EVOLUTIONARY BIOLOGY

Genomic evidence for the Chinese mountain cat as a wildcat conspecific (*Felis silvestris bieti*) and its introgression to domestic cats

He Yu[1†], Yue-Ting Xing[1], Hao Meng[1], Bing He[2], Wen-Jing Li[3], Xin-Zhang Qi[4], Jian-You Zhao[5], Yan Zhuang[1], Xiao Xu[1], Nobuyuki Yamaguchi[6], Carlos A. Driscoll[7], Stephen J. O'Brien[8,9], Shu-Jin Luo[1,9]*

The Qinghai-Tibet Plateau endemic Chinese mountain cat has a controversial taxonomic status, whether it is a true species or a wildcat (*Felis silvestris*) subspecies and whether it has contributed to cat (*F. s. catus*) domestication in East Asia. Here, we sampled *F. silvestris* lineages across China and sequenced 51 nuclear genomes, 55 mitogenomes, and multilocus regions from 270 modern or museum specimens. Genome-wide analyses classified the Chinese mountain cat as a wildcat conspecific *F. s. bieti*, which was not involved in cat domestication of China, thus supporting a single domestication origin arising from the African wildcat (*F. s. lybica*). A complex hybridization scenario including ancient introgression from the Asiatic wildcat (*F. s. ornata*) to *F. s. bieti*, and contemporary gene flow between *F. s. bieti* and sympatric domestic cats that are likely recent Plateau arrivals, raises the prospect of disrupted wildcat genetic integrity, an issue with profound conservation implications.

INTRODUCTION

The domestic cat (*Felis catus* or *Felis silvestris catus*), one of the most popular pets today, has an estimated worldwide population of over 600 million, including probably more than 100 million free-ranging feral cats (*1*). The origin and history of cat domestication have attracted wide public attention, as well as scientific interest (*2*). The first genetic study of the origin of domestic cats, based on a mitochondrial and nuclear DNA assessment of nearly 1000 specimens of domestic cats and their wildcat progenitors, *Felis silvestris*, revealed a single domestication event from the African wildcat (*F. s. lybica*) in the Near East (*3*). Ancient cat domestication coincided with the rise of both early agriculture and civilization in the Fertile Crescent and subsequently expanded across the world. Ancient DNA analysis of archeological cat remains reinforced this conclusion by showing that African wildcats from both the Near East and Egypt contributed to the modern domestic cats' gene pool at different historical times (*4*). Nevertheless, uncertainty remains as to whether multiple, independent cat domestication centers might exist, particularly given the lack of sampling in previous studies from East Asia.

The wildcat, *F. silvestris*, from which domestic cats arose, is widely distributed in the Old World and classified by controversial taxonomic systems, ranging from a monotypic taxon with multiple lineages to a species complex comprising at least two species (*5*). According to the most recent genetic study of wildcat samples collected worldwide (*3*), *F. silvestris* is resolved as a polytypic wild species including five distinct interfertile subspecies: *F. s. silvestris*, the European wildcat; *F. s. lybica* from the Near East and northern Africa; *F. s. cafra* from southern Africa; *F. s. ornata*, the Asiatic wildcat from central Asia east of the Caspian Sea; and *F. s. bieti*, the Chinese mountain cat endemic to the Qinghai-Tibet Plateau. However, the Felidae taxonomy by Kitchener *et al.* (*5*) merged *F. s. cafra*, *F. s. lybica*, and *F. s. ornata* into *F. lybica* to unify wildcats from Africa to central Asia, while maintaining *F. silvestris* in Europe and *F. bieti* in China their own species statuses.

Two wildcat taxa, the Chinese mountain cat and Asiatic wildcat, are found in China. The Asiatic wildcat (*F. s. ornata*) occurs from the eastern Caspian Sea north to Kazakhstan to western India, western China, and southern Mongolia. Its spotted coat pattern distinguishes it from other, usually striped, wildcat lineages. The Chinese mountain cat (*F. s. bieti*), also known as the Chinese desert cat or Chinese steppe cat, was first described as an independent species, *F. bieti*, in 1892 (*6*). With a restricted distribution on the Qinghai-Tibet Plateau, it is the only wild felid endemic to China and is characterized by a sand-colored fur with faint dark stripes, a thick tail, ear tufts, and light blue pupils (*7*). Molecular genetic studies suggested a reconsideration of the Chinese mountain cat as a conspecific of the wildcat based on its close association with other wildcat subspecies (*3*, *8*), but this taxonomic revision has not been unanimously accepted. Arguing against it, Kitchener *et al.* (*5*, *9*) wrote, "*F. bieti* is morphologically distinct and is supposedly sympatric with *F. l. ornata*, which would also preclude its recognition as a subspecies of *F. silvestris*/*lybica*." However, the presumed reproductive isolation between the Chinese mountain cat and Asiatic wildcat was based on their morphological divergence and possible overlapping distribution, either of which might not hold true given the two taxa's poorly defined ranges and possible misidentification or mislabeling of specimens in previous studies (*7*, *9*).

[1]The State Key Laboratory of Protein and Plant Gene Research, Peking-Tsinghua Center for Life Sciences (CLS), Peking-Tsinghua-NIBS (PTN) Program, School of Life Sciences, Peking University, Beijing 100871, China. [2]World Wide Fund for Nature, Beijing 100037, China. [3]CAS Key Laboratory of Adaptation and Evolution of Plateau Biota and Qinghai-Tibetan Plateau Museum of Biology, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, Qinghai 810008, China. [4]Tibetan Plateau Wildlife Zoo, Xining, Qinghai 810001, China. [5]Gansu Endangered Animals Protection Center, Wuwei, Gansu 733000, China. [6]Institute of Tropical Biodiversity and Sustainable Development, University Malaysia Terengganu, 21030 Kuala Nerus, Terengganu, Malaysia. [7]Galton Corp., Frederick, MD 21701, USA. [8]Laboratory of Genomic Diversity, Center for Computer Technologies, ITMO University, St. Petersburg 197101, Russia. [9]Guy Harvey Oceanographic Center, Halmos College of Arts and Sciences, Nova Southeastern University, Fort Lauderdale, FL 33004, USA.
*Corresponding author. Email: luo.shujin@pku.edu.cn
†Present address: Department of Archaeogenetics, Max Planck Institute for the Science of Human History, Jena 07745, Germany.

Recent advances in genomic studies of exotic species have demonstrated that hybridization between closely related taxa is common in nature and is important in shaping the genomes of modern animals (10–12). Intertaxa hybridization has also been documented in various Felidae lineages, such as the big cats (genus *Panthera*) and neotropical small cats (genus *Leopardus*) (8, 13, 14). In Northwest China, observations of cats possibly derived from interbreeding between Chinese mountain cats and domestic cats are occasionally reported, leading to the postulation that local wildcats may have contributed to the gene pools of domestic cats in China. As one of the world's oldest civilization centers, China has been involved in or has given rise to numerous domesticated animal varieties, including those of the dog and the pig (15, 16). Also, the earliest evidence of a commensal relationship between human and cat, in this case, the Asian leopard cat (*Prionailurus bengalensis*), was unearthed from a Neolithic site in Northwest China (17, 18), casting light on the existence of an environment conducive to a human-cat commensal process at that time in the East Asia.

On the other hand, genetic introgression from domestic species into their wild congeners has been documented in many taxa and, by introducing deleterious traits, it could threaten those wild populations by compromising their fitness in the wild (19, 20). In some regions of Europe, the anthropogenic spread of domestic cats has caused the expansion of feral cats' range and the subsequent hybridization with the European wildcats (21–23). Such widespread genetic infiltration from *F. s. catus* into *F. s. silvestris* is a substantial threat to the survival, distinctiveness, and genetic integrity of those sympatric European wildcat populations. On the Qinghai-Tibet Plateau where the Chinese mountain cat is endemic, most local domestic cats are free ranging, whose effect on wild conspecifics is a concern. However, the circumstance and the extent of genetic admixture between those two remain unknown, let alone its potential conservation impacts on local wildlife.

To resolve the phylogeny of one of the least studied felids in the world and to elucidate the evolutionary dynamics of the wildcats and domestic cats in East Asia, we assembled thus far the most comprehensive set of samples of the Chinese mountain cat over its entire range in the Tibetan region, the Asiatic wildcat from Xinjiang, and domestic cats across China, especially from those regions sympatric, parapatric, and allopatric with the Chinese mountain cat. Our data from both whole-genome sequencing (WGS) and uniparental mitochondrial DNA (mtDNA) and Y chromosome haplotype sequencing jointly showed that the Chinese mountain cat *F. s. bieti* and Asiatic wildcat *F. s. ornata* are equidistant and conspecific within the wildcat (*F. silvestris*). We also revealed an ancient introgression between *F. s. bieti* and *F. s. ornata* and a complex pattern of contemporary gene flow from *F. s. bieti* into domestic cats across, but not beyond, its range. Last, China's domestic cats share a Near Eastern origin with worldwide domestic cats, thus suggesting a single, not multiple, domestication event of cats arising from the African wildcat (*F. s. lybica*).

RESULTS

Range-wide sampling and initial genetic screening of wildcats and domestic cats

We sampled from a wide distribution of domestic cats in China and two of its wildcat congeners in Northwest China. From domestic cats, we collected blood, tissue, or saliva samples from 239 outbreed, unrelated individuals from 23 sites throughout China, including three locations within, three on the periphery of, and 17 distant from the Chinese mountain cat core distribution (Table 1). The wildcat

Table 1. Numbers of wildcat (*Felis silvestris bieti* and *F. s. ornata*) and domestic cat (*F. s. catus*) samples used in this study. MtDNA, mitochondrial DNA.

Scientific name	Common name	Sample source	Total no. of samples	MtDNA haplogroup				Y-chr haplogroup				No. of samples WGS*
				bieti	*ornata*	*catus*	Total	*bieti*	*ornata*	*catus*	Total	
F. s. bieti	Chinese mountain cat	modern	12	8	4	0	12	6	0	0	6	4
		museum	15	8	3	0	11	0	0	0	0	0
		Total	**27**	**16**	**7**	**0**	**23**	**6**	**0**	**0**	**6**	**4**
F. s. ornata	Asiatic wildcat	**Total**	**4**	**0**	**4**	**0**	**4**	**0**	**1**	**1**	**2**	**1**
F. s. catus	Domestic cat	*F. s. bieti* core range†	45	0	0	44	44	3	0	20	23	10
		F. s. bieti peripheral range‡	35	0	0	35	35	0	0	13	13	5
		Areas without *F. s. bieti*§	159	0	0	155	155	0	0	47	47	31
		Total	**239**	**0**	**0**	**234**	**234**	**3**	**0**	**80**	**83**	**46**

*WGS, whole-genome sequencing.　†*F. s. bieti* core range refers to western Qinghai and northwestern Sichuan on the Qinghai-Tibet Plateau.　‡*F. s. bieti* peripheral range refers to the junction area of northern Qinghai and southern Gansu on the edge of the Qinghai-Tibet Plateau.　§All other areas in China without any historical or present distribution of *F. s. bieti*.

Fig. 1. Wildcats (*F. s. bieti* and *F. s. ornata*) and domestic cats (*F. s. catus*) sampled from China. (**A**) Sampling localities and range of wildcats and domestic cats in China. Labels at each sampling site indicate the numbers of individuals in each of the following categories (separated by slashes): total sample size, with that of *F. s. catus* proportional to the circle area; samples with mtDNA (Mt) fragment data; samples with Y chromosome (Ychr) fragment data; and samples with WGS (autosome) data. Individual animal codes are in parentheses. Morphologically confirmed *F. s. bieti* individuals with *F. s. ornata* mtDNA haplotype and *F. s. catus* individuals with *F. s. bieti* Ychr haplotype are underlined in red and blue, respectively. The lower left panel summarizes sample sizes from each taxon and their population genetic backgrounds based on mtDNA, Ychr, and autosomal single-nucleotide variants (SNVs). Sympatry refers to domestic cats either from or not from the *F. s. bieti* range and gray, blue, and red correspond to the *F. s. catus*, *F. s. bieti*, and *F. s. ornata* clades, respectively. (**B**) Morphology of representative individuals from a "purebred" *F. s. bieti* (left), an *F. s. bieti* with an *F. s. ornata* mtDNA haplotype (middle), and an *F. s. catus* with an *F. s. bieti* Ychr haplotype (right). Photo credit: Shu-Jin Luo and Hao Meng, Peking University.

collection included four Asiatic wildcats *F. s. ornata* from Xinjiang and 27 Chinese mountain cats *F. s. bieti* across their full range on the Qinghai-Tibet Plateau spanning Qinghai, Gansu, and Sichuan Provinces. Twelve of the 27 *F. s. bieti* were tissues or blood from road kills or zoo animals, and 15 were pelts or bones from museums or local villages (Fig. 1A and data file S1).

A multilocus screening, based on partial mtDNA and Y chromosome sequencing, was performed in all samples (270 specimens for mtDNA and 103 for Y chromosome analysis) for an initial understanding of the genetic diversity patterns in the wildcat and domestic cat populations. A statistical parsimony network based on both markers revealed three distinct clusters that corresponded to the domestic cat *F. s. catus*, the Asiatic wildcat *F. s. ornata*, and the Chinese mountain cat *F. s. bieti* (Fig. 2A). Beginning with modern samples ($N = 255$), we amplified a 2620-bp (base pair) mtDNA fragment

spanning *ND5*, *ND6*, and *CytB* to distinguish 106 variable sites and 52 unique mtDNA haplotypes in 250 samples, including five haplotypes from 12 Chinese mountain cats, three from four Asiatic wildcats, and 44 from 234 domestic cats (data file S2). One-third (4 of 12) of the modern Chinese mountain cat specimens carried two mtDNA haplotypes that aligned with those of Asiatic wildcats, while the other eight individuals had three haplotypes exclusively found in the *F. s. bieti* clade. For degraded DNA extracted from museum samples ($N = 15$), we separately amplified four short fragments within the 2.6-kb mtDNA haplotype and concatenated them into 400 to 1000–base pair (bp) sequences (table S1). This yielded a similar proportion of individuals with the admixed genetic background, as 3 of the 11 succeeded Chinese mountain cat museum specimens were different from the rest and contained the Asiatic wildcat diagnostic variants (data file S2).

Fig. 2. Phylogenetic relationships among wildcat lineages and domestic cats. (**A**) Statistical parsimony networks of *Felis silvestris* and *F. s. catus* based on mtDNA and Ychr fragments. The larger a haplotype's circle, the more individuals share that haplotype. Colors represent the morphology-based taxonomic classifications of the animals (red, *F. s. ornata*; blue, *F. s. bieti*; gray, *F. s. catus*). (**B**) Bayesian phylogenies of *Felis* spp. based on the mitochondrial genome (excluding the control region) and the Ychr single-copy region. The branches are color-coded to coordinate with the morphology-based taxonomic classification of the taxon with the same-colored name. The shaded boxes are color-coded to correspond to the genetic affiliations of the three clades of interest in this study. Asterisks mark individuals with morphological appearances that disagree with their genetic affiliation based on certain genetic markers. (**C**) Phylogeny of *Felis* spp. based on genome-wide autosomal neutral SNVs reconstructed using the neighbor-joining method and a distance matrix calculated following Gronau's method, with the bootstrap support values marked on major nodes. The branches are color-coded as in (B) and the asterisks on certain branches correspond to the same individuals marked in (B).

We assembled two Y chromosome fragments from *DBY7* and *SMCY7* from 103 male cats and, based on six indels and single-nucleotide variants (SNVs) from the concatenated 1015-bp sequences, found three distinctive Y haplotypes from 91 succeeded samples, each representing one of the three *Felis* taxa in the study (table S1 and data file S3). The Y chromosome haplotype network revealed patrilineal introgression between wildcats and domestic cats. Three domestic cats, from Qinghai and Sichuan, which are within the

Chinese mountain cat *F. s. bieti* core range, shared the signature *F. s. bieti* Y haplotype, and one Asiatic wildcat *F. s. ornata* showed a Y chromosome haplotype typical for domestic cats *F. s. catus* (Fig. 2A).

Genome-wide phylogeny and taxonomy of the Chinese mountain cat

On the basis of adequate DNA quality, we selected 55 representative samples (8 Chinese mountain cats, 1 Asiatic wildcat, and 46 domestic

cats) for Illumina paired-end sequencing, subsequently generating mitogenome and WGS data for 51 of these samples (including four Chinese mountain cats *F. s. bieti*, B1, B2, B3, and B4) at 6.8 to 15.1 times coverage per individual. Only the mitochondrial genome was reconstructed for the other four Chinese mountain cats (B5, B6, B7, and B8) because of sample quality constraints (data file S4). Raw sequencing reads from 20 domestic cats and two black-footed cats (*Felis nigripes*) were downloaded from the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) (NCBI, Bethesda, MD). Our final dataset of 73 nuclear genomes had an average of 16× coverage and 20,425,451 biallelic autosomal single-nucleotide variants (SNVs) after quality filtering and masking. We also retrieved 66 different mitogenomes from 77 individuals, including six from eight *F. s. bieti* specimens (B1, B2/B5, B3/B8, B4, B6, and B7), and combined them with seven published genomes of *Felis* genus (one from *F. s. bieti*) (8) for downstream analyses.

Phylogenies reconstructed from mitogenome, Y chromosome, and the autosomal neutral region illuminated the evolution and taxonomy of the Chinese mountain cat in relation to other wildcats and domestic cats. Phylogenetic inference based on mitochondrial sequences, excluding the control region, clusters all taxa—including the Asiatic wildcat (*F. s. ornata*), European wildcat (*F. s. silvestris*), Chinese mountain cat (*F. s. bieti*), and a haplogroup containing all domestic cats (*F. s. catus*) and African wildcats (*F. s. lybica*)—into a single *F. silvestris* clade, with *F. s. ornata* situated as the basal lineage within the clade, although support of the node was not strong (Fig. 2B and fig. S1).

The patrilineal genealogy of the 929-kb Y chromosome single-copy region assembled from all available *Felis* spp. sequencing data also clustered *F. s. catus*/*F. s. lybica*, *F. s. bieti*, and *F. s. ornata* into one monophyletic group that is distinct from outgroup *F. nigripes*, despite an unresolved internal phylogeny among the three (Fig. 2B). In the neighbor-joining tree based on autosomal SNVs and average genomic divergence matrices (24), *F. s. bieti* (B1 to B4) and *F. s. ornata* (O1) formed a clade that diverged early before the domestic cat radiation (Fig. 2C). Notably, all phylogenomic inferences placed the Chinese mountain cat within the *F. silvestris* subspecies clade, distinguishing it from other congeneric outgroup species: the black-footed cat (*F. nigripes*), the sand cat (*F. margarita*), and the jungle cat (*F. chaus*). These genome-wide phylogenetic patterns provided robust evidence for a close association of the Chinese mountain cat with the other *F. silvestris* taxa and corroborated the previously suggested reclassification of *F. bieti* as a subspecies of *F. silvestris* (3, 8).

The phylogenies based on mtDNA or Y chromosome data showed that domestic cats from China were indistinguishable from those of other regions of the world, thus supporting a single domestication event for all domestic cats arising from the African wildcat (*F. s. lybica*). Nevertheless, all domestic cats from East Asia, including those from China and one from South Korea (W9; see data file S4), formed a monophyletic group in the autosomal phylogeny, thus indicating a recent association among East Asian domestic cats (Fig. 2C).

The discordant phylogenies inferred from maternal, paternal, and biparental genetic markers likely resulted from incomplete lineage sorting and/or hybridization among lineages (8). Consistent with the patterns from partial mtDNA and Y chromosome genealogies, mitogenomes from three voucher Chinese mountain cats *F. s. bieti* (B4, B6, and B7; Fig. 1) clustered within the Asiatic wildcat *F. s. ornata*,

and two domestic cats (C8 and C12; Fig. 1) carried *F. s. bieti* signature Y chromosome haplotypes (Fig. 2B). Genome-wide autosomal phylogeny (Fig. 2C) illustrated robust monophyly of individuals from *F. s. catus*, *F. s. bieti*, and *F. s. ornata*, with no apparent interlineage genetic admixture (thus excluding errors of morphological misidentification). In addition, both Bayesian coalescence analyses based on mitogenome and Y chromosome sequences estimated the time to the most recent common ancestor of *F. s. catus*, *F. s. bieti*, and *F. s. ornata* at around 1.5 million years (Ma) ago during the Middle Pleistocene (fig. S1), consistent with estimations from earlier studies (8, 25). Such a relatively rapid and recent divergence of these lineages may have led to the phylogenetic discordance observed in different genealogies.

Genetic introgression from Chinese mountain cats to domestic cats

Principal components analysis (PCA) of autosomal neutral SNVs detected strong signal partitioning among the three *F. silvestris* clades (Fig. 3A). The first PC (PC1), which maximized 36% of the variance, distinguished black-footed cats from the other *F. silvestris* taxa, thus indicating a species-level divergence. The Chinese mountain cat, Asiatic wildcat, and domestic cat were separated along PC2, which explained 10% of the variance and suggested a subspecies-level divergence. PC3 revealed the intraclade genomic diversity within domestic cats that segregated Chinese domestic cats from other, worldwide cat populations. Also, alternative pairwise population genetic difference estimates also revealed a similar hierarchical variance partitioning among the five groups (table S2), with the F_{ST} between *F. nigripes* and the other four groups larger than 0.7, the F_{ST} between *F. s. bieti*, *F. s. ornata*, and *F. s. catus* markedly lower (0.3 to 0.7), and the F_{ST} between Chinese and worldwide domestic cat populations as low as 0.1.

The ADMIXTURE Bayesian analysis of autosomal neutral SNVs clustered 72 cats into four groups whose primary genomic affiliations correlated with black-footed cats, Chinese mountain cats, Chinese domestic cats, or worldwide domestic cats (Fig. 3B and fig. S2) (*F. s. ornata* was excluded due to its limited sample size). Notably, domestic cats from the Chinese mountain cat's core range in Sichuan and Qinghai (N = 10, C6 to C15 in Fig. 1A) carried about 10% genomic ancestry from *F. s. bieti*, indicating an extensive introgression from Chinese mountain cats to their sympatric domestic cats.

D statistics further assessed the extent of genetic admixture between Chinese mountain cats and China's domestic cats while using the worldwide domestic cat data as a baseline. We quantified the level of wildcat genetic introgression in each domestic cat by determining the fraction of diagnostic sites, *f* statistics, and f_4 ratio test results (Fig. 3C and table S3). All 10 domestic cats sympatric with Chinese mountain cats displayed significant admixture signals in *D* statistics, with the average *z* score ranging from 6.9 to 11.4, and the fraction of introgression between 4 and 12%, a result consistent with the estimated ancestry proportion in population clustering analysis (Fig. 3B). We also detected introgression signals in five domestic cats (C1 to C5) collected from northern Qinghai and Gansu, a region peripheral to the Chinese mountain cat's range (see Fig. 1A). The exact proportion of *F. s. bieti* introgression in those individuals varied between 0.5 and 7% depending on the analysis method, but nevertheless significantly higher than that of domestic cats not from the Chinese mountain cat's geographic range (Figs. 1A and 3C and table S3). Overall, genetic introgression from Chinese mountain cats
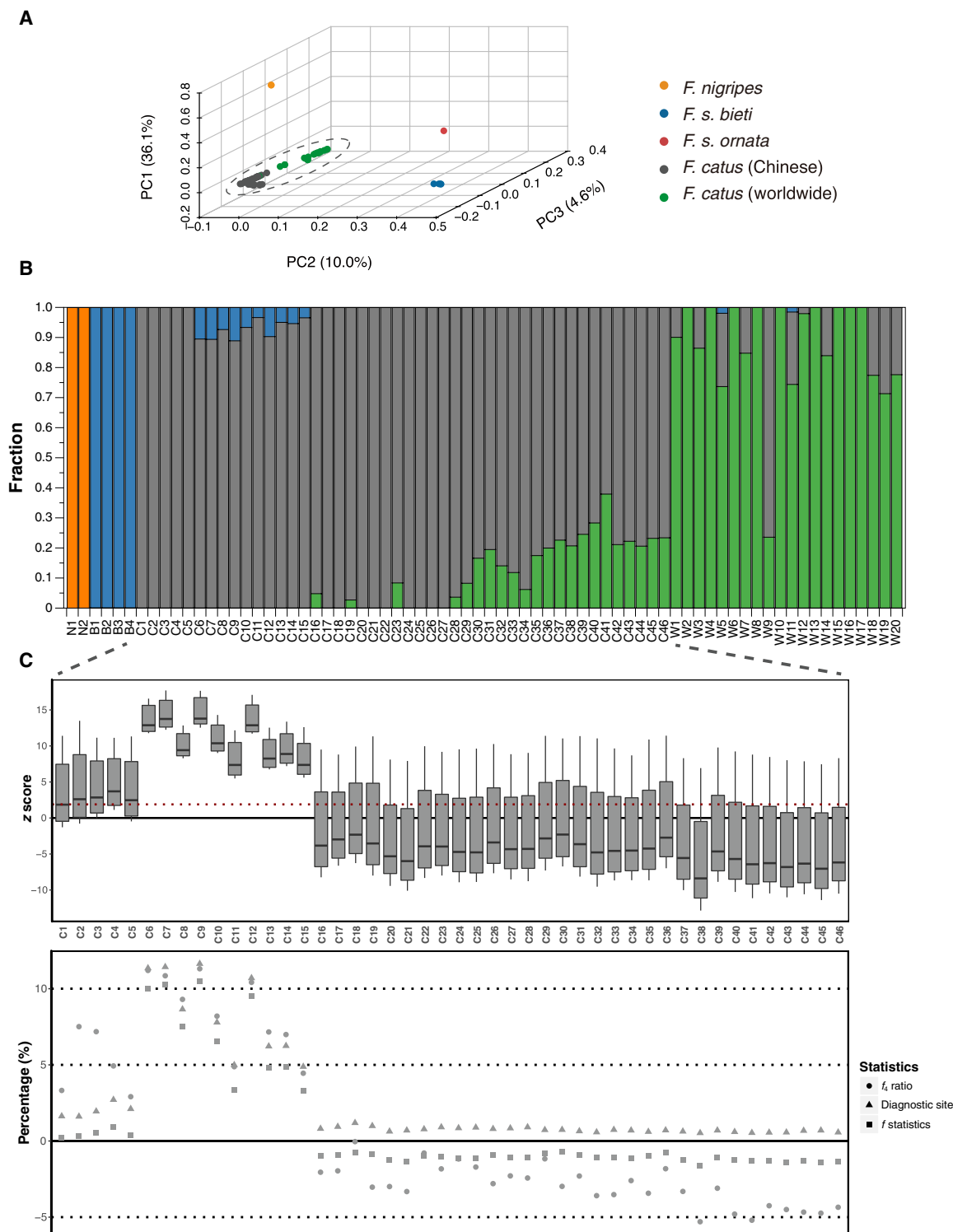
Fig. 3. Population genetic structure and introgression from Chinese mountain cats (*F. s. bieti*) to local domestic cats based on genome-wide neutral autosomal SNVs. (**A**) Principal components analysis (PCA) of 73 individuals showing only the first three PCs. Two black-footed cats (*F. nigripes*) were separated from the others with the first PC. The two wildcats, *F. s. bieti* and *F. s. ornata,* and *F. s. catus* (domestic cats) were separated with the second PC. *F. s. catus* individuals were partitioned along the third PC, with a moderate differentiation between domestic cats from China and those worldwide. (**B**) Population structure of 72 domestic and wildcat individuals estimated in ADMIXTURE with $K = 4$. The four clusters correspond to *F. nigripes*, *F. s. bieti*, *F. s. catus* from China, and *F. s. catus* worldwide, with 10 *F. s. catus* (C6 to C15) carrying about 10% genetic admixture from *F. s. bieti*. (**C**) Genomic admixture between *F. s. bieti* and *F. s. catus* from China (C1 to C46) estimated by D statistics, the f_4 ratio test, percentage of *F. s. bieti* diagnostic sites in the genome of *F. s. catus*, and f statistics. The D statistics results are summarized as boxplots showing the z-scores distribution of each *F. s. catus* and a significance level of $z > 2$ (red dotted line). Plotted percentages of diagnostic sites, f_4 ratio, and f statistics reveal the genomic admixture levels from *F. s. bieti* to each *F. s. catus* in the dataset.
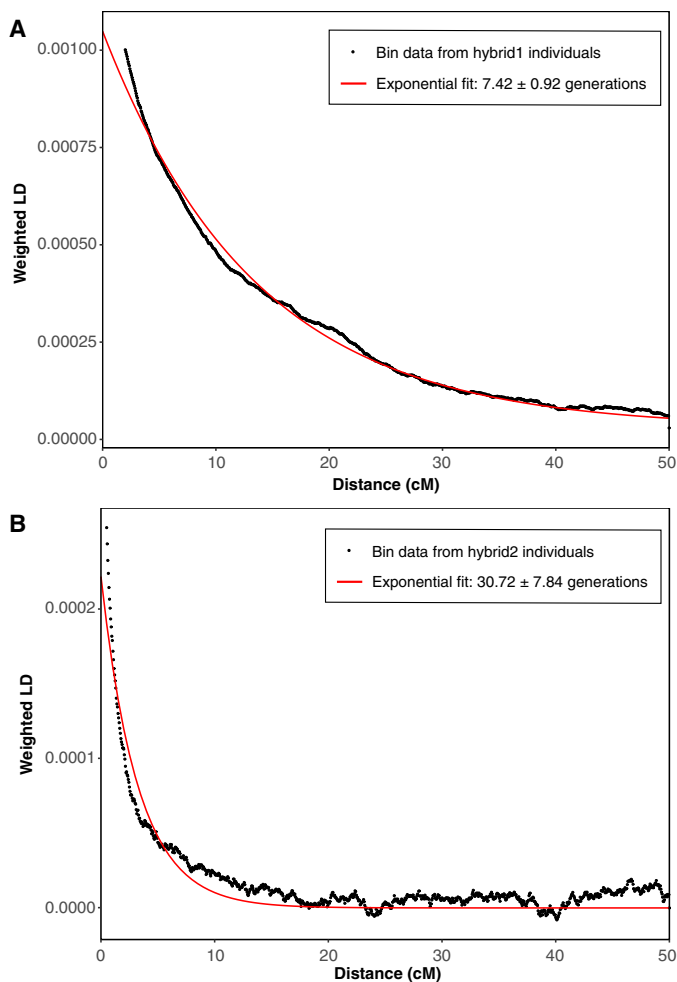
Fig. 4. Estimates of the timing of hybridization between Chinese mountain cats and sympatric domestic cats based on LD decay. Weighted LD curves with putative pure Chinese domestic cats and Chinese mountain cats as two reference populations for the (**A**) hybrid1 population with an exponential fit starting at 2.0 cM and (**B**) hybrid2 population with an exponential fit starting at 0.5 cM.

to domestic cats is restricted to the sympatric area in Qinghai, Sichuan, and Gansu, and the proportion of wildcat admixture in domestic cats decreases with increasing distance away from the Chinese mountain cat's core distribution. Notably, because none of the domestic cats with *F. s. bieti* genetic introgression appeared morphologically different from other domestic cats, morphological characters are likely not reliable diagnostic markers to identify hybrids.

We further examined the fine-scale distribution of the putative introgression regions within the genomes of the admixed domestic cats (C6 to C15) to determine whether the observed introgression in the sympatric domestic cats was introduced recently or was from ancient signals preserved in the population. On the basis of diagnostic SNVs, large continuous genomic segments (each more than 30 Mb) with Chinese mountain cat ancestry were identified in 6 of the 10 domestic cats (fig. S3). This indicated possible recent hybridization events between Chinese mountain cats and domestic cats because long-range linkage disequilibrium (LD) across the wildcat chromosomes had not been completely disrupted by recombination.

Individual C8, a domestic cat from eastern Qinghai that carried a Chinese mountain cat–like Y chromosome haplotype (Fig. 1B), displayed an extended, more than 30 Mb, homozygous region with both alleles from the Chinese mountain cat, a pattern consistent with a recent hybridization event that was reinforced by possible further interbreeding between the fertile hybrid offspring.

We dated the unidirectional introgression from the Chinese mountain cat *F. s. bieti* to its sympatric domestic cat population in the Tibetan area based on the extent of LD decay computed in ALDER (*26*). Domestic cats C6 to C15 from the core *F. s. bieti* range (namely, "hybrid1") and C1 to C5 from the *F. s. bieti* distribution periphery (namely, "hybrid2") were referred to as two admixed populations. The genomic introgression in the hybrid1 population was well supported ($P = 8.30 \times 10^{-16}$), with an exponential fit starting at 2 centimorgan (cM) (table S4), and was estimated to have occurred about 7.42 generations earlier (Fig. 4A). Using a generation time of 2 years for the domestic cat, hybridization between Chinese mountain cats and domestic cats on the Qinghai-Tibet Plateau occurred about 15 years ago. We also detected a significant admixture signal ($P = 8.90 \times 10^{-5}$) in the hybrid2 population, estimated to be about 30.72 generations or about 62 years ago (Fig. 4B).

Evolutionary history of wildcats and domestic cats

We used the pairwise sequential Markovian coalescent (PSMC) model to understand the demographic histories, dispersals, and divergences of the wildcat and domestic cat clades within China (Fig. 5A). Both the Chinese mountain cat *F. s. bieti* and the Asiatic wildcat *F. s. ornata* displayed a moderate population expansion 1 to 2 Ma ago, followed by a constant, gradual decline. The effective population size (*Ne*) of the African wildcat (*F. s. lybica*), as represented by the genomic diversity of the domestic cat (*F. s. catus*), experienced a drastic rise around 100 to 400 (Ka) ago during the Middle to Late Pleistocene, which may reflect an ancient range expansion and/or population growth.

We used the coalescent-based Generalized Phylogenetic Coalescent Sampler (G-PhoCS) to estimate the population divergence times and migration scenarios among *F. s. bieti*, *F. s. ornata*, and *F. s. catus*/*F. s. lybica* using *F. nigripes* as the outgroup for time calibration (Fig. 5B). Using a given topology based on the autosomal phylogeny (Fig. 2C), we performed 12 independent analyses using all the combinations between one of the three domestic cats (C20, C25, and W19) and one of the four Chinese mountain cats (B1 to B4; fig. S4 and table S5). The coalescent time of *F. s. catus* and *F. s. bieti*/*F. s. ornata* lineages was estimated to be around 1.87 Ma ago [95% highest posterior density (HPD) at 1.76 to 1.97 Ma ago], and then *F. s. bieti* and *F. s. ornata* coalesced around 1.27 Ma ago (95% HPD at 1.19 to 1.37 Ma ago). We detected four significant interlineage migration bands, indicating the presence of gene flow from *F. s. catus* to *F. s. ornata* and from *F. s. ornata* to *F. s. bieti*, with a total migration rate of about 0.1, and from the *F. s. bieti*/*F. s. ornata* lineage to *F. s. catus*, with a total migration rate of about 1.5 (Fig. 5B). The total migration rate from *F. s. catus* to *F. s. bieti* was minor and varied among different analyses from 0 to 0.09, with only one analysis that included B2 showing a significant level of gene flow. This observation confirmed that the hybridization between domestic cats and Chinese mountain cats was recent, and hence, the extent of genetic influence in *F. s. bieti* varied by individual. The effective population sizes estimated by G-PhoCS and PSMC were well correlated, with the *Ne* of the ancestor of *F. s. catus*/*F. s. bieti*/*F. s. ornata* lineages around 157,000, the *Ne* of
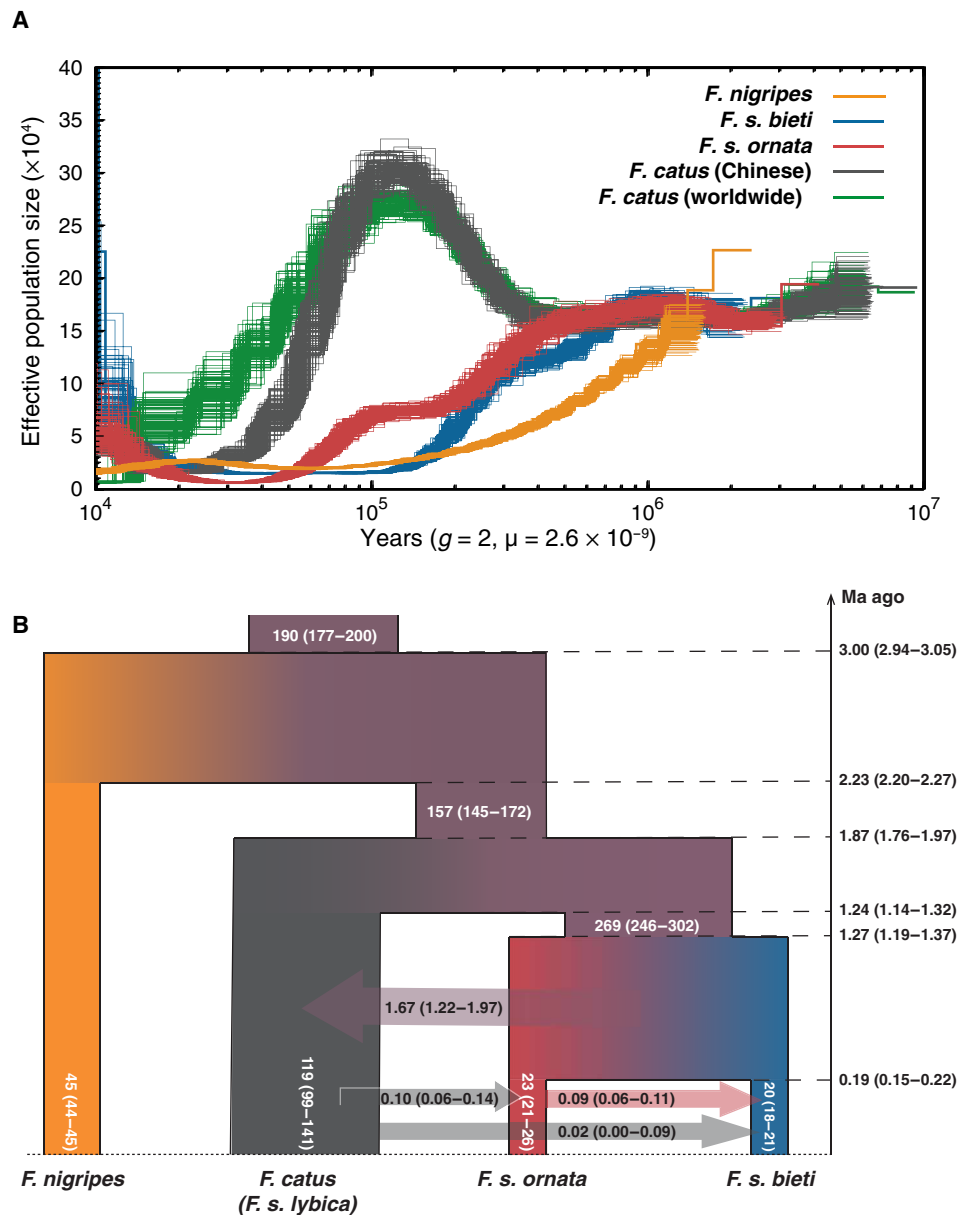
Fig. 5. Demographic history of wildcats and domestic cats estimated by PSMC and G-PhoCS. (**A**) Population dynamics estimated in a PSMC model of five individuals representing *F. nigripes*, *F. s. bieti*, *F. s. ornata*, *F. s. catus* from China, and *F. s. catus* worldwide, with 100 bootstrap replicates. The results from *F. s. catus* individuals represent the dynamics of their wild ancestor, *F. s. lybica*. *g*, average generation time; μ, mutation rate. (**B**) Demographic model with divergence and migration among *F. nigripes*, *F. s. bieti*, *F. s. ornata*, and *F. s. catus*, with the effective population sizes (in thousands), divergence times (in million years), and total migration rates estimated by the Generalized Phylogenetic Coalescent Sampler. Within the graph, the values and ranges outside and within the parentheses represent the average and combined 95% Bayesian credible intervals, respectively, of each estimated parameter, and the branch widths are proportional to effective population sizes.

the common ancestor of *F. s. bieti* and *F. s. ornata* lineages increasing to about 269,000, and the current population sizes of *F. s. bieti* and *F. s. ornata* shrinking to about 20,000 and 23,000, respectively.

DISCUSSION
Using WGS data generated from 46 domestic cats sampled across China, we found that both phylogenomic and population structure analyses clustered domestic cats from China and worldwide into one

panmictic group (Figs. 2 and 3A and table S2), thus supporting the single-origin scenario of all domestic cats being derived from the Near Eastern wildcat (*3*, *4*). However, autosomal phylogeny (Fig. 2C) and ADMIXTURE (Fig. 3B) also revealed a close genetic association among domestic cats from China and South Korea that distinguished them from other populations in the world. This pattern implies a certain degree of isolation of domestic cats in East Asia after they dispersed to or were introduced into this region. Although our sampling of domestic cats in China specifically targeted local cats and

avoided cat breeds originally from regions outside China, we also detected genetic introgression from the worldwide cat population in several individuals from southeastern China, which could be due to recent genetic interactions with introduced cats from other countries into the gene pool of local feral cats.

There is no statistical evidence suggesting a significant contribution from local wildcats into the genetic ancestry of modern domestic cats in East Asia, yet a complex hybridization scenario among domestic cat and wildcat lineages in the area was revealed. Genomic analyses indicate ancient admixture events between the Chinese mountain cat and the Asiatic wildcat, introgression from the domestic cat to the Asiatic wildcat (Figs. 2A and 5B), and recent genetic interaction between the Chinese mountain cat and its sympatric domestic counterparts (Figs. 2 and 3) on the Qinghai-Tibet Plateau.

First, an ancient, unidirectional introgression from the Asiatic wildcat *F. s. ornata* to the Chinese mountain cat *F. s. bieti* was evident, as we observed only the "misplacement" of *F. s. ornata* mtDNA haplotype in *F. s. bieti* but not vice versa (Fig. 2), and only the migration band from *F. s. ornata* to *F. s. bieti* was significant in the G-PhoCS analysis (Fig. 5B). The signal of *F. s. ornata* admixture in *F. s. bieti* was apparent only in the maternally inherited mitochondrial lineages, while a genome-wide autosomal phylogeny and clustering algorithm supported monophyly for all morphologically distinguishable *F. s. bieti*. This cytonuclear discrepancy is consistent with an ancient admixture scenario in which a female *F. s. ornata* mated with a male *F. s. bieti*, and then their offspring backcrossed with *F. s. bieti* for a long period of time. Such asymmetric hybridization has been reported in various mammalian lineages—including Neotropical wild cats (*Leopardus* spp.), canids in North America, and African savannah and forest elephants (*13*, *27*, *28*)—and was generally associated with population size contrasts and mating preferences when two lineages met (*29*). Likewise, the asymmetric introgression between the two wildcat lineages in Asia could be explained by the larger body size of *F. s. bieti* relative to *F. s. ornata*. Perhaps, larger males were preferred by female *F. s. ornata*, thus giving male *F. s. bieti* a mating advantage. When the ancient *F. s. bieti* population overlapped with the range of *F. s. ornata*, whose population size was supposedly large, such admixture could have occurred, leaving the signal in the contemporary *F. s. bieti* genome.

Another unidirectional *F. s. lybica*/*F. s. catus* to *F. s. ornata* introgression was revealed via Y chromosome genealogy and G-PhoCS analysis (Figs. 2A and 5B). That interlineage gene flow could also be explained by the difference in the population sizes of ancient African and Asiatic wildcat populations (Fig. 5A) and/or the dispersal of postdomestication *F. s. catus* into Central Asia during the last millenniums. However, we were unable to investigate further because of both our small sample size and the uncertainty regarding the exact geographic origin of the specimens. Further study may reveal whether the introgression occurred between the historical African and Asiatic wildcats before cat domestication or between free-ranging domestic cats and Asiatic wildcats, a scenario resembling the genetic infiltration of feral domestic cats into the native European wildcat population in Scotland (*30*).

Because the Chinese mountain cat is the only wildcat endemic to the Qinghai-Tibet Plateau of China, its genetic integrity has been a subject of scientific interest and conservation concern. Genomic introgression from the Chinese mountain cat to its sympatric domestic cats was widespread (Fig. 4) and was estimated to be a contemporary, not an ancient, event. We observed a gradual decrease of *F. s. bieti*

genetic contribution in domestic cats and older hybridization incidences as we progressed from the center (e.g., Aba in western Sichuan and Golog in eastern Qinghai) to the margins (e.g., Jiuquan in western Gansu and Xining in northern Qinghai) of the *F. s. bieti* range. The noticeable genetic admixture in domestic cat populations in the western Sichuan–eastern Qinghai boundary (*F. s. bieti* core range) and western Gansu–northern Qinghai area (peripheral range) dated back to 7 and 30 generations ago, respectively, corresponding to the beginning of the 21st century and mid-20th century. Because the signals of the earlier interbreeding could have likely been concealed by later events if multiple waves of population admixture recurred (*26*), the contrast between the timing of admixture in domestic cats from different locations may reflect a continuous gene flow from Chinese mountain cats to domestic cats during the last century. This scenario is also consistent with a pattern of more recent introgression in the areas occupied by abundant Chinese mountain cats that are in constant contact with domestic cats, whereas relatively older hybridization signals have been preserved in cats located in the peripheral *F. s. bieti* distribution.

Since the 1950s, Chinese population census data have recorded a marked increase in the numbers of households and residents on the Qinghai-Tibet Plateau (*31*), a trend that coincides with the earliest *F. s. bieti* to *F. s. catus* admixture in Qinghai as documented in this study. Unlike dogs, cats are not generally associated with the traditional pastoral nomadic Tibetan lifestyle, and it is likely that the arrival and establishment of domestic cats on the Plateau is relatively recent. Regional socioeconomic development, immigration into the highlands, and alterations in local livelihoods may have facilitated an expansion of free-ranging domestic cats, setting the stage for their close contact, frequent interaction, and possible interbreeding with the sympatric Chinese mountain cat. An exact population status of the Chinese mountain cat in the wild is unknown, but, nevertheless, it is sparse and at a low density (*32*). Therefore, the Chinese mountain cat could possibly face a similar crisis as that of the European wildcat and lose its genetic integrity and evolutionary adaptation to the local environment because of introgression from an increasingly dominant local domestic cat population (*22*, *33*).

Gene flow from the domestic cat to the Chinese mountain cat *F. s. bieti* was detected in the G-PhoCS analysis (Fig. 5B), despite a large variance in the estimates of total migration rates when different pairs of domestic cats and Chinese mountain cats were tested. Such fluctuation across individuals is consistent with recent introgression events in which the extent of introgression varies by individual within the Chinese mountain cat population (fig. S3). Unlike the abovementioned admixture analysis, no significant gene flow signals were detected from Chinese mountain cats to domestic cats in the G-PhoCS analysis. As the domestic cats used in G-PhoCS were from areas far from the Chinese mountain cat range, this scenario mostly likely resulted from a contemporary admixture that was restricted to the local sympatric cats and it exerted minor or no effect on domestic cat populations elsewhere.

The Felidae taxonomy by Kitchener *et al.* (*5*) considers the Chinese mountain cat its own species while maintaining the Asiatic wildcat as a subspecies. In our population genomic analysis, the Chinese mountain cat, the Asiatic wildcat, and the domestic cat are equidistant, corroborating a subspecies-level recognition of these groups. The WGS of the Chinese mountain cat, Asiatic wildcat, and domestic cat from China and worldwide, together with publicly available partial genomic data for the European wildcat and African

wildcat, provide support to the classification of the Chinese mountain cat as a wildcat subspecies, *F. s. bieti*. Phylogenetic analyses based on mitogenome, Y chromosome, and genome-wide autosomal markers (Fig. 2) demonstrated a monophyletic placement of the Chinese mountain cat and other wildcat subspecies (*F. s. catus*, *F. s. ornata*, and *F. s. silvestris*) within one clade, rather than a species-level distinctiveness between them (*34*). The estimated divergence time between those *F. silvestris* subspecies is around 1.5 Ma ago, which agrees with previous estimates based on nuclear sequence fragments and SNP arrays (*8, 25*) and is more recent than the divergence between the accepted *Felis* species (i.e., *F. chaus*, *F. margarita*, *F. nigripes, and F. silvestris)* at around 3 Ma ago. PCA results also reflect a threefold smaller genetic distance among *F. silvestris* subspecies compared to their species-level divergence with *F. nigripes*. Nevertheless, we do not exclude an alternative to resolve the conflict between the genomic pattern and current taxonomic nomenclature, which is to elevate all wildcat lineages, including the Asiatic wildcat (*F. s. ornata*) and African wildcat (*F. s. lybica*), to independent species statuses, or *F. ornata* and *F. lybica*, respectively, thus retaining the Chinese mountain cat as *F. bieti* to be consistent. This would however require a comprehensive analysis including whole-genome data from all wildcat taxa, especially those from *F. s. silvestris*, *F. s. ornata*, and *F. s. lybica*.

Evidently, this study shows that interlineage admixture of the Chinese mountain cat *F. s. bieti* and its closely related taxa further supports the inclusion of all lineages as wildcat conspecifics based on the biological species concept, which considers interbreeding as the prerequisite for a species (*35*). The key argument from the proponents for the species status of the Chinese mountain cat lies on its distinctive morphological characters, a presumed sympatric distribution with the Asiatic wildcat, and an absence of gene flow between free-ranging Chinese mountain cats and Asiatic wildcats (*9*). However, recent surveys in Northwest China showed that the range attributed to the Asiatic wildcat may have been overestimated and that its presumed presence on the Qinghai-Tibet plateau in northeastern Qinghai (*36*) may not be true. That assertion, if proven, would dispute the supposed sympatry of the two lineages. In addition, extensive genetic exchange between those two lineages was revealed through the presence of *F. s. ornata*–like mitochondrial lineages in voucher Chinese mountain cats (Fig. 2). A significant migration band (total migration rate of 0.09) from the Asiatic wildcat to the Chinese mountain cat was also detected in demographic analysis with G-PhoCS analysis (Fig. 5B). Such interbreeding could diminish the morphological distinctions between the taxa, as we observed when a Chinese mountain cat with an *F. s. ornata*–like mtDNA haplotype did not have the typical thick and fluffy tail (Fig. 1B). Answers to the remaining questions require more surveys and studies to fine map the Asiatic wildcat and Chinese mountain cat distribution in Northwest China; to delineate the subspecies boundaries or hybrid zones; to elucidate the ancestry, adaptation, and evolution of these taxa; and to resolve the historical and current patterns of gene flow among the wildcat and domestic cat lineages in the region.

In conclusion, this study examined the genetic ancestry, population structure, and demographic history of wildcat and domestic cat lineages in East Asia from a whole-genome perspective. Phylogenomic and population genomic analyses based on voucher specimens verified that the Chinese mountain cat, a traditionally delineated felid species endemic to the eastern Qinghai-Tibet Plateau of China, is equidistant with other currently recognized wildcat lineages such as the Asiatic wildcat (*F. s. ornata*) and hence should be recognized as a conspecific, *F. s. bieti*. We revealed ancient introgression between *F. s. bieti* and *F. s. ornata* as we found two deeply divergent mtDNA lineages within *F. s. bieti*. Domestic cats (*F. s. catus*) in China clustered with other cat populations worldwide, supporting the single, Near Eastern origin of cat domestication from the African wildcat (*F. s. lybica*), followed by the domestic cats' subsequent global spread. Contemporary genetic introgression from *F. s. bieti* into sympatric domestic cats is evident across, but not beyond, the range of *F. s. bieti*. The timing of admixture coincided with large-scale socioeconomic changes in the Tibetan area during the mid-20th century. That process likely led to an expansion of domestic cats into the region and suggests that domestic cats arrived rather late to the Plateau and thus had not encountered *F. s. bieti* until recently. The increasingly abundant local domestic cat population may pose a threat to the Chinese mountain cat and jeopardize its genetic integrity and evolutionary adaptation to high altitude, an issue with profound conservation implications and worth further study.

MATERIALS AND METHODS
Sample preparation
We collected samples from 27 Chinese mountain cats (*F. s. bieti*), 4 Asiatic wildcats (*F. s. ornata*), and 239 domestic cats (*F. s. catus*), all with known geographic locations. *F. s. bieti* specimens included feces, blood, skin tissues, dry pelt, and skulls from zoos, museums, or local villages in Qinghai, Sichuan, and Gansu; a collection effort that represents the largest ever range-wide sampling of this taxon (data file S1). *F. s. ornata* samples included blood or dry skin from southern Xinjiang. Last, we sampled buccal swab, blood, or skin tissues from outbred, unrelated *F. s. catus* from 23 sites across China, particularly areas that are sympatric, parapatric, or allopatric with the Chinese mountain cat (Fig. 1 and data file S1). All samples were recruited in compliance with the Convention on International Trade in Endangered Species of Wild Fauna and Flora through permissions issued to the School of Life Sciences (principal investigator: S.-J.L.), Peking University, by the State Forestry Administration of China.

We extracted genomic DNA from blood or skin tissues using the DNeasy Blood and Tissue Kit (QIAGEN, Valencia, CA, USA) and from fecal samples using the QIAamp DNA Stool Mini Kit (QIAGEN), both following the manufacturer's protocols. We collected DNA from buccal swab samples using a PERFORMAgene PG-100 collection kit (DNA Genotek, Ottawa, ON, Canada) and extracted DNA using the buffer and protocol provided by the kit. DNA concentrations and quality were examined with the NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and diluted to working solutions for further analysis.

Genomic DNA extraction from museum samples was performed in a dedicated ancient DNA laboratory and followed a modified silica-based spin column method and standard ancient DNA criteria while maintaining strict precautions to minimize contamination risk from modern DNA samples and facilities (*37*). For each specimen, 10 to 30 mg of skin tissue were pulverized in liquid nitrogen, washed twice with ddH$_2$O, and digested at 55°C overnight with 600 μl of ATL buffer from the DNeasy Blood and Tissue Kit (Qiagen), 24-mAU proteinase K (Qiagen), and 7 μl of 1 M dithiothreitol. After digestion, we purified the DNA using a silica column from a QIAquick polymerase chain reaction (PCR) purification kit (Qiagen) and kept the products at 4°C before subsequent downstream analysis.

Multilocus sequencing with mtDNA and Y chromosome DNA markers

We used PCR primers, redesigned based on published *F. silvestris* mtDNA sequences (*3*), to amplify a 2.7-kb mtDNA fragment spanning *ND5*, *ND6*, and *CytB*, and then selected four short fragments (200 to 400 bp each) within this region to amplify highly degraded DNA from museum samples. Two Y chromosome DNA fragments encompassing the *DBY7* and *SMCY7* intronic regions that had been used previously in mammals and Felidae (*38*, *39*) were amplified in all male individuals to examine their patrilineal ancestry.

The 2.7-kb mtDNA and the Y chromosome fragments were separately amplified in a 15 μl of PCR reaction system containing 1× GC buffer I, 1.0 mM deoxynucleotide triphosphates (dNTPs), 1 U of TaKaRa LA Taq DNA polymerase (Takara Bio, Shiga, Japan), 0.4 μM each of forward and reverse primers, and 10 to 20 ng of genomic DNA. For DNA extracted from museum specimens, we set up PCR reactions in an ancient DNA laboratory room and followed a previously published protocol (*37*), optimizing each step to amplify the short mtDNA fragments in a 25-μl PCR reaction system containing 1× PCR buffer II, 5.0 mM MgCl₂, 0.8 mM dNTPs, 10 μg of bovine serum albumin, 1 U of AmpliTaq Gold DNA polymerase (Applied Biosystems, Waltham, MA, USA), 0.2 μM each of forward and reverse primers, and 5 μl of genomic DNA. PCR products were cleaned and sequenced on an ABI 3730XL sequencing system (Applied Biosystems) as described previously (*37*). DNA sequences were inspected in Sequencher v5.0 (Gene Codes Corporation, Ann Arbor, MI, USA) and concatenated into haplotypes for downstream analyses.

Genome sequencing and next-generation sequencing data processing

We constructed Illumina sequencing libraries with 300- to 500-bp inserts from 55 genomic DNA extracts, following the manufacturer's protocols (Illumina, San Diego, CA, USA). The sample set included eight *F. s. bieti*, three of which carried *F. s. ornata* mtDNA haplotypes; one *F. s. ornata*; and 46 *F. s. catus* across China, two of which carried *F. s. bieti* Y chromosome haplotype (Fig. 1A). The libraries were sequenced on an Illumina HiSeq X Ten platform at Novogene Co. (Beijing, China) to generate 150-bp paired-end reads. For four Chinese mountain cats with either low DNA quality or endogenous DNA content, we produced 2-Gb sequencing data per individual for mitochondrial genome assembly. For the remaining 51 samples including four Chinese mountain cats, one Asiatic wildcat, and all domestic cats, 30- to 40-Gb sequencing data per individual were generated for WGS. For additional comparison, we downloaded WGS data of 20 domestic cats representing a worldwide distribution and two black-footed cats (*F. nigripes*) from the NCBI SRA and included that data in our analyses.

To exclude nuclear mtDNA segment (Numt) interference while assembling the mitogenomes, the sequencing reads from each individual were first mapped to a domestic cat mitogenome reference sequence (accession no. U20753) using the Burrows-Wheeler Aligner (BWA) minimum essential medium (MEM) algorithm (*40*). We then assembled the mapped reads into mitogenomes without the control region via a de novo genome assembly approach in Geneious v.9.1.5 (www.geneious.com). From the 77 individuals sequenced from this and previous studies, mitogenomes of 66 *Felis* spp. were assembled and identified for further analysis.

For genome-wide SNV identification and genotyping, we mapped the WGS reads of 73 individuals to the domestic cat reference

genome assembly felCat8 [downloaded from the UCSC (University of California, Santa Cruz) genome browser (UCSC, CA, USA)] and the domestic cat Y chromosome reference sequence (accession no. KP081775.1) using a BWA-MEM algorithm with default parameters. After removing PCR duplications and multitargeted reads with SAMtools (*41*), the local realignment of the uniquely mapped reads were performed via RealignerTargetCreator and IndelRealigner in GATK v3.7 (*42*). The reads realigned to autosomes and the X chromosome were piled up using SAMtools for SNV calling in BCFtools (*43*). The raw dataset of autosomal and X chromosome SNVs was filtered for downstream analysis, retaining only those biallelic SNVs with Phred-scaled quality scores of more than 20, raw read depths between 400 and 1600, genomic distances of more than 5 bp to the nearest indel, and no missing data across all individuals. We further excluded SNVs within repetitive regions, CpG island regions, and protein-coding regions of the domestic cat felCat8 reference genome annotations, resulting in a dataset of 20,425,451 variable sites from the putative neutral regions of the genome, for downstream phylogenetic and population genomic analyses. The statistics of the WGS reads of each sample are summarized in data file S4.

The realigned Y chromosome reads from 40 males—including 2 Chinese mountain cats, 36 domestic cats, 1 Asiatic wildcat, and 1 black-footed cat—were piled up in SAMtools, and genotypes were called as haploid using BCFtools. We filtered the initial dataset to keep only those biallelic SNVs with Phred-scaled quality scores of more than 20, raw read depth between 100 and 400, and more than 5-bp distances to the nearest indel. To eliminate X chromosome interference in this paternal genealogy analysis, we identified Y chromosome regions with X homologs by mapping sequencing reads from two female domestic cats to the cat Y chromosome. After filtering, only those SNVs located in the 929-kb single-copy Y chromosome region (*44*), with no mapped sequencing reads from females, were included in downstream Y-haplotype analysis.

Phylogenomic analysis

We aligned mtDNA and Y chromosome haplotypes with Clustal X v2.0.10 (*45*) and identified variable sites with MEGA v6.06 (*46*) (data files S2 and S3). Statistical parsimony networks were constructed using TCS v1.1.3 (*47*) to infer the phylogenetic relationships among domestic cats and wildcats (Fig. 2A).

The 66 mitogenomes assembled from high-throughput sequencing data were aligned along with published mitogenome sequences from the domestic cat (accession no. U20753) and other *Felis* spp. (accession no. KP202273.1 to KP202278.1) for phylogenetic reconstruction. We selected the best fit nucleotide substitution model using jModelTest v2.1.4 (*48*). A Bayesian approach with two parallel Markov chain Monte Carlo runs were performed in MrBayes v3.2.6 (*49*) for 1,000,000 generations, with sampling every 500 generations. Phylogenetic analyses based on maximum parsimony, maximum likelihood (ML) with a TrN (Tamura-Nei) + I + G model, and neighbor joining constructed from Kimura two-parameter distances were performed in PAUP v4.0b10 (*50*), and the statistical reliability of each node was assessed by 100 bootstrap replicates.

We reconstructed the Y chromosome phylogeny of 40 male cats following the same ML procedure with an HKY (Hasegawa-Kishino-Yano) + G model in PhyML v3.1 (*51*). The Bayesian trees based on mitochondrial genome and Y chromosome were illustrated with Figtree v1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/) (Fig. 2B), and the

bootstrap support or posterior probability of those tree topologies is marked in fig. S1.

We used BEAST v2.4.4 (52) to estimate the coalescence times of different wildcat lineages based on our mtDNA and Y chromosome SNVs. Mitogenome analysis was performed with TN93 + I + G as the substitution model, the lognormal relaxed clock model, the Yule tree prior, and the coalescence times of genus *Felis* (4 Ma ago) and *F. silvestris* subspecies (1.5 Ma ago) as two calibrations (8, 25). We performed Y chromosome analysis with HKY + G as the substitution model, the lognormal relaxed clock model, the Yule tree prior, and the coalescence times between *F. nigripes* and *F. silvestris* (3 Ma ago), and among *F. silvestris* subspecies as calibrations (8, 25). In both mitochondrial and Y chromosome coalescence analyses, we performed four parallel runs for 50,000,000 generations, with parameters sampled every 1000 generations, and then log files and tree files were combined with the first 10% of the generations as burn-in to achieve our final parameter estimations (fig. S1).

To reconstruct the genome-wide autosomal phylogeny, we computed a pairwise p-distance matrix based on the 73 individuals' autosomal SNVs following Gronau *et al.* (24) and used that matrix to build a neighbor-joining tree in the Ape package v4.0 in R v3.2.3 (53). We ran 100 bootstrap replicates by resampling the autosomal variants from 1-Mb nonoverlapping windows and summarized the support values using the method implemented in the Ape package of R.

Population genetic structure analysis

We performed PCA based on biallelic autosomal variants from all the individuals using smartpca in EIGENSOFT v6.1.4 (54, 55) without removing outliers (Fig. 3A). In addition, using VCFtools 0.1.15 (56), we estimated pairwise F_{ST} values among Chinese domestic cats, worldwide domestic cats, Chinese mountain cats, the Asiatic wildcat, and black-footed cats based on 1-Mb windows along the autosomes. Furthermore, we used autosomal SNVs to infer population genetic structure of domestic cats and Chinese mountain cats using ADMIXTURE with random seed (57). The Asiatic wildcat was excluded from the analysis because of its extremely small sample size ($N = 1$). The number of genetic clusters (K) was set from two to six, with five replicates for each setting and cross-validation enabled for choosing the best clustering number (fig. S2).

Gene flow detection and quantification

We applied *D* statistics (58) through ADMIXTOOLS (59) to detect gene flow between Chinese mountain cats *F. s. bieti* ("bieti") and local domestic cats *F. s. catus* within China ("X") while using worldwide domestic cats ("worldwide") for comparison and black-footed cats *F. nigripes* ("nigripes") as the outgroup and calculated all possible combinations of D (X, worldwide, bieti, and nigripes). The *z* scores of each *F. s. catus* from China were evaluated and those with the smallest *z* score of more than 2 were considered *F. s. catus* with genetic admixture from *F. s. bieti* (Fig. 3C and table S3). In addition, we adapted three statistical approaches to quantify the levels of genetic introgression from *F. s. bieti* to *F. s. catus*: the percentage of *F. s. bieti* diagnostic sites in *F. s. catus* genomes, *f* statistics (60), and the f_4 ratio test (61).

To identify autosomal SNVs specific to *F. s. bieti*, we compared the neutral genomic regions across four *F. s. bieti* to 20 worldwide *F. s. catus*, whose chances of interbreeding with *F. s. bieti* were extremely low. The resultant 531,395 variants unique to *F. s. bieti* were then used to calculate the portion of introgression in each of the admixed Chinese domestic cats.

Using ADMIXTOOLS, we calculated the f_4 ratio as

$$f_4 \text{ ratio} = \frac{f_4(\text{ornata}, \text{nigripes}; X, \text{worldwide})}{f_4(\text{ornata}, \text{nigripes}; \text{bieti}, \text{worldwide})} \quad (1)$$

and calculated *f* statistics with the *D* statistic parameters as

$$f - \text{statistics} = \frac{S(X, \text{worldwide}, \text{bieti}, \text{nigripes})}{S(\text{bieti1}, \text{worldwide}, \text{bieti2}, \text{nigrpies})} \quad (2)$$

where *S* (X, worldwide, bieti, nigripes) is the numerator of *D* of each domestic cat X and *S* (bieti1, worldwide, bieti2, nigripes) is the numerator of *D* with two randomly selected *F. s. bieti* designated as "bieti1" and "bieti2."

Genetic introgression dating

We first estimated the time of introgression from *F. s. bieti* to sympatric domestic cats by plotting the genome-wide distribution of *F. s. bieti*–specific alleles found in the 10 admixed domestic cats, along the 531,395 SNVs that distinguished *F. s. bieti* from the domestic cat (fig. S2). Large consecutive genomic segments carrying *F. s. bieti* ancestry within domestic cat genomes were identified based on diagnostic variants. We used ALDER v1.03 (26) to date hybridization events based on LD decay patterns in two domestic cat populations: (i) 10 cats from *F. s. bieti* core range (C6 to C15, labeled hybrid1) and (ii) five individuals from the edge of that range (C1 to C5, labeled hybrid2). One group with four *F. s. bieti* (B1 to B4) and the other with 31 domestic cats beyond *F. s. bieti* distribution area (C16 to C46) represented two ancestral populations in the analysis. To find the best fitting start point (d0), we performed 11 parallel runs with d0 set from 0.5 to 5 cM, subsequently selecting 2.0 and 0.5 cM as the best parameters for hybrid1 and hybrid2 populations, respectively, according to *P* values and *z* scores (table S4).

Demographic history inference

We applied the PSMC model (62) and G-PhoCS (24) approach to infer the demographic dynamics of wildcats and domestic cats in China, including historical population sizes, divergence times, and gene flow scenarios.

The PSMC model estimated effective population size changes through time based on autosomal consensus sequences of five individuals: N2, B4, O1, C25, and W19, representing *F. nigripes*, *F. s. bieti*, *F. s. ornata*, *F. s. catus* from China, and *F. s. catus* worldwide, respectively. The analysis was carried out at an individual-based level with 64 atomic time intervals under the default pattern "4 + 25 × 2 + 4 + 6," as described by Li and Durbin (62), and with the maximum coalescent time set to 20. The estimated θ values were then transformed to effective population sizes and plotted with a generation time (g) of 2 years and a mutation rate (μ) of 2.6×10^{-9} substitutions per site per generation (Fig. 5A), as calibrated in the G-PhoCS analysis. For each individual, we ran 100 bootstrap replicates to evaluate estimation robustness.

We used the G-PhoCS to estimate the demographic parameters such as historical population size, divergence time, and migration rate based on coalescent-based Markov chain Monte Carlo and a given topology (24, 63, 64). To identify neutral loci for the analysis, the autosomal sequences of the hard-masked domestic cat genome assembly (felCat8) were further masked to remove CpG islands and exons with 1-kb flanking regions based on UCSC genome annotations.

Following established procedures (*24*, *64*), we recognized 34,418 unlinked loci, each 1-kb long with a minimum interlocus distance of 50 kb and containing less than 10% masked sites.

We performed G-PhoCS analysis based on a given topology of the four *Felis* lineages and its estimated parameters (fig. S3A) and with 10 representative individuals, including four *F. s. bieti* (B1, B2, B3, and B4), three *F. s. catus* (C20, C25, and W19), one *F. s. ornata* (O1), and one *F. nigripes* (N2). To avoid possible interference between migration bands and the time cost correlated with the demography model's complexity, we performed a prior analysis to identify significant migration bands with C25, B2, O1, and N2. All 18 possible migration bands were considered in the model, two parallel runs were conducted with 500,000 generations sampled every 100 generations, and all results were cross-checked to ensure convergence. Four significant migration bands were detected in this preliminary run, with a total migration rate ($m_{tot} = m \times \tau$) around or more than 0.1 (fig. S3B).

Then, we ran 12 independent analyses with four individuals from each of the four lineages and the four migration bands detected in the prior analysis while considering all combinations of domestic cats and Chinese mountain cats. Each analysis was performed with two parallel runs of 1,000,000 generations each, sampled every 100 generations, and the trace files were combined to obtain final demographic parameter estimations, with the first 30% of the generations as burn-in (fig. S3C and table S5). The estimated parameters (θ and τ) were converted to the effective population size (Ne), divergence time (T), and coalescent time (T_{div}) according to Gronau's formulas (*24*): $\theta = 4 \times Ne \times \mu$, $\tau = T \times \mu/g$, and $\tau\_div = \tau + 0.5 \times \theta$. The mutation rate $\mu = 2.6 \times 10^{-9}$ was calibrated according to the divergence time between the black-footed cat and the domestic cat lineages (T_Felis_div), 3 Ma ago (*8*).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/26/eabg0221/DC1

View/request a protocol for this paper from *Bio-protocol*.

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