



The Dispersal of the Domestic Cat Paleogenetic and Zooarcheological Evidence

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Mummified cat, ancient Egypt, 2000–100 BCE. Science Museum, London. Wellcome Images (CC BY 4.0).

Domestication is one of the most interesting and challenging processes in human and animal evolution. The fundamental change in subsistence strategies from hunting and gathering to farming that took place for the first time in the Levant more than ten thousand years ago profoundly changed human culture and biology, and set the groundwork for population growth, migrations, the rise of civilizations, and wealth disparities (Bocquet-Appel 2011; Gignoux, Henn, and Mountain 2011; Kohler et al. 2017).

Animal domestication is a multifaceted and complex process consisting of multiple ecological and biological changes in both humans and animals (Marshall et al. 2014; Vigne 2011; Zeder 2012). Following trajectories of domestication processes has proven invaluable across multiple disciplinary fields for tracking cultural and economic transitions as well as migratory shifts in human (pre)history. In recent years genetics and in particular ancient DNA (aDNA) studies have largely contributed to such multidisciplinary efforts by providing times and modes of dispersal of domestic animals, in particular species used for food supply (livestock; Daly et al. 2018; Ottoni et al. 2013; Scheu et al. 2015) or transport (horse, donkey; Fages et al. 2019; Kimura et al. 2011).

More particularly, mitochondrial DNA (mtDNA) has proven to be a key tool for investigating the pattern of human-mediated dispersal of domestic animals across time and space. In most animals, the mtDNA is a small, circular, maternally transmitted

molecule contained in the energetic compartments of the cells: the mitochondria. Different from the nuclear DNA, which is contained in the nucleus of cells in two copies arranged in linear chromosomes maternally and paternally inherited, mtDNA is present in multiple copies (up to thousands) inside mitochondria. This feature makes the genetic information contained in mtDNA more easily accessible to laboratory investigations even after centuries and millennia.

By sequencing ancient mtDNA molecules, it is possible to define the peculiar set of mutations that an individual possessed in life, the so-called haplotype. Mutations accumulate stochastically over the time, and individuals living in geographic proximity possess closely related haplotypes, which are distinguished by a small number of mutations, as opposed to more distant individuals and geographically distinct populations. For this reason, haplotypes and groups (or, to use a more specific term, clades) of closely related haplotypes are geographically structured (the so-called haplogroups). The relationship between haplotypes and clades in terms of genetic distances (number of mutations differentiating them) is often represented in phylogenetic trees.

Wild animal populations are geographically structured and, through domestication and migration, humans reconfigure the mtDNA geographic signatures by moving animals from their original area of distribution—where the interaction with humans most likely started—to new areas where local animal populations of the same species possess distinct haplotypes and clades. The basic rationale behind aDNA studies of domestic animal species is to define the patterns of distribution of ancient

mtDNA haplotypes across time and space, in order to reconstruct animal translocations.

Cats as Archaeological Evidence

Of all domestic animals, cats are probably the most enigmatic, to the extent that one would even argue whether they are domestic. Pest-control agent, object and symbol of value in past civilizations, companion animal, and iconic celebrity of the internet in modern society, the cat has long held a unique position in our collective consciousness. The strong and intimate bond between cats and humans is the key to the evolutionary success of cats.

Until recently, the general belief was that the initial domestication of cats took place in ancient Egypt at the latest by 1600 BCE, during the Egyptian New Kingdom, mainly based on evidence from figurative art (Engels 1999; Málek 2006). In the first millennium BCE, the cat was associated with a local deity, the goddess Bastet, and its popularity reached its peak during the Ptolemaic period (323–30 BCE). Catteries were established in temple precincts and a huge number of cats of all ages were killed (Armitage and Clutton-Brock 1981) and mummified for votive offering. Animal mummies have been distinguished in various categories (Ikram 2012). “Food” mummies consisted of mummified victuals (steaks, ducks, geese) left as provisions for tomb owners. Animals believed to hold the essence of gods in their bodies are categorized as “sacred” mummies. “Votive” animal mummies were the most numerous in ancient Egypt, and were dedicated to specific deities. Each god had a totem, or symbolic animal, and the mummies of totem species were purchased by pilgrims and offered to the gods in dedicated shrines. Earlier cat–human interactions in Egypt are suggested by zooarchaeological evidence from the site of Hierakonpolis, where attempts at cat taming may have occurred as early as the Predynastic period, ~3,700 BCE (Van Neer et al. 2017). In fact, analysis of the age at death of six cats buried in a small pit shows that the natural reproductive cycle was disturbed as a result of human interference. These cats were held in captivity prior to their sacrifice and burial, indicating some kind of cultural control from humans (figs. 1, 2).

Zooarchaeological findings from Cyprus indicate that even earlier interactions between cats and humans took place in the Near East. Felids are not native to Cyprus and their presence on the island in Pre-Pottery Neolithic contexts of the ninth millennium BCE at the site of Klimonas suggests that they were introduced in tamed form by sea-faring Neolithic farmers (Vigne, Briois et al. 2012). A complete cat skeleton found at Shillourokambos in association with a human burial dated to ~7,500 BCE further suggests that cats had a close relationship with humans (Vigne, Guilaine et al. 2004). The overall general understanding is that the cat–human encounter most likely took the form of a commensal relationship—cats were attracted to settlements of Neolithic farmers as scavengers or following the arrival of anthropogenic commensal rodents (rats and mice), while humans in turn appreciated the presence of cats as they kept pests under control.

The Paleogenetics of Cat Dispersal

Despite the popularity of cats in present-day society, the study of their domestication has for long time lagged behind that of



Figure 1. Wim Van Neer excavating cat remains in the archaeological site of Hierakonpolis, Egypt. © Hierakonpolis Expedition.



Figure 2. Archaeological cat remains buried in a small pit in the archaeological site of Hierakonpolis, Egypt. © Hierakonpolis Expedition.

other domestic animals, in particular dogs and livestock. This is mostly due to the fact that cats were never primarily exploited for their economic or subsistence value. Cat remains were largely overlooked in zooarchaeological studies because they are rare in archaeological contexts and sometimes difficult to identify based on traditional metric analysis.

A seminal genetic study in 2007 (Driscoll et al. 2007) made a strong contribution to the understanding of cat domestication by revealing that only one of the *Felis silvestris* wild cat populations distributed in the Old World contributed to the genetic make-up of domestic cats worldwide: the North African and Near Eastern wild cat, *Felis silvestris libyca* (fig. 3). Yet, the limited sample coverage of the study in key

areas like North Africa and the Near East left open questions regarding the actual role and contribution of the two purported centers of cat domestication, the Near East and Egypt. Furthermore, the modern genetic data could not offer sufficient phylogenetic resolution to address more in detail the origin of five subclades described in the cat mtDNA phylogenetic tree (subclades A–E; fig. 3). In fact, the shallow representation of genetic variation provided by present-day wild and domestic populations is the result of demographic events that occurred in the past (such as migrations and population contractions and expansions), which remain undetected based on modern genetics alone.

The recent paleogenetic study that we undertook (Ottoni et al. 2017) has shed new light on the history of cat domestication. Our main objective was to provide temporal depth to the phylogeny described by the 2007 study so as to track the original phylogeographic signal of five subclades of domestic cats described in the mtDNA tree. That is, we sought to determine their original distribution prior to the worldwide cat dispersal. Through cutting-edge aDNA techniques, we successfully analyzed bones, teeth, claws, and even hairs of more than two hundred ancient cat specimens. We investigated the mtDNA of cats from various archaeological sites in Europe, Southwest Asia, and Africa (figs. 4, 5, table 1). The temporal depth and the geographic coverage of the samples made it possible to infer the original phylogeographic structure of cats (i.e. the geographic distribution of genetically distinct cat populations in the past), something that archaeological surveys and genetic analyses of modern cats could not previously detect.

By tracking the maternal ancestries of ancient cats, we succeeded in providing a better understanding of the distribution of wild cat populations and human-mediated translocation since prehistory. We found ancient European wild cat haplotypes (belonging to clade I, *F. s. silvestris*) exclusively in Europe, from the Mesolithic period to the eighth century BCE. However, quite surprisingly, we detected *F. s. lybica* haplotypes (called IV-A1) in Neolithic cats from southeast Europe and in a cat dated to 7700 BCE from Romania, prior to the arrival of farming communities in Europe during the Neolithic. On the other side of the Bosphorus, on the Anatolian peninsula, we found a different lineage of *F. s. lybica* (IV-A*). The occurrence of *F. s. lybica* in pre-Neolithic southeast Europe and in Neolithic Anatolia indicated that the native range of this subspecies most likely extended throughout Anatolia and beyond the Bosphorus for many millennia. IV-A* had a wide distribution ranging across Anatolia throughout the Neolithic, Bronze Age, and Iron Age, and as far south as the Levant, where we also found cats carrying clade IV-B. Such distribution indicates that cats that developed the earliest forms of commensal relationship with farming communities during the Neolithic period carried at least the mitochondrial lineages IV-A* and IV-B.

We found cats carrying the Near Eastern lineage IV-A* in late Neolithic contexts of southeast Europe by 4400 BCE

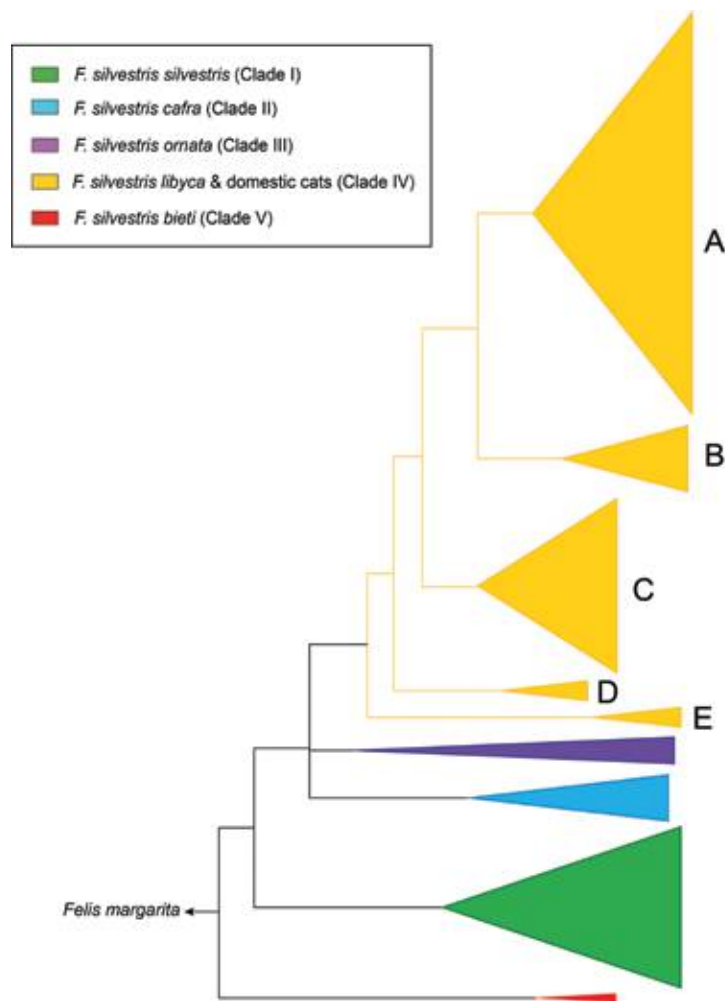


Figure 3. Phylogenetic tree of mtDNA lineages in wild and domestic cats, as from Driscoll et al. 2007. The tree shows that modern domestic cats possess the same maternal lineages as the Near Eastern and African wild cat *Felis silvestris lybica* (clade IV).

(fig. 6) suggesting that the human-mediated movement of cats began in prehistoric times, corroborating the interpretation of the first cats on Cyprus. Interestingly, a recent study showed that cats dated to 2900–2400 BCE from Poland carried lineages IV-A* and IV-B (Baca et al. 2018), providing further evidence of human-mediated dispersal of cats during the Neolithic. These data represent the first genetic evidence of cat translocations during the Neolithic. We believe that further paleogenetic analysis of cats from Neolithic sites in central, western, and southern Europe will help in the future to refine the timing of cat dispersal during the Neolithic.

The analysis of modern wild cats from central and eastern Africa and of ancient cats from Egypt, including cat mummies (fig. 5), has revealed that the mitochondrial clade IV-C was originally distributed in Africa. This clade marked a second, more relevant cat dispersal that occurred during classical antiquity, when we found it at sites in Turkey, Jordan, and Bulgaria (fig. 6). As noted above, cats were worshipped in Egypt, and during the Greco–Roman period they were kept in temple precincts to be mummified. They were at total ease in domestic contexts at least from the New Kingdom period, as witnessed by the depiction of the “cat under the chair” theme, and the peculiar social

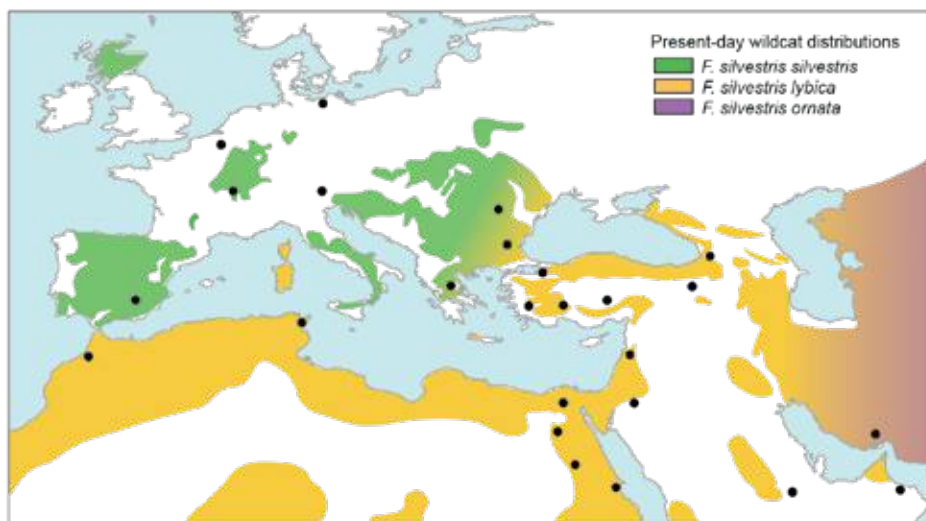


Figure 4. Map indicating the approximate geographic location of the sites analyzed in Ottoni et al. 2017.



Figure 5. Cat mummy from the collection of the Natural History Museum of London (UK).

and cultural context of Egyptian society may have facilitated the evolution of a more tolerant disposition of cats towards humans. From pest-control agents in farming communities, the cats in Egyptian households probably turned into the companions that we know today. The increasing popularity of cats among Mediterranean cultures (e.g., the Phoenicians, Carthaginians, Greeks, Etruscans, and Romans) and their usefulness on ships infested with pests—such as the black rat (*Rattus rattus*) and the house mouse (*Mus musculus*), which started spreading by sea routes in the Iron Age (Jones et al. 2013)—presumably sparked their dispersal across the Mediterranean from Egypt. Interestingly, cat representations in variations of the theme “cat under the chair” are found on coins and in literary and artistic sources in the Greek world by at least the sixth century BCE as well as in Etruscan tomb paintings (Engels 1999).

Cats spread even more rapidly in later European and Southwest Asian contexts, between the fifth and thirteenth centuries CE, when clade IV-C became significantly more frequent (up to 78% in Europe; fig. 6). Domestic cats remained absent outside the Roman territory until late antiquity, and they started

to appear north of the Alps after the Roman conquest. To corroborate our results, cats dated to the Roman era carrying the lineage C were recently found in Poland (Baca et al. 2018). Further expansion took place in the Middle Ages, when it was compulsory for seafarers to have cats on board to safeguard food (Johansson and Hüster 1987), ropes, and leather material from rodents and other pests. The trade in domestic cat pelts as cloth items in medieval Europe may also have fostered the dispersal of domestic cats (Ewing 1981; Lloveras et al. 2017).

The African clade IV-C appeared in the Viking trading port of Ralswiek, on the Baltic Sea, by the seventh century CE and the Iranian port of Siraf by the eighth century CE. Even longer cat dispersal distances were witnessed by the presence of an Asian lineage belonging to *F. s. ornata* (clade III, fig. 3) at the Roman–Egyptian port of Berenike on the Red Sea (first–second centuries CE) and at medieval coastal sites in Turkey. Cats may have accompanied humans across trade connections between South Asia and the Mediterranean basin via the Indian Ocean and Red Sea or via the Silk Road connecting central Asia with Anatolia (fig. 6). Similarly, the presence of the Southwest Asian haplotype IV-A* as far south as East Africa may be the result of maritime routes described in the first-century CE *Periplus* of the Erythraean Sea.

The last two clades observed in modern domestic cats (IV-D and IV-E) were found at very low frequencies in our aDNA dataset, and only in more recent historical contexts of Africa, Turkey, Germany, and Poland (Baca et al. 2018). Given their early divergence in the mtDNA phylogenetic tree, we believe they could be originally African, and were introduced into the genetic pool of domestic cats by admixture. In fact, upon their arrival at various destinations across the globe, introduced cats most likely interbred with local populations of wild (or tame) cats. Admixture episodes occurring at various times during the global dispersal of cats may have led to introgression of deeply divergent clades (such as IV-D and IV-E in Africa, or the Indian clade III in Asia) in the genetic pool of domestic cats.

The biological features of cats as pest controllers and (later) pets, and their adaptability to various ecological niches were the key factors that made their dispersal so successful, in some instances at the expense of other local, commensal species. For example, a recent study demonstrated that in Neolithic China a commensal relationship was present between humans and the leopard cat (*Prionailurus bengalensis*; Vigne, Evin et al. 2016). However, the leopard cat was never successfully domesticated and did not leave any genetic contribution to present-day domestic cats in China. Hence, it is possible that, once introduced from Southwest

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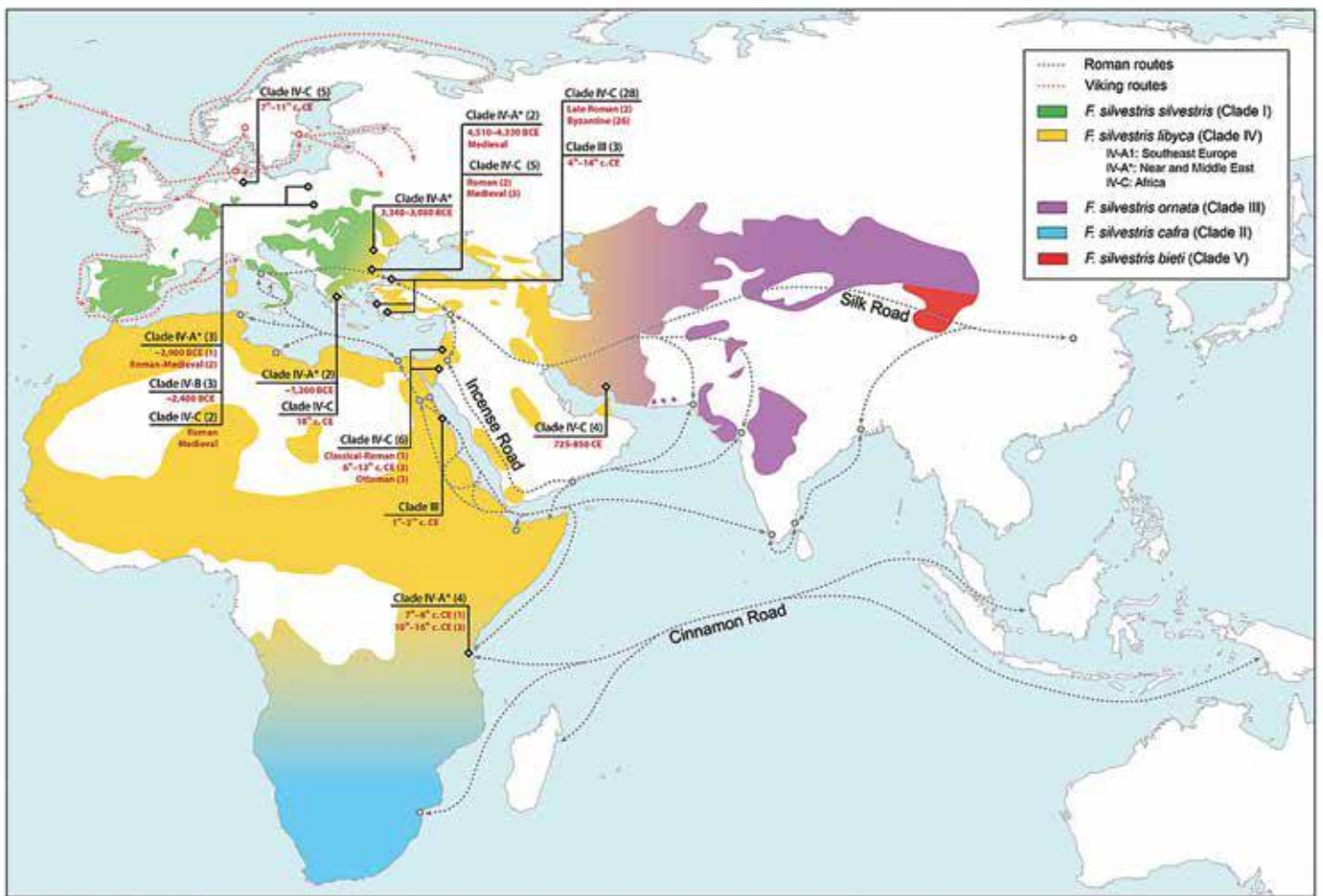


Figure 6. Human-mediated cat translocations as revealed by the presence of ancient mtDNA clades outside of their original phylogeographic distribution, as inferred in Ottoni et al. 2017. Approximate geographic location of sites investigated in Ottoni et al. (2017), and in Baca et al. (2018), is indicated, respectively, by black diamonds and circles (Poland). The number of cats found in each site is in parentheses. The map shows the present-day distribution of *Felis silvestris* with the geographic range of each subspecies (and of the mtDNA clades, as reported in the inset). A schematic representation of Roman and Viking trade routes is also depicted.

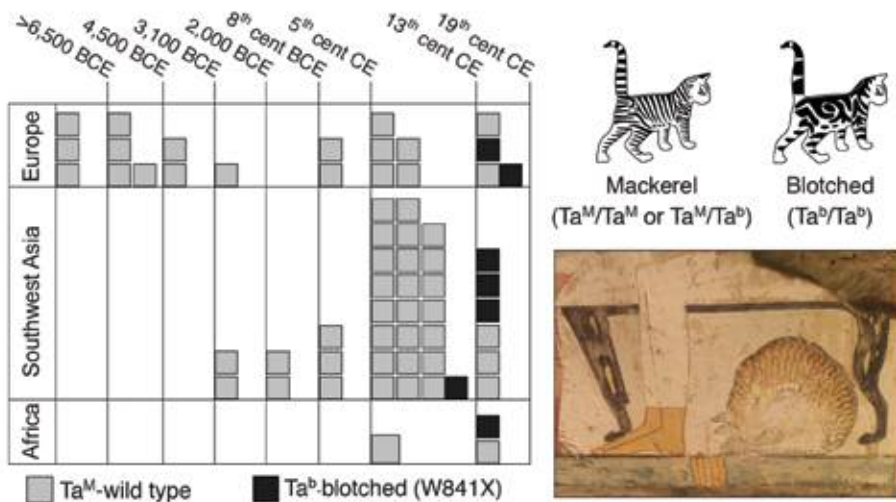
Asia to China, cats completely replaced the leopard cat from its purported commensal niche. Something similar may have happened to the weasel (*Mustela nivalis*, or other mustelid species) that were kept as house animals for rodent control by Greeks and Romans (Faure and Kitchener 2009) before being supplanted by domestic cats.

Changes in Physical and Behavioral Traits during Cat Domestication

The bulk of multidisciplinary evidence gathered over the last few years has continued to demonstrate that domestication is a complex and multistage process characterized by a gradient of mutualistic relationships between animal and human societies across increasing degrees of control and management of animals, from anthropophily to commensalism, captivity, and intensive breeding (livestock and pets; Vigne 2011). While in most animals the pathway of domestication leads to a common suite of morphological changes (Wilkins, Wrangham, and Fitch 2014), in cats few evident morphological or osteometric features differentiate wild and domestic forms. Recently, an unprecedented

study of thousands of cat bones from faunal assemblages encompassing almost two thousand years in Denmark, showed that domesticated cats grew in size by about 16 percent between the Viking Age and today (Bitz-Thorsen and Gotfredsen 2018), in contrast with a general trend of body-size reduction observed in other animals, in particular livestock. Increased supplies in the form of pests and food scraps associated with expanding towns from the Middle Ages may have determined the body growth, as suggested by the authors. However, other factors, such as direct breeding and selective pressure by humans, may have come into play in the Danish cats. Studies of such diachronic coverage tackled from multiple disciplinary sides (morphology, genetics, stable isotopes) may certainly help in the future to pinpoint changes in body size of cats during domestication, and to unravel whether the growth observed in Danish cats was a local event or rather a general trend in cats.

Most phenotypic variation in modern domestic cats occurs at the level of coat color and pattern, and fur length. In our study, we investigated a mutation in the nuclear *Taqpep* gene that shed light on the origins of coat pattern variation in ancient cats, in particular whether they possessed blotched or mackerel tabby



markings. The two variants of the tabby phenotype, mackerel and blotched, distinguish respectively wild and domestic cat populations. We demonstrated that in our dataset of ancient cats, the earliest occurrence of the mutation that causes the blotched tabby marking dates to the Ottoman Empire in Southwest Asia, and later increased in frequency in Europe, Southwest Asia, and Africa (fig. 7). The iconography from the Egyptian New Kingdom and European Middle Ages depicting cats with striped coats—corresponding to the mackerel-tabby pattern of the wild *F. s. lybica*—seems to corroborate our genetic results. Only starting from the eighteenth century CE were the blotched markings common enough to be associated with the domestic cat, as observed by Linnaeus (Kaelin et al. 2012).

Figure 7. From Ottoni et al. 2017, fig. 2: spatio-temporal representation of the alleles determining the phenotypic variation in the shape of tabby patterns, mackerel (Ta^M) and blotched (Ta^b). The image shows a “cat under the chair” with a tabby mackerel marking, typical of *F. silvestris lybica*. Anna (Nina) Macpherson Davies; copy of wall painting from private tomb 52 of Nakht, Thebes (I, 1, 99–102) cat eating fish; photo: © Ashmolean museum, Oxford, UK.

Table 1. Number of ancient cats (with approximate date range) analyzed in Ottoni et al. 2017. For more details see there.

Region	N	Dating (range from to)
Europe		
Armenia	2	second millennium BCE–medieval period
Belgium	1	>ninth millennium BCE
Bulgaria	17	fifth millennium BCE–Roman period
France	3	eighth century BCE–ninth century CE
Germany	7	seventh century CE–eighteenth century CE
Greece	8	second millennium BCE–eighteenth century CE
Italy	3	ninth millennium BCE
Romania	15	eighth millennium BCE–fifth millennium BCE
Spain	5	sixth millennium BCE–second millennium BCE
Southwest Asia		
Iran	15	first century CE–ninth century CE
Jordan	23	first millennium BCE–sixteenth century CE
Lebanon	1	second millennium BCE
Oman	5	fourteenth–fifteenth century CE
Saudi Arabia	1	seventeenth–eighteenth century CE
Syria	4	seventh century CE–fourteenth century CE
Turkey	71	eighth millennium BCE–fourteenth century CE
Africa		
Egypt	13	first millennium BCE–fifth century CE
Morocco	1	eighth century BCE
Senegal	3	eighteenth century CE
Tanzania	4	seventh century CE–sixteenth century CE
Tunisia	6	fourth–seventh centuries CE

This indicates that selection for coat pattern (and most likely following human-mediated breeding control) occurred rather late in the history of cat domestication, as opposed to other domesticates such as horses (Ludwig et al. 2009). The reason for that is that cats were never selected for a peculiar task by humans: They already possessed in their wild state the predatory skills that made them useful to human communities across (pre)history—hunting mice and other pests that infested human grain storages (or households, ships, and so on). On the contrary, human manipulation aimed at selecting specific traits that could assist humans (for example food supply, transport and traction in livestock and horses) played an important role in shaping phenotypic variation pretty early along the domestication pathway of other domestic animals. For example, the extreme variation in size and shape that we observe in domestic dogs may be the result of early attempts to select specific tasks such as hunting, protection, and sled-pulling (Driscoll et al. 2009).

On a similar note, it is important to mention that artificial selection aimed at creating breeds had a major role in generating physical variation in cats, but it was introduced only very recently. In cats it started in the nineteenth century, without any objective to select peculiar skills, except for generating “visible” aesthetic variation. This selection affected mostly the coat variation, less so the body shape and size, and led to the origin of most of the actual “fancy” breeds.

While cat domestication was not a matter of physical variation, a major change may have occurred at the level of behavior. A recent study showed that modern wild and domestic cat genomes are quite homogenous, while on the other hand, significant changes occurred at the level of behavioral traits, leading to reduced wariness and increased docility (Montague et al. 2014). Predisposition to tameness is probably the key feature to domestication in all animals, the trigger that makes animals more tolerant of human presence (Price 1999). Since the early encounter with humans in the Neolithic, cats acted for millennia

as pest-control agents in human settlements, towns, and on ships. However, beginning in the classical era, cats from Egypt dispersed in the Mediterranean (and then globally), accompanying humans along routes of trade and connectivity. Their relationship with humans turned into a more intimate bond, probably concurrently with the shift in behavior that is recorded in modern cat genomes. Selection for docility may have come into play in cats by acclimating them to human presence for food reward (Montague et al. 2014), and we speculate that this may have occurred in the favorable context of the Egyptian society, where cats were welcomed in households and developed a more tolerant attitude towards humans. More than pest hunters, cats became human companions, yet maintaining their innate predatory skills and a sort of aloofness that is still a hallmark of modern housecats. This, together with their adaptability, determined the evolutionary success of cats. In the future, analysis of complete ancient cat genomes may potentially help to pinpoint if and when selection of behavioral traits took place in cats, turning them into the pets that we know today.

We believe that aDNA investigations at the level of nuclear genomes will help in the future better to understand the times and places of human selective processes in the history of cat domestication, as well as the complex patterns of admixture that potentially occurred in overlapping and interbreeding populations of wild and domestic cats.

Future Perspective: The Evolution of Diet in Cats

The commensal relationship between cats and humans is unique. Cats are obligate carnivores and the access to food scraps, rodents, and other pest populations in Neolithic settlements of early farming communities was the spark that initiated their long-lasting and intricate bond. Domestic cats dispersed globally owing to their association with people and also to their capacity to adapt swiftly to novel dietary habits within the human food web. In particular, the global distribution of domestic cats is strictly associated with their presence on board ships, and we demonstrated that a significant dispersal of cats began in the classical through the Roman eras, when intense maritime trade routes connected civilizations across the Mediterranean and more widely the Old World. As already mentioned, cats on board ships were useful as pest-control agents to safeguard food and precious goods, and in medieval times it was compulsory to have cats on board. The link between cats, ships, and maritime environment is clear, and nowadays fish have entered the pet-food industry. However, it remains to be addressed how, when, and to what extent cats started to feed on marine sources and on cereal-based food. Recently, a study demonstrated that diet has a strong influence on the oral bacterial composition of modern cats, showing differences in the microbiome of cats fed on dry (highly refined, cereal-based typical of modern pet food industry) versus wet food (canned and/or fresh meat-based; Adler et al. 2016). Bioarchaeological approaches through, for example, stable isotope and oral microbiome analysis will certainly help in the future to address these questions, making it possible to follow diet shifts in cats associated with anthropogenic environments (including life

in confinement), across the transition from scavengers and pest-control agents to pets with easy access to food sources.

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