Rethinking dog domestication by integrating genetics, archeology, and biogeography

Greger Larson, Elinor K. Karlsson, Angela Perri, Matthew T. Webster, Simon Y. W. Ho, Joris Peters, Peter W. Stahl , Philip J. Piper, Frode Lingaas, Merete Fredholm, Kenine E. Comstock, Jaime F. Modiano, Claude Schelling, Alexander I. Agoulnik, Peter A. Leegwater, Keith Dobney, Jean-Denis Vigne, Carles Vilà, Leif Andersson, and Kerstin Lindblad-Toh

June 5, 2012

Rethinking dog domestication by integrating genetics, archeology, and biogeography

Greger Larson[a,1], Elinor K. Karlsson[b,c], Angela Perri[a], Matthew T. Webster[d], Simon Y. W. Ho[e], Joris Peters[f], Peter W. Stahl[g], Philip J. Piper[h,i], Frode Lingaas[j], Merete Fredholm[k], Kenine E. Comstock[l], Jaime F. Modiano[m,n], Claude Schelling[o], Alexander I. Agoulnik[p], Peter A. Leegwater[q], Keith Dobney[r], Jean-Denis Vigne[s], Carles Vilà[t], Leif Andersson[d,u], and Kerstin Lindblad-Toh[b,d]

[a]Durham Evolution and Ancient DNA, Department of Archaeology, University of Durham, Durham DH1 3LE, United Kingdom; [b]Broad Institute of MIT and Harvard, Cambridge MA 02142; [c]Faculty of Arts and Sciences Center for Systems Biology, Harvard University, Cambridge MA 02138; [d]Science for Life Laboratory Uppsala, Department of Medical Biochemistry and Microbiology, Uppsala University, SE-751 23 Uppsala, Sweden; [e]School of Biological Sciences, University of Sydney, Sydney NSW 2006, Australia; [f]Veterinary Sciences Department, Institute of Palaeoanatomy, Domestication Research and the History of Veterinary Medicine, Ludwig-Maximilian University, 80539 Munich, Germany; [g]Department of Anthropology, University of Victoria, Victoria, BC, Canada V8W 2Y2; [h]School of Archaeology and Anthropology, Australian National University, Canberra, Australian Capital Territory 200, Australia; [i]Archaeological Studies Program, University of the Philippines, Diliman, 1101, Quezon City, Philippines; [j]Department of Basic Sciences and Aquatic Medicine, Division of Genetics, Norwegian School of Veterinary Science, 0033 Oslo, Norway; [k]Faculty of Life Sciences, Division of Genetics and Bioinformatics, Department of Basic Animal and Veterinary Sciences, University of Copenhagen, 7-1870 Frederiksberg C, Denmark; [l]University of Michigan-Dearborn, Dearborn, MI 48128; [m]Department of Veterinary Clinical Sciences, College of Veterinary Medicine, University of Minnesota, St. Paul, MN 55108; [n]Masonic Cancer Center, University of Minnesota, Minneapolis, MN 55455; [o]Department of Animal Sciences, Swiss Federal Institute of Technology Zurich and Vetsuisse Faculty Zurich, University of Zurich, 8092 Zurich, Switzerland; [p]Department of Human and Molecular Genetics, Herbert Wertheim College of Medicine, Florida International University, Miami, FL 33199; [q]Department of Clinical Sciences of Companion Animals, Faculty of Veterinary Medicine, Utrecht University, 3508 TD Utrecht, The Netherlands; [r]Department of Archaeology, University of Aberdeen, Aberdeen AB24 3UF, Scotland, United Kingdom; [s]Département "Ecologie et Gestion de la Biodiversité", Muséum National d'Histoire Naturelle, "Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements," Centre National de la Recherche Scientifique-Institut Ecologie et Environement, F-75005 Paris, France; [t]Conservation and Evolutionary Genetics Group, Doñana Biological Station, 41092 Seville, Spain; and [u]Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, SE-75123 Uppsala, Sweden

Edited by Joachim Burger, Johannes Gutenberg-University, Mainz, Germany, and accepted by the Editorial Board April 17, 2012 (received for review February 20, 2012)

The dog was the first domesticated animal but it remains uncertain when the domestication process began and whether it occurred just once or multiple times across the Northern Hemisphere. To ascertain the value of modern genetic data to elucidate the origins of dog domestication, we analyzed 49,024 autosomal SNPs in 1,375 dogs (representing 35 breeds) and 19 wolves. After combining our data with previously published data, we contrasted the genetic signatures of 121 breeds with a worldwide archeological assessment of the earliest dog remains. Correlating the earliest archeological dogs with the geographic locations of 14 so-called "ancient" breeds (defined by their genetic differentiation) resulted in a counterintuitive pattern. First, none of the ancient breeds derive from regions where the oldest archeological remains have been found. Second, three of the ancient breeds (Basenjis, Dingoes, and New Guinea Singing Dogs) come from regions outside the natural range of *Canis lupus* (the dog's wild ancestor) and where dogs were introduced more than 10,000 y after domestication. These results demonstrate that the unifying characteristic among all genetically distinct so-called ancient breeds is a lack of recent admixture with other breeds likely facilitated by geographic and cultural isolation. Furthermore, these genetically distinct ancient breeds only appear so because of their relative isolation, suggesting that studies of modern breeds have yet to shed light on dog origins. We conclude by assessing the limitations of past studies and how next-generation sequencing of modern and ancient individuals may unravel the history of dog domestication.

genomics | phylogeography

Darwin speculated about the origins of several domestic animals and suggested that, given the vast morphological variation across numerous breeds, dogs must have had more than one wild ancestor (1). Recent genetic studies, however, support the notion that dogs are descended exclusively from the gray wolf (*Canis lupus*) (2).

Beyond questions regarding wild ancestry, geneticists and generations of archeologists have investigated not only how and why dogs were domesticated, but also when, where, and how many times it may have occurred. Unique among all domestic animals, the first unambiguous domestic dogs precede the appearance of settled agriculture in the archeological record by several thousand years. Identifying the earliest dogs is difficult, however, because key morphological characters established by zooarcheologists to differentiate domestic animals from their wild wolf ancestors (e.g., size and position of teeth, dental pathologies, and size and proportion of cranial and postcranial elements) were not yet fixed during the initial phases of the domestication process. Furthermore, the range of natural variation among these characters in ancient wolf populations and the time it took for these traits to appear in dogs are unknown. Free-ranging wolves attracted to the refuse generated by human camps most likely followed a commensal pathway to domestication that was neither deliberate nor directed (3). Because the process was not unidirectional, the telltale traits archeologists use to differentiate wolves and dogs probably took numerous generations to become apparent in the archeological record.

Despite the difficulties associated with the use of archeological evidence to pinpoint the timing of domestication, there is a general consensus that domestic dogs were present in the Levant (including Cyprus), Iraq, Northern China, and the Kamchatka peninsula in Far Eastern Russia by ~12,000 y ago, and in western Europe a few millennia before that. Recent studies have made claims that domestic (or incipient) dogs were present even earlier during the Late Pleistocene in Belgium (4), the Czech Republic (5), and southwestern Siberia (6). Morphological analyses suggest that although some of the early canid remains possess characteristics broadly similar to those found in modern dogs, it remains possible that the bones represent either wolves going through the initial phases of an incomplete domestication process (6) or a morphologically distinct local, now-extinct population of wolves.

The use of more advanced morphometric analyses is allowing zooarcheologists to have greater confidence in identifying early

Author contributions: G.L., E.K., and K.L.-T. designed research; G.L., E.K., A.P., F.L., M.F., K.E.C., J.F.M., C.S., A.I.A., P.L., C.V., and K.L.-T. performed research; G.L., E.K., M.T.W., S.Y.W.H., J.P., P.W.S., P.J.P., J.-D.V., C.V., L.A., and K.L.-T. analyzed data; and G.L., E.K., A.P., M.T.W., S.Y.W.H., J.P., P.W.S., P.J.P., J.F.M., K.D., J.-D.V., C.V., L.A., and K.L.-T. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. J.B. is a guest editor invited by the Editorial Board.

Freely available online through the PNAS open access option.

[1]To whom correspondence should be addressed. E-mail: greger.larson@durham.ac.uk.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1203005109/-/DCSupplemental.

dogs (7). Given the geographical breadth of these finds, archeologists have (generally) been reluctant to postulate exact locations where dogs may have been domesticated. Instead, they have broadly accepted the plausibility of the existence of numerous, independent centers of dog domestication beginning in the Late Pleistocene (8).

Many genetic studies of modern dogs and wolves have been less circumspect. Armed first with fragments of mitochondrial DNA and molecular clocks, the authors of one study concluded that dogs were domesticated 135,000 y ago (9). A separate study later analyzed a similar mitochondrial fragment sequenced from 654 dogs and, on the basis of regional patterns of modern dog diversity, deduced that dogs were domesticated just once in East Asia (10).

Both of these claims have since been challenged. First, it is highly likely that the use of deep fossil calibrations for molecular clocks has led to a significant overestimation of the timing of dog domestication (11). Second, analyses of African street dogs suggested that a single East Asian origin was too simplistic (12). A study of 48,000 SNPs in 912 dogs and 225 gray wolves concluded that both East Asian and Near Eastern wolf populations contributed DNA to modern dog breeds (13). Other studies that have incorporated nuclear markers also suggest diverse geographic origins of dogs (14), and with the application of a broader, more integrated approach, the genetic and archeological perspectives have become more closely aligned. However, despite the volume of new data, the estimates of when, where, and how many times dogs were domesticated remain disconcertingly imprecise.

One significant insight that genetic studies have yielded, using both microsatellites (15) and SNPs (13), is the identification of several genetically divergent modern dog breeds in well-supported basal positions on phylogenetic trees. This early-branching pattern has been used to designate these breeds as "ancient" (13). To avoid conflating genetic differentiation with presumed ancient heritage (16), we will instead refer to these lineages as "basal."

The term "breed" is also problematic. The focus on general classes of dogs (e.g., sight hounds, scent hunters, shepherd dogs, and giant dogs) likely has prehistoric roots and led to the development of broadly distinct forms of dogs. For example, three differently sized dog types have been recorded at the 8,000-y-old Svaerdborg site in Denmark (17). Modern breeding practices, focused on distinct breeds with strict aesthetic requirements and closed bloodlines, only emerged in the 19th century, and claims for the antiquity (and long-term continuity) of modern breeds are based upon little or no historical or empirical evidence. In fact, recent historical records clearly demonstrate that most modern breeds experienced significant population fluctuations within the past 100 y (Table S1). Here, we only use the term "breed" when referring to modern dog breeds recognized by kennel clubs.

To test the branching pattern of the previously identified basal breeds and to assess the status of unstudied breeds (Table 1 and Table S1), we used 49,024 SNPs typed in 19 wolves and 1,375 dogs from 35 breeds. In addition, we compiled a broad temporal and geographic survey of dog domestication by undertaking a global examination of the archeological record (Tables S2 and S3). By comparing the zooarcheological evidence with the geographical origins of the total set of modern breeds, we established a framework for understanding why some breeds have retained basal signatures and why most have not.

Results and Discussion

Genetic History of Modern Breeds. A neighbor-joining phylogenetic tree inferred using our data (Fig. 1) was broadly similar to those described previously (13, 15). A deep genetic split is evident between Old World and New World wolves (Table S4) at the base of the tree. From there, high bootstrap values (>95%) support the basal position and genetic distinctiveness of the so-called ancient (basal) breeds: the Akita, Basenji, Eurasier, Finnish Spitz, Saluki, and Shar-Pei (Fig. 1 and Table 1). Although the relationships between numerous breeds that have been crossed recently (e.g., Dachshunds) are well supported, and although each of nonbasal breeds is strongly monophyletic, the relationships between them are poorly resolved (Fig. 1).

When our results are combined with those from the two previous studies (13, 15), the total number of basal breeds increases to 16. Two of these basal breeds have shallow histories. The American Eskimo breed was deliberately created by crossing Keeshonds, Volpinos, and Pomeranians, and after World War II, Japanese Spitzes may also have been incorporated (18). The name "American Eskimo" was derived from the kennel that originally began breeding them, despite the fact that the breed never had an association with Inuits. The highly mixed heritage of the breed is evident from its position on the phylogenetic tree, which is dependent on the choice of analytical technique. The American Eskimo appears alongside the basal Samoyed in trees estimated using 10-SNP windows; however, it is positioned next to Pomeranians on a tree inferred using individual SNPs (13).

Table 1. A list of 16 breeds that were either labeled "ancient" in previous publications or were identified as basal in this study

Breed	Parker et al. (15)	Vonholdt et al. (13)	Present study
Afghan Hound[1]	y	y	
Akita[2]	y	y	y
Alaskan Malamute[3]	y	y	
American Eskimo (recent)		y*	
Basenji[4]	y	y	y
Canaan[5]		y	
Chow Chow[6]	y	y	
Dingo[7]		y	
Eurasier (recent)			y
Finnish Spitz[8]			y
New Guinea singing dog[9]		y	
Saluki[10]	y	y	y
Samoyed[11]	n	y	
Shar-Pei[12]	y	y	y
Shiba Inu[13]	y		
Siberian Husky[14]	y	y	

The letters "y", "n", and "y*" indicate basal breeds, nonbasal breeds, and an inconclusive result, respectively. The absence of a letter indicates the breed was not a part of the study in question. Superscripted numbers following breed names correlate with the numbers under the dog symbols in Fig. 2. Detailed descriptions of these breeds are provided in Table S1.

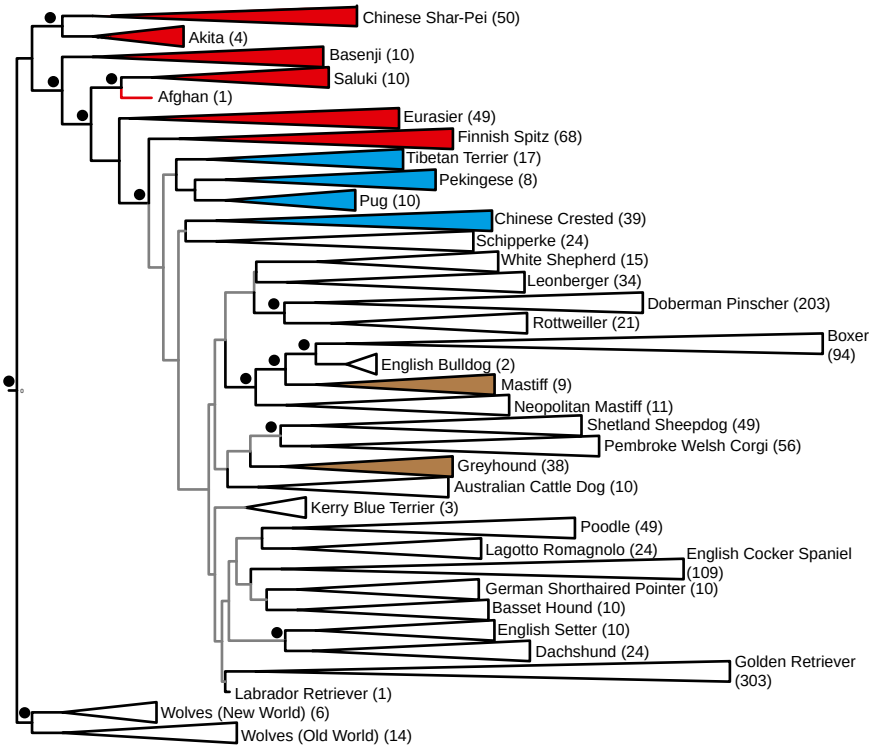

Fig. 1. A neighbor-joining tree depicting the relationships between 35 breeds (with sample sizes) and rooted with New and Old World Wolves. All clades have been collapsed. Gray branches are poorly supported, whereas black branches and black circles indicate bootstrap values >95%. Clade colors depict breeds that retain a basal signature (red), non-European breeds that are not basal (blue), and European breeds that are rumored to have deep histories but are not basal (brown). The well-supported relationships between Rottweilers and Doberman Pinschers, Neapolitan Mastiffs, Mastiffs, English Bulldogs, Boxers, Shetland Sheepdogs, and Pembroke Welsh Corgis are the result of known or suspected recent admixture between these breeds. The well-support relationship between Dachshunds and English Setters reflects a recent interbreeding between the Dachshund individuals used in this study with English Setters.

The Eurasier is also a recently created breed, developed deliberately and fixed in the 1960s by mixing Chow Chows with Keeshonds and a single Samoyed (18). Because the majority of the breeds used to create Eurasiers possess basal signatures (13, 15), Eurasiers also appear basal, although they are the only breed whose monophyly is weakly supported (33% bootstrap value).

The remaining 14 basal breeds [including Samoyeds, which do not appear basal on the phylogenetic tree inferred from microsatellite data (15), but are basal when using SNPs (13)] have generally avoided admixture with other breeds (Table S1). This avoidance is probably the only reason why they retain a genetic legacy that extends beyond the age of modern breeding and the establishment of kennel clubs during the second half of the 19th century (19).

Despite the long history of human selection for specific dog forms, there is a major disconnect between truly ancient dogs and modern breeds. For example, unsubstantiated claims have been made for the antiquity of the modern Irish Wolfhound. Wolfhound-type dogs were used to hunt wolves across Europe. In Ireland, wolves were exterminated by 1786 (20), after which the demand for Wolfhounds plummeted, and by 1840 the type was either extinct or all but extinct. George Augustus Graham revitalized (or recreated) the form by breeding one possible wolfhound to Scottish Deerhounds, and then incorporated Borzois and Great Danes to create the modern breed that retained the aesthetic of the original form, but not the genetic ancestry (18).

The story of the Irish Wolfhound is not unusual. Although the origin myths of the Cardigan and Pembroke Welsh Corgis state that their respective introductions to England differed by 2,000 y (21), both types were allowed to interbreed for centuries before being split into two modern breeds in the 1920s (18). Whatever their deeper history, these breeds form strongly supported sister clades on phylogenetic trees (13), meaning that their pre-admixture heritage is invisible even with the resolving power of tens of thousands of SNPs.

Both World Wars had a major impact on the genetic diversity of the domestic dog. In the United Kingdom, English Mastiffs were reduced to 14 individuals (18), Sussex Spaniels to 10 (22), and Manchester Terriers to 11 (18). Bernese Mountain Dogs (18) and Italian Greyhounds (22) vanished completely and many other breeds suffered significant bottlenecks (Table S1). Bolstering or recreating these breeds was accomplished by crossing numerous other breeds, a practice that obscured whatever genetic signatures of their early heritage that existed before the World Wars, and ultimately led to highly inbred modern populations (23). Interestingly, the recent genetic homogenization has occurred despite the increase in phenotypic disparity as breeders have simultaneously closed breeding lines and selected for extreme morphological traits (24).

Even the basal breeds identified in this and other studies experienced recent and significant demographic change. The Shiba Inu faced extinction in World War II and the modern breed is an amalgamation of three isolated and distinct Japanese lineages (18). The Finnish Spitz, supposedly used for millennia by Finno-Ugric people, was nearly extinct by 1880. A single breeder, Hugo Roos, set out to rescue the type by traveling to remote villages and collecting the few remaining individuals least likely to have been crossed (accidentally or purposely) with other breeds (18). The fact that Finnish Spitzes retain a basal genetic signature is testament to the success of Roos's efforts to obtain uncrossed individuals.

With the exception of the Alaskan Malamute, all 14 basal breeds have geographic origins in the Old World (Table S1); this is despite the fact that dogs were an integral part of the human occupation of the New World and that several modern breeds, including the Chihuahua, are thought to have been at least partly derived from domestic dogs native to the New World. The general lack of basal lineages in the Americas is likely because of the fact that European breeds, initially introduced only 500 y ago, have overwhelmed the native lineages. This finding was demonstrated by a recent study of mitochondrial variation among street dogs in South America, which concluded native maternal lineages were almost entirely absent in New World dogs (25).

Finally, numerous widely geographically distributed dog populations share identical mutations responsible for specific phenotypes. Chinese and Mexican breeds both possess the same hairless gene (26), sub-Saharan African and Thai breeds possess a ridged line of hair on their backs caused by the same genetic mutation (27), and at least 19 different breeds possess the

identical mutation for foreshortened limbs (28). These mutations are unlikely to have arisen multiple times independently, implying a significant degree of gene flow between breeds. This evidence, combined with known demographic fluctuations in numerous breeds, suggests that throughout history global dog populations experienced numerous episodes of diversification and homogenization. Each successive round further reduced the power of genetic data derived from modern breeds to infer the early history of dog domestication.

Dogs in the Archeological Record. Identifying dog remains in the archeological record is not always straightforward. First, it can be difficult to discriminate between dogs and wolves, because dogs were still morphologically wolf-like at the earliest stages of domestication. In addition, and in contrast to their modern patchy distribution, wolves were once dispersed across the Northern Hemisphere (29) (Fig. 2). As a result, zooarcheologists cannot establish the wild or domestic status of dog remains based solely on geographic location as they can for sheep and goats, the native wild ranges of which were much more restricted.

Second, identifying dogs can be confounded by the presence of several other extant and extinct species of similar-sized canids, including foxes (*Vulpes* spp.) and maned wolves (*Chrysocyon brachyurus*) in South America, dholes (*Cuon* spp.) in Europe and Asia, jackals in Africa and Asia (*Canis aureus*, *Canis adustus*, and *Canis mesomelas*), and African wild dogs (*Lycaon pictus*) (30). Recent efforts have been made to differentiate dogs from these canid species using shape analyses (7), and numerous early claims for domestic dogs have since been rejected because reanalyses have revealed contradictory designations (Table S2). This is often the case when preserved specimens are relatively scarce or fragmented, reducing the presence of specific distinguishing features necessary to discriminate between closely related forms.

Third, a variety of factors can introduce biases against the preservation of certain vertebrate taxa in the archeological record. These include taphonomic processes [particularly in humid tropical settings (31)], and the general paucity of canid remains relative to other prey and domestic animals in the fossil record. In addition, the absence of archeological excavations in many parts of the world biases our interpretation of domestication history. The universal human propensity to bury dogs either on their own or within human burials (32), however, has significantly enhanced the archeological visibility of dogs.

Finally, even when zooarcheologists can confidently attribute remains to *Canis familiaris*, dating can prove problematic. The earliest dogs in North America were originally reported from the Jaguar Cave site in Idaho with an associated date of 10,400 y cal B.P. (33). Subsequent direct dating of the bones revealed that two Jaguar Cave dogs are ~3,500 and ~1,000 y old (34).

An interesting pattern emerges when directly dated and confidently identified dog specimens (Table S3) are mapped onto the historic distribution of wolves across the Old and New Worlds (Fig. 2). First, remains ~12,000 y or older are present in numerous sites in Europe, the Levant, Iraq, Northern China, and the Kamchatka peninsula in the Russian Far East. Dogs appear in contexts older than 8,000 y everywhere else within the maximal distribution of wolves, suggesting independent domestications of local populations of wolves, migration of humans possessing dogs, or the secondary acquisition of dogs by groups that were not involved in the domestication process.

Dogs appear south of the original wolf distribution in the Old and New Worlds almost always with the arrival of agriculture. For example, despite the fact that human remains are present in much older contexts at Coxcatlan Cave in Mexico, dogs first appear only ~5,200 B.P. alongside the appearance of agricultural communities (35). The same is true in sub-Saharan Africa, where dogs appear after the advent of the Sudanese Neolithic ~5600 B.P. (36), in Peninsular Southeast Asia ~4,200 B.P. (37), and in Island Southeast Asia ~3,500 B.P. (38). Dogs only arrived in South Africa ~1,400 y ago following the arrival of cows, sheep, and goats a few hundred years before (39), and in southern South America ~1,000 y ago with the arrival of sedentary societies (40).

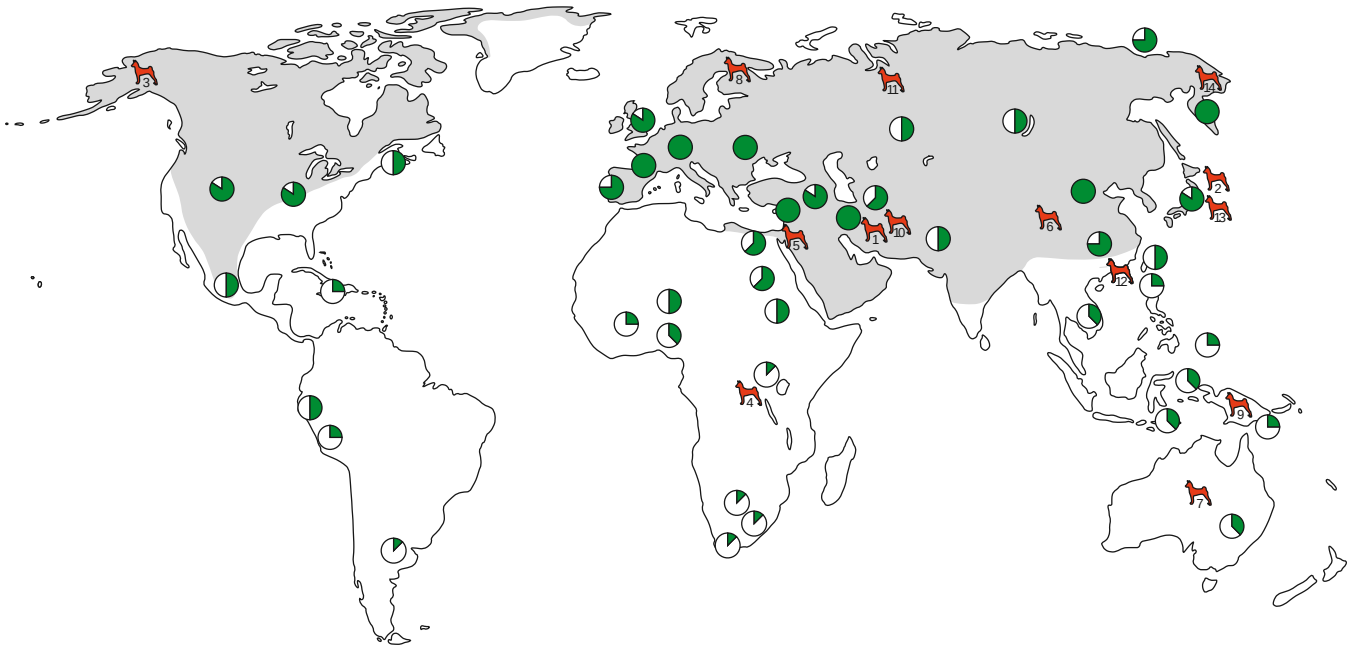

Fig. 2. A world map in which the approximate maximal range of gray wolves (*Canis lupus*) is shaded in gray (based on ref. 29). Green circles represent regions where confidently dated remains of domestic dogs have been described in at least one archeological site (Table S3). Circles are divided into eight segments, each of which represents 1,500 y, visually depicting the age of the oldest remains at sites in the region over which the circle sits. Filled circles represent remains older than 10,500 y. Each red dog represents a basal breed. The number under each dog refers to the breeds in Table 1; their locations are based upon their suspected geographic origins, described in Table S1.

Biogeographical Perspective. Mapping the geographic location of the 14 basal dog lineages onto the maximal wolf distribution and the archeological data reveals several counterintuitive patterns. First, although domestic dogs were present in numerous European archeological sites ∼15,000 y ago, and despite the fact that textual references or depictions superficially suggest temporally deep origins for 13 European breeds including the Pharaoh and Ibizan Hounds (Table S1), only the Finnish Spitz retains a basal signature. Second, although dogs reached Island Southeast Asia ∼3,500 y ago and southern Africa ∼1,400 y ago, the branches leading to three breeds from these regions (Basenjis, New Guinea Singing Dogs, and Dingoes) are located in basal positions on the tree (Fig. 1). This pattern confounds the expectation that basal breeds should originate from the regions that possess the oldest archeological dog remains, or at least the regions that possess the deepest historical records of types recognizable in modern breeds.

The two breeds closest to central Europe that retain basal signatures (the Finnish Spitz and the Israeli Canaan Dog), are both known to have been isolated from their European counterparts. Efforts to create modern breed standards included a policy of avoiding those individuals that had been bred with foreign, recently introduced breeds (18). Most basal breeds have hybridized with other lineages. If those breeds have either been crossed with other basal breeds (e.g., the Shiba Inu) or if a few of the least introgressed individuals are retained and bred [e.g., the Finnish Spitz or the Dingo; though at least 80% of wild dingoes have interbred with European breeds (41)], then a basal genetic signal is retained.

As discussed above, many basal breeds have also experienced severe bottlenecks that have exaggerated their unique genetic signatures. The extant captive population of the New Guinea Singing Dog is descended from only eight individuals (42), European Afghans went extinct during the World Wars and were re-established using just three imported dogs, and the modern European Basenji stock was initiated with just a handful of individuals collected in 1936 and supplemented with dogs acquired from central Africa in 1988 (21). The combination of introgression and bottlenecks suggests that basal breeds have little or no genetic connections to their ancestral populations, and that genetic distinctiveness alone cannot be used as a proxy to signify an ancient heritage.

The most predictive factor in determining whether a breed retains a basal signature is a lack of gene flow, or at least a lack of introgression with breeds that do not possess basal signatures. Thus, the unifying characteristic among the 14 basal dog lineages (Table 1) is geographic or cultural isolation from the primary center of dog breeding in Europe that began in the 19th century. If geography alone determined basal status, however, then the Africanis, Chihuahua, Chinese Crested, Lhasa Apso, Pekingese, Pug, Rhodesian Ridgeback, Shih Tzu, and Tibetan Terrier should also be basal. In these cases, however, a significant degree of introgression with European breeds is recorded or strongly suspected (Table S1). Although there is pictorial, written (43), and zooarcheological (44) evidence for toy dogs spanning at least the last 2,000 y, no toy breeds possess a basal signature, probably a result of the ease with which they can be transported and interbred with local dogs.

Populations of numerous taxa that live at isolated peripheries, including the Falkland Islands Wolf (45), *Homo floresiensis* (46), and woolly mammoths (47), often either outlived or appear different from their continental relatives. Island populations of dogs (both real and metaphorical) are more likely to retain their genetic integrity not because related populations on the mainland have gone extinct, however, but because peripheral populations have avoided amalgamation into a larger group that, as a consequence, has lost its genetic distinctiveness.

Conclusion

Though clear signs of the dog domestication process are visible 15,000 y ago, dogs were not present across every habitable continent until they reached South Africa and southern South America <1,400 y ago. The number of differentiated, isolated dog populations has since been reduced through human movement and trade that subsequently led to increased gene flow and population homogenization, and through warfare, which often resulted in extreme demographic fluctuations (including extinction). Each time a lineage that had been evolving in isolation came into contact with introduced dogs, the resulting descendant admixture blurred the genetic signature, making it more difficult to deduce their origins before the assimilation.

This pattern is not unique to dogs. When human populations transported domesticates into new regions, the most common result has been an admixed population of introduced and local varieties, many of which arrived during previous expansion episodes. Examples of this phenomenon include European domestic grapes (48), Central American maize (49), and Western Eurasian sheep (50).

Basal dog lineages fall outside the large, poorly supported clade that includes most modern dog breeds (Fig. 1). This result is not because they more closely approximate the earliest domestic dogs, but because they have mostly avoided recent admixture with other breeds that themselves possess a merged genetic heritage from dogs that evolved in a wide variety of geographic regions. It is far easier to avoid introgression by existing at the periphery, beyond landscape and cultural barriers. This theory explains why numerous basal lineages are from those regions where dogs only recently arrived, outside the natural range of wolves, and why no central European breeds retain an ancient signature despite the ∼15,000-y history of domestic dogs. The vast majority of modern breeds were only created in the past 150 y, emerging from what was a relatively homogeneous gene pool formed as a result of millennia of human migration and the subsequent merging of multiple, previously independently evolving dog lineages. This history, along with the closed gene pools and small effective population sizes associated with recent breed formation, also explains the strongly supported genetic monophyly of individual breeds and the lack of resolved relationships between them.

The shallow history of breed formation has eased the process of correlating known breed-specific phenotypes with, in some cases, their causal mutations (51). Unfortunately, our understanding of dog origins has been hampered by our reliance on limited marker sets that type a small portion of the 2.4 billion DNA bases that make up the dog genome (2). Even in datasets that type numerous individuals, methods that use mitochondrial sequences or even tens of thousands of SNPs are only capable of recovering signatures that have resulted from the effects of bottlenecks and reticulate evolution that took place during 19th and 20th century breed formation. As a result, our ability to investigate the deeper history of dog domestication has been severely hampered.

The advent of rapid and inexpensive DNA sequencing technology has made it possible to significantly increase the volume and commensurate resolving power of genetic data, thus allowing a greater time depth to be accessed. In humans, dense genotyping (millions of SNPs) and complete genomes of both ancient and modern individuals have revealed a far more complex history (including inter- and intraspecies admixture) than was previously available using sparser datasets (52). Comparable genetic analyses of modern and ancient domestic dog genomes and the resolving power they possess will soon yield equally complex insights into their domestication and subsequent evolution, thus revealing our deep, shared history with dogs.

Materials and Methods

Genetics. DNA was isolated from 1,375 domestic dogs (Table S1) and 19 wolves (Table S4) and genotyped for 49,664 SNPs on the Affymetrix canine v2 arrays using the snp5-geno-qc software package, with subsequent QC done using PLINK (53). SNPs on chromosome X and SNPs with genotyping rates <95%, were removed, yielding a dataset of 49,024 SNPs. Duplicate samples were identified and merged based on genome-wide average identity-by-state pairwise identity higher than 98%. Breed assignment was confirmed using principal component analysis with smartpca (part of the EIGENSOFT software

package) (54). All dogs included in the analysis had genotyping rates > 75% (median of 98% in dogs and 96% in wolves).

To construct phylogenetic trees, pairwise identity-by-state genetic distances between samples were first estimated across all SNPs that passed quality filters using PLINK (53). The distances were then used to construct a neighbor-joining tree using Phylip (55). The dataset was bootstrapped 1,000 times to obtain support values for each node.

Archeology. The survey of the archeological literature revealed numerous reports of remains, the details of which (species designation, status determination, and dating) the authors were confident. Many other claims were contentious. We created two tables. The first (Table S2) lists reports of domestic dogs and the rationales for not including them in Table S3, which lists all of the locations, sites, and elements used in Fig. 2. We applied a conservative approach when deciding whether or not to accept individual claims for remains that were identified as domestic dogs. The specific criteria and rationales are discussed in the *SI Results and Discussion*.

ACKNOWLEDGMENTS. We thank April McMahon, Alan de Quieroz, Matthew Breen, Gary Johnson, and Hannes Lohi for comments on the manuscript. G.L. is currently a Research Councils United Kingdom Academic Fellow and was supported by a European Molecular Biology Organization postdoctoral fellowship; K.L.-T. is a European Young Investigator award recipient funded by the European Science Foundation, and was supported by grants from the Swedish Research Council; and A.P. was supported by the British Association for Japanese Studies.

1. Darwin C (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (John Murray, London).
2. Lindblad-Toh K, et al. (2005) Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature* 438:803–819.
3. Zeder MA (2012) Pathways to animal domestication. *Biodiversity in Agriculture: Domestication, Evolution and Sustainability*, eds Gepts P, et al. (Cambridge Univ Press, Cambridge).
4. Germonpré M, et al. (2009) Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. *J Archaeol Sci* 36:473–490.
5. Germonpré M, Lázničková-Galetová M, Sablin MV (2011) Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. *J Archaeol Sci* 39:184–202.
6. Ovodov ND, et al. (2011) A 33,000-year-old incipient dog from the Altai Mountains of Siberia: Evidence of the earliest domestication disrupted by the Last Glacial Maximum. *PLoS ONE* 6:e22821.
7. Pionnier-Capitan M, et al. (2011) New evidence for Upper Palaeolithic small domestic dogs in South-Western Europe. *J Archaeol Sci* 38:2123–2140.
8. Crockford SJ (2000) A commentary on dog evolution: Regional variation, breed development and hybridisation with wolves. *Dogs Through Time: An Archaeological Perspective*, ed Crockford SJ (Archaeopress, Oxford, UK), pp 295–312.
9. Vilà C, et al. (1997) Multiple and ancient origins of the domestic dog. *Science* 276: 1687–1689.
10. Savolainen P, Zhang YP, Luo J, Lundeberg J, Leitner T (2002) Genetic evidence for an East Asian origin of domestic dogs. *Science* 298:1610–1613.
11. Ho SYW, Larson G (2006) Molecular clocks: When times are a-changin'. *Trends Genet* 22:79–83.
12. Boyko AR, et al. (2009) Complex population structure in African village dogs and its implications for inferring dog domestication history. *Proc Natl Acad Sci USA* 106: 13903–13908.
13. Vonholdt BM, et al. (2010) Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature* 464:898–902.
14. Gray MM, Sutter NB, Ostrander EA, Wayne RK (2010) The IGF1 small dog haplotype is derived from Middle Eastern grey wolves. *BMC Biol* 8:16.
15. Parker HG, et al. (2004) Genetic structure of the purebred domestic dog. *Science* 304: 1160–1164.
16. Miklósi Á (2007) *Dog Behaviour, Evolution, and Cognition* (Oxford Univ Press, New York).
17. Henriksen BB, Sørensen KA, Sørensen I (1976) *Sværdborg I: Excavations 1943–44: A Settlement of the Maglemose Culture* (Akademisk, Köbenhavn).
18. Morris D (2002) *Dogs: The Ultimate Dictionary of Over 1,000 Dog Breeds* (Trafalgar Square, North Pomfret, VT).
19. Arman K (2007) A new direction for kennel club regulations and breed standards. *Can Vet J* 48:953–965.
20. Hickey KR (2000) A geographical perspective on the decline and extermination of the Irish wolf *Canis lupus*: An initial assessment. *Ir Geogr* 33:185–198.
21. American Kennel Club (2006) *The Complete Dog Book* (Ballantine, New York), 20th Ed.
22. Wilcox B, Walkowicz C (1993) *Atlas of Dog Breeds of the World* (TFH Publications, Neptune, NJ), 4th Ed.
23. Calboli FCF, Sampson J, Fretwell N, Balding DJ (2008) Population structure and inbreeding from pedigree analysis of purebred dogs. *Genetics* 179:593–601.
24. Drake AG, Klingenberg CP (2010) Large-scale diversification of skull shape in domestic dogs: Disparity and modularity. *Am Nat* 175:289–301.
25. Castroviejo-Fisher S, Skoglund P, Valadez R, Vilà C, Leonard JA (2011) Vanishing native American dog lineages. *BMC Evol Biol* 11:73.
26. Drögemüller C, et al. (2008) A mutation in hairless dogs implicates FOXI3 in ectodermal development. *Science* 321:1462.
27. Salmon Hillbertz NH, et al. (2007) Duplication of FGF3, FGF4, FGF19 and ORAOV1 causes hair ridge and predisposition to dermoid sinus in Ridgeback dogs. *Nat Genet* 39:1318–1320.
28. Parker HG, et al. (2009) An expressed fgf4 retrogene is associated with breed-defining chondrodysplasia in domestic dogs. *Science* 325:995–998.
29. Nowak RM (2003) Wolf evolution and taxonomy. *Wolves: Behavior, Ecology, and Conservation*, eds Mech L, Boitani L (Univ of Chicago Press, Chicago), pp 239–258.
30. Macdonald DW, Sillero-Zubiri C, eds (2004) *The Biology and Conservation of Wild Canids* (Oxford Univ Press, Oxford).
31. Van Neer W (2000) Domestic animals from archaeological sites in Central and West-Central Africa. *The Origins and Development of African Livestock: Archaeology, Genetics, Linguistics and Ethnography*, eds Blench R, MacDonald K (Routledge, New York), pp 163–190.
32. Morey DF (2006) Burying key evidence: The social bond between dogs and people. *J Archaeol Sci* 33(2):158–175.
33. Lawrence B (1968) Antiquity of large dogs in North America. Tebiwa. *The Journal the Idaho State University Museum* 11(2):43–48.
34. Gowlett JAJ, Hedges R, Law I, Perry C (1987) Radiocarbon dates from the Oxford AMS system: Archaeometry datelist 5. *Archaeometry* 29(1):125–155.
35. Flannery KV (1967) Vertebrate fauna and hunting patterns. *The Prehistory of the Tehuacan Valley*, ed Byers DS (Univ of Texas Press, Austin), pp 132–177.
36. Gautier A (2002) The evidence for the earliest livestock in North Africa: Or adventures with large bovids, ovicaptrids, dogs and pigs. *Droughts, Food and Culture: Ecological Change and Food Security in Africa's Later Prehistory*, ed Hassan FA (Kluwer Academic/Plenum, New York), pp 195–207.
37. Higham CFW (1998) Archaeology, linguistics and the expansion of the East and Southeast Asian Neolithic. *Expansion of East and Southeast Asian Neolithic in Archaeology and Language II: Archaeological Data and Linguistic Hypotheses*, eds Blench R, Spriggs M (Routledge, New York), pp 103–114.
38. Bellwood P (1998) The archaeology of Papuan and Austronesian prehistory in the Northern Moluccas, Eastern Indonesia. *Expansion of East and Southeast Asian Neolithic in Archaeology and Language II: Archaeological Data and Linguistic Hypotheses*, eds Blench R, Spriggs M (Routledge, New York), pp 128–140.
39. Plug I, Voigt EA (1985) Archaeozoological studies of Iron Age communities in southern Africa. *Advances in World Archaeology* 4:189–238.
40. Prates L, Prevosti FJ, Berón M (2010) First records of prehispanic dogs in southern South America (Pampa-Patagonia, Argentina). *Curr Anthropol* 51:273–280.
41. Corbett LK (1995) *The Dingo in Australia and Asia* (Comstock/Cornell, Ithaca, NY).
42. Koler-Matznick J, Yates BC, Bulmer S, Brisbin IL (2007) The New Guinea singing dog: Its status and scientific importance. *Aust Mammal* 29:47.
43. Toynbee JMC, Oost SI (1973) Animals in Roman life and art. *History: Reviews of New Books* 2(2):34–34.
44. Peters J (1998) *Roman Animal Keeping and Breeding: A Synthesis Based on Zooarchaeological Analysis and the Written and Pictorial Record* (in German). (Leidorf, Rahden, Germany).
45. Slater GJ, et al. (2009) Evolutionary history of the Falklands wolf. *Curr Biol* 19: R937–R938.
46. Brown P, et al. (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:1055–1061.
47. Vartanyan SL, Arslanov KA, Karhu JA, Possnert G, Sulerzhitsky LD (2008) Collection of radiocarbon dates on the mammoths (*Mammuthus primigenius*) and other genera of Wrangel Island, northeast Siberia, Russia. *Quat Res* 70(1):51–59.
48. Myles S, et al. (2011) Genetic structure and domestication history of the grape. *Proc Natl Acad Sci USA* 108:3530–3535.
49. van Heerwaarden J, et al. (2011) Genetic signals of origin, spread, and introgression in a large sample of maize landraces. *Proc Natl Acad Sci USA* 108:1088–1092.
50. Chessa B, et al. (2009) Revealing the history of sheep domestication using retrovirus integrations. *Science* 324:532–536.
51. Karlsson EK, et al. (2007) Efficient mapping of mendelian traits in dogs through genome-wide association. *Nat Genet* 39:1321–1328.
52. Stoneking M, Krause J (2011) Learning about human population history from ancient and modern genomes. *Nat Rev Genet* 12:603–614.
53. Purcell S, et al. (2007) PLINK: A tool set for whole-genome association and population-based linkage analyses. *Am J Hum Genet* 81:559–575.
54. Patterson N, Price AL, Reich D (2006) Population structure and eigenanalysis. *PLoS Genet* 2:e190.
55. Felsenstein J (1993) *PHYLIP (phylogeny inference package), version 3.5 c* (Joseph Felsenstein, University of Washington, Seattle).

Supporting Information

Larson et al. 10.1073/pnas.1203005109

SI Results and Discussion

Sample Information. For this study we genotyped 1,375 dogs and 19 wolves on the dog genome-wide SNP array. Table S1 lists the sample size of each of the 35 breeds included in this study, as well as the sample sizes of breeds from two previous studies (1, 2).

Survey of Archeological Dogs. As discussed in the main text, the identification and dating of early dog remains can be difficult. To establish a record of the timing of the first appearance of dogs in the archeological record, we have adopted a conservative approach. Table S2 lists those remains that were considered but not included in Table S3, which lists the earliest dog remains from each region, the status and dating of which are well supported. The most common reason for including a specific dog in Table S3 was not because the original claim was controversial, but because earlier remains from the same region have been reported and are included in Table S2.

The literature contains numerous claims of early domestic dogs, but many of those claims have since been questioned for a variety of reasons. First, as discussed in the main text, a lack of secure dating has led to a revision of the antiquity of some early dog remains. Second, fragmented remains often lack diagnostic characters to confidently exclude the possibility that they derive from local wild canid species. In those cases where other species can be eliminated, differentiating between dogs and wolves, especially during the early stages of domestication, is problematic. By listing these ambiguous samples on Table S2, and by not including them in the data depicted in Fig. 2, we are not claiming that the remains are not domestic dogs. They may well be. To apply a consistent standard of acceptance, however, we biased our selection to only include those claims that have been robustly argued. We are aware that deciding whether or not to include a controversial claim is itself controversial, but we are confident that the inclusion or exclusion of specific claims has no effect on either the overall temporal and geographic pattern of global dog domestication, or the conclusions derived from the data.

Supplementary Tables. Table S1 lists the 35 breeds included in this study, as well as all breeds investigated in two previous studies (1, 2). The cells in which the breeds are listed are colored according to the colored clades in Fig. 1 and represent breeds that retain a basal signature (red), non-European breeds that are not basal (blue), and European breeds that have deep histories but do not sit in basal positions on phylogenetic trees (brown). Numbers beneath in the publication headings columns represent the number of samples in each study. The regional origin column lists the suspected geographic origin of each breed, although in many cases the precise origins are unknown. The word "Europe" in parentheses indicates that although that breed is known to have spent time in a different region, it was either imported from or admixed with breeds from Europe. The breed notes column gives succinct breed information gleaned from several encyclopedic entries (3–6).

Table S2 lists those samples that were considered but not used to create Fig. 2. This table lists: the country, site, dates (reported in calibrated years before present), the elements reported in the publication, a reference that discusses the remains, and the reference from which information about the dating was gleaned. The column labeled "notes" possesses pertinent information about the remains, and the final column lists a rationale for excluding the sample from being included in Table S3.

Table S3 lists those samples that were used to create Fig. 2. The table lists the general location where the pie charts in Fig. 2 were placed, followed by the country, site, dates (reported in calibrated years before present), the elements reported in the publication, a reference that discusses the remains, and the reference from which information about the dating was gleaned. The final column lists additional information in support of the status determinations. Outlined boxes in each region correspond to a single pie chart in Fig. 2.

Table S4 lists the wolf samples analyzed in this study. C.V. provided the DNA extracts and the sample codes are his.

Note on Biogeography and Basal Breeds. A possible exception to the general rule that domestic dog remains found south of the natural distribution of wolves are only found in association with an agricultural package may be southern China. Although the presence of wolves in this region is questionable, preliminary results suggest that dogs may have been present in late hunter-gatherer sites before the introduction of agriculture (7) (but see Table S2).

More generally, the pattern of significantly earlier dates in the Northern Hemisphere than in the Southern Hemisphere supports Diamond's (8) observation that human movement along latitudes is far simpler than along longitudes. People and dogs migrated more easily east and west not only because doing so required less of an adjustment to shifting climatic and daylight patterns, but also because landscape features (e.g., rainforests, mountains, and deserts) in South America, Central and East Asia, and Africa presented significant geographical barriers to north-south movement.

Because three of the basal breeds (Basenjis, Dingoes, and New Guinea Singing Dogs) are found beyond the natural wolf range, the implication is that these dogs would have had numerous opportunities to interbreed with a wide variety of dogs and wolves before moving south. The relatively late dates for the appearance of dogs in these regions, combined with the long history of probable hybridization before their arrival, suggests these dogs are not directly descended from the first domestic populations despite their genetic distinctiveness.

1. Vonholdt BM, et al. (2010) Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature* 464:898–902.
2. Parker HG, et al. (2004) Genetic structure of the purebred domestic dog. *Science* 304: 1160–1164.
3. Morris D (2002) *Dogs: The Ultimate Dictionary of Over 1,000 Dog Breeds* (Trafalgar Square, North Pomfret, VT).
4. American Kennel Club (2006) *The Complete Dog Book* (Ballantine, New York), 20th Ed.
5. Wilcox B, Walkowicz C (1993) *Atlas of Dog Breeds of the World* (TFH Publications, Neptune, NJ), 4th Ed.
6. Clark AR, Brace A, eds (1995) *The International Encyclopedia of Dogs* (Howell Book House, New York).
7. Zhang C, Hung H-C (2012) Later hunter-gatherers in southern China, 18000–3000 BC. *Antiquity* 86:11–29.
8. Diamond J (2002) Evolution, consequences and future of plant and animal domestication. *Nature* 418:700–707.

Other Supporting Information Files

Table S1 (DOCX)
Table S2 (DOCX)
Table S3 (DOCX)
Table S4 (DOCX)

Table S1. A list of breeds analyzed in two previous publications and in this study, their purported geographic origins, and notes derived from four encyclopedic sources. The cells in which the breeds are listed are colored according to the colored clades in Figure 1 and represent breeds that retain a basal signature (red), non-European breeds that are not basal (blue), and European breeds that have deep histories but do not sit in basal positions on phylogenetic trees (brown). Numbers beneath each study represent sample sizes.

Breed	Parker *et al.* 2004(1)	vonHoldt *et al.* 2010(2)	This Study	Regional Origin(3-6)	Breed Notes(3-6)
Afghan Hound	5	12	1	SW Asia	Though several regional varieties existed in Afghanistan, this breed was only discovered by the west in the 19th century when they were imported. They later went extinct during the World War 1. The breed was then reintroduced and most of the modern western individuals are descended from three individuals.
Africanis		3		Africa	Though this breed is from South Africa, there are reports of admixture with exotic breeds after the 19th century. Given its geographic origin, it should retain an ancestral signature, but the recent admixture has been sufficient to eliminate this genetic heritage.
Airedale Terrier	4			Europe	This breed was deliberately developed in 1840 in Yorkshire by mating Otterhounds, and English Black and Tan Terriers.
Akita	5	12	4	Japan	From northern Japan, this breed nearly went extinct until an effort was made to preserve it in the 1920s by admixing a number of regional varieties.
Alaskan Malamute	5	11		N America	Used as a sled dog by tribes native to Eastern Alaska, this breed was nearly extinct as a result of 18th century efforts to breed in other bloodlines to increase the speed of the dogs for races. Two people collected the most pure examples of the breed and recreated it in the 1920s.
American Cocker Spaniel	5	12		N America (Europe)	Derived from early land spaniels, possibly in Spain, this breed was brought to England where it was bred with English Setters and then imported into the USA. Until the 1930s there were no differences between the American and the English breed, but the two were split and recognized as separate breeds in 1946.
American Eskimo		7		N America (Europe)	German immigrants brought white spitz dogs that were the result of crosses between Keeshonds, Volpinos, and Pomeranians to the USA in the 19th century. Their German origin fell out of favor during the world wars their name was changed to American Eskimo to reflect the name of the kennel that bred the dogs and was possibly responsible for breeding in Japanese spitzes into the bloodline.
American Hairless Terrier	5			N America (Europe)	A naked puppy appeared in a litter in 1972. This individual was then mated with its sisters to create the foundation of the hairless variety of this breed, originally imported from Europe.
American Water Spaniel	5			N America (Europe)	A large number of different lineages were combined to create this breed in the USA.
Australian Cattle Dog			10	Australia (Europe)	The original dogs introduced to Australia to assist with the cattle industry were not hardy enough. Multiple attempts were made in the 19th century to mate a wide variety of breeds (including dingoes) in order to create a breed that could handle the Australian climate.
Australian Shepherd	5	12		N America (Europe)	Basque shepherds resident in Australia travelled to the west coast of the USA in the 19th century where the dogs that accompanied them were admixed with several other breeds.
Australian Terrier	5	12		Australia (Europe)	A 19th century admixed breed created by mating Yorkshire, Norwich, Cairn, Scottish, and Irish terriers.
Basenji	5	13	10	Africa	Known for its lack of a bark, this breed is from the Congo basin in sub-Saharan Africa. Individual dogs were first brought to the UK in 1895 though they did not survive. Additional dogs were imported to England in the 1930s and an additional trip to Zaire in 1987 added more dogs in order to increase the breeding pool. Importantly, it is claimed that this breed has never been bred with European dogs either in Africa, Europe or North America.
Basset Hound	4	11	10	Europe	This breed was first mentioned in the 16th century in France. It possessed a mutation that gave it short legs and was used to hunt rabbits in heavy cover. Following World War 2, there were very few individuals remaining in England and additional individuals from France were imported to save the breed.
Beagle	5	10		Europe	Though this is supposed to be an ancient breed, the modern variety was created in 1830s in the UK from several similar breeds of small hounds.
Bedlington Terrier	4			Europe	Several breeds were used in the development of this breed in the 1820s including whippets, a wire-coated terrier and possibly a hound.
Belgian Sheepdog	5			Europe	Though flock-herding dogs were used in Belgium for centuries (during which interbreeding was common since the dogs were selected for performance and not for aesthetics), the modern breed was deliberately developed in the 1880s by mating several representatives of the breed that existed at the time.
Belgian Tervuren	4			Europe	This breed has a similar origin to that of the Belgian Sheepdog and nearly went extinct during the World Wars.
Bernese Mountain Dog	5	11		Europe	This breed supposedly came into being when Roman guard dogs 2,000 years ago were introduced to Switzerland and mated with local mountain dogs. From there, four local varieties were recognized, nearly all of which had gone extinct before the 1890s when two men tracked down the least contaminated members of the breed and bred them together. During World War 2, the breed died out completely in the UK.
Bichon Frisé	4			Europe	This small dog was associated with sailors for centuries and was transported around the Mediterranean to and from Islands as far away as the Canaries. They were often favorites of royal courts in Europe and were likely interbred with small dogs across Europe.
Bloodhound	5	9		Europe	Scent hounds have been used to hunt large game in Europe for centuries since the dogs could follow the scent of a wounded animal. Roman records mention scent hounds with a similar appearance and it is possible the breed was introduced to the UK in 1066. Only 12 animals remained in the UK after World War 2. In order to save the breed, individuals were imported from Canada and bred with the local remaining dogs.
Border Collie	5	12		Europe	The origin myth for these dogs imagines that Romans introduced herding dogs to the UK in the 1st century AD. Vikings then brought their own herding dog derived from northern spitzes. All modern representatives of this breed, however, descend from a single individual born in 1893.
Borzoi	5	12		Europe	The romantic narrative for this breed imagines that thirteenth century Mongols introduced sight hounds into Russia where, centuries later, the Russian aristocracy used them to hunt wolves though the middle of the 19th century when they began to decline before nearly vanishing in Russia after 1917. The modern breed was developed by a small number of breeders in the late 19th century.
Boston Terrier		6		N America (Europe)	This breed was developed in the USA in the 1820s by crossing five separate breeds including English Bulldogs, White English Terriers, Pit Bulls, Boxers, and French Bulldogs.
Boxer	5	12	94	Europe	This breed was developed deliberately in the 1880s when a resident of Munich crossed a mastiff type of dog called a French Bullenbreisser to a local dog. English bulldogs and Great Danes are purported to have also been involved in the creation of this breed.
Briard		12		Europe	The legend for this breed maintains that it was developed in France as a sheep guard dog from mixes between local breeds and those introduced by eastern cultures who invaded Europe in the Middle Ages.
Brittany Spaniel		12		Europe	This breed is descended from a pointing tradition and is therefore not technically a spaniel. And though the general type of dog existed for centuries, this particular breed arose in the second half of the 19th century and was likely crossed with English pointing dogs.
Brussels Griffon		7		Europe	Developed as a pest controller in Belgian cities, this breed was mated with many other small dogs including Afenpinschers, Yorkshire Terriers, Pugs, and King Charles Spaniels.
Bulldog (English)	5	11	2	Europe	This breed was developed for bull baiting and though its original ancestors were related to mastiffs, it was also mated with pugs in England before the sport was outlawed in 1835.
Bull Terrier		3		Europe	This breed was created in 1835 after bull baiting was made illegal by crossing English Bulldogs with several breeds including Black and Tan Terriers, Spanish Pointers, English White Terriers, Dalmatians, Greyhounds and Whippets in order to create a dog breed that would fight other dogs.
Bullmastiff	5	12		Europe	At the end of the 19th century, British estate owners required a breed that could protect their land from poachers so a deliberate effort was made to cross Bulldogs and Mastiffs, and from 1924 the breed was closed to further introgression.
Cardigan Welsh Corgie		12		Europe	One of two small droving dogs from Wales, the origin myth of the Cardigan maintains that it originated from Celts who introduced the dog in 1,200 BC. These dogs interbred with other herders including Collies and freely interbred with Pembroke Welsh Corgis until the two breeds were split in 1927.
Cairn Terrier	5	12		Europe	Numerous working terriers existed across Scotland from at least the 16th century. All the different breeds were collectively referred to, and treated as, a single population of Scottish Terriers until 1873, when the different breeds were split from one another.
Canaan Dog		3		Middle East	The legend for these dogs claims that they were introduced to the Levant when the Romans drove out the Israelites 2,000 years ago. A population of these dogs existed in the Nagev desert in a feral form until the 1930s, when deliberate efforts were made to re-domesticate them.

Breed	Parker *et al.* 2004(1)	vonHoldt *et al.* 2010(2)	This Study	Regional Origin(3-6)	Breed Notes(3-6)
Cavalier King Charles Spaniel	5	12		Europe	Tapestries from the 15th and 16th centuries depicted this breed that was possibly mixed with Pugs. The breed all but disappeared before being revived in the 1920s in a slightly different form, but then suffered a significant bottleneck during World War 2.
Chesapeake Bay Retriever	5			N America (Europe)	Created and developed in the USA from two Newfoundland dogs and local Retrievers from Maryland, this breed was likely crossed with Pointers, Irish Water spaniels, and even native American dogs.
Chihuahua	5	9		N America	There are numerous conflicting stories about the origin of this breed. The most likely scenario is that it, like numerous others associated with ocean trading, has a long history of interbreeding with multiple small dogs including Papillons, Pomeranians, hairless breeds native to Mexico, and possibly East Asian dogs. There has been significant selection for more juvenile characteristics including the domed head and round eyes that has likely involved bottlenecks.
Chinese Crested			39	East Asia	Like other small hairless breeds, the geographical origins of this breed are uncertain. European merchants reported seeing dogs of this description in both East Asian and Mexican ports in the 1500s and they became popular along trade routes in Spain, Mexico, China and South Africa.
Chinese Shar-Pei	5	12	50	East Asia	The legends maintains that this breed began as a guard dog during the Han Dynasty in 200 BC in the southern Chinese province of Kwantung. It nearly went extinct during the Cultural Revolution and by 1978, only 60 individuals remained. The modern breed is descended from the few dogs that were kept and bred initially by breed clubs in Hong Kong and Taiwan, and then by breeders in the USA. Like the Chow Chow, they possess a blue-black tongue suggesting the two breeds are closely related.
Chow Chow	5	11		East Asia	Depictions of Chow-like dogs date to 150 BC in China, and the Chinese Tang Emperor is thought to have had several thousand Chow Chows in the 8th century AD. They were first brought to Europe in 1780 by members of the East India Company and displayed in London zoo. This breed has supposedly remained free of admixture since a breed club formed in 1895.
Clumber Spaniel	5			Europe	Supposedly imported to the UK in 1770 from France, several additional breeds were admixed into this line to create the Clumber.
Cocker Spaniel (English & American)	10	24	109	Europe	Descended from Spanish Spaniels, flushing spaniels were readily interbred with other dogs of the group. Two sizes were developed: the springer and the cocker that were then split into separate breeds in 1893.
Collie	5	12		Europe	Collie like dogs have been in use shepherding for millennia and the origin myth maintains that the breed traces its ancestry to introduced Roman dogs 2,000 years ago. The modern version is derived from Scottish varieties that had both rough and smooth coats, came in a variety of colors, and may also have interbred with the Borzoi.
Dachshund	5	12	24	Europe	Short-legged dogs have been known for 4,000 years and they have been employed to root out badgers, foxes, and rabbits from their underground tunnels. The modern breed has been mixed with French, German, and English hounds and terriers and possibly Basset hounds as well. The breed also suffered a big population decline during World War 1.
Dingo		12		Australia	The earliest archeological evidence for dogs in Australia dates to ~3,500 years ago (see Table S3) and though the modern Dingo may be extinct in the wild due to heavy introgression with modern European breeds, those individuals who have avoided this mixing may be the oldest breed still in existence.
Doberman Pinscher	5	6	203	Europe	This breed was deliberately developed in 1890 by Louis Doberman. He initiated a series of complicated crosses to create a dog that would act as a personal guard dog. There is no record of what breeds he used, but it is possible the following breeds were involved: Rottweiler, Greyhound, Manchester Terrier, and a short haired pinscher.
English Setter			10	Europe	Originating from Spanish land spaniels, there were a wide variety of similar dogs in both England and the continent, all of which were routinely crossed. The dogs date to at least 400 years ago in England in the USA and Canada, at least two types have diverged in the past 100 years.
English Springer Spaniel		6		Europe	These dogs were developed to flush game and like the Setter, probably had Spanish origins in the past few hundred years. Cocker and Springer spaniels were often born in the same litter and their separation into distinct breeds is a recent phenomenon.
Eurasier			49	Europe	Though genetically ancient, this breed was deliberate developed starting in the 1940s and fixed in the 1960s by crossing Chow Chow males with Keeshounds bitches, the offspring from which were later crossed with a Samoyed. Originally called a Wolf Chow, they have been called Eurasiers since 1973.
Finnish Spitz			68	Europe	Originally kept by Finno-Ugric people in Central Russia, the dogs were moved to Finland when the culture migrated. The breed was nearly extinct by 1880 because of introgression from other breeds, but one breeder sought pure individuals and carefully bred them together to rescue the breed, which today retains an ancient genetic signature.
Flat-coated Retriever	5	12		Europe	After the development of the gun, it became desirable to possess a dog that could retrieve dead birds. All the dogs that did this were called retrievers and they were allowed to freely interbreed. As the modern breed was developed, several crosses between Newfoundlands, setters, sheepdogs, and spaniel-like water dogs. This breed nearly died out during World War 2.
French Bulldog	4	12		Europe	Supposedly developed solely as a companion dog, many breeds are known to have been involved in its modern form including: terriers, English bulldogs, and possibly Pugs.
German Shepherd Dog	5	12		Europe	This breed was deliberately developed in 1899 in Germany by Max von Stephanitz in an effort to create a sheep-herding dog. Numerous breeds were involved in its creation as well as wild wolves.
German Shorthaired Pointer	5	12	10	Europe	This breed was developed in the 17th century by mating old Spanish pointers with German bird dogs, and English pointers (a heavily admixed breed itself). Lots of admixture continued until 1870, when a studbook was created and the line was closed.
Giant Schnauzer	5	11		Europe	Derived from large cattle drovers, this breed was developed by mating Great Danes, Rottweilers, Bouvier des Flanders and local sheep dogs living near Munich. The breed's numbers declined in World War 2 and several additional large breeds were used to re-establish it.
Glen of Imaal Terrier		12		Europe	Supposedly derived from crosses between Kerry Blue, soft-coated, and Irish terriers, this breed was nearly extinct in 1950 before being rescued.
Golden Retriever	5	12	303	Europe	In 1865, a single yellow puppy was born in a litter of black, wavy-coated retrievers. The yellow puppy was selected and bred to a water spaniel, and the four resulting yellow pups became the foundation of the modern breed that also included admixture with Red Setters and possibly a Bloodhound.
Great Dane	5	12		Europe	Large mastiff-like dogs existed in Europe for millennia and were favorites of the Romans who used them as dogs of war. There have been dozens of different breeds with a wide variety of coat colors and it's possible that the modern populations stems from a mix of English Mastiffs and Irish Wolfhounds.
Greater Swiss Mountain Dog	5			Europe	This breed shares a similar history to the Bernese Mountain dog. The legends for both breeds maintain that they arose from crosses between Roman guard dogs and local Swiss dogs 2,000 years ago. The breed was thought to be extinct in 1908 when two breeders found a handful of surviving individuals and recreated the breed from no more than 8 individuals, during which time they may have been mated with Saint Bernards as well.
Greyhound	5	12	38	SW Asia	One of the oldest types of dogs, there are depictions of greyhound-like dogs in 6,000 year-old Egyptian tombs and in 1,000 year-old texts. There are at least 40 different varieties of Greyhound across the world. Their true origins are unknown, though the modern breed does not possess a basal genetic signature.
Havanese		12		Europe	Part of the Bichon family, these small dogs associated with Mediterranean and Atlantic sailors may have originated on Malta before being imported to Cuba. After 1959, 11 were exported to the USA where the breed was rescued from extinction.
Ibizan Hound	5	11		Europe	Closely related to the Pharaoh Hound, the origin myth of this breed maintains that it was introduced to the island of Ibiza by the Phoenicians in the 8th or 9th century BC. The island has been settled numerous times since, and the modern breed stems from about eight puppies that were transported to the USA in 1956, when they may have been admixed with other breeds.
Irish Setter	5			Europe	This breed shares a similar history to all other setters and has existed in Ireland since the 1700s. Several other breeds were involved in both its early and later creation including Bloodhounds, Pointers, and Borzois.
Irish Terrier	4			Europe	Possibly the oldest terrier in Ireland, it interbred freely with other terriers during its early history and even during the 1870s the breed possessed a tremendous amount of size and color variation that resulted from crosses with breeds, including non-terriers.
Irish Water spaniel		11		Europe	Though retrieving dogs have been used for millennia, this breed was created in the 1830s by mixing several dogs including extinct English Water Spaniels and possibly Poodles.

Breed	Parker *et al.* 2004(1)	vonHoldt *et al.* 2010(2)	This Study	Regional Origin(3-6)	Breed Notes(3-6)
Irish Wolfhound	5	12		Europe	The legend of these dogs maintains that they were already present in the British Isles when the Romans invaded in 393 AD and that Romans sent individuals back to Rome. Similar breeds are known from the Icelandic Sagas and Cromwell made it illegal to export the breed since wolves presented so much of a threat. They were used to hunt wolves to extinction in Ireland by 1786, and demand for the dogs plummeted along with the population. An Army officer in 1862 restored the breed by admixing Scottish Deerhounds, Russian Wolfhounds, and Mastiffs. It is likely that the modern version of the breed bears no genetic relationship to the original breed. (See main text.)
Italian Greyhound	5	13		Europe	Possibly the first breed to be developed solely for companionship, it has been popular with royalty for at least 2,000 years. It was nearly extinct in the 1890s, but was rescued using about 40 individuals. The populations declined dramatically in World War 2 as well so individuals from the USA and Canada were used to bolster the breed in Europe.
Jack Russel Terrier		12		Europe	This breed was deliberately developed in 1819 in Oxford, England using a single dog that was itself had been admixed from several terriers. The original breed was nearly (or entirely) extinct in World War 2 and was recreated using Dachshunds, Corgis, and several toy breeds.
Keeshond	5			Europe	This breed was possibly derived from Northern spitz dogs and was common on barges in the Netherlands. Political change in Holland nearly led to the breed's extinction. In 1920, an effort was made to find the few remaining individuals to regenerate the breed.
Kerry Blue Terrier	5		3	Europe	Like other Irish terriers, this breed interbred with a wide variety of terriers in Ireland and the modern variety is the result of numerous admixtures.
Komondor	5			Europe	This breed is related to many similar breeds that were used throughout Europe for centuries to protect livestock flocks while smaller dogs herded them. They may have descended from large dogs introduced earlier into Europe, though they suffered a significant population decline during World War 2.
Kuvasz	5	12		Europe	This breed's history mirrors the Komondor and other Eastern Euorpean flock guardings dogs. They were nearly wiped out in World War 2 when as few as 12 remained, but a few isolated individuals were discovered and then mated with Great Pyrenees to rescue the breed.
Labrador Retriever	5	12	1	Europe	Originally from Newfoundland, this breed was popular in England in the 1830s when it was bred with various retrievers and spaniels before going extinct in Canada.
Lagotto Romagnolo			24	Europe	This water breed was known in the Northeast of Italy from at least the 15th century after which it became a truffle-hunting dog and mated with numerous other breeds to improve its smelling capability.
Leonberger			34	Europe	As breeders were attempting to rescue the Saint Bernard in the 1830s by introducing imported Newfounlands, the dogs they chose not to keep became Leonbergers. The breed was reduced to five and eight individuals in the successive World Wars.
Lhasa Apso	5			East Asia	The legend maintains that this breed was kept by Tibetan Monks, though it may have also come from in Mongolia. Individuals were imported to Europe where they interbred with similar dogs including Tibetan Terriers. The breed virtually disappeared in World War 1, but was re-established in 1922 when a Colonel brought six dogs back from Sikkim. They were officially separated from Tibetan Terriers in 1934 and then experienced another decline in World War 2.
Manchester Terrier – Toy	4			Europe	This breed is an improved version of the extinct Black and Tan Terrier that was bred with Whippets, Greyhounds, and Dachshunds. The populations declined during World War 2 and only 11 dogs were registered at the end of the conflict.
Mastiff (English)	5	12	9	Europe	Large mastiff-like dogs have been used as watchdogs for millennia and dogs resembling this breed were present in the British Isles when the Romans invaded in 55 BC. The word 'dog' originally described mastiff-type dogs, and when the Normans invaded Britain, there were so many of them that the word ‘dog’ came to describe all dogs, not just large mastiff-like individuals. The breed suffered large population decreases when dog fighting was disallowed, and after both World Wars when there were only 8 individuals of breeding age in 1945. In every case, other breeds were used to recreate and rescue the breed.
Miniature Bull Terrier	5	12		Europe	This breed was deliberately developed in the early 19th century by crossing Bulldogs with the now extinct white English terrier and possibly a Black and Tan Terrier. Spanish Pointers may also have been bred into this line to increase the breed's size.
Miniature Pinscher		12		Europe	This breed is older than the Doberman Pinscher and was created by mixing several breeds including German and Italian Greyhounds and possibly Dachshunds.
Miniature Schnauzer	5			Europe	This breed was developed by mating smaller individual standard Schnauzers with Affenpinshers and Poodles. Other breeds that may have been involved include: Pomeranians, Fox terriers, and Scottish Terriers.
Neapolitan Mastiff			11	Europe	Farmers in Southern Italy used these large mastiff-like dogs. They suffered a significant population decline in World War 2 and English Mastiffs may have been involved to rescue the breed.
New Guinea Singing Dog		12		New Guinea	Dogs were present in New Guinea by at least 2,500 years ago, though Westerns first encountered the New Guinea Singing Dog in 1897. Breeding pairs were sent to Western Zoos beginning in the 1950s and there were at least 100 individuals in zoos in 1997, all of which were descendants of no more than 14 individual dogs. Given the size of New Guinea, it is likely that regional variants of this breed had developed on the island, though they all may not be extinct through admixture with introduced western breeds.
Newfoundland	5	3		N America (Europe)	One origin myth for this breed states that sailors brought Pyrenean mountain dogs to Canada that then mated with local breeds to create a working dog. Other stories involve a Viking introduction. Regardless, this breed was present in Newfoundland by the early 18th century though the modern breed is derived from individuals that were brought from Canada to the UK and likely mated with English breeds.
Norwegian Elkhound	5			Europe	The legend of this breed maintains that it closely resembles the bones of Scandinavian dogs found in archaeological sites 6,000 years ago. The Vikings are said to have hunted with this dog and it was brought to the UK at the end of the 19th century where it likely interbred with other hounds before a breed club was formed for this breed in 1936.
Norwich Terrier		12		Europe	This breed was developed in the 1880s by interbreeding numerous terriers from Yorkshire, Ireland, and Southern England.
Old English sheepdog	5	10		Europe	This breed was a cattle drover and not a sheepdog. It was developed in the early 19th century by interbreeding several different drover dogs with collies and numerous European breeds including Bergamascos and Ovtchartkas.
Papillion		12		Europe	This breed has been associated with royal courts for centuries including Marie Antoinette and Louis the XIV. Toy dogs were traded and sold after being carried on the backs of mules as they moved from country to country where they interbred with local small dogs.
Pekingese	5	12	8	East Asia	Dogs resembling this breed have been known in China since the 8th century AD. Three examples were brought back to the UK following the English siege of the Imperial Palace in Beijing in 1860. The dogs became extinct in China in 1908, and the appearance of the breed in the UK changed dramatically through the second half of the 19th century as a result of selection pressures and likely admixtures with other toy breeds.
Pembroke Welsh Corgi		11	56	Europe	The origin myth for this breed maintains that these dogs were introduced to Wales in 1107 AD by Flemish Weavers. This cattle droving breed routinely interbred with Cardigan Welsh Corgis until 1930 when they were separated.
Perro de Presa Canario	5			Europe	This breed is the result of interbreeding between the native dogs that were present on the Canary islands and introduced Mastiffs and Bulldogs that arrived in the 19th century. The admixed breed was nearly extinct in the 1960s when a few individuals from remote corners were collected and used to rescue the breed in the 1970s.
Petit Basset Griffon Vendeen		12		Europe	Part of a continuum of dogs used to hunt differently sized game, this version was used to hunt small game. It was not distinguished from the larger dogs within the population until 1975 when all crossing was forbidden and the Petit and the Grand versions became separate entities.
Pharaoh Hound	4			Europe	This type of site hound has been used for millennia and drawings on Egyptian tombs of dogs resembling this breed date back more than 6,000 years. The Legend maintains that Phoenician traders introduced these dogs to Malta and many other Mediterranean islands where they were used to hunt rabbits. Eight examples of this breed were imported to England in 1968 and were called Pharaoh Hounds because of their resemblance to the Egyptian depictions. Given its remote island home, some scholars have suggested that this breed has not been admixed with the numerous purebred lines that were also present on the island, though the genetic results suggest that this breed has not escaped admixture with European breeds.
Pointer	5			Europe	This breed appeared throughout Europe in the 17th century and has been used to point at prey and as a guard-dog. Though their regional origins are unknown, different pointer breeds were often admixed, either deliberately or accidentally. Breeds they have been crossed with include: Foxhounds, Greyhounds, and Bloodhounds throughout (at least) the 19th century.
Pomeranian	5	12		Europe	The larger version of this dog was derived from Northern sled dogs. The Pomeranian was bred into a smaller breed and was brought to the UK by Queen Victoria who first encountered them in Italy. At that time Pomeranians were often 30 pounds, but they are now typically four to five pounds.
Poodle	5	12	49	Europe	Poodles are depicted in 15th century art and water-retrieving dogs were likely present for a long time before that. The modern breed was standardized in Germany and may have been mated with various terriers.

Breed	Parker *et al.* 2004(1)	vonHoldt *et al.* 2010(2)	This Study	Regional Origin(3-6)	Breed Notes(3-6)
Portugurese Water Dog	5	12		Europe	When and where this breed emerged is unknown. There has been some speculation that water dogs were known in Central Asia in 700 BC. Moors may have introduced waterdogs to Europe in the 8th century AD where they were common on the Portuguese coast for several hundred years. As demand for the breed dropped, their numbers fell and by 1960 there were only 50 individuals left before a breeding program rescued them from extinction.
Pug Dog	5	12	10	Asia	Morris(3) lists eight separate theories regarding the origin of the Pug, though it most likely originated in Asia. The Dutch East India company brought dogs resembling Pugs to the Netherlands in 1572. These dogs were mated with numerous other breeds including Affenpinschers and miniature Bulldogs, and populations fluctuated with fashion over several centuries. Additional individuals including the first black versions were imported into the UK in 1877 and though for a time two breeds were recognized, they have since merged again.
Rhodesian Ridgeback	5	12		Africa (Europe)	When European farmers moved to South Africa they brought their dogs with them. In the 17th century, these farmers recognized the value of the local dogs and began deliberately mating their dogs to the local individuals. Two of these mixed heritage dogs were then taken to Zimbabwe in 1875 where they were mated with Greyhounds, English pointers, Bulldogs, Rough Collies and Great Danes to create what became known as Van Rooyen's Lion Dogs. A few desirable individuals were then selected as the foundation of the breed that was set in 1922.
Rottweiler	5	3	21	Europe	Romans used large dogs to drive cattle so that armies could eat meat while travelling. These large dogs were used to guard herds until the middle of the 19th century when they were replaced by railroads. By 1882, only a single individual remained and it was used as the basis for the re-emergence of the breed, though the new population nearly went extinct during World War 2.
Saint Bernard	5	12		Europe	The legend maintains that the dogs that accompanied Romans across the Alps are interbred with local Swiss dogs. These admixed dogs were then used as watchdogs by Monks living in the valleys in the 11th century AD. The breed then became rescue dogs in the 18th century when they were possibly mated with Great Danes and Bloodhounds. In 1810, a handful of individuals were imported into England to replenish the English Mastiff population. The modern breed is known to have been mated Newfoundlands.
Saluki	5	12	10	Near East	Dogs resembling this running sight-hound have been present throughout the Near East and North Africa for millennia, and a legend maintains that they were imported to the UK following the Crusades after which they were assimilated into the native dog population. In desert regions, the dogs were carried on camelback and released after birds of prey had been spotted. Once the camels arrived the dogs would have already captured and killed the game. Examples of this breed were imported into the UK in middle of the 19th century and though the numbers suffered in World War 2, additional fresh imports helped to sustain the breed.
Samoyed	5	12		Siberia	Used as sled-pulling dogs in northern Siberia by the Samoyedic reindeer herders, 19th century traders acquired a few individuals and introduced them into the UK. Both Shakleton and Scott used them for their polar expeditions. It is possible that the entire modern breed descends from just 12 individuals.
Schipperke	4		24	Europe	Possibly derived from northern spitz dogs, this breed is thought to be the first participant in a dog show in 1690. The modern breed has likely been admixed with Pomeranians and numerous terriers.
Scottish Deerhound		6		Europe	Large shaggy Greyhounds have been known in Scotland for more than 500 years. Like their Irish cousins, they were originally bred to hunt wolves. Once the wolf became extinct, demand for the dogs fell. They were then used to hunt deer until the deer population collapsed. The breed suffered additional population collapses with the break up of the clan system in 1769, and in World War 2.
Scottish Terrier		12		Europe	Possibly the oldest of the many various types of terrier found in Scotland, the rough coated breed was identified in 1879 and in 1882 the breedlng line was closed. Prior to that however, all of the different terriers interbred freely.
Shetland Sheepdog	5	12	49	Europe	Traders brought dogs from Greenland and Scandinavia to Shetland in the 18th century where smaller versions of cattle and ponies were present. This breed, a smaller version of a collie, was standardized in 1906, but was crossed with standard collies after a population crash in World War 1.
Shiba Inu	5			Japan	Dogs are known from the early Jomon period in Japan where they evolved in isolation, though there is the suggestion that native dogs were admixed with dogs imported from the Asian continent in the third century AD. Local varieties developed across many regions of Japan, though by 1920, the purebred dog were rare given a surge in popularity of foreign breeds. A program was begun in 1928 to rescue the breed, though the breed was nearly extinct by the end of World War 2. A second attempt to save the breed was launched by mating three distinct breeds (the Mino Shiba, the Sanin Shiba, and the Shinshu Shiba) to develop the modern version.
Shih Tzu	5	10		East Asia	Also called the Lion dog, an origin myth maintains that this breed was the result of a 17th century (or earlier) cross between Lhasa Apsos of Tibet and the Pekingese from China. These dogs were unknown in the west until the early 20th century when a few were imported to the UK and Norway. They mixed freely with Lhasa Apsos in the west until they were separated in 1935. In 1952, backcrosses were made with Pekingese to overcome inbreeding issues.
Siberian Husky	5	12		Siberia	The Chukchi tribe from Northeast Siberia has been breeding sled dogs for millennia. They were imported into Alaska in the early 20th century where they may likely mixed with local sled-pulling dogs, and the modern breed stems from these imports.
Soft Coated Wheaten Terrier	4			Europe	Known as the poor man's wolfhound, this terrier was present in Ireland for centuries during which time it freely interbred with other local terrier breeds such as the Kerry Blue and Irish Terrier.
Staffordshire Bull Terrier		12		Europe	The early history of this breed is identical to the Bull Terrier which was a cross between a Bulldog and a Black and Tan Terrier. This breed is the result of a deliberate cross between a Bull Terrier (itself a mix of a Bulldog and a Black and Tan Terrier) and a smaller terrier (possibly a Manchester Terrier or a White Terrier).
Standard Schnauzer	5	12		Europe	This breed is the oldest of the three sizes of Schnauzers. Known as a wire-haired pinscher and more likely closer to a terrier, the breed performed several jobs as far back as the 14th century and deliberate crosses in the 19th century with Wolfspitzes and Poodles produced a mottled coloring. Additional crosses were used to create the miniature and giant versions.
Sussex Spaniel		5		Europe	Used to flush game, the breed was deliberately developed in the 18th and 19th centuries by crossing several spaniel and hound breeds. Always rare, the breed was reduced to eight individuals following World War 2, and the modern populations stems from this group.
Tibetan Terrier	5		17	East Asia	A close relative of the Lhasa Apso, this breed is not related to European terrier breeds despite its name. The breed was introduced slowly into the West as numerous travelers acquired them and brought them back to Europe where they were confused with other East Asian and Tibetan breeds such as the Lhasa Apso with which it freely interbred. The two breeds were later separated.
Toy Poodle		12		Europe	This breed was developed in the first half of the 20th century by selecting small versions of standard Poodles in an effort to develop a toy version.
Welsh Springer Spaniel	5			Europe	Prior to the 20th century, all spaniel breeds were used to flush out small game and were not divided into separate breeds. Welsh and English Spaniels were even judged together at dog shows until 1873, before being split into two breeds. This breed was recognized in 1902.
West Highland White Terrier	5	12		Europe	Terrier dogs were common in Scotland and were allowed to freely interbreed. In the 19th century, a colonel accidentally shot and killed his favorite brown terrier. He then began deliberately developing a more visible white version of the breed. White puppies often appeared in the litters of Cairn Terriers and these were selected as the basis for this breed.
Whippet	5	12		Europe	Known as the poor man's greyhound, this breed was developed in the 19th century as a rabbit courser by crossing greyhounds with spaniels and terriers.
White Shepherd			15	Europe	White versions of German Shepherds were often ignored after they were first mentioned in 1882. They were virtually eliminated in Europe but found favor in North America before being reintroduced to Europe in the 1970s.
Yorkshire Terrier		8		Europe	Among the wide variety of Scottish terrier breeds, some were deliberately crossed with local terriers in Yorkshire in the 1870s. In all, up to eight separate breeds were used to create the modern breed, the smallest of which was a 10 oz. adult.

References:

1. Parker HG, *et al.* (2004) Genetic structure of the purebred domestic dog. *Science* 304(5674):1160-1164.
2. vonHoldt BM, *et al.* (2010) Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature* 464(7290):898-902.
3. Morris D (2002) *Dogs: The Ultimate Dictionary of Over 1,000 Dog Breeds* (Trafalgar Square).
4. American Kennel Club (2006) *The Complete Dog Book* (Ballantine Books, New York) 20th Ed.
5. Wilcox B & Walkowicz C (1993) *Atlas of dog breeds of the world* (TFH Publications) 4th Ed.
6. Clark AR & Brace A eds (1995) *The international encyclopedia of dogs* (Howell Book House).

Table S2. A list of canid remains that have not been included in Figure 2, along with a rationale for excluding them.

Country	Site	Dates (cal BP)	Element(s)	Dog Reference	Dating Reference	Notes	Rationale for exclusion
EUROPE							
Ukraine	Mezin	14,700 - 14,300	2 skulls	(1)	(2)		Benecke (1) concludes that the two skulls may represent either wolves or dogs at an initial stage of domestication.
Sweden	Skateholm	7,000	complete skeletons	(3)	(3)	10 canine graves, some with ochre.	Older dog remains are found nearby.
Belgium	Goyet	31,700	skulls	(4)	(4)		Though the skulls possess some characters that suggest they are domestic dogs, these remains could also represent an extinct population of wolves (2).
Czech Republic	Předmosti	~27,000 - 26,000	7 complete skulls, 26 skull fragments and 44 canines	(5)	(5)	Of the seven skulls, three are described as dogs, one as a wolf, and the remaining three could not be assigned.	Like other reports of late Pleistocene dogs, these skulls share characteristics with modern domestic dogs, but they could also belong to an extinct population of wolves.
Denmark	Svaerdborg	8,400 - 7,800	14 bone fragments	(6)	(6)	Though there are only 14 fragments of bones, the authors suggest that three types of dogs were present at the site: large Greenland sledge-like dogs, medium-sized dogs and small dog like the modern Lappish Spitz.	Older dog remains are found nearby.
Latvia	Zvejnieki	7,434 - 7,200	complete skeletons	(7)	(7)		Older dog remains are found nearby.
Italy	Palidoro Rock Shelter	18,551 - 17,330	mandibular ramus of large Canis, no teeth	(8)	(8)		The authors suggest that this specimen is probably a wolf.
ANATOLIA, LEVANT, CENTRAL ASIA							
Israel	Kebara Cave	12,500 - 12,000	mandible	(9)	(9)		The dating of this site and the determination of the mandible are uncertain. Contemporary remains of elements that can more confidently be assigned to domestic dogs are found nearby.
EAST ASIA							
Russia, Altai Mountains	Razboinichya Cave	33,500 - 33,000	skull mandibles and teeth	(10)	(10)		Uncertain determination since though these remains could be 'incipient' dogs, they could also represent an extinct population of wolves.
Vietnam	Phung Nguyen	Early 5th millennium BP	no description	(11)	(11)		The dating is uncertain, there is no description of the material, and there are numerous robust reports of contemporary and established dog remains nearby.
Vietnam	Man Bac	4,000 - 3,500	4 maxillae, 1 mandible, 2 isolated teeth from at least 2 individuals	(12)	(13)		Recorded as *Canis sp*. The authors suggest the remains are *Canis familiaris*, and though they are likely to be domestic dogs since domestics are known in southern China at this time, no analysis is presented that can distinguish *C. aureus* and *C. lupus* remains.
China	Bancun I	8,000 – 7,000	2 remains	(14)	(14)		There is no description of how the dating or the status of these remains was determined. The large number of reported canid remains at sites along the Yellow River Valley suggests the possibility that dogs were not uncommon.
China	Baijiacun	8,000 – 7,000	8 remains	(14)	(14)		There is no description of how the dating or the status of these remains was determined. The large number of reported canid remains at sites along the Yellow River Valley suggests the possibility that dogs were not uncommon
China	Zijing I	8,000 – 7,000	2 remains	(14)	(14)		There is no description of how the dating or the status of these remains was determined. The large number of reported canid remains at sites along the Yellow River Valley suggests the possibility that dogs were not uncommon
China (southern Guangxi)	Dingsishan Shell Midden	7,000	“bones”	(15)	(15)	The dog bones at this site were not found in association with other domestic animals such as pigs or water buffalo. This raises the possibility that these remains may be the first known example of domestic dogs moved outside of the distribution of wolves not in association with a complete agricultural package.	There is no description of how the dating or the status of these remains was determined. In addition, the reference to these remains is an unpublished PhD thesis completed in 2010. It is likely that once the full descriptions of these results are published, these dog bones can be moved to Table S3.
ISLAND SOUTHEAST ASIA, AUSTRALIA							

Country	Site	Dates (cal BP)	Element(s)	Dog Reference	Dating Reference	Notes	Rationale for exclusion
Philippines	Ille Cave	More recent than 2000 and perhaps more recent than 1500	complete skeleton	(16)	(16)		The dating is insecure due to reworking of the material, and there are established, contemporary dog remains at other sites in the Philippines.
Philippines	Callao Cave, Luzon	3,650 - 3,470	3rd left metacarpal	(17)	(18)		Insecure dating with associated charcoal.
Papua New Guinea	Akari & Beri in the Ramu Lowlands	5,500	2 teeth and 1 tooth at each site	(19)	(19)		The chronology of these sites has recently been called into question (20).
AFRICA							
Kenya	Hyrax Hill	modern	complete skeleton	(21)	(21)		This specimen was originally thought to date to the Iron Age but a directly dated long bone revealed that it was a modern dog.
Democratic Republic of the Congo	Matupi	700 - 600	1 premolar	(22)	(22)	The likelihood of finding preserved faunal remains in this region is low due to both the acidic soils in the region and because there have been few excavations.	According to the author, the single premolar find could easily be derived from one of two jackals living in the region: *Canis adustus* or *Canis mesomelas*.
South Africa	Diamant	1,430	cranial, tooth, and limb fragments	(23)	(23)		The report of these dogs was never published, and there are numerous, better documented reports of dog remains in the region.
Sudan	Kerma	4,050 - 3,750	complete skeletons	(22, 24)	(22, 24)	Dogs co-buried with humans.	These dogs are more recent than several other dog remains from earlier Sudanese Neolithic sites.
Sudan	Um Direiwa	6,000 – 5,500	numerous fragmentary elements	(25)	(25)		These remains are from the earliest Neolithic layers and could easily be derived from jackals.
Sudan	Shaqadud Cave	4,742 - 4,424 & 4,064 - 3,812	numerous fragmentary elements	(26)	(26)		The fragmentation precludes definitive a status and earlier definite dogs are described nearby.
Egypt	Maadi	4,600 - 4,400	121 bones and 1 complete skeleton	(27)	(27)		Though these remains can be ascribed to dogs, there are remains that predate these in the same region.
Botswana	Bosutswe	700 AD	no mention	(23)	(23)		Plug 1996 (23) cites Plug 1997 (28). This reference discusses only cows from the site and not dogs. There are numerous contemporary dogs from sites nearby.
NORTH AND CENTRAL AMERICA							
Alaska, USA	Fairbanks area	430-220	skulls	(29, 30)	(29-31)		Though these dogs found by gold miners in the 1920s were initially reported to be ~10,000 years old(29, 30), radiocarbon dating of 11 remains(31) demonstrated that these dogs were not more than 430 years old.
California, USA	Thousand Springs, San Nicolas Island	7,207 - 6,550 & 5,264 - 4,301	2 "elements"	(32)	(32)		The association and status of the elements is uncertain.
California, USA	Daisy Cave, San Miguel Island	"Early Holocene"	left mandible	(33)	(33)		The mandible "appears to have come from the early Holocene midden" and there is no additional description or comparison of the element.
Idaho, USA	Jaguar Cave	10,400 original, 3,689-3,315 and 1,095 - 740 revised	maxilla and mandibles	(34)	(34, 35)		The original published date for this material was 10,400 cal BP. Direct dating on two dog bones established that the stratigraphic dates were off by several thousand years.
Texas, USA	Hinds Cave	9,430 - 9,090	1 skull fragment (within human paleofecal sample)	(36)	(36)		Though the genetic sequence may have derived from endogenous DNA, there is also the possibility that the sequence represents an exogenous source. In addition, the publication does not present a morphological analysis related to the status determination and skull fragments are not known to have many diagnostic characteristics.
Mexico	Tula	2,646 - 2,865	26 dog remains	(37)	(37)		Numerous older dogs have been described from nearby sites.
SOUTH AMERICA							
Chile	Fell's Cave	10,340 - 10,020	lower right 4th premolar and molars	(38-42)	(38, 40, 41)		Clutton Brock's (38) description concluded that the canid remains were similar to dogs. Amorosi *et al.* (39) re-analyzed the material and concluded the remains were likely derived from an extinct native canid (*Dusicyon avus*).

Country	Site	Dates (cal BP)	Element(s)	Dog Reference	Dating Reference	Notes	Rationale for exclusion
Peru	Uchcumachay	9,000 - 7,500 & 6,200 - 4,500	1 axis, 1 canine	(42, 43)	(43)		Uncertain determination and uncertain dating.
Peru	Panaulauca	7,500 - 6,200	1 tooth	(42, 43)	(43)		Uncertain determination and uncertain dating.
Ecuador	Chobshi Cueva Negra	10,705 - 7,585	1 unspecified tooth	(42, 44)	(44)		Uncertain determination and uncertain dating.
Argentina	Los Toldos	9,230 - 8,270	3 unspecified elements	(40, 41, 44)	(44)		Determination revised from *Canis familiaris* to *Canis avus* by Caviglia (40, 41).
Argentina	Arroyo Seco 2	12,300 - 8,400	unspecified elements	(45)	(45)		Determination revision Reassignment of taxa to gymnocercus or brachyrus (46).
Argentina	Cueva Tixi	10,400 - 10,000	unspecified elements	(45)	(45)		Originally identified as *Canis avus* in Mazzanti (47) and therefore has an uncertain determination.
Colombia	El Abra	9,520 - 8,580 & 7,350 - 7,150	2 unspecified elements	(42, 48)	(48)		Uncertain determination.
Argentina	La Moderna	6,710 - 6,390	1 hemimandible	(49)	(49)		Uncertain determination and uncertain dating.
Peru	La Paloma	8,825 - 5,543	single canine	(50)	(50)		The single dog canine could not be definitively identified as dog since it could also be a fox *(Dusicyon sp*).
Mexico	San Lorezo (Olmec)	3,200 - 2,900	numerous dogs	(51)	(51)		Though the remains can confidently be assigned to dog, there are numerous dogs in earlier sites nearby.
Peru	Puente	7,050 - 6,380	distal humerus, phalanx, tooth, 4 maxilla, 3 distal metapodia	(42, 52)	(52)		Uncertain determination.
Peru	Pachamachay	6,200 - 4,500	unspecified elements	(42, 43)	(43)		Uncertain determination and uncertain dating.
Peru	Lauricocha	6,200 - 4,500	unspecified elements	(42, 43)	(43)		Uncertain determination and uncertain dating.

References

1. Benecke N (1987) Studies On Early Dog Remains From Northern Europe. *J. Archaeol. Sci.* 14(1):31-49.
2. Pionnier-Capitan M*, et al.* (2011) New evidence for Upper Palaeolithic small domestic dogs in South-Western Europe. *J. Archaeol. Sci.* 38(9):2123-2140.
3. Larsson L (1990) Dogs in Fraction – Symbols in Action. *In Contributions to the Mesolithic in Europe*, eds Vermeersch PM & Van Peer P (Leuven University Press, Leuven), pp 153-160.
4. Germonpré M*, et al.* (2009) Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes. *J. Archaeol. Sci.* 36(2):473-490..
5. Germonpré M, Lázničková-Galetová M, & Sablin MV (2011) Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. *J. Archaeol. Sci.* 39(1):184-202.
6. Henriksen BB, Sørensen KA, & Sørensen I (1976) *Sværdborg I: Excavations 1943-44: a settlement of the Maglemose culture* (Akademisk Forlag (København)).
7. Löugas L (2006) Animals as subsistence and bones as raw material for settlers of prehistoric Zvejnieki. *Back to the Origin: New Research in the Mesolithic-neolithic Zvejnieki Cemetery & Environment, Northern Latvia,* Acta Archaeologica Lundensia, eds Larsson L & Zagorska I (Almqvist & Wiksell Intl, Lund), pp 75-89.
8. Verginelli F*, et al.* (2005) Mitochondrial DNA from prehistoric canids highlights relationships between dogs and South-East European wolves. *Mol Biol Evol* 22(12):2541-2551.
9. Dayan T (1994) Early Domesticated Dogs of the Near East. *J. Archaeol. Sci.* 21(5):633-640.
10. Ovodov ND*, et al.* (2011) A 33,000-Year-Old Incipient Dog from the Altai Mountains of Siberia: Evidence of the Earliest Domestication Disrupted by the Last Glacial Maximum. *Plos One* 6(7):e22821.
11. Higham CFW (1998) Archaeology, linguistics and the expansion of the East and Southeast Asian Neolithic. *Expansion of East and Southeast Asian Neolithic in Archaeology and Language II: Archaeological Data and Linguistic Hypotheses*, eds Blench R & Spriggs M (Routledge, New York), pp 103-114.
12. Sawada J, Thuy NK, & Tuan NA (2011) Faunal Remains at Man Bac. *Man Bac: The Excavation of a Neolithic Site in Northern Vietnam: The Biology,* Terra Australis, eds Oxenham MF, Matsumura H, & Dung NK), Vol 33, pp 105-116.
13. Matsumura H & Oxenham MF (2011) Introduction: Man Bac biological research objectives. *Man Bac: The excavation of a Neolithic Site: The Biology,* Terra Australis eds Oxenham MF, Matsumura H, & Dung NK), Vol 33, pp 1-8.
14. Jing Y & Flad RK (2002) Pig domestication in ancient China. *Antiquity* 76(293):724-732.
15. Zhang C & Hung H-C (2012) Later hunter-gatherers in southern China, 18000 – 3000 BC. *Antiquity* 86:11-29.
16. Ochoa JT (2005) In dogged pursuit: A reassessment of the dog's domestication and social incorporation. *Hukay* 8:37-65.
17. Piper PJ, Amano N, Yang H-Y, & O'Connor T (submitted) The terrestrial vertebrate remains, . *Archaeology in the Batanes Islands: The early movements of Austronesian-speaking populations.*, eds Bellwood P & Dizon E).
18. Mijares ASB (2007) *Unearthing prehistory: the archaeologyof Northeastern Luzon, Philippine Islands* (John and Erica Hedges Ltd. , Oxford).
19. Bulmer S (2000) Lapita dogs and singing dogs and the history of the dog in New Guinea. *The Archaeology of Lapita Dispersal in Oceania: Papers from the fourth Lapita Conference, June 2000*, eds Clark GR, Anderson AJ, & Vunidilo T (Terra Australis, Canberra, Australia), Vol 17.

20. O'Connor S*, et al.* (2011) The Power of Paradigms: Examining the Evidential Basis for Early to Mid-Holocene Pigs and Pottery in Melanesia. *Journal of Pacific Archaeology* 2(2):1-25.
21. Kyule M (1997) The Sirikwa economy. *AZANIA: Journal of the British Institute in Eastern Africa* 32(1):21-30.
22. Van Neer W (2000) Domestic animals from archaeological sites in Central and West-Central Africa. *The origins and development of African livestock: archaeology, genetics, linguistics and ethnography*:163-190.
23. Plug I (1996) Domestic Animals during the Early Iron Age in Southern Africa. *Aspects of African Archaeology: Papers from the 10th Congress of the Pan African Association for Prehistory and Related Studies*, eds Pwiti G & Soper R (University of Zimbabwe Publications, Harare), pp 515-519.
24. Thompson A, Chaix L, & Richards MP (2008) Stable isotopes and diet at ancient Kerma, Upper Nubia (Sudan). *J. Archaeol. Sci.* 35(2):376-387.
25. Tigani El-Mahi A (1988) *Zooarchaeology in the Middle Nile Valley. A Study of four Neolithic Sites near Khartoum* (BAR International Series, Oxford).
26. Peters J (1991) The faunal remains from Shaqadud. *The Late Prehistory of the Eastern Sahel. The Mesolithic and Neolithic of Shaqadud, Sudan.*, eds Marks AE & Mohammed-Ali A (SMU Press, Dallas), pp 197-235.
27. Boessneck J, von den Driesch A, & Ziegler R (1989) Die Tierreste von Maadi und Wadi Digla (The animal remains from Maadi and Wadi Digla). *The non-lithic small finds and the structural remains of the predynastic settlement*, eds Rizkana I, Seeher J, & Maadi I (von Zabern, Mainz), pp 87-128.
28. Plug I (1997) Cattle remains in some pre- and protohistoric socieies of the central cattle pattern in southern Africa. *Anthropozoologica* 25-26(Proceedings of the 7th ICAZ Conference):747-752.
29. Olsen SJ (1985) *Origins of the domestic dog: the fossil record* (University of Arizona Press Tucson).
30. Clutton-Brock J (1995) Origins of the domestic dog: domestication and early history. *The domestic dog: its evolution, behavior, and interactions with people*, ed Serpell J (Cambridge University Press, Cambridge), pp 8-20.
31. Leonard JA*, et al.* (2002) Ancient DNA evidence for Old World origin of New World dogs. *Science* 298(5598):1613-1616.
32. Bleitz DE (1993) The prehistoric exploitation of marine mammals and birds at San Nicolas Island, California. *Third California Islands Symposium: Recent Advances in Research on the Californian islands*, ed Hochberg FG (Santa Barbara Museum of Natural History, Santa Barbara, CA), pp 519-536.
33. Erlandson JM (1994) *Early Hunter-Gatherers of the California Coast* (Plenum Press, New York).
34. Lawrence B (1968) Antiquity of large dogs in North America. *Tebiwa: The Journal the Idaho State University Museum* 11(2):43–48.
35. Gowlett JAJ, Hedges R, Law I, & Perry C (1987) Radiocarbon dates from the Oxford AMS system: Archaeometry datelist 5. *Archaeometry* 29(1):125-155.
36. Tito RY*, et al.* (2011) Brief communication: DNA from early Holocene American dog. *American Journal of Physical Anthropology*.
37. Azúa RV, Gudiño BP, & Galicia BR (1999) Entierros de Perros descubiertos en la antigua ciudad de Tula. *Latin American Antiquity* 10(2):180-200.
38. Clutton-Brock J (1988) The carnivore remains excavated at Fell's Cave in 1970. *Travels and archaeology in South Chile by Junius B. Bird*, ed Hyslop J (University of Iowa Press, Iowa City), pp 188–195.
39. Amorosi T & Prevosti FJ (2008) A preliminary review of the canid remains from Junius Bird's excavations at Fell's and Pali Aike caves, Magallanes, Chile. *Current Research in the Pleistocene* 25:25-27.
40. Caviglia SE (1985) Nuevos Restos de Canidos Tempranos en Sitios Arqueológicos de Fuego-Patagonia [New Early Canid Remains in Archaeological sites of Fuego-Patagonia]. Spanish. *Anales del Instituto de la Patagonia, Serie Ciencias Sociales* 16:85-93.
41. Caviglia SE, Yacobaccio HD, & Borrero LA (1986) Las Buitreras: Convivencia del Hombre con Fauna Extinta en Patagonia Meridional [Las Buitreras: Co-existence of Humans with Extinct Faunas in Southern Patagonia]. Spanish. *New Evidence for the Pleistocene Peopling of the Americas*, ed Bryan AL (Center for the Study of Early Man, Orono), pp 295-317.
42. Stahl PW (in press) Interactions Between Humans And Endemic Canids In Holocene South America. *Journal of Ethnobiology*.
43. Pires-Ferreira JW, Pires-Ferreira E, & Kaulicke P (1976) Preceramic animal utilization in the Central Peruvian Andes. *Science* 194(4264):483.
44. Lynch TF & Pollock S (1981) La Arqueología de la Cueva Negra de Chobshi [The Archaeology of Cueva Negra de Chobshi]. Spanish. *Miscelánea Antropológica Ecuatoriana* 1:92-119.
45. Gutiérrez MA & Martínez GA (2008) Trends in the Faunal Human Exploitation during the Late Pleistocene and Early Holocene in the Pampean Region (Argentina). *Quaternary International* 191:53-68.
46. Fidalgo F*, et al.* (1986) Investigaciones Arqueológicas en el Sitio 2 de Arroyo Seco (Odo. De Tres Arroyos-Pcia. de Buenos Aires-República Argentina) [Archaeological Investigations en Site 2 of Arroyo Seco (Tres Arroyos department, Buenos Aires Province, Republic of Argentina]. Spanish. *New Evidence for the Pleistocene Peopling of the Americas*, ed Bryan AL (Center for the Study of Early Man, Orono), pp 221-269.
47. Mazzanti DL & Quintana CA (1997) Asociación Cultural con Fauna Extinguida en el Sitio Arqueológico Cueva Tixi, Provincia de Buenos Aires, Argentina [Cultural Association with Extinct Fauna en the Archaeological Site of Cueva Tixi, Buenos Aires Province, Argentina]. Spanish. *Revista Español de Antropología Americana* 27:11-21.
48. Ijzereef GF (1978) Faunal remains from the El Abra rock shelters (Colombia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 25(1-2):163-177.
49. Politis GG (1986) Investigaciones Arqueológicas en el Área Interserrana Bonaerense [Archaeological Investigations in the Interserrana Bonaerense Area]. Spanish. *Etnia* 32:7-52.
50. Reitz EJ (1988) Preceramic animal use on the central coast. *Economic Prehistory of the central Andes*, eds Wing ES & Wheeler JC (BAR International Series 427, Oxford), pp 31-73.
51. Wing ES (1978) Uses of Dogs for Food: An Adaptation to the Coastal Environment. *Prehistoric Coastal Adaptations: The economy and ecology of maritime middle America*, eds B.L. Stark BL & Voorhies B (Academic Press, New York).
52. MacNeish RS & R.K. V (1983) The Preceramic way of life in the Thorn Forest Riverine Ecozone. *Prehistory of the Ayacucho Basin, Peru: The Preceramic Way of Life*, eds MacNeish RS, Vierra RK, Nelken-Terner A, Lurie R, & Cook AG (University of Michigan Press, Ann Arbor), Vol 4, pp 48-129.

Table S3. A list of dog remains depicted in Figure 2. Boarded boxes in each geographic region (listed in bold above each section) represent all the dogs included in specific pie charts present in each region.

Pie Location	Country	Site	Dates (cal BP)	Element(s)	Dog Reference	Dating Reference	Notes
EUROPE							
United Kingdom	United Kingdom	Star Carr	11,658-10,633	skull fragment, single tooth, femur, tibia	(1)	(1)	Bones identified as both dog and wolf are found at this site.
United Kingdom	United Kingdom	Seamer Carr	11,866-11,246	6 vertebrae	(1)	(1)	
Central Europe	Germany	Bonn-Oberkassel	14,708 - 13,874	maxillary fragments, vertebrae frag, ulna frag, humorous frag	(2)	(3)	
Central Europe	Germany	Oelknitz	15,770 - 13,957	phalanges, metapodia and part of distal humerus and tibia	(4)	(3)	Musil (4) states that when considered together, the finds at the contemporaneous sites Oelknitz, Kniegrotte and Teufelsbruecke are likely to be derived from domestic dogs.
Central Europe	Germany	Kniegortte	16,700 - 13,800	partial maxillary fragment with teeth	(4)	(3)	Musil (4) states that when considered together, the finds at the contemporaneous sites Oelknitz, Kniegrotte and Teufelsbruecke are likely to be derived from domestic dogs.
Central Europe	Germany	Teufelsbrucke	15,770 - 13,957	proximal metapodial fragment and first phalanx	(4)	(3)	Musil (4) states that when considered together, the finds at the contemporaneous sites Oelknitz, Kniegrotte and Teufelsbruecke are likely to be derived from domestic dogs.
Central Europe	Switzerland	Kesslerloch Cave	14,600 - 14,100	partial skull frag with some maxilla / zygo / palatine and a few teeth	(5)	(5)	A morphometric analysis suggests these remains are equivalent to domestic dogs.
Central Europe	Switzerland	Hauterive-Champréveyres	15,200 - 13,900	metatarsal and two teeth, second phalanx	(6, 7)	(3, 7)	
Central Europe	France	Saint-Thibaud-de-Couz	12,027 - 11,311	skull, right mandible, atlas, axis, some teeth, left humerous	(8)	(3)	
Central Europe	France	Pont d'Ambon	12,952 - 12,451	39 skull, limb, mandible,vertebal, and tooth fragments	(3, 9, 10)	(11)	
Central Europe	France	Montespan	15,500 - 13,500	1 atlas, 1 femur, 1 baculum	(3)	(3)	
Central Europe	France	Le Closeau	14,999 - 14,055	7 fragments including mandible, meta carpal, metapodial and phalanxes	(3)	(3)	
Central Europe	France	Noyen-sur-Seine	10,200	2 complete skulls, several post-cranial bones	(12)	(13)	These skulls are as big as wolf skulls, but they possess domestic characteristics. According to Vigne (12), these remains are likely derived from a local population of wolves.
Western France - Spain	Spain	Erralla	19,000 or 12,500	1 humerus	(14-16)	(14, 15)	According to Vigne (15), the bone belonged to a small dog.
Western France - Spain	France	Pont d'Ambon	12,952 - 12,451	39 skull, limb, mandible,vertebal, and tooth fragments	(3, 9)	(11)	
Portugal	Portugal	Moita do Sebastiao	8,023 - 7,849	complete skeleton	(17)	(17)	
Western Russia	Russia	Eliseevichi I	16,945 - 16,190	two skulls	(18)	(3)	
ANATOLIA, LEVANT, CENTRAL ASIA							
Iraq	Iraq	Palegawra	13,000	Mandible	(19)	(19)	Zeder (20) states that this specimen shows clear evidence of tooth size reduction and crowding in a smaller jaw.

Pie Location	Country	Site	Dates (cal BP)	Element(s)	Dog Reference	Dating Reference	Notes
Iraq	Iraq	Jarmo	9,000 - 8,500	53 cranial and mandibular fragments, 18 of which positively identifiable as dog	(21)	(21)	The dog bones were compared with remains from the local wolf, *Canis lups pallipes*.
Anatolia	Turkey	Çayönü	9,200 - 9,100	complete skeleton	(22)	(22)	
Anatolia	Turkey	Cafer Höyük	9,500-8,300	complete skull, 14 other elements	(23)	(24)	Digested bones and gnawing marks indicate that dogs were living in the village.
Levant, Syria, Cyprus	Cyprus	Shillourokambos	12,400-12,300	multiple elements	(25, 26)	(26, 27)	The dog bones are associated with the earliest layers of the site (early phase A) and are clearly represent very small dogs.
Levant, Syria, Cyprus	Cyprus	Klimonas	11,120-10,615	one phalanx	(26, 28)	(26)	This phalanx is consistent with a very young dog. Gnaw marks on the ungulate bones at the site confirms that these dogs lived together with humans.
Levant, Syria, Cyprus	Syria	Aswad-Damascus	10,200-9,400	a few tens of elements	(29)	(30)	
Levant, Syria, Cyprus	Syria	Tell Mureybet	11,500 - 11,300	skull and left and right mandibles	(31)	(32)	Morphological features and metrical comparison with *Canis lupus pallipes* confirms the domestic status of this specimen.
Levant, Syria, Cyprus	Israel	Ain Mallaha	11,500	co-burials with humans, one skeleton juvenile and one adult, and one partial mandible	(33, 34)	(34)	One complete specimen is a puppy buried with a woman whose hand is resting on the dog. The second complete individual is an adult positioned underneath a human burial.
Levant, Syria, Cyprus	Israel	Hayonim Cave and Terrace	12,000 - 11,000	complete skeleton	(34)	(34)	
Turk-menistan	Turkmenistan	Jeitun	8,200 - 7,700	multiple elements	(35)	(35)	
Kazakhstan	Kazakhstan	Botai	5,650	complete skeleton	(36)	(36)	
Kazakhstan	Kazakhstan	Botai	5,550-5,050	several bones	(37)	(37)	

EAST ASIA

Kamchatka	Russia	Ushki I	12,900 - 12,600	complete skeleton	(38)	(38)	
Siberia	Russia (Cis-Baikal region)	Shamanka	7450 - 7280	complete skeleton	(39)	(39)	Canid remains (both dog and wolf) are also found in several nearby sites.
North Siberian Islands	Russia	Zhokhov	8480 - 8175	2 mandibles, maxilla, canine, radius, ribia	(40)	(40)	
Peninsular Southeast Asia	Thailand	Ban Chiang	3,200 - 2,600	crania in human coburial, several mandibles, and long bones	(41)	(42)	
Peninsular Southeast Asia	Thailand	Ban Non Wat	3,700	~20 fragments	(43)	(44)	Recovered from Neolithic layers.
Peninsular Southeast Asia	Thailand	Khok Phanom Di	3,800 - 3,700	numerous fragments	(45)	(46, 47)	
Peninsular Southeast Asia	Vietnam	An Son	4,200 - 3,500	109 fragments including 8 mandibles, 4 maxillae from at least 5 individuals	(48)	(49)	These dogs appear to have been butchered and eaten. Separated from *C. aureus* and *C. lupus* based on the morphology of the maxillary and mandibular M1s
Japan	Japan	Natsushima Shell (Kanagawa Prefecture)	9,300	complete skeleton	(50)	(50)	Shigehara and Hongo (51) report that dog remains have been found in 282 sites (including Torihama and Shigehara), 22 of which date to the earliest Jomon phase.

Pie Location	Country	Site	Dates (cal BP)	Element(s)	Dog Reference	Dating Reference	Notes
Japan	Japan	Kamikuroiwa (Ehime)	8,500 - 8,000	complete skeleton	(50)	(50)	
Pakistan	Pakistan	Harappa	4,600	complete skeleton	(52)	(52)	
Central China	China	Jiahu	9,000 - 7,800	complete skeleton co-burial with humans	(53)	(53)	
Northern China	China	Nanzhuangtou	12,790 – 10,747	>31 fragments including a complete mandible	(54, 55)	(56)	

ISLAND SOUTHEAST ASIA, AUSTRALIA

Australia	Australia	Madura Cave	3,545 - 3,355	unspecified remains	(57)	(57)	
Australia	Australia	Fromm's Landing	3,091 - 2,909	complete skeleton	(58)	(58)	
Philippines	Philippines, Northern Luzon	Nagasabaran, Luzon	2,500	Complete skeleton – burial	(59)	(60)	
Philippines	Philippines, Batanes Islands	Savidug, Sabtang Island	2,500 - 2,300	3 fragments: a basioccipital, right scapula and right mandibular condyle	(61)	(62)	Transverse cut marks on the neck of the mandibular condyle suggests butchery, possibly for consumption.
Taiwan	Taiwan	Nanguanli	4,800	Complete skeletons from burials	(63)	(63)	
Lesser Sundas	Indonesia, Timor	Matja Kuru 2	3,375 - 3,076	complete skeleton	(64)	(64)	
Mollucas Islands	Indonesia, N. Moluccas	Uattamdi site, Kayoa Island	3,500	1 lower molar	(65)	(66)	Bellwood (67) states that dog remains are found in the region beginning about 3500-3000 cal BP, always in association with evidence of rice agriculture. This site in particular has evidence of human occupation before dogs are introduced.
Micronesia	Federated States of Micronesia	Fais Island	1,780 - 600	45 tooth and bone fragments	(68)	(68)	Intoh (68)states that similarly aged dog remains are found on several other Micronesian sites including Nukuoro Atoll and Fefan Island in Chuuk.
New Guinea	Papua New Guinea	Taurama	2,500 - 2,000	complete skeleton	(69)	(69)	Bulmer (69) reports that contemporaneous dog remains have been found at several sites from this time period including Oposisi, and Mailu 01.

AFRICA

Northern Egypt	Egypt	Merimde Beni-Salame (Nile Delta)	6,800 - 6,520	20 dog bones	(70)	(70)	This multi-layered site (Layers I to V) produced 514 dog bones and a few remains from jackals. Layer I, the oldest layer dating to the first half of the 7th millennium cal BP produced 20 bones, Layer II is particularly rich in finds (n = 162).
Southern Egypt	Egypt	Nabta Playa and Bir Kaseiba	6,500 - 6,000	17 dog remains	(71)	(72)	According to Gautier (71) dogs may have been present at Nabta Playa during the Middle Neolithic (*c*. 7,000-6,500 BP), when livestock husbandry was also practised. Given this possibility, four postcranial remains have been tentatively attributed to dogs.
Central Sudan	Sudan	Esh Shaheinab	5,600 - 5,000	1 upper jaw and 7 lower jaws	(73)	(73)	Gautier (74) states that there are no claims for dogs in Early Neolithic sites, but that several sites in the Middle Neolithic possess dog remains that were likely brought into North Africa alongside domestic sheep and goats.
Central Sudan	Sudan	El Kadero	5,280 - 5,030	coprolites	(75)	(75)	The presence of cows and goats and the evidence of a pastoralist community at this site suggest that the carnivore coprolites are more likely to be derived from dogs than jackals.
Central Sudan	Sudan	El Kadada	5,645 - 5,491 & 5,466 - 5,170	Several complete skeletons in burials	(76)	(76)	Dog remains are found in many different contexts at the site.

Pie Location	Country	Site	Dates (cal BP)	Element(s)	Dog Reference	Dating Reference	Notes
Niger	Niger	Chin Tafidet	4,619 - 4,141	3 complete skeletons	(77)	(77)	
Nigeria	Nigeria	Gajiganna A	3,200 - 3,000	2 scapula, 2 femur, 1 calcaneus, 1 phalanx	(78)	(78)	Numerous additional dog remains have been excavated from early layers at this site.
Nigeria	Nigeria	Gajiganna B1	3,500 - 3,000	1 ulna, 1 femur, 1 tibia	(78)	(78)	Numerous additional dog remains have been excavated from early layers at this site.
West North Africa	Burkina Faso	Oursi	2,000 - 1,500	1 maxilla	(78)	(78)	These two sites are the earliest of several sites in Burkina Faso. All of the later sites possess numerous dog remains.
West North Africa	Burkina Faso	Oursi village	2,000 - 1,500	1 metatarsal	(78)	(78)	These two sites are the earliest of several sites in Burkina Faso. All of the later sites possess numerous dog remains.
West North Africa	Mali	Jenne-Jeno	2,250 - 1,600	1 M2, 3 distal radius	(79)	(79)	
Central Africa	Uganda	Ntusi	1,218 - 845	complete skeleton	(80)	(80)	
North S Africa	Zambia	Isamu Pati Mound	1,050 - 1,000	7 dog remains, skulls and limb bones	(81)	(81)	
North S Africa	Botswana	Commando Kop	1,100 - 900	1 fragment	(82)	(83)	Three publications (82, 84, 85). state that domestic cattle, sheep and goat are common in the first few centuries AD in sites across this region. This evidence suggests that the lack of early dog remains is not exclusively taphonomic, though Voigt (86) suggests that the acidic soil may explain the dearth of sites before 600 AD.
North S Africa	Botswana	Taukome	1,200 - 1,000	2 fragments	(85)	(85)	
South S Africa	South Africa, Natal	Ntshekane	1,200 (no earlier than)	Left mandible, maxilla and skull fragments	(82)	(82)	
South S Africa	South Africa, Natal	Wosi	1,400- 1,350	1 fragment	(86)	(87)	
South S Africa	South Africa, Natal	Wosi	1,250- 1,150	11 fragments	(86)	(87)	Voigt and Peters (86) noted domestic dogs of two sizes in this assemblage (p. 108).
South S Africa	South Africa, Natal	Magogo	1,400 - 1,200	3 fragments	(85)	(85)	
South S Africa	South Africa, Transvaal	Mapungubwe	1,000 - 940	Skull, right mandible fragment, M3	(82)	(83)	
South S Africa	South Africa, Transvaal	Schroda	1,300 - 1,200	anterior portion of skull with both mandibles	(82)	(83)	
South S Africa	South Africa, Transvaal	Pont Drift	1,200 - 900	3 fragments	(85)	(85)	
South S Africa	South Africa, Transvaal	K2	1,200 - 1000	3 fragments	(85)	(85)	
Southern South Africa	South Africa, S Coast	Cape St. Francis	1,222- 1,020	complete skeleton	(88)	(82)	A juvenile dog buried in the lap of a person.

NORTH AND CENTRAL AMERICA

Western USA	Utah	Danger Cave	10,000 - 9,000	1 skull fragment, 2 mandibles (18 wolf specimens)	(89, 90)	(89, 90)	
Eastern USA	Illinois, USA	Koster	9,700 - 9 130	complete skeleton	(91)	(91)	
Eastern USA	Illinois, USA	Modoc Rock Shelter	8,000 - 7,650	complete skeleton	(92)	(92)	
Eastern USA	Tennessee, USA	Anderson	7,200 - 6,700	complete skeleton	(93)	(93)	

Pie Location	Country	Site	Dates (cal BP)	Element(s)	Dog Reference	Dating Reference	Notes
Eastern Canada	Newfoundland, Canada	Port au Choix	4,869 - 4,042	complete skeleton	(94)	(94)	
Caribbean	Puerto Rica, Vieques Island	Socre	2,000 - 1,500	567 bones from at least 22 individuals	(95)	(95)	Wing (96) comments that dog remains have been found on 16 Caribbean Islands and are often found associated with human burials.
Central America	Mexico	Coxcatlan Cave	5,200	teeth and mandibles	(97)	(97, 98)	Flannery (97) suggests because dogs are not present in earlier layers at this site, despite significant numbers of human bone remains, that dogs were therefore not kept in the Tehuacan Valley until considerable agricultural efficiency had been reached. The dogs appear to be characteristic of early village farming, but not any earlier stage.
Central America	Mexico	Purron Cave	4,500	teeth and mandibles	(97)	(97, 98)	Flannery (97) suggests because dogs are not present in earlier layers at this site, despite significant numbers of human bone remains, that dogs were therefore not kept in the Tehuacan Valley until considerable agricultural efficiency had been reached. The dogs appear to be characteristic of early village farming, but not any earlier stage.

SOUTH AMERICA

Ecuador	Ecuador (SW)	Real Alto	4,400 - 4,100	complete skeleton	(99)	(99)	
Ecuador	Ecuador (SW)	Loma Alta	5,000 - 4,500	18 elements, MNI=3	(100, 101)	(100, 101)	
N Chile - Peru	Peru	Sipán	1,700- 1,450	complete skeletons	(102)	(102)	There are two human burials at this site in which a dog has been placed in close proximity to the people.
N Chile - Peru	Peru	Rosamachay	5,620 - 5,420 & 5,450 - 5,150	2 dog burials	(103)	(103)	
N Chile - Peru	Peru	Ilo	3,350 - 2,900	43 dog burials	(104)	(104)	
N Chile - Peru	Peru	Telarmachay	3,620 - 3,420 & 3,560 - 3,360 & 2,740 - 2,650	7 elements including intentional puppy burial	(105)	(105)	
N Chile - Peru	Chile	Arica	2,500 - 500	8 mummified dogs	(106)	(106)	Medium sized dogs with short straight hair and curly tails.
Pampa-Patagonia	Argentina	Chenque 1	975 - 832	complete skeleton	(107)	(107)	
Pampa-Patagonia	Argentina	Angostura 1	990 - 790	dental fragments including M1, P4, I3	(107)	(107)	

1. Clutton-Brock J & Noe-Nygaard N (1990) New osteological and C-isotope evidence on Mesolithic dogs: companions to hunters and fishers at Star Carr, Seamer Carr and Kongemose. *J. Archaeol. Sci.* 17(6):643-653.
2. Street M (2002) Ein wiedersehen mit dem hund von Bonn-Oberkassel. *Bonner Zoologische Beitrage* 50(3):269-290.
3. Pionnier-Capitan M*, et al.* (2011) New evidence for Upper Palaeolithic small domestic dogs in South-Western Europe. *J. Archaeol. Sci.* 38(9):2123-2140.
4. Musil R (2000) Evidence for the domestication of wolves in central European Magdalenian sites. *Dogs through time: an archaeological perspective*, ed Crockford SJ (British Archaeological Reports, Oxford, England), pp 21-28.
5. Napierala H & Uerpmann HP (2010) A 'new' palaeolithic dog from central Europe. *International Journal of Osteoarchaeology*.
6. Morel P & Müller W (2000) *Un campement magdalénien au bord du lac de Neuchâtel, étude archéozoologique (secteur 1)* (Musée cantonal d'archéologie, Neuchâtel).
7. Müller W (2004) Les vestiges osseux. *Témoins d'implantations magdaléniennes et aziliennes sur la rive nord du lac de Neuchâtel*, eds Leesch D, Cattin M-I, & Müller W (Archéologie neuchâteloise), pp 96-109.
8. Chaix L (2000) A preboreal dog from the northern Alps (Savoie, France). *Dogs Through Time: An Archaeological Perspective*, ed Crockford SJ (Archaeopress), pp 49-60.
9. Crabtree PJ (1993) Early animal domestication in the Middle East and Europe. *Archaeological method and theory*, ed Schiffer M (University of Arizona Press, Tucson), Vol 5, pp 201-245.

10. Célèrier G & Delpech F (1978) Un chien dans l'Azilien de" Pont d'Ambon"(Dordogne)? *Bulletin de la Société préhistorique française* 75(7):212-215.
11. Célèrier G, Tisnerat N, & Valladas H (1999) Données nouvelles sur l'âge des vestiges de chien à Pont d'Ambon, Bourdeilles (Dordogne)/New data on the age of Canis remains at Pont d'Ambon, Bourdeilles (Dordogne, France). *Paléo* 11(1):163-165.
12. Vigne JD & Marinval-Vigne MC (1988) Quelques rèflexions prèliminaires sur les Canidès mèsolithiques de Noyen-sur-Seine (France) et sur la domestication du Chien en Europe occidentale. *Archaezoologia* 2(1-2):153-164.
13. Mordant C & Mordant D (1992) Noyen-sur-Seine: a Mesolithic waterside settlement. *The Wetland Revolution in Prehistory*, ed Coles BW (The Prehistoric Society-WARP), pp 55-64.
14. Altuna J & Mariezkurrena K (1985) Bases de subsistencia de los pobladores de Erralla: Macromamiferos. *Munibe* 37:87-117.
15. Vigne JD (2005) L'humèrus de chien magdalènien de Erralla (Gipuzkoa, Espagne) et la domestication tardiglaciaire du loup en Europe. *Homenaje a Jesus Altuna*, Munibe), Vol 57, pp 279-287.
16. García-Moncó C (2005) *El perro en la Prehistoria de la Península Ibéric. Estudio crítico de la documentación arqueozoológica anterior al Calcolítico en su contexto euroasiático. Trabajo de Investigación de Tercer Ciclo* (Universidad de Cantabria, Santander).
17. Detry C & Cardoso JL (2010) On some remains of dog (Canis familiaris) from the Mesolithic shell-middens of Muge, Portugal. *J. Archaeol. Sci.* 37(11):2762-2774.
18. Sablin MV & Khlopachev GA (2002) The Earliest Ice Age Dogs: Evidence from Eliseevichi 11. *Curr. Anthropol.* 43(5):795-799.
19. Turnbull PF & Reed CA (1974) *The fauna from the terminal Pleistocene of Palegawra Cave: a Zarzian occupation site in northeastern Iraq* (Field Museum of Natural History).
20. Zeder MA (2012) Pathways to animal domestication. *Biodiversity in Agriculture: Domestication, Evolution and Sustainability*, eds Gepts P, Famula TR, Bettinger RL, Brush SB, Damania AB, McGuire PE, & Qualset CO (Cambridge University Press, Cambridge).
21. Lawrence B & Reed CA (1983) The dogs from Jarmo. *Prehistoric Archaeology Along the Zagros Flanks*, eds Braidwood LS, Braidwood RJ, Howe B, Reed CA, & Watson PJ (Oriental Institute, University of Chicago, Chicago), pp 485-489.
22. Özdoğan A (1999) Çayönü. *Neolithic in Turkey: the Cradle of Civilization*, eds Özdoğan M & Başgelen N (Arkeoloji ve sanat Yayinlari, Istanbul), pp 35-63.
23. Helmer D (2008) Révision de la faune de Cafer Höyük (Malatya, Turquie): Apports des méthodes de l'analyse des mélanges et de l'analyse de Kernel à la mise en évidence de la domestication. *Archaeozoology of the Near East VIII: actes des Huitièmes Rencontres internationales d'archéozoologie de l'Asie du Sud-Ouest et des régions adjacentes*, eds Vila E, Gourichon L, Choyke AM, & Buitenhuis H (Travaux de la Maison de l'Orient et de la Méditerranée), pp 169-195.
24. Cauvin J, Aurenche O, Cauvin M-C, & Balkan-Atlı N (1999) The Pre-Pottery Site of Cafer Höyük. *Neolithic in Turkey: The Cradle of Civilization*, ed Özdoğan M (Arkeoloji ve Sanat Yay, Istanbul), pp 87-103.
25. Vigne JD (2011) Les petits et microvertébrés terrestres (chéloniens, squamates, oiseaux, rongeurs et carnivores): contribution à l'histoire du peuplement reptilien et mammalien de Chypre. *Shillourokambos. Un établissement néolithique pré-céramique à Chypre. Les fouilles du Secteur 1, Editions Errance*, eds J. G, Briois F, & Vigne J-D (Ecole Française d' Athènes, Paris), pp 847-870.
26. Vigne JD, Carrère I, Briois F, & Guilaine J (2011) The Early Process of Mammal Domestication in the Near East. *Curr. Anthropol.* 52(S4):255-271.
27. Guilaine J, Briois F, Perrin T, Vigne J-D, & Gérard P (2011) La périodisation proposée. *Shillourokambos. Un établissement néolithique pré-céramique à Chypre. Les fouilles du Secteur 1, Editions Errance*, eds J. G, Briois F, & Vigne J-D (Ecole Française d' Athènes, Paris), pp 583-586.
28. Vigne J-Dwe (2011) Preliminary data on a new early Pre-Pottery Neolithic site on Cyprus (Ayios Tychonas - Klimonas, ca. 9000 cal. BC). *Neo-Lithics* 1(11):3-18.
29. Helmer D & Gourichon L (2008) Premières données sur les modalités de subsistance à Tell Aswad (Syrie, PPNB moyen et récent, néolithique céramique ancien) - Fouilles 2001-2005. *Archaeozoology of the Near East VIII: actes des Huitièmes Rencontres internationales d'archéozoologie de l'Asie du Sud-Ouest et des régions adjacentes*, eds Vila E, Gourichon L, Choyke AM, & Buitenhuis H (Travaux de la Maison de l'Orient et de la Méditerranée), pp 119-151.
30. Stordeur D*, et al.* (2010) Le PPNB de Syrie du Sud à travers les découvertes récentes à tell Aswad [The South Syrian PPNB based on the recent discoveries at Tell Aswad]. French. *Hauran V La Syrie Du Sud Du Néolithique À L'antiquité Tardive Recherches Récentes Actes Du Colloque De Damas 2007*, eds Al-Maqdissi M, Braemer F, & J-M. DBeyrouth), pp 41-68.
31. Gourichon L & Helmer D (2008) Étude archéozoologique de Mureybet [Archaeozoological study of Mureybet]. French. *Le site néolithique de Tell Mureybet (Syrie du Nord). En hommage à Jacques Cauvin*, ed Ibáñez JJ (BAR International Series, Oxford), Vol 1, pp 115-228.
32. Évin J & Stordeur D (2008) Chronostratigraphie de Mureybet. Apport des datations radiocarbone [Chronostratigraphy of Mureybet. Contribution of the radiocarbon dating]. French. *Le site néolithique de Tell Mureybet (Syrie du Nord). En hommage à Jacques Cauvin*, ed Ibáñez JJ (BAR International Series, Oxford), Vol 1, pp 21-32.
33. Davis SJM & Valla FR (1978) Evidence for domestication of the dog 12,000 years ago in the Natufian of Israel.
34. Tchernov E & Valla FF (1997) Two new dogs, and other Natufian dogs, from the southern Levant. *J. Archaeol. Sci.* 24(1):65-95.
35. Harris D*, et al.* (1993) Investigating early agriculture in Central Asia: new research at Jeitun, Turkmenistan. *Antiquity* 67(255):324-338.
36. Olsen SL (2000) The secular and sacred roles of dogs at Botai, North Kazakstan. *Dogs Through Time: An Archaeological Perspective*, ed Crockford SJ (Archaeopress), pp 71-92.
37. Benecke N & von den Driesch A (2003) Horse Exploitation in the Kazakl Steppes during the Eneolithic and Bronze Age. *Prehistoric steppe adaptation and the horse*, eds Levine MA, Renfrew C, & Boyle KV (McDonald Institute Monographs, University of Cambridge, Cambridge), pp 69-82.
38. Dikov NN (1996) The Ushki sites, Kamchatka Peninsula. *American Beginnings: the Prehistory and Palaeoecology of Beringia*, ed West FH (University of Chicago Press, Chicago), pp 244-250.
39. Losey RJ*, et al.* (2011) Canids as persons: Early Neolithic dog and wolf burials, Cis-Baikal, Siberia. *Journal of Anthropological Archaeology*.
40. Pitul'ko VV & Kasparov AK (1996) Ancient Arctic hunters: material culture and survival strategy. *Arctic anthropology*:1-36.
41. Higham C, Kijngam A, & Manly B (1980) An analysis of prehistoric canid remains from Thailand. *J. Archaeol. Sci.* 7(2):149-165.
42. Higham C, Higham T, & Kijngam A (2011) Cutting a Gordian Knot: the Bronze Age of Southeast Asia: origins, timing and impact. *Antiquity* 85(328):583-598.
43. Kijngam A (2010) The mammalian fauna. *The origins of the civilization of Angkor Vol. IV: The excavation of Ban Non Wat: The Neolithic occupation*, eds Higham CFW & Kijngam A (Thai Fine Arts Dept, Bangkok), pp 189-197.
44. Higham C & Higham T (2009) A new chronological framework for prehistoric Southeast Asia, based on a Bayesian model from Ban Non Wat. *Antiquity* 83(319):125-144.

45. Higham C (2004) Mainland Southeast Asia from the Neolithic to the Iron Age. *Southeast Asia: from prehistory to history*, eds Glover I & Bellwood P (Rutledge Curzon, London), pp 41-67.
46. Higham CFW & Bannanurag R eds (1990) *The Excavation of Khok Phanom Di: Volume I, The Excavation, Chronology and Human Burials* (The Society of Antiquaries of London and Thames and Hudson, London), p 387.
47. Higham CFW & Bannanurag R eds (1991) *The Excavation of Khok Phanom Di: Volume II: The Biological Remains Part 1* (The Society of Antiquaries of London and Thames and Hudson, London), p 388.
48. Piper P, *et al.* (2012) Early evidence for pig and dog husbandry from the Neolithic site of An Son, Southern Vietnam *International Journal of Osteoarchaeology*.
49. Bellwood P (in press) An Son and the Neolithic of Southern Vietnam. *Asian Perspectives*.
50. Nishinakagawa H, Matsumoto M, Otsuka J, & Kawaguchi S (1992) Skeletal Remains of Domestic Dogs from Jomon and Yayoi Sites in Kagoshima Prefecture. *Journal of the Anthropological Society of Nippon* 100(4):485-498.
51. Shigehara N & Hongo H (2000) Ancient remains of Jomon dogs from Neolithic sites in Japan. *Dogs Through Time: An Archaeological Perspective*, ed Crockford SJ (Archaeopress).
52. Meadow RH (1991) Faunal Remains and Urbanism at Harappa. *Harappa Excavations 1986-1990 A Multidisciplinary Approach to Third Millennium Urbanism,* Monographs in World Archaeology, ed Meadow RH (Prehistory Press, Madison, Wisconsin), pp 89-106
53. Jing Y (2008) The origins and development of animal domestication in China. *Chinese Archaeology* 8:1-7.
54. Jing Y (2010) Zhongguo gu dai jia yang dong wu de dong wu kao gu xue yan jiu (The zooarchaeology of domesticated animals in ancient China). *Quaternary Sciences* 30(2):298–306.
55. Jing Y (2010) Research report of the faunal remains from Nanzhuangtou site, XuShi of Hebei Province. (Translated from Chinese) *Acta Archaeology Sinicaq* 2010:385-391 (in Chinese).
56. Cui J & Zhou S (2008) Zhongguo xin shi qi shi dai wen hua yan bian dong li fen xi (An analysis of the evolutionary forces of Neolithic period cultures in China). *Zhongguo li shi di li lun cong* 23(2):33-45.
57. Milham P & Thompson P (1976) Relative antiquity of human occupation and extinct fauna at Madura Cave, south-eastern Australia. *Mankind* 10:175-180.
58. Macintosh JWG (1964) A 3,000 year old Dingo Skeleton from Shelter 6. An appendix to Mulvaney, D.J., Lawton, G.H., Twidale, C.R., Archaeological excavation of Rock Shelter No. 6 Fromm's Landing, South Australia. *Proceedings of the Royal Society of Victoria* 77:479-516.
59. Amano N (2012) The Faunal Remains of Nagsabaran in Cagayan, Northern Philippines: Subsistence Strategies in the Neolithic and Metal Age. Masters (University of the Philippines, Manilla`).
60. Hung H, *et al.* (2011) The first settlement of Remote Oceania: the Philippines to the Marianas: supplementary information on radiocarbon dating of the Nagsabaran site. *Antiquity* 85(329).
61. Piper PJ, Amano N, Yang H-Y, & O'Connor T (in press) The terrestrial vertebrate remains. *Archaeology in the Batanes Islands: The early movements of Austronesian-speaking populations*, eds Bellwood P & Dizon E).
62. Bellwood P (in press) The chronology of Batanes prehistory. *Archaeology in the Batanes Islands: The early movements of Austronesian-speaking populations*, eds Bellwood P & Dizon E).
63. Tsang CH, Li KT, & Chu CY (2006) *Xian min lv ji (Footprints of Ancestors: Archaeological Discoveries in Tainan Science-Based Industrial Park)* (Tainan County Government, Tainan) (Chinese).
64. Spriggs M, O'Connor S, & Veth P (2003) Vestiges of early pre-agricultural economy in the landscape of East Timor: recent research. *Fishbones and Glittering Emblems: Proceedings from the EurASEEA Sigtuna Conference*, eds Kallen A & Karlstrom A (Museum of Far Eastern Antiquities, Stockholm), pp 49-58.
65. Flannery T, *et al.* (1995) Fossil marsupials (Macropodidae, Peroryctidae) and other mammals of Holocene age from Halmahera, North Moluccas, Indonesia. *Alcheringa* 19(1):17-25.
66. Flannery T, *et al.* (1998) Mammals from Holocene archaeological deposits on Gebe and Morotai islands, northern Moluccas, Indonesia. *Australian Mammalogy* 20:391-402.
67. Bellwood P (1998) The archaeology of Papuan and Austronesian prehistory in the Northern Moluccas, Eastern Indonesia. *Expansion of East and Southeast Asian Neolithic in Archaeology and Language II: Archaeological Data and Linguistic Hypotheses*, eds Blench R & Spriggs M (Routledge, New York), pp 128-140.
68. Intoh M & Shigehara N (2004) Prehistoric pig and dog remains from Fais Island, Micronesia. *Anthropological Science* (0):409290019.
69. Bulmer S (2000) Lapita dogs and singing dogs and the history of the dog in New Guinea. *The Archaeology of Lapita Dispersal in Oceania: Papers from the fourth Lapita Conference, June 2000*, eds Clark GR, Anderson AJ, & Vunidilo T (Terra Australis, Canberra, Australia), Vol 17.
70. von den Driesch A & Boessneck J (1985) *Die Tierknochenfunde aus der neolithischen Siedlung von Merimde-Benisalâme am westlichen Nildelta [The animal remains from the Neolithic settlement of Merimde Beni-salame in the western Nile Delta]. German* (Uni-Druck, München).
71. Gautier A (2004) The Early to Late Neolithic Archeofaunas from Nabta and Bir Kiseiba. *Holocene Settlement of the Egyptian Sahara*, eds Wendorf F & Schild R (Kluwer Academic Press and Plenum Publishers, New York), Vol 1, The Archeology of Nabta Playa, pp 606-635.
72. Wendorf F & Schild R eds (2004) *The Early to Late Neolithic Archeofaunas from Nabta and Bir Kiseiba* (Kluwer Academic Press and Plenum Publishers), Vol 1, The Archeology of Nabta Playa.
73. Peters J (1986) A revision of the faunal remains from two Central Sudanese sites: Khartoum Hospital and Esh Shaheinab. *Mélanges publiés à l'occasion du 5e Congrès International d'Archéozoologie, Août 1986*, (La Pensée Sauvage Editions), pp 11-33.
74. Gautier A (2002) The evidence for the earliest livestock in North Africa: Or adventures with large bovids, ovicaptrids, dogs and pigs. *Droughts, Food and Culture: Ecological Change and Food Security in Africa's Later Prehistory*, ed Hassan FA (Kluwer Academic / Plenum Publishers, New York), pp 195-207.
75. Gautier A (1984) The fauna of the neolithic site of Kadero (central Sudan). *Origin and early devleopment of food-producing cultures in North Eastern Africa*, eds Krzyzaniak L & Kobusiewicz M (Polish Academy of Sciences and Poznam Archaeological Museum, Poznan), pp 317-319.
76. Gautier A (1986) La fauna de l'occupation néolithique d'el Kadada (Secteurs 12-22-32) au Soudan Central. *Archéologie du Nil Moyen* 1:59-111.
77. Paris F (2000) African livestock remains from Saharan mortuary contexts. *The Origins and Development of African Livestock*, eds Blench RM & MacDonald KC (UCL Press, London, England).
78. Linseele V (2007) *Archaeofaunal Remains from the Past 4000 years in Sahelian West Africa: Domestic livestock, subsistence strategies and environmental changes.* (Archaeopress, Oxford, England) 70 Ed.

79. MacDonald KC (1995) Analysis of the mamalian, avian, and reptilitan remains. . *Excavations at Jenne-Jeno, Hambarketolo, and Kaniana (Inland Niger Delta, Mali), the 1981 season,* Anthropology, ed McIntosh SK (University of California Press, Berkeley), 20 Ed.
80. Clutton-Brock J (1997) Animal Domestication in Africa. *Encyclopedia of Precolonial Africa: Archaeology, History, Languages, Culture, and Environment*, ed Vogel JO (AltaMira, London), pp 418-424.
81. Degerbøl M (1967) Dogs from the Iron Age (c. A.D.950-1000) in Zambia with remarks on dogs from primitive cultures. *Iron Age Cultures in Zambia,* The Robins Series, ed Fagan BM (Chatto & Windus, London), pp 198-207.
82. Voigt EA (1983) *Mapungubwe: An Archaeozoological Interpretation of an Iron Age Community* (Transvaal Museum., Pretoria).
83. Plug I (1996) Domestic Animals during the Early Iron Age in Southern Africa. *Aspects of African Archaeology: Papers from the 10th Congress of the Pan African Association for Prehistory and Related Studies*, eds Pwiti G & Soper R (University of Zimbabwe Publications, Harare), pp 515-519.
84. Smith AB (2000) The origins of the domesticated animals of southern Africa. *The Origins and Development of African Livestock: archaeology, genetics, linguistics and ethnography*, eds Blench R & Macdonald KC (UCL Press, London, England), pp 222-238.
85. Plug I & Voigt EA (1985) Archaeozoological studies of Iron Age communities in southern Africa. *Advances in world archaeology* 4:189-238.
86. Voigt EA & Peters J (1994) The faunal assemblage from Wosi in the Thukela Valley. *Natal Museum Journal of Humanities* 6:105-117.
87. van Schalkwyk L (1994) Wosi: an Early Iron Age village in the lower Tukhela Basin, Natal. *Natal Museum Journal of Humanities* 6(65-96).
88. Chappel CA (1968) A strandloper skeleton found at Cape St. Francis. *Diastema* 2(3):37-39.
89. Grayson DK, Parmalee PW, Lyman RL, & Mead JI (1988) Danger Cave, Last Supper Cave, and Hanging Rock Shelter: the faunas. Anthropological papers of the AMNH; v. 66, pt. 1.
90. Lupo KD & Janetski JC (1994) Evidence of domesticated dogs and some related canids in the eastern Great Basin. *Journal of California and Great Basin Anthropology* 16(2):199-220.
91. Morey DF & Wiant MD (1992) Early Holocene domestic dog burials from the North American Midwest. *Curr. Anthropol.* 33(2):224-229.
92. Fowler ML (1959) Modoc Rock Shelter: an early Archaic site in southern Illinois. *American Antiquity* 24(3):257-270.
93. Dowd JT & Breitburg E (1989) *The Anderson site: Middle Archaic adaptation in Tennessee's central basin* (Tennessee Anthropological Association).
94. Tuck JA (1976) *Ancient people of Port au Choix: the excavation of an Archaic Indian cemetery in Newfoundland* (Institute of Social and Economic Research, Memorial University of Newfoundland).
95. Wing ES (1991) Dog Remains form Socre Site on Vieques Island. *Beamers, Bobwhites, and Blue-Points: Tributes to the Career of Paul W. Parmalee*, eds Purdue JR, Klippel WE, & Styles BW (Illinois State Museum Scientific Papers, Springfield), Vol 23, pp 379-386.
96. Wing ES (2001) Native American use of animals in the Caribbean,. *Biogeography of the West Indies: Patterns and Perspectives*, eds Woods CA & Sergile FE (CBC Press, Boca Raton, Lousiana), 2nd Ed, pp 481-518.
97. Flannery KV (1967) Vertebrate fauna and hunting patterns. *In the Prehistory of the Tehuacan Valley*, ed Byers DS (University of Texas Press, Austin), pp 132-177.
98. Smith BD (2005) Reassessing Coxcatlan Cave and the early history of domesticated plants in Mesoamerica. *Proc. Natl Acad. Sci. U. S. A.* 102(27):9438.
99. Salomon IB & Stahl PW (2008) Un Enterramiento Canino en Real Alto: Implicaciones para el Estudio del Perro Prehispánico en el Nuevo Mundo [A Dog Burial in Real Alto. Implications for the Study of the Prehispanic Dog in the New World]. Spanish. *III Congreso Ecuatoriano de Antropología y Arqueología*.
100. Byrd KM (1976) Changing Animal Utilization Patterns and their Implications: Southwest Ecuador (6500 B.C.-A.D. 1400). Ph.D. (University of Florida, Gainesville).
101. Stahl PW (1984) Tropical Forest Cosmology: The Cultural Context of the Early Valdivia Occupations at Loma Alta. Ph.D. (University of Illinois, Urbana-Champaign, Illinois).
102. Alva W & Donnan CB (1993) *Royal tombs of Sipán* (Fowler Museum of Cultural History, University of California).
103. MacNeish RS & Vierra RK (1983) The Preceramic way of life in the Thorn Forest Riverine Ecozone. *Prehistory of the Ayacucho Basin, Peru, Vol.4 The Preceramic Way of Life*, eds MacNeish RS, Vierra RK, Nelken-Terner A, Lurie R, & Cook AG (University of Michigan Press, Ann Arbor), pp 48-129.
104. Vásquez Sánchez VF, Rosales Thom TE, & Dorado G (2009) Morphotypes and Breeds of Dogs (Canis lupus familiaris L.) from the Moche Period. *Archaeobios* 3:20-23.
105. Wheeler J, Cardoza CR, & Denise Pozzi-Escot D (1977) Estudio Provisional de la Fauna de las Capas II y III de Telarmachay. *Revista del Museo Nacional* 43(97-109).
106. Allison MJ, Focacci G, & Santoro C (1982) The pre-Columbian dog from Arica, Chile. *American Journal of Physical Anthropology* 59(3):299-304.
107. Prates L, Prevosti FJ, & Berón M (2010) First Records of Prehispanic Dogs in Southern South America (Pampa-Patagonia, Argentina). *Curr. Anthropol.* 51(2):273-280.

Table S4. A list of the individual wolves analyzed in this study.

Macro-region	Country	Region	Sample Code
Old World	Belarus	Belowieza Forest	13
Old World	Belarus	Gomel, Khoyniki	104
Old World	Russia	Smolensk, Vjazmad	460
Old World	Russia	Pskov, Ostrov	520
Old World	Russia	Petersburg, Gatchina district	523
Old World	Bulgaria	Bulgaria	719
Old World	China	N. Hulunbard Grasslands, Inner Mongolia	8
Old World	China	N. Hulunbard Grasslands, Inner Mongolia	9
Old World	Spain	Hoz de Arreba, N. Burgos (CyL)	SP1
Old World	Spain	Asturianos, Zamora (CyL)	SP2
Old World	Spain	Piezu, Ponga (Asturias)	SP3
Old World	Spain	Covadonga (Asturias)	SP4
Old World	Italy	N. Pesaro (Serra S. Abbondio)	ItalyW1
Old World	Italy	C. Rieti (Pescoracchiano)	ItalyW2
New World	Canada	Alberta	CanadaW1
New World	Canada	Alberta	CanadaW2
New World	Canada	N.W. Territories	CanadaW3
New World	Canada	N.W. Territories	CanadaW4
New World	Canada	N.W. Territories	CanadaW5
New World	USA	SE Alaska	AKW1