Redefining the timing and circumstances of cat domestication, their dispersal trajectories, and the extirpation of European wildcats

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Abstract

Despite the domestic cat's (*Felis catus*) close association with humans, the timing and circumstances of its domestication and subsequent introduction to Europe are unresolved. Domestication of its wild progenitor, the African wildcat (*F. lybica*), is widely attributed to the emergence of farming. Wildcats are said to have been attracted to settled communities by the rodent populations that were thriving within this new agricultural niche. Some claim the African wildcat even reached Europe during the Neolithic, though many credit the Romans with their dispersal. Through a program of zooarchaeological analysis, genetic identification and radiocarbon dating, we redefine the established chronology for the cat's domestication and dispersal across Europe. We argue that early human-cat relationships were more complex than the commensal and mutualistic pathways that have been proposed, and that both the domestication and translocation of cats were linked to its association with deities. Our results suggest domestic cats first arrived in Europe prior to Roman expansion during the early first millennium BCE, and that successive populations of domestic cats with unique mitochondrial signatures were introduced during the Roman, Late Antique and Viking periods. Lastly, by characterising the spatiotemporal representation of both domestic cats and the native European wildcat (*F. silvestris*), we argue that the introduction of domestic cats precipitated a decline in native European wildcat populations.

Main Text

Introduction

Genetic analyses have determined that the progenitor of domestic cats (*Felis catus*) is the African wildcat (*F. lybica*) (1). Beyond this, neither the timing nor circumstances of the domestic cat's emergence and subsequent dispersal are well-established. Resolving the biocultural history of domestic cats has proved difficult for several reasons. Cats are not typically part of the human diet so their remains are underrepresented in zooarchaeological assemblages. Like other small animals, felid bones are susceptible to stratigraphic movement and, without direct radiocarbon dating, reconstructions of their spatio-temporal distribution lack confidence (2, 3). For instance, Ottoni et al.

(3) directly dated a cat bone from a Bronze Age context in Tiryns, Greece, and found it to be a modern intrusion.

The identification of felid remains to species is equally problematic. While morphological analyses can aid discrimination, wildcats and domestic cats frequently overlap in size (4, 5). For example, the purported *F. lybica* in Neolithic China (6) and Predynastic Egypt (7) were later shown to be the remains of leopard cat (*Prionailurus bengalensis*) (8) and jungle cat (*F. chaus*) (9), respectively.

Given these challenges, existing hypotheses for the cat's domestication and early dispersal are not robustly supported. One popular model posits that domestication began in the Neolithic when populations of *F. lybica* were attracted to small rodents, who themselves were enticed by cereal processing and storage by early Near Eastern settled agricultural communities (1, 10). The principal evidence marshalled in support of this model is a ~9,500-year-old felid interred at the edge of a human burial on Cyprus (10). Identified as an African wildcat based upon morphological analysis, the specimen's tame status was inferred from its depositional context in close proximity to the human. Poor preservation, however, has prevented genetic analyses or direct radiocarbon dating from corroborating either the date or the species assignment.

Claims have also been made for the presence of cats with Near Eastern ancestry in Neolithic Central and Southeastern Europe based on a mitochondrial DNA (mtDNA) signature associated with *F. lybica* (3, 11, 12). Recently, however, Jamieson et al. (13) showed that European wildcats (*F. silvestris*) can also carry *F. lybica* mtDNA due to ancient gene flow between the two species. This result indicates the IV-A genetic signature alone is not a sufficient proxy to distinguish between European wildcats and domestic cats in the archaeological record of continental Europe.

Early Egyptian cultures are regularly cited as the originators of cat domestication based upon both iconographic depictions and the inclusion of cats in human graves (14, 15). Inferring domestic status based on their appearance in tomb wall paintings can be problematic as these may portray other felid species. Similarly, the nature of the relationship between humans and cats interred together is difficult to establish and interpretations may be shaped by modern attitudes. Evidence for human control over cat reproduction has been claimed at Predynastic Hierakonpolis (~3700 BCE) based on the presence of six juvenile cats from a single burial with age profiles suggesting that the natural reproduction cycle was disturbed (16). These remains are dated 2,000 years prior to the period when cat remains are commonly found in archaeological contexts, and when they are depicted within domestic settings (14, 17).

The human-mediated dispersal of cats out of Egypt is thought to have occurred by maritime traders from Phoenicia and Greece (18), although the timing and routes are unclear. It is commonly stated that the Romans were responsible for the spread of domestic cats across and beyond the Mediterranean (19). In fact, some authors have stated that domestic cats did not appear north of the Alps until after the Roman conquest, and were absent beyond Roman territory until Late Antiquity (3, 20, 21). These narratives have often been repeated without critique or the recognition that zooarchaeologists have presented evidence for domestic cats in pre-Roman contexts in Italy (22) and Britain (23). Whilst the Romans may not have been responsible for the domestic cat's initial introduction to Europe, the greater abundance of cat remains during the early first millennium CE suggest that expansion of the Roman Empire helped to increase their range and population size (24).

The impact of the domestic cat's arrival on native European wildcat populations is also uncertain. The decline and local extirpation of the wildcat is thought to have begun in the 18th-19th centuries CE as a result of habitat loss and overhunting (25). More recently, overlapping ecological niches, hybridisation, and disease transmission from domestic cats have also been cited as challenges to

wildcat restoration and conservation (26, 27). The archaeological record offers the opportunity to examine dynamics of wildcat populations and their interactions with domestic cats over the last three millennia.

Here, in order to characterise the origins and dispersal of domestic cats in Western Eurasia, we combined zooarchaeological and biomolecular analyses of ancient felid remains. This included an examination of each specimens' contextual information including biological age, deposit type, and site type. We integrated our results with evidence from archaeology, historical sources, and iconography. The emergent phylogeographical patterns enabled us to re-evaluate the circumstances and cultural contexts which led to the domestication and human-mediated spread of domestic cats, and to map the decline of the European wildcat.

Results and Discussion

To morphologically distinguish European wildcat and African wildcat/domestic cat remains, we collated 2,456 measurements from ancient and modern felids from across Europe (Dataset 1). We then cross-referenced these values with genetic species assignments from many of the same individuals (Dataset 2) that allowed us to identify a metrical threshold to delimit the two species (Fig. 1).

We also assessed the shifting spatiotemporal distributions of the six primary mitochondrial haplogroups (I, IV-A, IV-B, IV-C, IV-D, and IV-E) previously identified in European wildcats, African wildcats and domestic cats (1, 3) (Fig. 2A). We did so by collating the haplotype calls assigned to 350 individual felids derived from eight publications (2, 3, 11, 12, 24, 28, 29), and mapped the location and haplogroup assignments of felids across Western Eurasia in a series of temporally defined maps that were supported by a programme of radiocarbon dating (Fig. 2B-E).

We obtained direct radiocarbon dates from 24 specimens. Of these, four were more recent than their contextually assigned date. Specifically, a tibia from Almosen, Denmark (P141), thought to be from a ritualised bog deposit dated to 10th-5th centuries BCE, was directly dated to the 20th century. A cat bone from Gyngstruplund Nordøst, Denmark (P166), was phased to 1st-2nd centuries CE, but directly dated to the 17th-20th centuries CE. A specimen from Howe, Orkney (AJ517) was phased to the 2nd-1st centuries BCE, but directly dated to the 8th-10th centuries CE. An immature wildcat skeleton from Owslebury (AJ340) was determined to date to the 7th-8th centuries CE, and not the 1st-3rd centuries CE as suggested by its depositional context. These results were combined with 92 published radiocarbon dates (2, 3, 11, 12, 24, 28–33).

Differentiating wild and domestic felids

Current hypotheses for the earliest domestication of the cat rest heavily on the felid buried at the edge of a human grave at the Neolithic Shillourokambos, Cyprus, dated to ~7,500 BCE (10). Though identified morphologically as a subadult African wildcat (34, 35), comparison of its cranial and postcranial measurements with those of known species indicates that its size is consistent with that of the European wildcat (Fig. 1, Fig. SI 1). Whilst the size of African wildcats during the early Holocene is poorly defined, our analysis raises the possibility that it was European wildcats that were transported to Cyprus from Anatolia during the Neolithic. This interpretation corresponds with the presence of imported Anatolian obsidian at the site (36), and indications that the earliest settlers at Shillourokambos were of Anatolian origin (37).

Claims for African wildcats in Neolithic Central and Southeastern Europe are similarly uncertain (3, 11, 12). Most derive from cave deposits with few or no domestic taxa, and in some instances, a complete absence of evidence for an anthropogenic presence (11, 38, 39). Measurements from these felids indicate they are consistent with the native European wildcat (Figure 1). The presence of *F. lybica* mtDNA in these individuals is likely the result of ancient, natural hybridisation between the

two species (13). Indeed, a recent analysis of nuclear DNA derived from a number of these specimens concluded that they are European wildcats that possess mitochondrial haplotypes of African wildcats (24).

There is a gap of >2,500 years between these Neolithic claims for cats of Near Eastern ancestry in Europe and those arising in the Iron Age. The earliest claim for domestic cats in pre-Roman Western Europe is from Fidene on the eastern outskirts of Rome (22). Here a complete felid skeleton was recovered from a food storage building that, according to radiocarbon dating, burnt down ~1000–800 BCE (40). The remains were identified as those of a domestic cat on the basis of its morphology and location, though some have cautioned against inferring either its species or status from its depositional context since it could have been a hunted European wildcat that was placed in the structure prior to the fire (41). While most of its postcranial measurements are consistent in size with *F. lybica/catus* (Fig. 1), they are unlikely to be reliable indicators of its species. The bones were unfused and therefore the individual was not fully grown, and their exposure to high temperatures during the fire has resulted in heat-induced warping and potentially heat-induced shrinkage.

At Entzheim in France, an isolated mandible, radiocarbon dated to 766–420 BCE, was found to possess *F. lybica* IV-A mtDNA and submitted as further evidence for the presence of domestic cats in Iron Age Europe (3). Metrical analysis, however, indicates that the felid was particularly large and more comparable with the European wildcat (Figure S2). The lack of additional contextual evidence to support its domestic status suggests that this too is a European wildcat that possessed mitochondrial haplogroup IV-A as a result of gene flow from African wildcats.

While the IV-A genetic signature alone is not sufficient to confirm the presence of domestic cats in continental Europe, it is unlikely that hybridised wildcats reached Britain from their glacial refugia (42) before the island became separated from the continent ~8,000 years ago. No ancient wildcats from Britain or Ireland exhibit discordance between their mitochondrial and nuclear genomes (SI Figure S4). Indeed, wildcats in Britain dating from both the Mesolithic and early modern period are devoid of *F. lybica* ancestry (13). Limited introgression from *F. lybica* may also account for the boldness of the flank stripe in the pelage of modern wildcats in Western Europe, in contrast to their virtual absence in Eastern European wildcats (43). There is no evidence for the presence of IV-A in Britain or Ireland prior to ~400 BCE (13, 24). From this point until ~700 CE, the only *F. lybica* haplotype present on both islands is IV-A. This includes an individual from Fishbourne Roman Palace (AJ86) whose status as a domestic cat is supported by the fact that its genome clusters with modern domestics, and that it does not possess any detectable levels of admixture with European wildcats (13). Furthermore, measurements of the Fishbourne specimens, together with metrics from other British cats that possess the mitochondrial haplogroup IV-A (n=22), are all consistent with domestic morphologies (Fig. 1, Dataset S1).

The earliest example of the IV-A haplotype in Britain comes from Gussage All Saints where the skeletons of five neonatal kittens were recovered from a single deposit dated to 339–51 calBCE (AJ98, AJ100). The genetic result appears to confirm their original identification as domestic cats (23). Juvenile felid bones are frequently labelled as domestic cats on the assumption that if wildcats were hunted for their fur, adults would be preferentially selected (23, 44). Similarly animals found as partial skeletons or Associated Bone Groups (ABGs) are assumed to have been deliberately buried by humans (45) and so felid ABGs are often interpreted as domestic cats, though this assumption has rarely been tested.

To examine the correlation between species, age and whether they were recovered as isolated bones or as ABGs, we integrated genetic results with the samples' contextual information. Beyond the Gussage All Saints kittens, we found no relationship between these variables. Other sub-adult cats from Gussage All Saints (AJ343), together with those from Danebury (AJ343) and Quarry Field

(AJ107), had previously been identified morphologically as domestic cats, but were determined genetically to be European wildcats. Two complete skeletons - one from Iron Age Owslebury (AJ340) another from Roman Dorchester (AJ93) (both Britain) - were also shown genetically to be European wildcat. By contrast disarticulated bones from Fishbourne Roman Palace (AJ85, AJ86) were identified genetically as domestic cats.

Religion motivated the domestication and spread of cats

Our results do not support a Neolithic origin for domestic cats. Instead they suggest that the closening of human-cat relationships occurred more recently, in the first-millennium BCE. This timeframe suggests that Egypt was the locus of domestication, especially in light of the cultural evidence (see SI Text).

Cats are closely associated with the Egyptian goddess *Bastet.* She first appeared in the third-millennium BCE depicted with a lion's head, but during the 9th-7th centuries BCE she was increasingly represented with the head of an African wildcat (46). This transformation was coincident with the rise of cat sacrifice, whereby millions of free-ranging and specifically-reared cats were mummified as offerings to the goddess (14, 17, 18). Temples and sanctuaries to *Bastet* were situated within vast arable landscapes, which likely sustained large populations of rodents and their wildcat predators. This would have provided the context for the tighter relationship between people and cats that led to the wildcat's domestication, motivated by their newly acquired divine status.

Cults and religions are often drivers for animal translocations. For instance, the spread of fallow deer has been directly linked to the cults of *Artemis* and *Diana* (47), while chickens were associated with *Mercury* and *Mithras* (48, 49). In the same way, the cult of *Bastet* (50) could feasibly have facilitated the dispersal of *F. lybica.*

Haplogroup IV-C is first detected in mummified cats from Egypt dating to the Ptolemaic and Roman period (~300 BCE to 500 CE). Cats with this haplotype have subsequently been found in Roman period deposits in Jordan, Turkey, Bulgaria (3), and at Sławsko Wielkie and Łojewo in Poland, which were both radiocarbon dated to the 1st-3rd centuries CE (2, 12). A cat of this haplogroup, whose nuclear genome clusters with modern cats, was identified at the legionary fort of Petronell-Carnuntum in Austria, and radiocarbon dated to 60–210 calCE (24). This haplogroup may have spread to Europe following the Greek and Roman conquests of Egypt, after which the cat was incorporated into their religions and became a symbol of the goddesses *Artemis* and *Diana* (18).

Haplogroup IV-A was equally widespread in Egypt during the Roman period, and has been identified at the sites of Berenike (50–400 CE) and Shenhur (400–700 CE). While it is accepted that this haplogroup was transported across the Roman Empire to sites such as Fishbourne Palace in southern Britain (13, 24), pre-Roman cats possessing the IV-A haplogroup are frequently dismissed as hybridised wildcats. This has led to the belief that domestic cats were not present in northern Europe prior to the Roman Empire (21). In Britain, however, where IV-A cats are not native, the Gussage All Saints kittens provide compelling evidence that these were domestic cats and they were introduced to the island in the 4th-2nd century BCE. Additional evidence for close human-kitten interactions in Iron Age Britain is provided by a pottery sherd from the site of Shinfield, Berkshire, on which a kitten paw is imprinted (51) (Fig. S5). That cats also held a religious significance at this time is indicated by depictions of human-cat hybrids, including one that is thought to be a headdress used in a trance-experiencing shamanistic ritual (52).

Between the 4th century BCE and the ~7th century CE, IV-A is the only *F. lybica* haplogroup present in Britain. Domestic cats were not introduced to Ireland until the 7th century CE and the first to arrive also possess Haplogroup IV-A. This includes the specimen from Ratoath (AJ249) radiocarbon dated to 602–653 calCE. Some have linked the arrival of cats in Ireland with the growth of Christian monasticism, where cats provided companionship and protection to manuscripts from being

damaged by rodents (53–55). Caring for a cat features prominently in the hagiography of many saints from Britain and Ireland in the 7th-9th centuries CE, where it is volunteered as a demonstration of their virtue (55).

The presence of Haplogroup IV-E in Britain may also be linked to the spread of Christianity. A cat of this haplogroup was identified at the royal monastery of Lyminge, radiocarbon dated to 672–818 calCE (AJ76). This mitotype was identified in a Sardinian cat, dated to the 3rd–1st centuries BCE, that possessed a North African ancestry distinct to modern domestic cats (24). Haplogroup IV-E is more common in Turkey from the early-medieval period, with 17% of cats (4 of 23) possessing this lineage between 500–1200 CE, and 10% (1 of 10) between 1200–1900 CE. As such the presence of this cat at a monastery in Britain patronised by royalty may reflect ecclesiastical trade routes with Byzantium following the conversion of the Anglo-Saxon kingdoms to Christianity (56).

We first detected domestic cats with Haplogroup IV-D in Denmark from the 9th-11th centuries CE. In Britain, this haplogroup was associated with areas of Viking-influence, and cats that possessed this lineage were identified in the Danelaw settlements of York (978–1151 calCE) and Lincoln, as well as the Viking-controlled archipelagoes of Orkney (Howe: 775–993 calCE; Jarlshof: 989–1029 calCE) and Shetland. This lineage was also present on the Baltic coast of Poland at Gdańsk and inland at sites along the Vistula River (Starogród: 990–1154 calCE), at Bernhardsthal in Austria (770–980 calCE), as well as the coastal settlement of Galway, Ireland.

The transportation of cats by the Vikings has previously been interpreted as an effort to limit rodent populations on board ships (57). The domestic cat's continued association with goddesses—in this instance *Freyja*, a Norse goddess associated with fertility, magic, and death—may have additionally motivated its translocation. As Freyja's companion animal, cats held an important role in Norse mythology and ritual practice, and cat bones were often found in high-status graves and at cult sites across Scandinavia and Iceland (58). Cat skins were highly valued and treated as a talisman of their patron deity (59). The *Sagas* make specific reference to witches who wore white cat fur, which encouraged the deliberate breeding of white cats in Viking and Medieval Ireland (53).

Early decline of European wildcat populations

The reduction in both the extent and abundance of the European wildcat is thought to have begun in the 17th-19th centuries CE and is commonly attributed to habitat loss and increased persecution by people (25). To test this chronology, we examined spatio-temporal trends in the presence of wildcat bones identified through metrical and genetic analyses (Fig. 3).

The proportion of archaeological felid bones identified genetically as European wildcat decreased dramatically from the first millennium CE onwards. Metrical separation of domestic cat and wildcat bones from before the 6th century CE is challenging due to the larger size of domestics during this period (60, 61), but in later centuries domestic cats are smaller. We identified only a few large felids dating from the 6th-9th centuries CE which are likely to be European wildcats, though they have not been confirmed genetically. Many of these presumed wildcats were excavated at high-status sites, including Łęczyca Castle (Poland), Visegrád Castle (Hungary) and Clarendon Palace (England). These sites yielded extensive faunal evidence for hunting, though wildcat bones were present only in very low numbers, suggesting they were uncommon in the landscape. Other surveys of European zooarchaeological data have similarly observed a decline in wildcat abundance from the early-first millennium CE, and their extirpation from large parts of the species' maximum Holocene extent by the medieval period (62–64).

The archaeological record suggests that the decline in wildcat abundance began earlier than previously believed and was coincident with the expansion of domestic cat populations during the Roman period. The arrival of domestic cats would have introduced competition for resources and niches that wildcats once dominated, particularly during the Dark Age Cold Period (~400–800 AD)

when many small mammal species experienced a population decline (65). Native wildcat populations may also have been affected by new diseases, which can readily transmit between the two species, and pose a challenge to modern wildcat reintroduction efforts (26, 66).

Conclusion

Our reassessment of the archaeological evidence indicates that both the domestication of the cat and its subsequent introduction to Europe were relatively late phenomena. We contend that a closer relationship between humans and the African wildcat emerged in Egypt during the early-first millennium BCE, and that they then rapidly spread northwards. This more recent timeframe is also consistent with evidence demonstrating that domestic cats did not reach China until the 8th century CE (67).

Rather than the product of a commensal and mutualistic relationship centred on the predation of rodent populations around settlements, our evidence points instead to the importance of religion in both the domestication and dispersal of cats. This can be seen in the consilience of the goddess *Bastet* changing depiction from lion-headed to cat-headed, the rise of offering mummified cats in her honour, and the cat's introduction to Europe, all of which occurred in the first millennium BCE.

The cat's connection to female goddesses continued subsequent to their introduction to Europe, after which they became associated with *Artemis*, *Diana* and *Freyja*. Positive attitudes towards the cat continued in early Christian Europe and our evidence suggests that cats were spread via an international network of Christian monastic houses. However, a shift in theology during the 12th century CE reframed cats as a symbol of heresy and evil (54). Though the species kept its (now negative) female association as the archetypal witches' 'familiar' (46).

Our results also challenge the belief that cat translocation to northern Europe did not occur before the Roman period. Three independent lines of evidence - zooarchaeological, biomolecular and material culture - suggest that domestic cats were present in Britain by the 4th-2nd century BCE. While it is logical to link animal translocations with the spread of Empires, other detailed single-species studies, including fallow deer (47), chickens (48) and rats (68), have demonstrated the two are often uncorrelated. Furthermore, these studies have highlighted that species are often repeatedly introduced, and that each wave has its own circumstances, meaning and impact. The same is true for domestic cats, and successive populations with unique mitochondrial signatures were moved across Europe during the Iron Age, Roman, Late Antique and Viking periods.

The focus on domestic cats within this paper, and the wider archaeological literature, is not to suggest that human relationships with other felids were not important. Wildcat synanthropy around settlements (6, 12), the ritualised burial of European wildcats in Bronze Age Sicily (69) and Roman Britain (70), and the intentional burial of leopard cats in Han Dynasty China (71) and Predynastic Egypt (72), are just some examples of the complex relationships people have formed with wildcats globally.

Humans have been influencing wildcat populations for millennia. In some cases, they have facilitated range expansion by deliberately introducing wildcats to islands, as seems to be the case in Neolithic Cyprus (10) and pre-Roman Sardinia (24). More commonly, people have instigated the contraction of wildcat range through overhunting and anthropogenic environmental degradation (25). The negative impact of domestic cats on wildcat populations is recognised today (27), and our study suggests this competition has a greater time-depth than previously recognised. The European wildcat was once widespread across the continental mainland, Britain and Ireland, and their range began contracting only as the distribution of domestic cats increased. Rewilding programs focussed on the introduction of wildcats should therefore consider the density of domestic cats in the region since their presence has negatively influenced the European wildcat since their introduction.

Methods

Zooarchaeological analysis

Metrical analysis was undertaken to assist with the identification of archaeological *F. silvestris* and *F. lybica/catus* remains (Dataset 1, Table S1 and S2). For this we analysed 2,416 measurements from archaeological felids recovered from 206 archaeological sites. These were analysed using linear metrics and the logarithmic size index method where measurements were standardised to the mean value for all samples. Additional information relating to data generation can be found in Appendix SI.

Radiocarbon Dating

To refine the chronology of the domestic cat's translocation and check for issues of stratigraphic migration, published radiocarbon dates were collated (n=92) and 24 specimens were directly dated: 19 at the University of Oxford's Radiocarbon Accelerator Unit, UK and 5 at Beta Analytica, USA.

Genetic Analysis

For the purposes of species identification, we screened mitochondrial genomes sequenced in Jamieson et al. (1) using HAYSTAC (73). This provided species assignments to 23 samples which had not previously been identified to species (Dataset 1).

For this, runs from multiple sequencing lanes were merged into single fastq files. Sequencing adapters were removed using AdapterRemoval2; any reads shorter than 15 base pairs were excluded. We built a database containing a single (longest and complete) mitochondrial genome for each of the six felid species available on NCBI using the database module of HAYSTAC. The database included the following species and accession combinations: *Felis bieti* (KP202273.1), *Felis catus* (NC_001700.1), *Felis chaus* (NC_028307.1), *Felis lybica* (KP202275.1), *Felis margarita* (NC_028308.1), *Felis silvestris* (NC_028310.1).

Fastq files (after adapter removal) were processed with the analysis module of HAYSTAC. Species assignment probabilities were calculated using the "probabilities" analysis mode implemented in HAYSTAC using default options ("haystac analyse –mode probabilities"). For a confident species call for a given sample, we required more than 50 aligned reads as well as an assignment posterior probability higher than 0.5.

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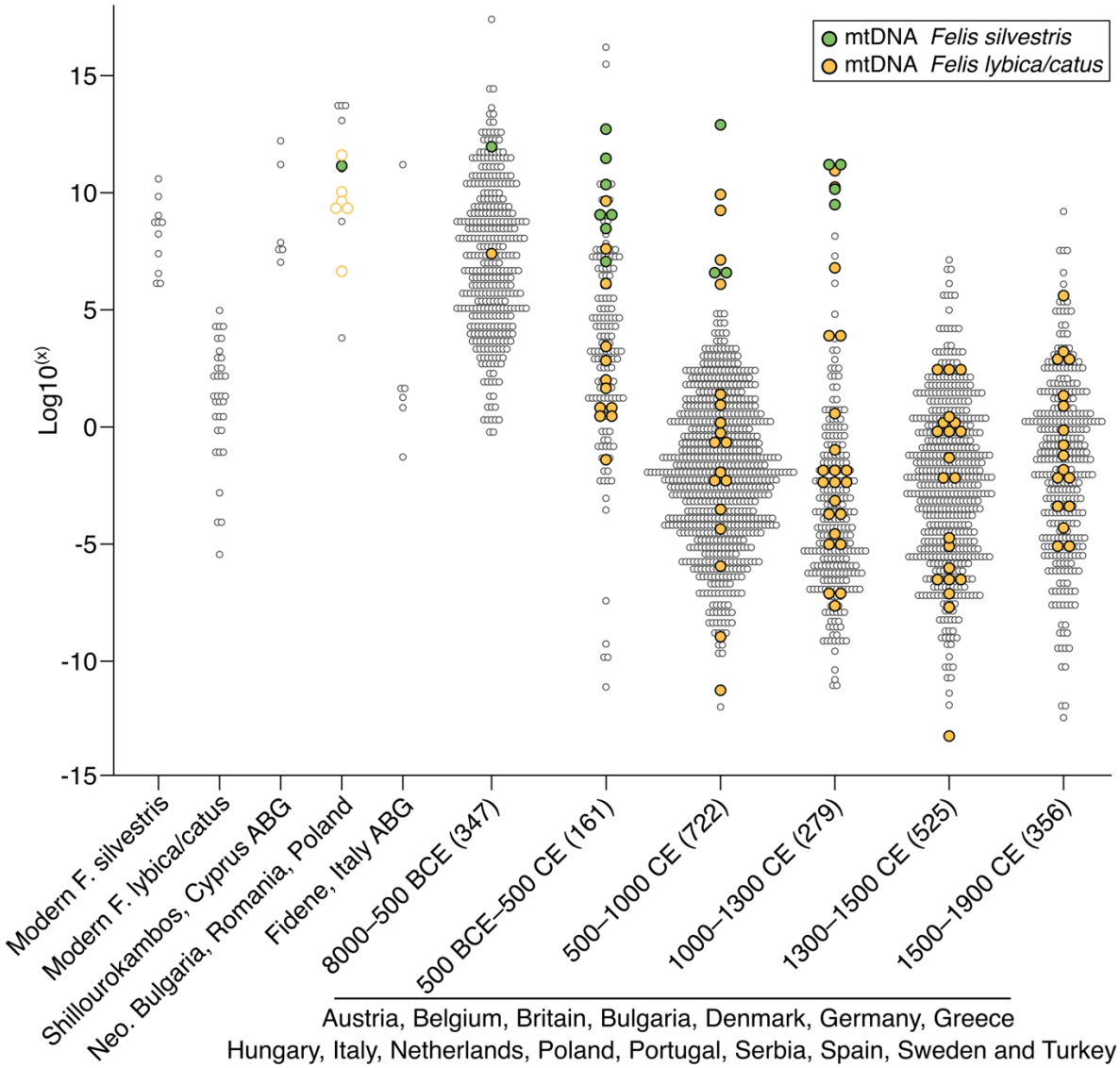
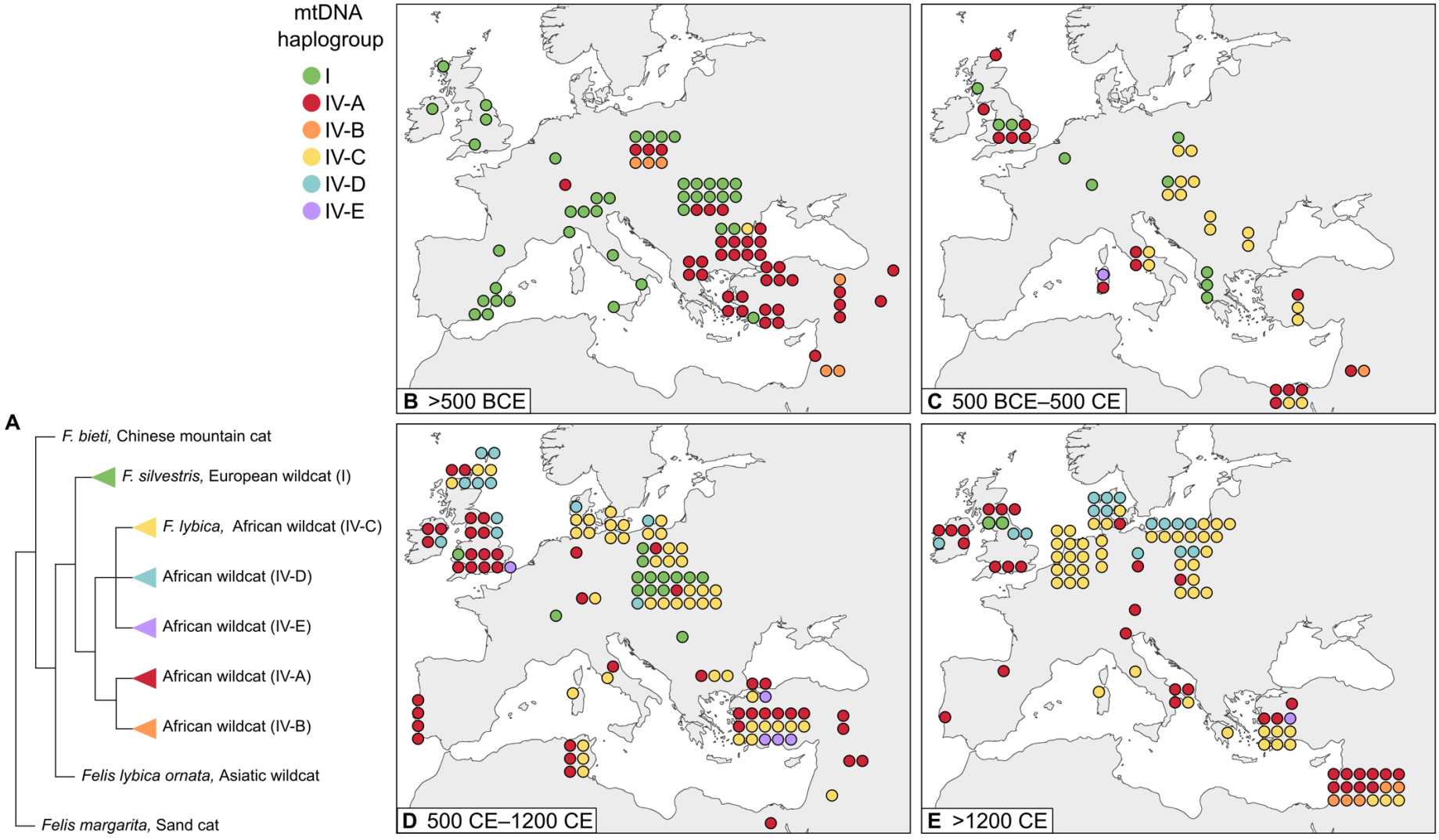
Fig 1. A comparison of archaeological post-cranial felid bone breadth measurements from across Europe with known European wildcats (green circles) and African wildcats/Domestic cats (yellow circles) via log size ratio analysis (the number of specimens is shown in parentheses). Where available, values are coloured coded according to mtDNA species assignments (Dataset 2). This framework provides a reference for the separation of wildcats and domestic cats in the absence of genetic information (grey circles). Recent analyses (13, 24) suggest the *F. lybica* mtDNA present in felids from Neolithic Central and Southeastern Europe is most likely the result of natural gene flow between European and African wildcats. Given this uncertainty, these specimens are presented as open circles with a yellow border.

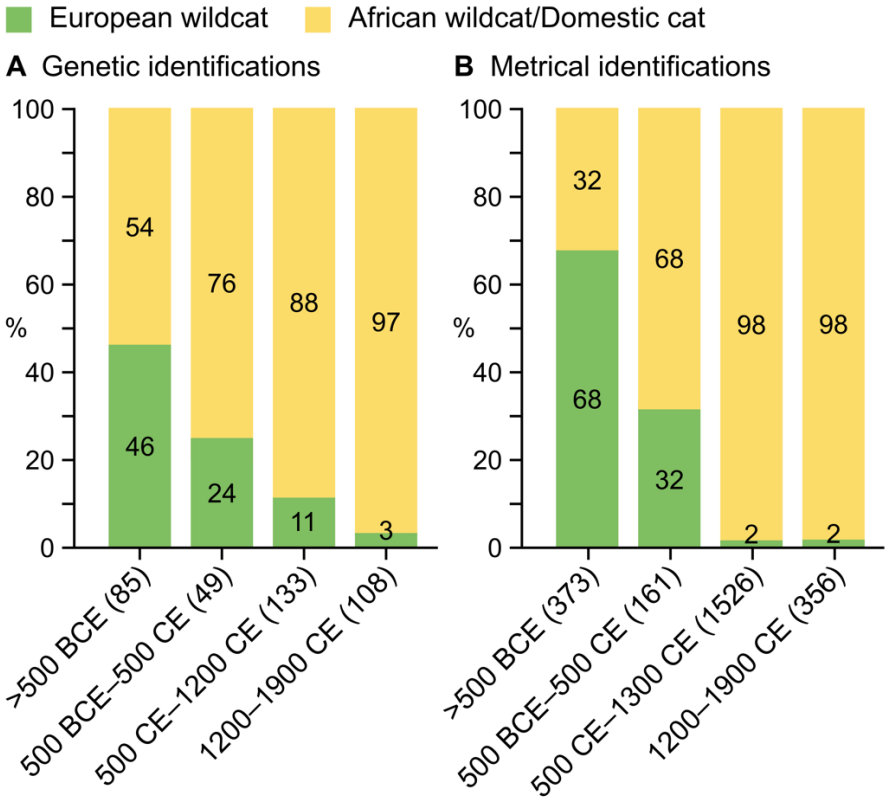


618 **Fig 2.** Four temporally constrained maps that sequentially depict the presence of archaeological felid samples that possess mitochondrial sequences that fall
619 into one of six well-supported (coloured) haplogroups (data from Dataset 2). Individual colour circles correspond to each of the six clades in panel A.
620 Mitochondrial haplogroup assignments drawn from (3, 28, 29).



621

622 **Figure 3:** Species identification of archaeological felids remains in Europe using (A) mtDNA and (B)
623 metrical analyses



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