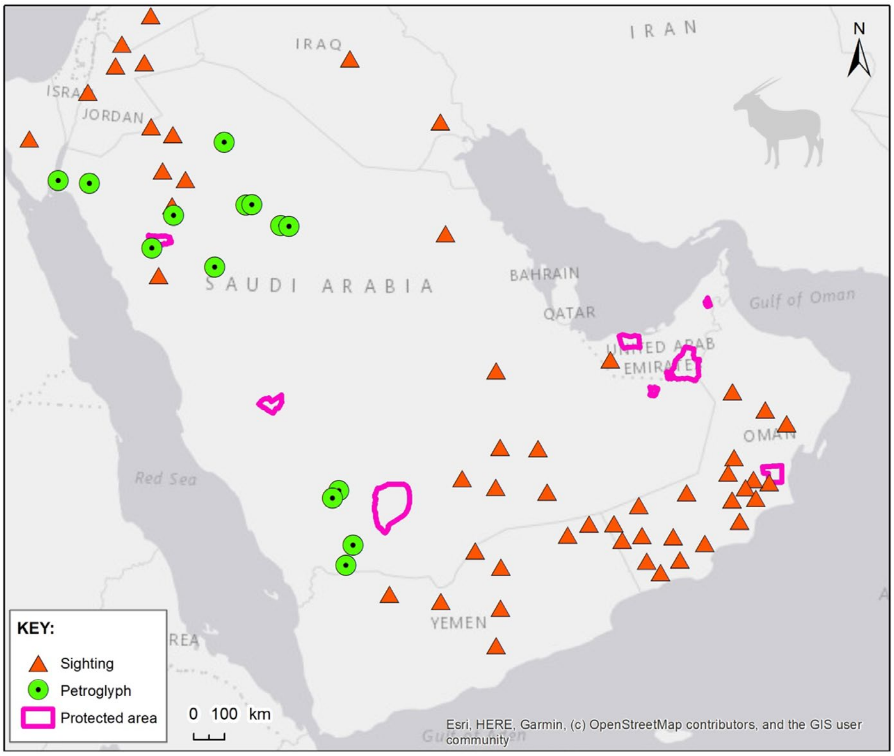


FIGURE 24 | Anthropocene and Holocene Distribution of Arabian oryx in the AP. *Sources*: Harrison and Bates (1991), Guagnin et al. (2016), MacGlennon et al. (2016); https://www.arabianoryx.org; Icon by Jan A. Venter, Herbert H. T. Prins, David A. Balfour & Rob Slotow (vectorized by T. Michael Keesey), https://creativecommons.org/licenses/by/3.0/.

				
Olsen (2013: 201)	Magna, KSA (Christopher Clarke)	Wadi Damm, Tabuk, KSA (Christopher Clarke)	Jabal Yatib, Hail, KSA (Christopher Clarke)	Jabal Yatib, Hail, KSA (Christopher Clarke)

FIGURE 25 | Selected oryx petroglyph drawings.

returned so long as other source populations remain, either as wild populations outside the AP or within zoos and collections.

Oryx are easy to speciate in petroglyphs with their long slightly inwardly curved horns pointing backwards. Curiously, the horns are sometimes shown pointing forwards (Figures 25 and 26). Petroglyphs expand their range but only to edges of mountainous areas. The interior of these rocky areas, despite being well endowed with rock art, do not have any depictions of oryx according to the sources used for this study.

3.2.8 | Wild Sheep

In the literature, several species bear the name wild sheep. One of these is the Asiatic mouflon or urial (*Ovis orientalis* Gmelin, 1774). According to McCorriston and Martin (2009), this species is native to the well-watered foothills and grassy plains of the Fertile Crescent, though Mallon et al. (2023) place it in Iran up to the Turkish border. It has never been associated with the wild fauna of Arabia, and is only found as an introduced domesticate (McCorriston and Martin 2009). On the other hand, Harrison and Bates (1991) provide evidence of a different species of wild sheep being native to Arabia, known as the Argali or mouflon (*Ovis ammon* Linnaeus, 1758). A specimen of this species from Arabia was shot in Wadi Khabora, Oman in 1967 (Harrison and Bates 1991). At that time, it was common in this part of Jabal Akhdar. In 1968, a wild sheep was recorded by a person who came from Sharawrah on the SE edge of the Rub al Khali, Saudi Arabia. The last record dates from 1981 and is of several sheep taken from the Hatta area, UAE (Harrison and Bates 1991).

Wild sheep are mentioned as part of the bounty from 10th century AD hunting expeditions to SW Arabia by the Yemeni scholar

FIGURE 26 | Oryx petroglyph photographs.

FIGURE 27 | Wild sheep being hunted by dogs. Dogs have been coloured beige to make the image clearer. Note two upturned (dead) sheep and two halves of a third sheep (from Robin, 2018).

Al Hamdani, though no exact location is specified (Robin 2018). This is supported by petroglyphs from Hima in SW Saudi Arabia showing sheep being hunted (Figure 27). The sheep petroglyphs are thought to be associated with adjacent inscriptions, which would date them to the literate era, post 750 BC (Robin 2018). The distribution of wild sheep records shows two clusters, one in northern Oman/UAE, the other in the southern Saudi Arabia close to the Yemen border (Figure 28).

3.2.9 | Wild Goat

The world population of wild goat or bezoar (*Capra aegagrus* Erxleben, 1777) used to extend to near Al Manama, UAE, until the 1960s (Harrison and Bates 1991). No other records from Arabia are known south of northern Syria. Since then, the animal has become extirpated from the AP and its current range extends from south-east Pakistan to south-west Turkey (Mallon et al. 2023). In the Neolithic, it ranged as far south as northern Oman (McCorriston and Martin 2009) and inhabited the central and northern regions of the Levant into the mid-Holocene (Horwitz and Goring-Morris 2000). Although the wild goat no longer is found in Oman or the UAE, five native Omani goat populations originate from *Capra aegagrus* (Al-Araimi et al. 2017).

Determining the Holocene distribution of the bezoar is rendered complicated by the fact that it is difficult to distinguish its bones from domestic goat species (Tsahar et al. 2009). It can also be hard to distinguish between goat and ibex petroglyphs. Ibex are the only caprine with transverse bosses along the horn, so where these are indicated, speciation is clear (Horwitz 2005). Having said this, absence of markings to show bosses does not mean ibex are not intended, so rock images of a goat without bosses could either be ibex or bezoar. Olsen (2013, 198) proposes that caprine rock engravings that show long curved, smooth horns with patterns on the coat (in the form of raised surfaces) are the bezoar goat, and the aforementioned features separate them from ibexes since they do not have patterned coats. She provides one example in Olsen (2013, 198) which is from Shuwaymis according to the website saudi-archaeology.com[23] (Figure 29). Also Khan (2007, 186) provides another image from Shuwaymis that shows a goat with the distinct vertical stripe and a horn with a spiral tip. Nayeem (2000, 275) displays an image of a goat with a stripe from Najran. Neither Khan nor Nayeem speciate to bezoar. Anati (1974, 137, 147) shows caprine images at Alam Massif with the distinctive central band. Close to the Alam Massif, at Najran, Mashael bin Abdullah posts on X an image of two goats on a boulder where the artists indicate different coloration of the front and back parts[24] through pecking technique.

Atallah Mardy Jalbakh uploaded a photograph of a rock engraving from the suburbs of Tayma[25] that well fits a wild goat and not an ibex. The distinctive vertical stripe down the flanks is shown as well as the blackened head. Another goat with the distinctive vertical stripe is shown in Harrigan (2008) from Jubbah. The panel shows the goat being surrounded by dogs. Also, Angás et al. (2021) provide images of a number of caprines from Khatm al Maleha, Sharjah, UAE. Although they consider these to be ibexes rather than *Capra aegragus*, one image shows the distinct vertical black stripe of the wild goat. Three fragments of bezoar horn core have been discovered at Shumah in southwest Yemen (Cattani and Bökönyi 2002). The Holocene and Anthropocene distribution of bezoar is shown in Figure 30.

4 | Discussion

4.1 | Summary of Extinct and Extirpated Species

The common perception is that a handful of large animals have become extinct from Arabia. For example, Boland and Burwell (2021) and the NCWCD (2004) cite Asiatic wild ass, lion, cheetah, oryx and Saudi gazelle as lost species for Saudi Arabia. Mallon et al. (2023) expand the assessment to include the AP as well as Jordan, Syria, Iraq and Israel and list five species: the Saudi gazelle and Yemen gazelle as Extinct (according to IUCN classification) and lion, cheetah and onager as Regionally Extinct.

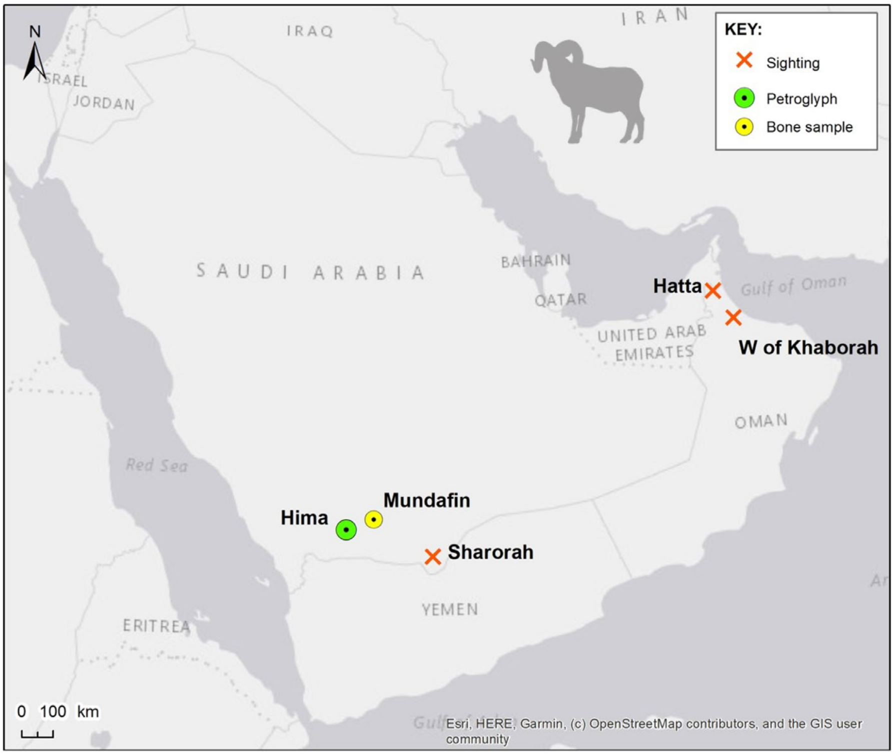


FIGURE 28 | Anthropocene and Holocene Distribution of Wild Sheep in the AP. *Sources*: Wadi Kharbora (Khabora), Oman (Harrison and Bates 1991); Sharorah (Sharawrah), KSA, (Harrison and Bates 1991); Hatta, UAE (Harrison and Bates 1991), Mundafin, KSA, (Robin 2018); Hima, KSA, (Robin 2018).

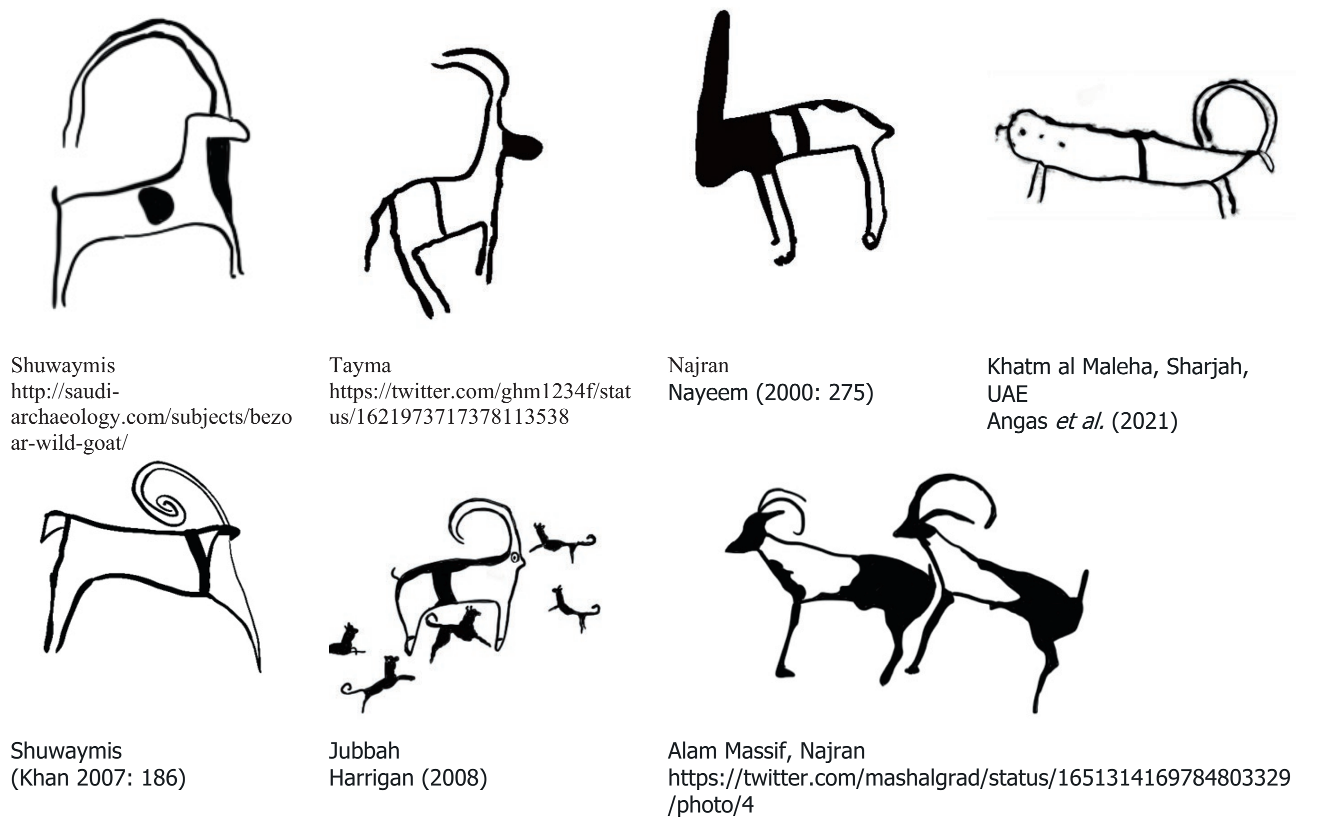


FIGURE 29 | Wild goat petroglyphs.

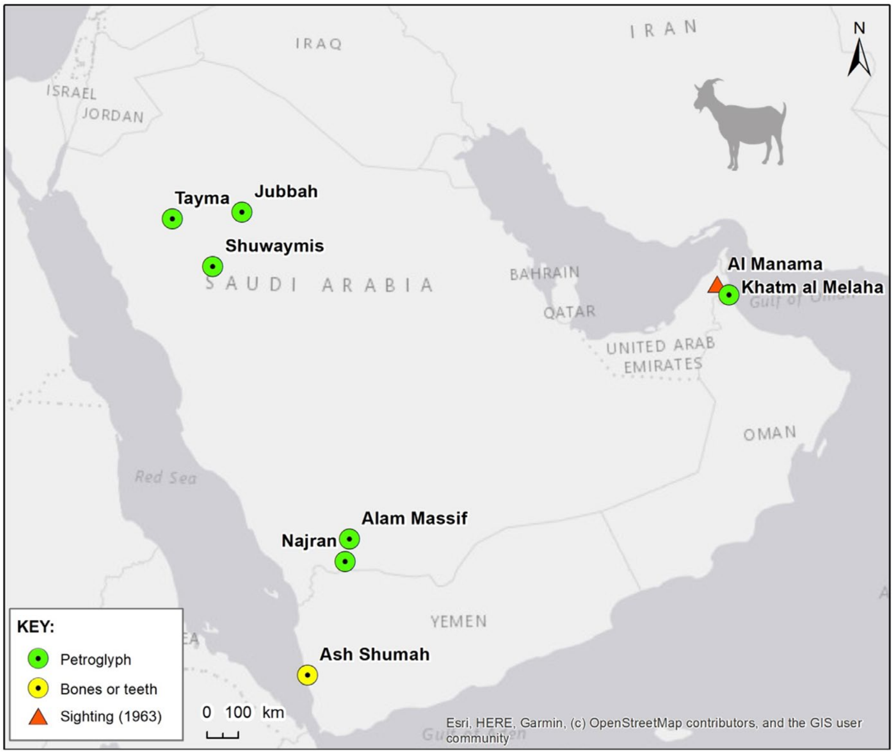


FIGURE 30 | Anthropocene and Holocene evidence of bezoar/wild goat in the Arabian Peninsula. *Sources*: 1—Tayma, https://twitter.com/ghm1234f/status/1621973717378113538/photo/1. 2—Jubbah; Harrigan 2008. 3—Shuwaymis; Olsen 2013, 198. 4—Al Manama; Harrison and Bates 1991. 5—Khatm el Melaha; Angás et al. 2021. 6—Alam Massif, Anati 1974, 137, 147. 7—Najran, https://twitter.com/mashalgrad/status/1651314169784803329/photo/4. 8—Ash Shumah; Cattani and Bökönyi 2002. Icon from Public Domain, created by Katy Lawler.

However, this study has shown that the AP used to have a much greater taxonomic breadth of large mammals than previously recognised, with no less than 15 large mammal species having become extinct or extirpated since the beginning of the Holocene. This compares with Africa that has lost 24 large mammal species during the Late Pleistocene and Holocene (Faith 2014), while Egypt has lost 29 large mammals (>4 kg) during the last 11,000 years (Yeakel et al. 2014). Faith (2014) claims that in Africa most losses occurred between 13,000 and 6000 years ago, while Yeakel et al. (2014) believe that Egypt lost 24 species since the end of the African Humid Phase (5500 years BP).

Furthermore, this study proposes two additional species to be included in the faunal inventory of the Holocene for which no previous evidence of their existence in the AP has been published. These are the greater kudu (known from two petroglyphs) and Somali wild ass (known from one petroglyph). There are no archaeological remains for these two these species from anywhere in the AP, neither from the Holocene nor any previous period. Their presence in the faunal record will need to be confirmed by other petroglyphs or osteological remains.

Results from this study also show that there is a disparity between the zooarchaeological and petroglyphic record (similar to the findings of Hill et al. 2020), and in general, the rock engravings provide a much clearer picture of faunal diversity than archaeological finds (Table 5) but no source provides a complete picture. This result has also been noted for the middle Sahara where rock engravings of hippos, oryx, warthog, African giant buffalo, African buffalo, giraffe, hartebeest and rhino have been inscribed on rocks but poorly represented in the zooarchaeological and paleontological record (di Lernia 2021). Also, Potts (2001) highlights ostrich, for which no bone samples have ever been found in the AP, yet for which there are abundant literary and rock engravings not to mention finds of ostrich shells. It is hoped that the development of ancient DNA (of which there are few studies to date in the AP) will add another source for finding lost species[26].

4.2 | Incorrectly Interpreted Petroglyphs

When Doughty (1888a, 1888b) wrote of his explorations in the AP, he named his book *Travels in Arabia Deserta*, using an ancient Latin name coined by the Roman geographer Claudius Ptolemy who drew from Greek sources. Ptolemy's book, *Geography*, written around 150 AD, influenced map makers up to one and a half millennia after publication. European maps drawn between the 1400s and 1800s[27] placed an imaginary boundary across the north of the AP across which they wrote *Arabia Deserta*[28]. This boundary continues to influence scientists to this day; not in geographical maps but in the perception that south of an artificial line lies a vast and inhospitable desert, that is deserted, or empty (in this case of biodiversity, Al-Nafie 1989). Even biogeographers are swayed such that historical distribution maps of lion and aurochs are drawn skirting *Arabia Deserta* (e.g., Bertola et al. 2016; de Manuel et al. 2020; van Vuure 2014), despite rock art and archaeological findings indicating otherwise. And when rock engravings of species not currently found in the AP are encountered, the conclusion is

TABLE 5 | Holocene and Anthropocene lost species sources.

Lost species	Origin	Rock art	Rock inscription	Sighting/skin/horns/ancient literature	Excavated bones, teeth, or horns	Toponym
African giant buffalo	African				●	
African wild ass	African	●	*ʿfr*		●	
Aurochs	African	●	*ḥwrw/ ḥwry*	●	●	
Bezoar	Eurasian	●		●	●	
Cheetah	African	●	*nmr*	●		●
Greater kudu	African	●				
Lesser kudu	African	●		●		
Lion	African	●		●		●
Oryx	Endemic	●		●		
Bilkis gazelle	Endemic			●		
Saudi gazelle	Endemic			●		
Somali wild ass	African	●				
Syrian wild ass	Eurasian	●	*ʾrd*	●	●	
Wild dromedary	Eurasian	●			●	
Wild sheep	Eurasian					

Note: Sources for rock inscriptions are from Robin (2018).

mostly that the artist had seen that animal elsewhere[29] rather than recording a species found locally because it is considered impossible for African and Levantine animals to have existed in deserted Arabia. By contrast, findings of lost species in the central and eastern Sahara are treated differently, interpreted as indicating that the Sahara once was habitable for that species (e.g., Drake and Blench 2017; Guagnin 2014; see also Judd 2011 for Egypt's eastern desert). Likewise, rock engravings and paintings found in Namibia are interpreted as being from the immediate vicinity (Joubert 1971).

The Suez Canal has prevented the spread of large mammals into Arabia since its completion in 1869 (Al-Nafie 1989). Before the canal existed, North Africa east of the Nile and Arabia were sufficiently vegetated during wetter periods to allow animal dispersion. Indeed, the Nile would have provided a perfect corridor for species movements from central to North Africa (de Manuel et al. 2020; Drake and Blench 2017) and the Sinai coastal belt that runs along the Mediterranean would have acted as a longitudinal corridor from the Nile to Arabia (and vice versa according to Manlius 1998). Unlike the much drier rest of the Sinai Peninsula, this coastal belt comes under the maritime influence of the Mediterranean Sea with a relatively short dry season (attenuated) and annual rainfall ranging between 100 and 200 mm (Zahran and Willis 2009). Table 6 lists the mammals that managed to cross the Sinai, from Africa to Asia and vice versa during the Holocene or Pleistocene. The Sinai was therefore no obstacle to migration for some species.

However, while there is widespread acceptance that a considerable number of large mammals made it across the Sahara to North Africa, any African savannah animal found in Arabia is immediately interpreted as representing an animal that was imported or seen elsewhere. Also, the African lost species presented in this paper taken aside (Somali wild ass, greater kudu), evidence of other African mammals confirmed for the Arabian Holocene such as lesser kudu, hartebeest, hamadryas baboon, African giant buffalo and African wild ass makes it possible that other African savannah species could also have been part of the Holocene Arabian fauna.

Petroglyphs depicting animals that are not part of the current native fauna are sometimes interpreted as depicting imported species. Examples of species importation include apes and peacocks imported by King Solomon to Jerusalem at the beginning of the first millennium BC (Holy Bible, 2 Chronicles 9: 21), Julius Caesar's import of exotic animals from Africa in 46 BC to Italy (Petzold et al. 2020), the Roman prefect Plautianus' expedition to the east African coast to capture zebras in the 3rd century AD (Mallan 2019), and the king of India sending two giraffe and an elephant from Ethiopia to Gaza and then on to Constantinople in 496 AD (Kruk 2001; Plumb and Shaw 2018; Zohar 2008).

Such importations may have influenced the numerous Near Eastern mosaics from the Byzantine era churches, monasteries, synagogues and villas that depict exotic animals including zebra, rhino, elephant and giraffe (Masseti 2015; Zohar 2008), some

TABLE 6 | Large mammals that have managed to cross the Sinai during the Pleistocene and/or Holocene.

	From Africa to Asia	From Asia to Africa
Previous studies	Lion (de Manuel et al. 2020; Jhala et al. 2019) Spotted hyaeana (Hooijer 1961; Stewart 2019) Striped hyaena (Rohland et al. 2005) African giant buffalo (Drechsler 2007; Garcia et al. 1991; Kallweit 2001) African wild ass (Kimura et al. 2011) Hippopotamus (Delany 1989) Lesser kudu (Guagnin, Shipton, et al. 2018) Dorcas gazelle (IUCN 2017b) Hartebeest (Tsahar et al. 2009; Uerpmann 1987)	Asiatic cheetah (Charruau et al. 2011) Persian fallow deer (Yeakel et al. 2014) Wild boar (Albarella et al. 2009) Brown bear (Mallon et al. 2023; Manlius 1998)
Proposed from this study	Somali wild ass Greater kudu	

with such realism that they may have been directly observed by the artists (Zohar 2008). However, with the exception of elephant (see Appendix 1), we argue that these Mediterranean area imports are not applicable to petroglyphs in the AP. Such imports must have been rare because in the case of the Mount Nebo mosaic, the giraffe is shown incorrectly as a camel with leopard spots. This error traces back to Agatharchides (2nd century BC: Burstein 1989) and Pliny the Elder (64 AD) who called a giraffe 'camel-leopard' because it had a head and tail like a camel and spots like a leopard (Petzold et al. 2020). The artist who made the mosaic in Mount Nebo church (see Masseti 2015) clearly had never seen a giraffe, and based his animal on Pliny's description made hundreds of years previously by drawing an outline of a camel and adding leopard spots. Zohar (2008, 137) makes the same interpretation of the Beth Shean giraffe mosaic, stating that 'the craftsmen heard a description of the "leopard-camel" and decided to reproduce their own visual interpretation'. By contrast, the five petroglyphs we present from the AP, southern Jordan and the Sinai all correctly depict the giraffe's silhouette.

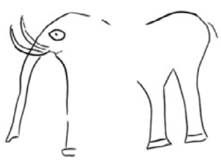
Also, the animals depicted in mosaics are imports to Rome, Constantinople or the Levant. Just because animals were imported to these areas by wealthy kingdoms cannot be extrapolated to say that animals found on rocks etched by Beduin in remote parts of the AP depict imported animals. As Garcia et al. (1991, 1202) state about Yemeni petroglyphs, 'We cannot imagine that the fauna drawn on the walls is not the same that was living around the prehistoric artists'. Support for Garcia's claim comes from Robin's (2018) investigations of the petroglyphs of Hima in SW Saudi Arabia. Robin notes that nearly all inscriptions associated with petroglyphs are in the local Hima'ite script (indicating local origin), rather than the South Arabian script (associated with foreign travellers).

Another argument that has been used against petroglyphs depicting local animals is that the climate became too dry to support them, so they could not have existed at the time they were engraved. However, taking an example from elephants, parietal evidence from across the Sahara during the Holocene indicates widespread presence albeit at low density, even within the last 4000 years (Judd 2011; Lafrenz 2004). In Egypt, the last records can be dated between 4580 and 4645 BP (Yeakel et al. 2014). Furthermore, within the Sahara, elephants were not only restricted to the mountainous areas but also the plains (Lafrenz 2004). The presence of elephants during the dry phase that postdates the African Humid Phase, does not indicate a lush climate but instead illustrates their high ecological tolerance (Gautier et al. 1994; cited in Lafrenz 2004). Even today, elephants in the Namib survive within an area of between 50 and 250 mm per year (Craig et al. 2021), exploiting wadi systems with more lush vegetation and travelling across sandy deserts to reach different systems. Kingdon (1997) states that they are so adaptable, they can survive in any habitat, save true deserts. Also, for reasons beyond the scope of this paper, it appears that southern Arabia (Yemen) at least was much more heavily vegetated than present even within the last 2000 years (Robin 2018). Accounts of hunting expeditions yield remarkable catches of animals from areas that today are totally desolate. Robin (2018) comments that the dessication that started around 4000 BC did not lead to a rapid disappearance of large animals. Instead, the savannah vegetation established during the humid phase disappeared very slowly with some areas still preserved until around 1000 years ago.

4.3 | Other Species That May Also Have Existed in the AP

While this study has expanded our knowledge of the large mammal fauna of the AP during the Holocene, it is likely that some species are still missing but for which no data has yet appeared, or for which speciation is ambiguous. Examples of species that potentially could have been present in the AP include those that had been able to cross the Sahara during a previous wetter period but so far not found in the AP. If the climate had been suitable enough for them to cross the Sahara, then it would have also been suitable for them to move across from North Africa to the AP via the Sinai. Table 7 shows these latter species plus their justification. Note that there are even species present in the AP (such as lesser kudu) for which there is no evidence of them having crossed the Sahara (Drake and Blench 2017), illustrating that the list of animals that potentially could have been found may be even greater than Table 7 suggests. Examples of such species include lesser kudu (Harrison and Bates 1991; Guagnin, Shipton, et al. 2018) and greater kudu (shown to be present from this study).

TABLE 7 | Large mammals from Africa that may have colonised the AP but conclusive evidence is lacking.

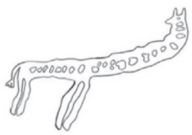
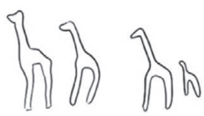
Species name	Justification
Elephantidae	
Elephant sp. Genus Elephas Linnaeus, 1758  Dedan, KSA, RCU   Madinah, Sultan Alsharif 	This study has uncovered no fewer than 11 petroglyphs across the AP, plus a further four that the finders claim to be elephant but too stylistic to confirm speciation (e.g., Anati 1972; Khan 1993). The distribution of these shows three distinct clusters: northern Oman, southwestern Saudi Arabia and northern Saudi Arabia. Explanations to this distribution pattern should note that engravings of elephants do not automatically mean they are native to the area of the engraving. This is because elephants have been imported to areas outside their natural range for military campaigns, as explained further in Appendix 1. As the Omani and southwestern Saudi engravings depict domesticated imported elephants they are not discussed further here. Instead, attention is given to two elephant petroglyphs for which there is no evidence of any association with elephantine military expeditions. Dayton (1968) was the first to publish rock art depicting an elephant in Arabia at Dedan, near Al Ula. The artwork, quality of the engraving and general setting is impressive, and there is no possible doubt about this being an elephant. Its position within the mountain helps to provide a *terminus post quem* date as it is found within a rock-cut niche that dates to the Lihyanite or Dedanite era that started around the 7th century BC (Al-Ansary 1999). The niche is approximately 30 m high, and the engraving is situated 10 m above the ground. Close to the engraving lies a text written in Dadanitic about a flute player, and another inscription on the edge of the niche is an epitaph, written in Dadanitic script but is a mixture of Arabic and Dadanitic text (M. Macdonald, pers. comm). The Dayton elephant is considered by Nayeem (2000) to date to the last quarter of the 6th century AD (as he associates it with Abraha the Ethiopian) while Dayton considers it to be much older, dating to the 13th century BC (Dayton 1968). Apart from Dayton's elephant, the only other unambiguous elephant drawing comes from the Madinah area, discovered in November 2021 by Mohammad Almugathawi[a] (see adjacent image). The whole body is represented, and there is both a trunk and tusk with the forked end of the trunk visible. The location near Madinah makes any association with Abraha the Ethiopian unlikely (see Appendix 1), but more evidence is required to confirm that elephants were native to the AP during the Holocene. Apart from the Holocene rock art mentioned above, most recent elephantid remains found in the AP date to the Pleistocene where fossils have been found overlaying sediment dated to 117 ± 8 ka and 99 ± 7 ka (Stewart et al. 2020). These are only identified to genus level as Elephantidae Gray 1821. No Proboscideans have been reported from any Late Pleistocene deposits of the eastern Saharo-Arabia region (Stewart 2019). Elephant were found all over Egypt until 4000 BC (Judd 2009) and there are 41 elephant petroglyphs in a small area of the eastern Egyptian desert (Judd 2011). Should elephants be native to Holocene Arabia, their speciation remains unclear. Dayton (1968) favoured the African elephant (*Loxodonta Africana* Anonymous, 1827) on the basis of the saddle-back and tip of the trunk. On the other hand, the long, upward curling tusks could point to the extinct Syrian elephant (*Elephas maximus asurus* Deraniyagala, 1950), a subspecies of Asian elephant (Dayton 1968). The discovery of bones at Qatna in Syria (along the Orontes river) are thought to be of this elephant that was indigenous to the area until its extinction during the iron Age (Pfälzner 2016). Remains of Syrian elephants have been recorded as far south as southern Lebanon (Çakırlar and Ikram 2016). However, the African elephant remains a plausible alternative. An extinct subspecies of this elephant, the north African elephant (*Loxodonta africana pharaohensis* Deraniyagala, 1948) was found along the African seabord of the Red Sea in classical times (Sinervä 2019), and was the species used by Hannibal in his campaign to conquer Rome. Osteological remains from the Holocene in the AP are needed to settle this speciation question.

(Continues)

Species name	Justification
Equidae	
Zebra sp.  Madinah, Dr. Abd Alrazzaq Alromaihy, with permission	A petroglyph of a striped animal has been found by Dr. Abd Alrazzaq Alromaihy 50 km south west of Madinah (see adjacent image). It is clearly not a hyaena, that has a totally different body shape, which leaves zebra as a possible alternative, though the head shape is too small. The petroglyph may be recent as suggested by the coloration of the engraving, and therefore may not be indicative of zebra being local to the area. More data will need to be found to confirm this species as being native, as no osteological remains of zebra have ever been found in the AP. If it is a local zebra, it could be one of several species. Zebra (*Equus quagga*) crossed the Sahara during the HHP (Drake and Blench 2017) and two zebra species, *Equus quagga* and *Equus grevyi*, were last recorded in Egypt before 11,700 BP (Yeakel et al. 2014).
Suidae	
Sus scrofa (Linnaeus, 1758) or *Phacochoerus aethiopicus* (Pallas, 1766)    	Wild boar used to occur in the Nile delta (Manlius and Gautier 1999), as well as coastal Libya and the mountain regions of Algeria, Tunisia and Morocco. The authors suggest a near eastern origin of this animal in North Africa. This is confirmed by Albarella et al. (2009) who tested mandible, teeth and post-cranial bones of wild boar around the world from museum collections and recently caught specimens to understand geographical variations in size. On the basis of this, he notes that the one specimen from Egypt that dates to the Napoleonic Wars is closer in size and proximity to the Near Eastern wild boar (*S. s. lybicus* Gray, 1868) than to its northwest African counterpart. Wild boar still occur in north Jordan (Christopher Clarke, pers. obs.) and south of the Dead Sea in Israel (Anati 1974, 242). While they disappeared from the Nile valley c. 1900 (Albarella et al. 2009), there is still a chance they may be found there (Yeakel et al. 2014). We consider that if they had been able to cross the Sinai from the Levant to the Nile, they would surely also have been able to colonise the AP. Anati (1974, 240) lists 6 Suid engravings found in Wadi Dahthami in SW Saudi Arabia (top two images shown adjacent). They are illustrated as tracings in Anati (1972, 61, 67), as a photograph (rock B15) in Anati (1972), and as a tracing in Anati (1974, 70). Tchernov (in Anati 1974, 214) speciated to these petroglyphs to wild boar (*Sus scrofa* Linnaeus, 1758). A large petroglyph showing a multitude of animals at Al Musaiqrah near Riyadh includes an image of a Suid (Nayeem 2000, 221), though the author does not mention this animal (see adjacent image, 3rd down) The upturned tail is more characteristic of warthog (*Phacochoerus sp.* F. Cuvier, 1826) than wild boar though both animals raise their tails when running (Manlius 2005). An engraving of an animal from Al Hail could be a Suid[b] though it could also be a dog (lowest adjacent picture). The quality of the drawing is very high, and the artist has pecked away the centre of the animal but left small ovals possibly to indicate the ear and tusks. On the same panel there is a cow, and it is possible the boar was inscribed on top as its feet encroach on the cow's horns. Other cow engravings are found nearby. It is not possible to be certain if the images are warthog or wild boar, though J. Kingdon (*pers. comm.*) favours warthog. In Africa, there are two species of warthog: the desert warthog (*Phacochoerus aethiopicus* subsp. *delamerei* Lönnberg, 1909) and the common warthog (*Phacochoerus africanus* Gmelin, 1788). Of these, desert warthog is more specialised for extremely arid environments than the common warthog (D'Huart and Grubb 2001), but the common warthog is more widely distributed and currently extends further north along the Red Sea (de Jong et al. 2023). Desert warthog remains from between 10,000 and 6000 cal BP have been found at Dakhleh Oasis, SW Egypt, west of the Nile (di Lernia 2021). Also, a warthog tooth dating to the Holocene has been found west of the Nile at El Nabta, Egypt, dating to between 7000 and 3500 BC (Manlius 2005). A *Phacochoerus sp.* has been found in the Levant from the late Pleistocene (Stewart 2019). A petroglyph found at Dakhleh Oasis depicts a member of the Suidae, that could be either warthog or wild boar (Manlius 2005). While a Suid once did roam the Holocene AP, it is still not clear whether it was a warthog, wild boar or even both species coexisting.

(Continues)

TABLE 7 | (Continued)

Species name	Justification
Giraffidae	
Giraffa camelopardalis Linnaeus, 1758  G1  G2  G3  G4  G5  G6  G7	Doughty (1888a, 1888b, 116) was the first to report giraffe (*Giraffa camelopardalis* Linnaeus, 1758) petroglyphs in the AP. Local people told him they were found at a place called the Khusshm es Sefsafa near Khaybar in Saudi Arabia though Doughty himself never saw them. The first published petroglyph of a giraffe appeared over a 100 years later from Jebel Magraisha on the Jordanian side of the northern Nafud, dated to after the 2nd century AD (Borzatti von Löwestern and Masseti 1991; Masseti 2015, G1: adjacent top figure). It has not been possible to locate any of the places mentioned above. Within the AP, Khan (2007) was the first to report an engraving as being a giraffe from an area east of Tayma and west of Hail in Saudi Arabia, and on first glance, the engraving may look like a goat with an exaggerated neck (G2: adjacent figure). The neck appears short for a giraffe but this is because of the angle of photography, for the same petroglyph taken head on shows the true proportions and here the neck is longer[c], the withers are well defined and the head shape is correct for giraffe. Khan (2007) considers it to be very early, from 11,000 years BP. Further examples of giraffe engravings come from unpublished websites such as Twitter or X. One of these[d] (G3) illustrates the spots on the neck and body of the giraffe plus the bony knobs (ossicones) on the top of the head and cannot be mistaken from any other species. The author gives the location as Tayma in Saudi Arabia. Engraving G4 depicts a herd with young numbering four individuals, located in Tabuk region. The extensive desert varnish suggests an early date. None of the giraffe petroglyphs mentioned above have been seen by us, and they do not appear in any other publications, apart from G2 that appears both within Majeed Khan's book and in a posting on X. For these reasons, we assume they must be found in very remote or inaccessible locations. Apart from the petroglyphs mentioned in this paper, evidence for giraffe in Asia come from bones dating much earlier than the Holocene, and only two locations to date have yielded these. Bones of *Giraffa cf. camelopardalis* have been found in Bethlehem, Palestine (Rabinovich and Lister 2014), in a layer considered to be from at least 3 Mya (3 million years BP: Rabinovich and Lister 2017). Also, a fragment of an ossicone (giraffe horn) from *Giraffa camelopardalis* from Latamne in the Orontes river in Syria has been found (Guérin et al. 1993) dating to around 500,000 years ago. This raises the question as to the inspiration for the giraffe petroglyphs in Arabia. There are two theories: First, they are depictions of local animals, and second, they are of animals seen elsewhere. It is interesting to note that all four giraffe engravings in Arabia are found only in the northwest (Tabuk and Tayma regions or extreme south of Jordan). A giraffe engraving has been found in southern Sinai, at Jabal Sarabit (see adjacent figure G5)[e], and there are no fewer than 59 giraffe petroglyphs in Egypt's eastern desert (Judd 2011; see adjacent figure G6 & G7). Osborn (1998) states that the distribution of giraffe petroglyphs in Egypt indicate giraffe inhabited the whole country south of Memphis (near Cairo). It is thought they were extirpated around 3000 BC as increased aridity caused them to damage crops. The above details would support the theory that giraffe colonised the AP via the Sinai, and would have spread during historical wet periods such as during the HHP. Kingdon (1997) reports that giraffe have a catchment area of 80 km^2, and can cover up to 600 km^2 in a year. The scarcity of giraffe petroglyphs in Arabia compared to eastern Egypt would suggest that few made it all the way there, or they were extirpated long before the populations in Egypt's eastern desert disappeared. The most likely subspecies to have made the journey through to Arabia would have been *Giraffa c. camelopardalis*, based on its historic distribution. *G. camelopardalis* is currently found in South Sudan (Petzold et al. 2020). In the 1700s, giraffe were found in Sudan as far north as the Egyptian border (GCF 2019). The last record from within Egypt was between 4810 and 5050 years BP (Yeakel et al. 2014). Giraffe remains from the Late Pleistocene or early Holocene have been recorded from SW Egypt (di Lernia 2021). Giraffe still occur in very dry areas of Africa, such as the Skeleton Coast National Park in Namibia, where rainfall does not exceed 100 mm per year (Stander 2019). The other theory is that giraffe petroglyphs in Arabia, southern Jordan and the Sinai depict animals seen elsewhere. Support for this theory comes from the rarity of the petroglyphs in the AP. Given that there are 59 petroglyphs of giraffe in Egypt's eastern desert (Judd 2011), the five examples from the AP, Jordan and Sinai do not provide sufficient evidence for their existence in the Holocene AP.

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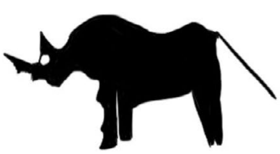
Species name	Justification
Hyaenidae	
Spotted hyaena (*Crocuta crocuta*)	Spotted hyaena crossed the Sahara during the HHP (Drake and Blench 2017), with the last record from Egypt between 11,700 and 5950 years BP (Yeakel et al. 2014). Osteological remains of this species from Ksar Akil (Lebanon) date to the Pleistocene (Hooijer 1961). Also, Late Pleistocene remains have been found in Kebara and Dederiyeh Cave, both in the Levant (Stewart 2019).
Rhinocerotidae	
Rhinoceros (*Diceros bicornis* Linnaeus, 1758 or *Ceratotherium simum* Burchell, 1817)  Alam Massif, KSA Anati 1974:142 & 144  Jabal Yatib, KSA, Christopher Clarke   Madinah, KSA, Sultan Alsharif 	The Philby-Ryckmans-Lippens expedition archives (1951/1952) describe a rock engraving from the Suleimat mountains of KSA that they call a 'type rhinoceros'[f], but we believe is most likely to be a caprine. Nevertheless, the characteristic head of a rhino from the Alam Massif (south-east of Qahra[g] KSA) was described by Anati (1972, 235) using Philby's 1951/52 expedition photographic collection (see adjacent image), and although no photograph of the image is given, there is a tracing (Anati 1974, 142, 144). The head lacks horns and most of the body is missing. E. Tchernov (in Anati 1974) dates it to 10,000 years BP. Another possible rhino engraving was found in Jabal Yatib, near Hail, discovered by Christopher Clarke (see adjacent image). The heavy body with thick legs, rounded ears and long front horn do not fit any other species. Like the ibex engraving above it, there is a front and back leg and an oversized tail, as thick as a leg. It would be reasonable to conclude that both animals were drawn by the same artist. The raised ears of the 'rhino' are odd and are reminiscent of some of the elephant petroglyphs in the eastern Egyptian desert that also have large raised ears (Judd 2011). Judd notices that elephant petroglyphs are less realistic than giraffe petroglyphs at this location despite both animals being represented by a similar number of images (around 50). His interpretation is that those who drew elephants did not draw them as they were seeing them, but either from memory or from descriptions from travellers. We consider the latter option highly unlikely, but the former is plausible. Applying this interpretation to the engraving in Hail would suggest that rhinos could have been rare and the artist is drawing one seen in the past. An additional potential rhino petroglyph from the Madinah area discovered by Mr. Muhammad Almugathwi (lowest two adjacent images) resembles a rhino, with both horns shown plus the high withers. None of the petroglyphs mentioned here are of sufficient quality and convincing to confirm the presence of rhino in the AP during the Holocene If these are rhino engravings, it would be surprising, given the total absence of osteological remains of rhino within the AP. In Africa during the HHP, they were able to spread into Egypt (Delany 1989), but it is notable that no rhino petroglyphs have been found in the eastern desert of Egypt (Judd 2011), yet there are 59 giraffe and 41 elephant images. In Egypt, the last records of rhino date to between 5350 and 5050 BP (Yeakel et al. 2014).

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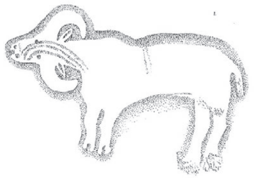
Species name	Justification
Bovidae	
African buffalo (*Syncerus caffer* Sparrman, 1779) 	No bones have been found of this buffalo within the AP, but 6th millennium BC rock art found in Yemen's Sa'ada highlands have been interpreted as being of this species (Rachad 2007a, 2007b; cited in McCorriston and Martin 2009, see adjacent image). The authors narrow down speciation to either the African buffalo (*Syncerus caffer* Sparrman, 1779) or the African giant buffalo (*Syncerus antiquus*), noting that no bone fragments of the former have been found, whereas the latter is supported by archaeological remains. A rock engraving from the same area is shown in Garcia et al. (1991) and Nayeem (2000, 465 & back cover), presumably the same referred to by McCorriston and Martin (2009). Nayeem (2000) adds that it was found in Shob Homeid in Wadi Hazira but speciates to cow. The characteristic wide handlebar horns of the African giant buffalo do not fit the petroglyph, though Garcia et al. (1991) consider this the most likely species when comparing African giant buffalo against Asian water buffalo. Alternatively, the image could just be of a sheep, and the one petroglyph is too ambiguous to confirm the presence of this species in the AP. The African buffalo used to reach the Red Sea coast of Sudan (Smitz et al. 2013). Moreover, remains of this buffalo dating to the early Holocene are attested at Dakhla, quite far north in Egypt's Western Desert (di Lernia 2021; Jousse 2017; Yeakel et al. 2014) as well as Toukh, north of Cairo and east of the Nile (di Lernia 2021).
Hartebeest (*Alcelaphus buselaphus* Pallas, 1776)   Madinah, Sultan Alsharif   Madinah, Sultan Alsharif  Badia Bani Amr[h]	The hartebeest used to be found in the open country of the southernmost regions of the southern Levant (Tsahar et al. 2009; Uerpmann 1987), and actually became more abundant here during the Late Pleistocene compared to the Middle Pleistocene (Stewart 2019). This was considered the northern limit of its range; it also being found in Egypt, at several locations east of the Nile (di Lernia 2021). This would mean that it would have also occurred in Sinai in order to have spread to the southern Levant. It was extirpated from Egypt between 100 and 1555 years BP (Yeakel et al. 2014) though it was extirpated much earlier in Israel, between 1200 and 586 BC during the local Iron Age (Tsahar et al. 2009). Martin et al. (2009) thought the presence of the grassland-dwelling hartebeest in the AP was not certain but cannot be dismissed, citing a similar comment made by Uerpmann (1987, 83). Two possible hartebeest petroglyphs have been found near Madinah by Sultan Alsharif. The characteristic back pointing horn in profile view and the lyre shape in frontal view are characteristic of hartebeest. A further possible hartebeest petroglyph has been found in Badia Bani Amr, Namas Govenorate, KSA[i], though the finder did not speciate it. These images are not convincing enough to confirm speciation as they could be badly drawn goats or even cows. Archaeological or DNA evidence will be required to confirm the presence of this species A tooth fragment found in the Empty Quarter dating from the Late Pleistocene (26,660–21,090 years BP) may be of this species (Edgell 2006; McClure 1984; Stewart et al. 2019).
Wildebeest (*Connochaetes gnou*, Zimmerman, 1780) or (*Connochaetes taurinus* Burchell, 1823)  Dahthami wells, KSA Anati (1972:55)	A tracing of an engraving of what Anati (1972, 55) calls 'Khaniq style' oxen on Rock B13 in Dahthami wells, KSA, looks more like wildebeest than oxen. The two animals clearly have a mane, and the shape of head and horns fits that of wildebeest. Drake and Blench (2017) show that both black wildebeest (*Connochaetes gnou*, Zimmerman, 1780), and blue wildebeest (*Connochaetes taurinus* Burchell, 1823) crossed the Sahara into North Africa during the green Sahara period. The last record of *C. taurinus* in Egypt dates to between 5950 and 11,700 years BP (Yeakel et al. 2014). As there are no records for black wildebeest from Egypt, from where wildebeest would have spread into Arabia, the most likely wildebeest species found in Arabia would be the blue wildebeest. The petroglyph at Dahthami Wells is the only potential rock art of this species in the AP

(Continues)

TABLE 7 | (Continued)

Species name	Justification
Nile lechwe (*Kobus megaceros*, Fitzinger, 1855)	The last record from Egypt dates from between 5350 and 5050 BP (Yeakel et al. 2014).
Clarke's gazelle (*Ammodorcas clarkei* Thomas, 1891)	The last record from Egypt dates from between 5350 and 5050 BP (Yeakel et al. 2014).
Rhim gazelle (*Gazella leptoceros* F.Cuvier, 1842)	Still occurs in north western Egypt (El Alqamy and El Din 2006) and formerly to the Nile (Huffman and Leslie Jr 2023).
Dorcas gazelle (*Gazella dorcas* Linnaeus, 1758)	This gazelle is mainly African species formerly found in the Sinai, but still occurs in Israel, Palestine and Jordan (IUCN 2017b; Mallon et al. 2023). Harrison and Bates (1991) show dorcas gazelles extend from Iran to East Africa, but these have since been split into dorcas gazelles for Africa, the Sinai and Jordan, and Saudi gazelles for western Saudi Arabia and Yemen. The Iraqi and Iranian records must refer to *Gazella subgutturosa* (Güldenstaedt, 1780) or *Gazella marica* (Thomas, 1897).
Soemmerring's gazelle (*Nanger soemmerringii* Cretzschmar, 1828)	Soemmerring's gazelle was extirpated from Egypt between 4295 and 4140 BP (Yeakel et al. 2014).
Barbary sheep (*Ammotragus lervia* Pallas, 1777)	During the Neolithic period, this wild sheep's range extended across the whole Sahara to Asia, from Suez to the Dead Sea (Manlius et al. 2003). At the beginning of the 19th century found in the whole of Egypt except the Sinai but the range has now contracted to the south eastern and south western extremities of the country.
Scimitar-horned oryx (*Oryx dammah* Cretzschmar, 1827)	Pleistocene or Early Holocene remains from SW Egypt (di Lernia 2021). The last record from Egypt is between 100 and 1550 BP (Yeakel et al. 2014).
Gemsbok (*Oryx beisa* Rüppell, 1835)	Last record from Egypt between 3735 and 3520 BP.
Roan antelope (*Hippotragus equinus* Desmarest, 1804)	Late Pleistocene to early Holocene remains have been found at Qantir, Egypt, close to the Sinai (di Lernia 2021). The last record from Egypt is between 4084 and 3735 BP (Yeakel et al. 2014).
Addax antelope (*Addax nasomaculatus* Blainville, 1816)	Texts written in the ancient South Arabian script refer to an animal called *ḥwry*, which Maraqten (2015) states is to be identified with the Addax, though no reasons are given for this interpretation. In the same article, the word *ryym* has also been taken to mean Addax, though it sounds like the Arabic *rym*, which means gazelle. Addax used to live across the entire Sahara up to the Egyptian Nile (Hempel et al. 2021). Remains from the Late Pleistocene or early Holocene have been recorded from SW Egypt (di Lernia 2021) and the last record for Egypt is between 0 (i.e., the 1950s) and 1550 BP (Yeakel et al. 2014), while Manlius (2000) brings the extinction date to the 1960s. With similar habitats, the possibility of it having occurred in the AP cannot be ruled out (Martin et al. 2009; McCorriston and Martin 2009).
Bohor reedbuck (*Redunca redunca* Pallas, 1767)	Remains from the Late Pleistocene or early Holocene have been recorded from SW Egypt (di Lernia 2021).
Kob (*Kobus kob* Erxleben, 1777)	The last record from Egypt is between 5350 and 5050 BP (Yeakel et al. 2014).
Sitatunga (*Tragelaphus spekeii* Speke, 1863)	Last record in Egypt between 5950 and 11,700 BP (Yeakel et al. 2014).
Eland (*Taurotragus oryx*Pallas, 1766)	Crossed Sahara during the HHP (Drake and Blench 2017). Last record in Egypt was between 5050 to 4810 BP (Yeakel et al. 2014).

[a]https://twitter.com/mohammed93athar/status/1458537798231896064.
[b]https://twitter.com/Meshari_0000/status/1531316748322062336/photo/4.
[c]https://twitter.com/hzemhzem10/status/1731636292201382055.
[d]https://twitter.com/Asd92074605/status/1456945416671531011.
[e]https://Www.Flickr.Com/Photos/Mumbleshead/6780462180.
[f]archives.uclouvain.be/ark:/33176/dli000000hHjC.
[g]Probably the same as Jabal al-Qara in the map of Arbach (2019).
[h]https://twitter.com/thoomaly11/status/1668700404241035265/photo/3.
[i]https://twitter.com/thoomaly11/status/1668700404241035265/photo/3.

Table 8 presents another smaller list of Palaearctic animals that could have colonised the AP during the HHP, based on their current occurrence in the Levant, or extirpation in the Levant during the modern era, Holocene or Late Pleistocene. Examples include Persian fallow deer (Anati 1974), brown bear (Manlius 1998) and wild sheep.

TABLE 8 | Large mammals from Eurasia that may have colonised the AP during the Holocene but for which evidence is lacking.

Species name	Justification
Cervidae	
Persian fallow deer (*Dama mesopotamica* Brooke, 1875)  Jabal Kaukab, Khan (2007: 217)   Wadi Dahthami, Anati (1972: 81; 1974:217).	Khan (2007, 217) shows an image of an ostrich and what he calls a goat at Jabal Al Kaukab, KSA. The body shape does not match that of a goat, and the size relative to the adjacent ostrich is more akin to that of a deer than a goat, though engravings are not always drawn to scale. More importantly, there are antlers with the characteristic branches unlike the unbranched horns of antelope, caprines and gazelle. Also, an engraving of an animal with antlers was found in Wadi Dahthami[a] on rock B19 and illustrated with both photograph and tracing by Anati (1972, 81). Tchernov (in Anati 1974, 217) interprets this as the Persian fallow deer, no doubt due to the antlers. A photograph of another engraving of the same species is given in Anati (1974, 52) with a tracing in Anati (1974, 53). Again, the antlers are diagnostic. Luciani (2023) describes deer as being part of the decorated motifs of Qurrayah Painted Ware that were produced at Qurayyah in NW Saudi Arabia between the 12th and 14th century BC but does not publish any images of them. The quality of the images mentioned here are insufficient to provide conclusive evidence that fallow deer once occurred in the AP. Persian fallow deer are found in19th and 20th century records from north Jordan and Palestine (Harrison and Bates 1991) and Upper Galilee, Israel (Anati 1974, 239), but there are no literary records within the AP. In Egypt, their last record dates to between 3520 and 3270 years BP (Yeakel et al. 2014), overlapping the period of the Qurayyah pottery mentioned above. The presence of this deer in Egypt would suggest a continuous distribution up to Jordan. A *Dama* species, presumably *D. mesopotamica*, has been recorded in the Negev of southern Israel dated to the Late Natufian (Horwitz and Goring-Morris 2000). By 1950, the deer had become extinct in Israel but were reintroduced from a core of individuals taken from Iran and bred in Europe (Zidon et al. 2017).
European roe deer (*Capreolus capreolus* Grey, 1821)	Roe deer are found in 19th century records from Palestine (Harrison and Bates 1991). The last roe deer was shot on Mt. Carmel, Israel in 1910 (Anati 1974, 239).
Red deer (*Cervus elaphus* Linnaeus, 1758)	Bones of red deer in southern Israel were recorded until the Bronze Age (Tsahar et al. 2009).
Equidae	
European wild ass (*Equus hydruntinus* Regalia, 1897)	The European wild ass inhabited Europe and the Middle East for more than 30,000 years and is found in the Upper Pleistocene in Libya and in Israel and Jordan (Orlando et al. 2006).
Wild horse (*Equus ferus* Boddaert, 1785)	Surviving populations of wild horse were found in the Levant during the mid Holocene (Shev 2016), though the argument for it not originating in Arabia is presented by Schiettecatte and Zouache (2017).

(Continues)

TABLE 8 | (Continued)

Species name	Justification
Ursidae	
Brown Bear (*Ursus arctos* Linnaeus, 1758)	Brown bears are currently found in Syria, yet recorded west of the Sea of Galilee, Israel, in the 19th century (Harrison and Bates 1991). Mallon et al. (2023) show that the bears' original distribution included the Levant and Sinai. In the Sinai, they may have existed until the 1500s in the high mountains (Manlius 1998). The historian Herodotus (484-c. 425 BC) states that Egyptians used to bury bears where they found their corpses. Manlius (1998) explains that this would be of bears that had wandered from the forested Sinai mountains down to the lowlands and died of starvation or thirst. His theoretical map of brown bear distribution extends beyond the Isthmus of Suez almost to the Nile and also extends into NW Saudi Arabia (NEOM region). According to him, there is nothing to prevent populations of bears spreading from Palestine (recorded in Biblical accounts such as two Kings) to Sinai in historic times. Bears are mentioned in the list of animals found by Anati who reported on the rock engravings found by the Philby-Ryckmanns expedition (Anati 1972, 26) but not described in later sections of the volume.
Felidae	
Lynx (*Lynx lynx* Kerr, 1792)	An unconfirmed record of lynx from Palestine in the 19th century (Harrison and Bates 1991)

[a]Identified in Google Earth as Dalhami, but local people call them Dhathami.

TABLE 9 | Summary of lost species finds.

First for Arabia	Range extension	No added information
Greater kudu Somali wild ass	African wild ass Arabian oryx Aurochs Bezoar/Wild goat Cheetah Lion Lesser kudu Syrian wild ass Wild dromedary Wild sheep	African giant buffalo Saudi gazelle Yemen gazelle

Regarding species which may have colonised the AP, it should be noted that while Indian water buffalo *Bubalus bubalis* subsp. *arnee* (Kerr, 1792) has been quoted as occurring there, the records are erroneous. This confusion may be due to species sharing the same generic name *Bubalus*. Holm (1960) refers to water buffalo being found in deposits underlying sand dunes in the SW Empty Quarter but does not provide the scientific name. *Bubalus bubalis* has the synonym *Bos bubalis* (Linnaeus, 1758). Garcia et al. (1991) record water buffalo being found at Jabal Makhroug 2 (MK2: Saada, Yemen) and and Wadi Robia 3 (Saada), but say it might be the African giant buffalo *Pelorovis antiquus*. They refer to a study by Djillali Hadjouis of 55 bone fragments found at MK2 that include aurochs (*Bos primigenius*), *Pelerovis antiquus* or *Bubalus arnee*. Kallweit (2001) describes rock engravings in Yemen as being of water buffalo and gives the genus name *Bubalus*. In the same article, he also refers to *Bubalus antiquus, Bos primigenius and Bos taurus*. While this species is now found on all five continents, its domestication has been traced to the western region of the Indian subcontinent (ca. 6300 BP), reaching Mesopotamia by 2500 BC (McIntosh 2007) and arriving in Egypt by the early Middle Ages (Zhang et al. 2020). This rules out its presence in Yemen thousands of years before reaching the Near East.

4.4 | Diversity, Distribution and Origin of Large Mammal Fauna

The rock engravings illustrate not only a wider species diversity but also a wider distribution of animals within the Holocene AP than previously thought (Table 9); the best examples being that of Arabian oryx, aurochs, bezoar/wild goat, cheetah, lesser kudu, lion, Syrian wild ass and wild dromedary. Also, the distributions are still far from complete, with large gaps. For some species such as the African giant buffalo, it is not known if their Holocene distribution was widespread or limited to certain refugia, such as the montane areas of Yemen.

The lost large mammals of the AP are more closely related to the African fauna than the Eurasian. For example, eight out of 15 species are African in origin while four are Eurasian, and three species are endemic (Table 5). This aligns with the evidence from earlier humid phases during the Middle and Late Pleistocene, where mammals had a stronger African than

Levantine affinity (Groucutt et al. 2021). Yet it contradicts other works that claim the zoogeographic separation of North Africa and the Levant from sub Saharan Africa goes back to the Early to Middle Pleistocene (O'Regan et al. 2005).

The pattern of dispersal of humans during the Early to Middle Pleistocene was one of cycles of colonisation during wet climatic phases and regression or extirpation during dry phases (Stewart et al. 2020). This would also hold true for some large mammal species such as hippotami that would not have been able to survive during dry phases. On the other hand, other species may have been able to persist through the dry phases, or retreat to localised highland refugia such as SW Saudi Arabia, Yemen, Dhofar and Jabal Al Akhdar in Oman and other isolated upland areas (Stewart et al. 2019). A similar pattern would be expected for the Holocene, with some animals colonising during the HHP from Africa or Eurasia, or from localised refugia within the AP.

4.5 | Implications for Re-Wilding

The findings made as part of this paper have important implications for re-wilding of the AP. The first point is to underline the importance of going back beyond the modern era to the middle Holocene (5000 BP) as the target fauna to re-establish. The argument for this holds as true for the AP as it does for Europe: That this should be the conservation benchmark because this is the time when human-induced extinctions started and also the last point of natural colonisation of large mammals.

The second point is that the diversity of species that occurred during the HHP is greater than previously thought to be actually found to be existing in the AP during the Holocene. As these species coexisted with humans, the possibility of their extinction occurring due to human-induced habitat loss or overhunting rather than exclusively to climate change cannot be ruled out.

Support for the idea that anthropogenic factors caused extinction will depend on dating of rock engravings. It would be natural to assume that most of the large mammals mentioned in this paper became extinct at the end of the HHP (around 6000 years BP), when the climate became significantly drier. These animals would not be good candidates for re-wilding purposes as the land cannot naturally support them. To test this theory requires accurate dating of petroglyphs which has so far been problematic (Olsen 2013). Petroglyphs are not permanent and can disappear within as little as 5000 years but can last up to 10,000 years (Bednarik and Khan 2017)[30]. Before they disappear due to weathering, engravings are covered in a layer of desert varnish that becomes thick enough to hide any colour contrast between the engraving itself and the surrounding rock. The lack of colour differentiation and the reduced profile then makes them difficult to detect. Andreae et al. (2020) estimate that the varnish on rock becomes indistinguishable from its surroundings between 7000 and 8000 years BP. Bednarik (2017) analysed a number of rock art sites in Saudi Arabia using a variety of advanced dating methods. Of 13 petroglyphs assessed, only anthropomorphs and cupules dated from the HHP[31], while all other rock art was more recent. Notable in his assessments is a caprine from Jabal Raat, that has a thick desert varnish indistinguishable from surrounding rock, yet dated between 6000 and 5300 years BP. Also, a bovid from Fardat Shamous South site has attained a full desert varnish and is dated to a similar period of 5650–5010 years BP. These two examples show that a full desert varnish can even develop for engravings that postdate the HHP. The implication from this is that where a petroglyph does have a colour contrast, it is likely to be younger than the HHP, especially for a vivid contrast. In such cases, if the petroglyph is of a lost species, it more likely would have become extinct/extirpated through anthropogenic rather than climatic factors.

In a dating study of 110 petroglyphs in the Hima region of Saudi Arabia, that included animals, inscriptions and human figures, by far the majority were found to date to well after the onset of the dry climate (Macholdt et al. 2019). Only female anthropomorphs with skirts could possibly have extended back to the HHP, but most likely (based on manganese concentration of desert varnish) were more recent. Oxen were included among the animals assessed, that normally are thought to date to the HHP only, yet for which scientific analysis showed they existed much more recently than previously thought (Macholdt et al. 2019; Robin 2018).

With the strong recent political support for hunting control and habitat restoration, the argument for bringing back lost species is greater than ever. Even back in 2011, Price (2011) considered the timing to be right. Support for re-wilding lost species comes from the awareness that an ecosystem cannot be properly restored unless the original faunal component is also present, otherwise the plant communities will develop in a trajectory at variance from the original. The conservation value of lost species was underlined by Boland and Burwell (2021) who compared a few of the lost species with the existing terrestrial fauna and ranked them according to conservation priority in Saudi Arabia in the hypothetical situation that they would be reintroduced. The lost species ranked as follows: Saudi gazelle 3rd; cheetah 18th; lion 20th; and Asiatic wild ass 25th. This ranking did not take into account flagship or economic value that would raise the ranking of lost species, some of which would be able to increase the revenue of reserves in the same way they do in Africa (Child 2000). Sadly, the gazelle and wild ass are extinct, but lion and cheetah can still be brought back. On the other hand, Boland and Burwell (2021) emphasise the risk of diverting conservation resources from protecting existing threatened species to bringing back lost species.

Therefore, bringing back each lost species needs evaluation on a case by case basis taking account of cost, conservation benefit, range, risk to humans, cause of extinction, availability of donor species, availability of large fenced sites with suitable habitat, potential economic returns, and national and international conservation priorities. Ideally, climatic suitability modelling for range should also be done using the method employed by Cooper et al. (2021) for lions in the AP. We believe that the establishment of new populations of lost species in the AP can have international conservation benefit, so long as the animals are sourced correctly from areas where local populations are thriving. Also, the reintroduction of carnivores will require a prior reintroduction and build-up of suitable prey populations, such as gazelles.

When considering climatic suitability, caution is advised regarding interpretation of current species distributions as a determiner of a species' suitable climate range. Certain large mammals have retreated away from drier areas during the modern era (compare current distribution of giraffe in South Sudan (Petzold et al. 2020) to 1700s distribution at the Sudan/Egypt border [GCF 2019]), not because they cannot survive in dry climates, but because they are more vulnerable to predation, hunting, or persecution. Also, dry areas have been more prone to vegetation clearance which further increases species' vulnerability. Faurby and Araújo (2018) emphasise that many species have been extirpated from areas of suitable climate, which causes models to negatively bias suitable ranges.

The AP lies at the intersection of the Palearctic, Afrotropical and Indo-Malay faunas (Price 2011). The original fauna was a unique mix of elements from each of these realms and re-wilding efforts should aim to bring back as many lost species as practicable from each. The case for bringing back lost species is not only to increase diversity but also to increase the ecological resilience of restored lands. An example of this is how ingestion of seeds by some lost species improve germination. In a study from South Africa, acacia seeds infested by the bruchid beetle were more likely to regenerate if giraffe and kudu had eaten the seeds beforehand (Miller 1994). Large carnivores prevent over grazing, and while an alternative approach is removal of herbivores through culls or hunting, this can lead to a long-term reduction in soil nutrients (Abraham et al. 2021). The implication from these examples is that the lost animals of Arabia would not only benefit from the regreening of the AP but also actually assist and increase its chance of success by restoring ecosystem functions.

Author Contributions

Both authors carried out fieldwork to search for petroglyphs and critically commented on the results and their interpretation; Christopher Clarke led the writing of the manuscript and produced a first draft, which was further improved by Sultan Alsharif.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Endnotes

[1] https://www.greeninitiatives.gov.sa/.

[2] The original target was 0.40 million km^2 but this has since increased to 0.75 million km^2.

[3] https://www.bonnchallenge.org/.

[4] We follow Schnitzler (2011)'s time scale for the Early and Middle Holocene (9600–3500 calibrated BC), 3500 BC–AD 500 for the Late Holocene 1 and AD 500–1500 for Late Holocene 2. The Pleistocene predates the Holocene (Tsahar et al. 2009), and the modern era post dates it.

[5] The precise duration of the HHP varies and may not have been uniform across the AP. Delany (1989) places the HHP between 11,000 and 6000 BP. Guagnin et al. (2015) consider the start of the HHP in northern regions to be between 10,000 and 9000 BP while Guagnin, Shipton, et al. (2018) mention early phase of lake formation at Jubbah in northern KSA around 12,000 BP with humidity peaking between 9000 and 8000 BP and the dry period starting around 5900 BP. Drechsler (2007) considers the dry period to have started between 6500 and 6000 cal BC.

[6] https://www.bradshawfoundation.com/middle_east/saudi_arabia_rock_art/index.php.

[7] http://saudi-archaeology.com/overview/arabian-rock-art-heritage-project/.

[8] Available online at https://archives.uclouvain.be/items/browse?collection=63&page=2.

[9] To save confusion, all references to *Equus hemionus* or *Equus hemionus hemippus* are referred to in this section as *Equus hemippus*.

[10] This image is much clearer in http://saudi-archaeology.com/subjects/onager-or-african-wild-ass/attachment/wild-ass-at-shuwaymis-west_/ and here the vertical lines at the hind legs are visible.

[11] Or Wadi al-Thayyilah (Martin et al. 2009).

[12] For example, see Sa'ib. Musamma, scène de chasse et graffites dont copie GR », 13 janvier 1952, Archives de l'Université catholique de Louvain, BE A4006 FI 387-P-R4209. *Source:* UCL Archives | archives.uclouvain.be/ark:/33176/dli000000gpN8.

[13] https://destinationksa.com/qaryat-al-faw-arabias-forgotten-city/.

[14] https://spa.gov.sa/en/w2143092#.

[15] https://www.arabnews.com/node/2144896/saudi-arabia.

[16] The domesticated horse (*Equus ferus* subsp. *caballus*, also called *Equus caballus*) arose from the wild horse (*Equus ferus*). The latter existed in the Levant during the mid Holocene (Shev 2016).

[17] https://twitter.com/ProfAlghazzi/status/1712092326451974501.

[18] A better image can be found in https://twitter.com/mash10000/status/1064529484802596866/photo/1.

[19] https://twitter.com/Lazzam_mawan06/status/1362104679514189824.

[20] https://twitter.com/bm0167/status/1190913321316290560.

[21] https://twitter.com/Meshari_0000/status/1526601100916400130/photo/1.

[22] https://twitter.com/SAldhmshy50207/status/1746661405938298992/photo/2.

[23] http://saudi-archaeology.com/subjects/bezoar-wild-goat/.

[24] https://twitter.com/mashalgrad/status/1651314169784803329/photo/4.

[25] https://twitter.com/ghm1234f/status/1621973717378113538/photo/1.

[26] For example, analysis of extinct cave hyaena (*Crocuta crocuta* subsp. *spelaea* Goldfuss, 1823) droppings in Germany has revealed the presence of the woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1799) according to Seeber et al. (2023).

[27] See, for example, John Cary (1811) *A New Map of Arabia including Egypt, Abyssinia, the Red Sea &c, &c.*

[28] Ptolemy's *Arabia Deserta* was actually north of the line; the south was called *Arabia Felix* (Happy Arabia), but map makers often made Yemen *Arabia Felix*, with the northern part of the AP *Arabia Deserta*.

[29] Examples do exist of rock art depicting images seen elsewhere, such as the Egyptian Nile boat found near Tabuk, NW Saudi Arabia (Aksoy 2020) but Guagnin, Shipton, et al. (2018) and Judd (2011) consider most petroglyphs of animals to be restricted to sightings from a localised area.

[30] These dates should be interpreted with caution as there is a fundamental problem with trying to date rock art. This is because the rate of deposition of varnish is dependent on several factors: (i) The amount of exposure to wind, rain and other climatic conditions which the particular area of the rock bearing the carving receives after it is carved; (ii) the technique in which the petroglyph is carved: thus, for instance, on the same area of rock, thin incisions tend to patinate more quickly than hammered or scraped areas (M. Macdonald, pers. comm.). Olsen (2013, 37) considers the oldest petroglyphs to date to the HHP, also known as the Holocene Wet Phase.

[31] Compare with the chronology suggested by Guagnin et al. (2016) not based on rock specific dating methods.

[32] https://twitter.com/hilal_alqasmi/status/1557311607063060482.

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Appendix 1

Petroglyphs of Elephants Imported for Military Campaigns

The classic example of elephants used for military campaigns is of Hannibal's campaign against Rome in 218 BC, where 37 elephants from North Africa were driven through Spain and France and across the Alps to attack Rome from the north (Walbank 1979). The following year, in 217 BC, another battle occurred in Rafah, Gaza, in which two Greek kingdoms pitched African and Asian elephants against each other (Brandt et al. 2014). Besides these campaigns, there were a further 12 battles involving Rome and its enemies in which elephants were used (Sinervä 2019).

Other literary sources suggest that there were an additional two battles involving elephants in the AP not involving Rome. In Oman (that was known at the time as Mazoon), Persian occupiers fought against Malik bin Fahm Al Azdi using war elephants in the 2nd century AD (Ross 1984). All four elephant engravings found in Oman are located between the battle site of Salut and coastal areas opposite Persia[32]. Of these four engravings, the two images that are visible online both show domesticated elephants. One of these shows a litter on the elephant (Nayeem 2000); the other a rider on the animal. The connection between the Omani engravings and the Persian campaign cannot therefore be discounted (Gracey 2017), and for this reason, the Omani engravings do not provide evidence for native populations of elephants occurring there during the Holocene.

Literary sources dating to the 8th century AD speak of a campaign by the Ethiopian King Abraha to attack the tribes of Saudi Arabia during the 6th century using war elephants (Robin et al. 2014). The invasion would have come from Yemen, where Abraha was based. Five elephant engravings from SW Saudi Arabia bear a rider, a further one has a saddle and only one has no indications of being domesticated, but found in the same location as a petroglyph with a rider. All are located along the route of the ancient frankincense road as described by de Maigret (1997). This therefore discounts the possibility of these engravings being of wild elephants.