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# Using palaeogenetics to unravel the impact of humans on animal populations in the past

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## Abstract

Palaeogenetics has the potential to reconstruct past genetic diversity of species and/or populations and to reveal evolutionary processes that would otherwise remain hidden when relying only on modern genetic data. After a general presentation of the limits and potentials of palaeogenetics, we summarize a series of studies from our lab that allow us to compare the evolution of genetic diversity of various animal species since the end of the Pleistocene, that have had different relationships with humans with respect to their domestication or avoidance therefrom. We show that, even though domestication initially involved only a subset of a larger wild population, regular gene flow from wild to domestic animals allowed the latter to retain a higher genetic diversity than related wild populations many of which experienced a severe, human-driven population reduction during the Holocene.

## Zusammenfassung

Mithilfe der Paläogenetik können potentiell sowohl die einstige genetische Vielfalt von Arten und/oder Populationen als auch evolutionäre Prozesse aufgedeckt werden, die andernfalls verborgen blieben, verließ man sich nur auf moderne genetische Daten. Nach einer generellen Darstellung von Grenzen und Potential der Paläogenetik präsentieren wir eine Reihe von Studien aus unserem Labor, die es erlauben, die Entwicklung der genetischen Vielfalt von diversen Tierarten seit dem Ende des Pleistozäns vergleichend zu betrachten - Spezies, die jeweils unterschiedliche Bindungen zum Menschen besaßen, entweder im Zuge der Domestikation oder durch die Vermeidung derselben. Wir zeigen auf, dass obwohl in den Domestizierungsprozess ursprünglich nur ein Teil einer größeren Wildtierpopulation einbezogen wurde, durch den regulären Genfluss von den Wild- zu den Haustieren letztgenannte eine höhere genetische Diversität innehaben als die Wildpopulationen.

Denn viele davon haben während des Holozäns eine durch den Menschen verursachte Schrumpfung ihrer Bestände erfahren.

**Keywords:**

Palaeogenetics, potential, limits, gene flow, genetic diversity, wild versus domestic species

Paläogenetik, Potential, Grenzen, Genfluss, genetische Vielfalt, Wild- vs. Haustiere

**Introduction**

Humans exploit other animals in the most diverse ways. As it is generally true for carnivorous and omnivorous animals, humans exploit other animals as food source. Compared to animals, however, humans progressively developed more sophisticated and efficient hunting techniques, a development that profoundly changed the predator-prey relationship at the expense of the prey animals. Moreover, humans discovered other ways to use animals, for example, as a resource for hides, hoofs, horns, and, later, secondary products such as milk, wool, dung, and also as beasts of burden for work and transportation, for military purposes, and as carriers of symbolic value. These various uses had different impacts on the animal species and populations concerned, some of them disappeared and some thrived. Even when not the focus of human intervention, animals have been victims of anthropogenic actions dating back to the Pleistocene, characterized by an ever-growing impact until modern times. It is of interest to trace back the evolution of animals since the Pleistocene in order to understand the mechanisms at work that led to their present-day situation.

*Palaeogenetics and Palaeogenomics*

One of the most powerful ways to measure the impact of human action on animal populations is genetics, because genetic diversity is an adequate measure for the status of an animal population. For instance, high genetic diversity argues for a healthy population with greater chances for long-term survival, whereas low genetic diversity suggests that the population is on the decline. To understand the evolution of genetic diversity of extant populations, including population replacements and migrations, and to put it into a spatio-temporal perspective, it is necessary to obtain a glimpse of their past diversity. This can be achieved through palaeogenetic and palaeogenomic analyses of remains of the species under consideration. Indeed, palaeogenetic data obtained from dated ancient specimens from secure archaeological or palaeontological contexts allow a journey into the past of the corresponding species while avoiding pitfalls that hamper genetic analyses of extant populations. Entire sequences of mitochondrial genomes or, even better, whole genomes of dated ancient specimens provide the opportunity to date divergence events via Bayesian analyses, and thus to reconstruct the evolutionary paths of species.

### *Methodological aspects of palaeogenetic and palaeogenomic analyses*

The analysis of ancient DNA is by no means a simple task. Ancient DNA molecules are heavily degraded, by about 5 million-fold with respect to the size of DNA molecules in living cells. These tiny DNA fragments are diluted in DNA from soil microorganisms that in most cases amount to 99-99.9% of the DNA content in an archaeological bone extract. In very rare exceptional cases the endogenous ancient DNA content can reach up to 70% of the total DNA content of an extract, such as in the extracts of both a finger and a toe phalanx preserved in the Denisova Cave in the Altai mountains, the high coverage genomes of which showed that they belonged to a Denisovan and a Neanderthal individual, respectively (Meyer et al. 2012; Prüfer et al. 2014). For less well preserved archaeological remains in which endogenous DNA makes up only 0.1-1% of the total DNA content, the methods for DNA amplification or library construction have to be optimized (e.g., Bennett et al. 2014; Guimaraes et al. 2017). The extremely low endogenous DNA content is also responsible for contamination, with modern DNA molecules being a major concern. This is particularly true for all ancient DNA studies performed with powerful PCR-based approaches that are very sensitive to contamination with modern DNA molecules. These can originate either from contamination of the archaeological remains with DNA from excavators etc., DNA molecules produced in the course of previous experiments in the laboratory (Pruvost et al. 2005) or from DNA molecules contaminating the reagents used to extract, purify and amplify DNA (Champlot et al. 2010). To avoid contamination during and after excavation and to preserve DNA from post-excavation degradation, archaeological remains predestined for a palaeogenetic analysis should be excavated aseptically and stored at low temperature (Pruvost et al. 2007). To minimize contamination with products of previous DNA amplification reactions, our laboratory chemically labels all amplified DNA molecules and enzymatically destroys them prior to new PCR amplifications (Pruvost et al. 2005). Moreover, we also eliminate DNA molecules that contaminate reagents, such as DNA from modern cattle that is found in a large variety of reagents compromising studies of ancient bovine remains (Champlot et al. 2010). In doing so, we ensure that the PCR products we obtain and sequence reflect the authentic endogenous ancient DNA molecules. We also apply these precautionary measures to the construction of DNA libraries for next-generation sequencing, an approach that is less prone to contamination because amplification of DNA molecules is only performed once the adaptors are ligated to the extracted molecules, but which are not exempt of erroneous sequences due to contaminated reagents (Bennett et al., in prep.). Moreover, in cases where very little endogenous DNA is preserved, which is the rule rather than the exception and is particularly true for remains buried in hot environments, capture approaches are used that again are contamination-prone since they rely on extensive PCR amplification steps. Furthermore, DNA extraction, purification,

amplification and library construction entail biases with respect to DNA molecule length and base composition that have to be taken into account or, better, minimized (Gorgé et al. 2016). Finally, the bioinformatics analyses of the DNA sequences obtained are not devoid of mapping problems linked to the short size of the ancient DNA fragments and to the sequence changes caused by diagenetic modifications of DNA, thus causing both false negative and false positive mapped reads that need to be addressed to minimize sequencing errors (Kircher 2012).

Bearing these constitutive pitfalls of ancient DNA analyses in mind, this approach definitely possesses great potential for the study of the evolution of genomes, and its practical applications are numerous: revealing unknown human species (Meyer et al. 2012), admixture between archaic human populations (e.g., Prüfer et al. 2014), as well as migrations and population admixture and replacements (e.g., Allentoft et al. 2015; Fu et al. 2016) have been discovered. The progress made in these analyses of ancient humans is also beneficial to the study of population dynamics and domestication of animals.

Bayesian phylogenetic analysis of ancient DNA sequences allows for estimating the dates of radiation events of the various clades of a species or genus studied by using (i) plausible estimates of the origin of the present lineages based on fossil evidence, (ii) estimates of the rates of sequence evolution within the mitogenome based on other mammals and (iii) the information contained within the DNA sequence of dated ancient specimens. Complete mitogenomes of various individuals distributed throughout the phylogenetic tree provide species-specific estimates of the molecular clock ticking on the mitogenome. This in turn yields valuable estimates of the ages of the various radiations. The ages of these divergence nodes, the age of the samples and their geographic origin allow us to reconstruct the evolution of the various populations, their migrations and replacements.

The palaeogenetic and -genomic studies of our laboratory described here aim at understanding the evolution of mammalian populations. The studies we present focus on a comparison between wild and domestic species of the same genus. This allows us to separate the influence that humans have on the evolution of species from that of natural selection due to adaptation to changing environments. To identify general trends of the impact of humans on the evolution of the genetic diversity of wild and domesticated animal populations, we will compare three different species pairs of the genus *Equus* (*E. hemionus*-*E. caballus*), the subtribe Bovina (*Bos*-*Bison*) and the family Felidae (*Acinonyx*-*Felis*).

## Results

### *The genus Equus*

Little is known about the phylogeography of wild asses outside of Africa and no comprehensive palaeogenetic study has been performed so far. We have analysed the hypervariable region of the mitochondrial DNA in archaeological bones and teeth that are dated from ca. 100,000 years ago to the present and were determined as *E. hydruntinus*, *E. hemionus*, *E. kiang*, and “small equid”. The DNA sequences allowed us to construct a phylogeny corresponding to the genetic distance between individual sequences and the establishment of groups or clades. Differences in the genetic determination of numerous specimens with respect to their identification based on morphological criteria led us to carry-out a blind study in which four or five osteologists independently assigned the specimens to a subspecies. To our surprise, there were numerous specimens for which no consensus was reached and we had to conclude that the morphological criteria for the determination of equid teeth and bones were insufficient (Bennett et al. 2017; Geigl & Grange 2012). The genetic results, however, and their Bayesian analysis enabled us to reconstruct the ancient population structure of Eurasiatic wild asses and to show that most of the former populations have disappeared and with them, most of their genetic diversity. We could also show that *E. hydruntinus* corresponds to a population or subspecies of *E. hemionus* to the same extent as *E. h. hemionus*, *E. h. hemippus*, *E. h. kulan*, *E. h. khur*, or *E. kiang* (Bennett et al. 2017). Thus, our results question the definition of species and conservation units of this taxon. Moreover, the analysis of remains from the equid burials at Umm el-Mara, a Bronze Age elite cemetery in Syria, allowed us to show for the first time that these male equids were hybrids between female domesticated donkeys and male *E. h. hemippus* (Bennett et al., in prep.). This genetic determination lends support to what until now has only been a hypothesis based on the tooth wear, i.e., that these animals were the kungas, prestigious equids used as draught animals to pull the chariots of nobles (Weber 2008). Thus, if hemiones were not domesticated *per se*, they participated transiently to the production of “domesticated” yet sterile animals, a practice that became marginal when domesticated horses became available.

The loss of population and mitochondrial diversity in Eurasiatic wild asses is contrasted by the situation of another species of the genus *Equus*, the domestic horse *E. caballus*. Indeed, the mitochondrial diversity in horses is very high (Cieslak et al. 2010; Lippold et al. 2011b) and so is the size of the population. The diversity of the Y chromosome in *E. caballus*, however, is very low (Lippold et al. 2011a) suggesting that only a limited number of wild stallions had been domesticated whereas wild female horses have been recruited across time in many places and at many occasions (Lippold et al. 2011b).

### *The subtribe Bovina*

Our study of 57 partial and whole mitogenomes of Bison remains from Europe, the Caucasus and Siberia dating to the last ~50,000 years and their Bayesian analysis uncovered the population dynamics of bison in Western Europe. The dates of divergence of the various branches that are estimated in this Bayesian analysis as well as the presence of mitochondrial haplotypes at various periods and areas could be correlated to the climate and the paleoenvironment (Massilani et al. 2016). Three bison populations colonized Western Europe via three successive waves, the first between 57,000 and 34,000 years ago when the climate was temperate during Marine Isotope Stage (MIS) 3. During the subsequent MIS2, this first population of ancient European bison (wisent) was replaced by the steppe bison, *B. priscus*, the ancestor of the present-day American bison. As suggested by paintings from the French Chauvet Cave, both bison types were present in Southern France between 39,000 and 34,000 years ago. During the last glacial period however, France was inhabited solely by the steppe bison. When the climate became mild again 14,500 ago, a new wisent population coming from the Lesser Caucasus colonized Western Europe, the genetic diversity of which gradually decreased until their disappearance in the wild in 1918. A wild herd was reconstituted after World War I starting from 12 zoo-animals. Our study indicates that climatic and environmental changes and human pressure play a major role on the population dynamics of the megafauna, of which the wisent is the largest representative still alive in Europe. Indeed, climate-induced environmental changes seem to be responsible for the movements of populations and species during the Pleistocene, while human-induced environmental changes, competition with livestock, and increased hunting pressure seem to be responsible for the bottlenecks and extinctions of the Holocene populations. The present-day genetic diversity of these populations was severely reduced during the Holocene. Parallel to this, we studied the population dynamics over the last ~10,000 years of wild aurochs populations and the process of their domestication in Southwest Asia, Southern Europe (France, Spain, Slovakia, Italy, Greece) and Northeast Africa (unpublished study of the Geigl/Grange laboratory: Guimaraes, Massilani, Pruvost et al., in prep.). We screened ca. 750 archaeological remains to obtain more than 200 sequences of the mitochondrial hypervariable region and 30 whole mitochondrial genomes. Through Bayesian phylogenetic analyses of the whole mitogenomes we could deduce the dynamics of aurochs populations during the Late Pleistocene and Early Holocene and correlate it to environmental conditions. Moreover, the data obtained from the Neolithic to the Middle Ages could be interpreted in light of the established framework of aurochs population dynamics.

European aurochs went through a major bottleneck during the Last Glacial Maximum (LGM) and we have no evidence for their domestication. In the course of the Holocene, their mitochondrial genome was almost completely lost except for a few occurrences in present-day East Asia revealing

past gene flow between female European aurochs and male domestic cattle. In modern British cattle breeds, however, small parts of the genome of a ca. 6,750-year-old British aurochs have been recognized suggesting (if contamination with modern bovine DNA in the aurochs genome can be excluded) past hybridization events between ancient European aurochs and domestic cattle (Park et al. 2015). We found the mitochondrial lineages of present-day taurine cattle in Neolithic and Bronze Age remains in Southwest Asia indicating that their domestication took place in this region. The age estimates suggest that an expanding aurochs population has been domesticated which thrived in an environmental optimum owing to the climatic changes after the last glaciation. We find the same haplotypes in our European Neolithic samples. During the Bronze Age, however, this initial diversity collapsed and was reduced to the present-day diversity dominated by one haplogroup. We found evidence for a similar process taking place in Northeast Africa.

Although mitochondrial DNA is maternally transmitted, does not recombine and therefore cannot testify admixture events, we have indirect evidence for introgression of local aurochsen in the domesticated cattle. Indeed, the appearance of the Anatolian haplotypes in skeletal remains that have been diagnosed as belonging to wild animals because of their convincingly large size, is an indication for introgression in the domestic gene pool of aurochs lineages, i.e., for male aurochsen interbreeding with female domesticates. In Europe, Southwest Asia and Northeast Africa, we found evidence for such introgression events that may have been either deliberately sought for by the people who managed and bred the domestic form of cattle or may result from accidental events that were exploited in some instances.

Altogether, the mitochondrial DNA genetic diversity preserved in the modern domestic cattle population corresponds to a large fraction of that existing at the beginning of the Holocene, whereas that of the remaining wild aurochs populations was reduced during the Holocene prior to the extinction of the wild lineage.

### *The family of Felidae*

The members of this family are informally grouped together as “cats”, all of which are carnivores and efficient apex predators. Here, we will report our studies on two members of this family, the *genera* *Acinonyx* and *Felis*, the cheetah and the “real” cat.

The cheetah, *Acinonyx jubatus*, a species that in the past had a wide distribution over most of Africa, Southwest and South Asia, is now recognized by the International Union for Conservation of Nature and Natural Resources (IUCN) as a vulnerable species (Durant et al. 2015). The cheetah was tamed but never domesticated. From Egyptian iconography, such as the hieroglyph depicting leashed cheetahs from the tombs of Deir el-Bahari from the 15<sup>th</sup> century BCE, we know that it was already held by the ancient Egyptians as a tamed animal, but also by the aristocracy in Medieval Europe (see



a painting by Benozzo Gozzoli depicting Giuliano de' Medici with a cheetah behind him on horseback; "Procession of the Magi" in the Chapel of the Magi, "Casa de Magi", Florence, Italy), and in Persia and India where it was also used to kill game at hunts owing to its prowess at hunting. In India the so-called "hunting leopard" was kept by kings and princes to hunt gazelle and the Moghul emperor Akbar kept them for hunting gazelle and blackbucks as known from depictions. According to the IUCN, the Asiatic subspecies, *A. j. venaticus*, has been classified as critically endangered (Durant et al. 2008) and suspected to have disappeared by the present day even in Iran (Durant et al. 2015).

We performed a genetic study of modern cheetah specimens from each of the four African subspecies and on ancient cheetah specimens from Iran (Charruau et al. 2011). We showed that the specimens from Northern Africa and the Asiatic cluster are in different groups that are monophyletic for mitochondrial DNA. Our ancient DNA results from the Iranian specimens dated to the 9<sup>th</sup> and 10<sup>th</sup> century CE show that the critically endangered or already extinct Iranian cheetahs are an autochthonous, monophyletic population and the last representatives of the Asiatic cheetah (ibid.). The species is now globally endangered without efficient conservation programs.

Five subspecies of the genus *Felis* are recognized (IUCN 2016), but only *Felis silvestris* became domesticated, and in particular the subspecies *F. silvestris lybica* whose natural range extended from Northern Africa to Southwest Asia. This unambiguous result was obtained when the mitochondrial DNA of wild, feral and domestic cats were analyzed showing that domestic cats and the wild cat from Northern Africa/Southwest Asia belong to the same clade (Driscoll et al. 2007). The European wild cat, on the contrary, belong to a distinct mitochondrial clade (ibid.). The place and timing of domestication was unclear up to now. The archeological record revealed a cat in a Neolithic human burial in Cyprus indicating that a special cat-human relationship had already been established by early farmers and that cats accompanied humans on their maritime trips (Vigne et al. 2004). Later in time in Egypt, during the predynastic period, there is archeological evidence for cat taming (Van Neer et al. 2014). The richest records for the development of a particular cat-human relationship, however, comes from the Egyptian iconography where cats are shown during the Middle (2,055-1,650 BCE) and New Kingdom (1,550-1,069 BCE) in various contexts, such as Tomcat slaughtering the serpent, as "cat in the marsh" hunting birds and, since the 1<sup>st</sup> millennium BCE, as "cat under the chair" of nobles (Engels 2001; Málek 1993-2006). The evolution of the iconographic representation could be interpreted as describing the process of cats penetrating more and more into the human niche. Yet, the understanding of the domestication of the cat did not go beyond this limited knowledge. To shed light on the domestication history of the cat, we analyzed the mitochondrial DNA of a large sample of 351 cat specimens, including 80 samples from mummified Egyptian cats, from around 60 archeological sites in Europe, Southwest Asia and Africa as well as museum collections covering roughly the last 9,000 years (Ottoni et al. 2017). Despite its large size, the

dataset is patchy, but allowed us nevertheless to elucidate some important aspects of the history of cat domestication, the most important being that the cat became early on an animal that accompanied humans on their trips over sea and land. This can be deduced from the appearance in our data set of the mitochondrial lineage from Southwest Asia in other areas suggesting translocation events (ibid.). We conclude that it was the cat from the Fertile Crescent that was the first to travel around the Mediterranean Sea with the Neolithic farmers. We see another mitochondrial lineage showing up in Egypt during the 1<sup>st</sup> millennium that very quickly and efficiently spread to Anatolia and Southeast Europe and, during the Middle Ages, to Viking ports at the Baltic Sea (ibid.). Thus, the spreading pattern coincides with the major routes of human mobility in the Ancient World in pre-, proto- and historic times suggesting that soldiers, merchants, and seafarers were responsible for the cat's conquest of the world where it is now present with about 600 million individuals in all continents and environments except Antarctica.

In contrast, the European wild cat, *F. silvestris silvestris* that was never domesticated or tamed but hybridized with the domesticated African wild cat *F. silvestris lybica* experienced a reduction of its population size and a reduction of habitats and is now a protected species (Yamaguchi et al. 2015). The high degree of hybridization with domestic cats, however, and concomitant transmission of diseases still represent a major threat to the European wildcat.

## Discussion

These few studies show a general trend: evolutionary speaking, domestication provides benefits to a species, at least in the short term, while related wild mammalian species suffer reductions and extinctions in the Anthropocene. Humans reshape the biodiversity and create new and complex niches that finally lead to extinctions, extirpations and shifts in species composition, diversity and community structure (Boivin et al. 2016). Our data from related domestic and wild populations show that although domestication starts with a genetic bottleneck because only animals with desirable characteristics were selected from larger wild populations, there was more or less regular gene flow between the early domesticates and the wild populations. This led to preservation of a significant part of the ancient diversity even after the corresponding wild population was extinct. Species that were not domesticated suffered a more severe reduction in their genetic diversity following hunting pressure, habitat fragmentation and reduction, and competition with domestic animals. Paleogenomic studies have the potential to unravel the processes leading to biodiversity shifts and to contribute to a better understanding of how humans influenced animal populations and changed their evolutionary pathways.

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