Geographical Origin of the Domestic Dog

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The domestic dog (Canis familiaris) is considered to be the oldest domestic animal in the world. World-wide mitochondrial deoxyribonucleic acid (mtDNA) studies clearly indicate a single origin in time and place in Southeast Asia less than 16 000 years ago including a high number of female foundation wolves resulting in 10 subhaplogroups within three haplogroups. Later hybridisation events in East Asia, the Middle East, Scandinavia and possibly North America formed 3–4 small haplogroups. In contrast, the archaeological record, favours other, sometimes multiple, regions for dog domestication (mainly Europe and Middle East), but suffers from a lack of samples from Southeast Asia and is problematic, because of the difficulty of distinguishing between wolf and dog in fossil remains. Future studies including, for example, paternal markers such as the Y-chromosome, autosomal markers like SNPs, and ancient DNA samples of both wolves and dogs may give new insights into early domestication history and the dog’s migration routes.

Introduction

The domestication of plants and animals was the crucial step in the Neolithic transition from a hunter-gather to a sedentary lifestyle which led to the advanced agricultural societies and eventually to modern civilisations (Diamond, 2002). Therefore, domestication is considered to be the most significant innovation in history for human society (Diamond, 2002). The study of domestication may tell us not only something about the domestic animal, but also about the human cultural context, thus giving insights about human societies throughout the world (Bruford et al., 2003). Until 20 years ago, the origin of the domestic dog was a total riddle. It was not clear if the wild ancestor was wolf (Canis lupus), jackal (Canis aureus; Clutton-Brock, 1995) or coyote (Canis latrans) or if all three or a combination of two of these contributed to the gene pool of the dog. Even more contention existed in the field when it came to the questions ‘where’, ‘when’ and ‘how many times’ the dog was domesticated. Since then, especially through genetical studies, the picture has become increasingly clearer, for example, most importantly, pointing out that the wolf is the only ancestor of the dog (Figure 1; Olsen and Olsen, 1977; Wayne, 1993; Vila et al., 1997; Leonard et al., 2002; Lindblad-Toh et al., 2005). However, the

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Figure 1 The dog’s ancestor, the wolf (Canis lupus). Image courtesy of Gary Kramer, US Fish and Wildlife Service.
The domestic dog is a good illustration of how different scientific evidence (of different nature) may result in diverse interpretations. Therefore, there is not full agreement about the details of dog domestication, but the picture becomes increasingly clearer.

The dog is generally considered to be the earliest domestic animal (e.g., Zeder et al., 2006; Wang and Tedford, 2008) and has been unparalleled in its success as a companion in human society. It is the only animal which in ancient times accompanied humans to all continents and, in contrast to other domestic animals, it serves a large number of different ‘roles’ as hunting, herding, guarding, guiding, searching and rescuing companion (Figure 2). In some countries it is also a source of food and fur and it has lately also become a model organism for medical and genetical research, because it has, in addition to a countless morphological variety, diseases similar to those of humans (Sutter and Ostrander, 2004; Ostrander and Wayne, 2005). Scientists as nonscientists alike are therefore fascinated by the history of the domestic dog.

However, there is still considerable controversy among scientists as to whether the dog has a single or multiple origins, and to where and when the dog was domesticated. In Eurasia, two principal ancient domestication centres have been identified in which most of the current livestock species were domesticated: The Middle East (mainly Fertile Crescent) and China/Southeast-Asia (Diamond, 2002; Bruford et al., 2003). However, the dog is not a typical domestic animal, because it was probably not domesticated solely as livestock and it is a carnivore and therefore might have been domesticated outside the classical domestication centres. Here, we review the different lines of evidence (the archaeological record and genetical studies), discuss the advantages and limitations of each approach, and propose a probable scenario for dog origins.

**Archaeological Record**

Studies of the archaeological record may give insights into the history of domestication and potentially deliver answers about ‘where’, ‘when’ and ‘how many times’ domestication occurred. However, the archaeological record for dogs is fragmentary (Napierala and Uerpmann, 2010) and only a few fossils considered to be remains of potential early domesticated dogs have been described (Table 1). Further, there is an ongoing intensive discussion about the question: Is this fossil really a dog or is it a small ancient wolf? Naturally, the further we go back in time, the more similar the early domestic dogs would have been to their ancestors, the wolves (Figure 1; Wang and Tedford, 2008). The situation is further complicated by the fact that remains are normally incomplete, consisting only of a few bones or teeth (Wang and Tedford, 2008), which makes a comprehensive examination impossible. Additionally, there is considerable bias in the geographical distribution of excavations carried out with a strong focus on Europe and the Middle East, giving the perhaps false impression that these areas are more likely to be areas of origins for the dog just because a larger number of early Canid specimens have been found there (see Table 1 for a review of the earliest archaeological findings proposed to be dog).

However, wolves were formerly distributed throughout North America and Eurasia (Nowak, 2003; Napierala and Uerpmann, 2010). Logically it follows that a comprehensive picture of dog domestication can only be validated if fossil of dog/wolf remains from all parts of the Old World are studied. Nevertheless, it is generally agreed by many scientists that either Chinese or Middle Eastern wolves were the ancestors of the domestic dog (Olsen and Olsen, 1977), because these southern wolves are smaller in size and might have been easier to handle than the much larger wolf types from Northern Europe, Russia and Siberia.

**Measurements in Archaeological Research**

Measurements of bones and teeth have been among the most commonly used techniques in osteological research (e.g., Street, 2002; Germonpré et al., 2009; Detry and Cardoso, 2010; Napierala and Uerpmann, 2010). Since domestication was accompanied by a decrease in body size (Davis, 1981; Dayan, 1994), somewhat smaller fossil remains have been interpreted as being those of domestic dog. However, two of the earliest findings, from Israel (Davis and Valla, 1978) and Bonn-Oberkassel in Germany (Table 1; Street, 2002; Napierala and Uerpmann, 2010) are from subadult specimens. Therefore, smaller body size in these cases is possibly related to younger age rather than evidence for domestication. Further, Napierala and Uerpmann (2010) point out that the finds from, for example Eliseevichi I, and Kniegrotte (Table 1) cannot be clearly assigned to domestic dogs, because tooth measurements (upper carnassials, $P^4$) are within the range of variability found in teeth size of wolf populations. In contrast, the Kesslerloch Cave find is clearly smaller. Furthermore, the Eliseevichi I find from western Russia, in layers C-14 dated to 13 000–17 000 BP (Sablin and Kholopachev, 2002) are questioned by Wang and Tedford (2008) since only some of the morphological characteristics are dog-like (similar to a Siberian husky), while others are more wolf-like. The same applies to the very early Belgian canid (Table 1; Germonpré et al., 2009). Napierala and Uerpmann (2010) emphasise that the find by Germonpré et al. (2009) must therefore be re-evaluated in comparison to unambiguous wolf and dog samples rather than to questionable finds from Eliseevichi I (Russia), and other findings from Mezin and Mezhrich (Ukraine). Likewise, the feature of a broadened snout, which is often taken as a sign of domestication, is an unreliable morphological character. Napierala and Uerpmann (2010) suggest other influences, such as individual age or changes in predator–prey relations, to potentially impact the modification of this character. There are additional osteological traits used
The domestic dog (*Canis familiaris*) comes in different shapes and sizes. The (a) Tibetan Mastiff (guarding dog) originates from Central Asia and is a representative of an ancient dog group, the Mastiffs. (b) The Sloughi, a representative of the ancient group of Hounds, originates from (North-) Africa and is traditionally used for hunting. Representatives of modern breeds are the (c) Fox Terrier (fox hunting), (d) Swedish Vallhund (herding/guarding) and (e) Wirehaired Dachshund (hunting). Other presumably old dog breeds include the (f) Bergamasco Sheepdog (herding) and (g) Naked Peruvian Inca Orchid (unclear role; probably connected to spiritual rituals and food), the latter has no fur except for the head hair. (a) Reproduced from http://commons.wikimedia.org/wiki/File:Candra_Du_Domaine_De_Toundra,_CAC.jpg under the wikimedia commons license; (b) and (c) Copyright Dr. Dominique de Caprona, reproduced with permission; (d) reproduced from http://commons.wikimedia.org/wiki/File:V%C3%A4stg%C3%B6taspets1.jpg under the wikimedia creative commons license; (e) reproduced from http://commons.wikimedia.org/wiki/File:Wire-haired_Dachshund_R_01.JPG under the wikimedia creative commons license; (f) reproduced from http://en.wikipedia.org/wiki/File:Ortensia_di_Valle_Scrivia.jpg under the wikimedia creative commons license and (g) reproduced from http://commons.wikimedia.org/wiki/File:Perro_sin_pelo_del_Per%C3%BA.JPG under the wikimedia creative commons license.
to distinguish domestic dogs from wolves, for example
crowding of the teeth caused by shortening of the facial
region (Clutton-Brock, 1995). However, these traits are
sometimes found also among wolves (Musil, 2000), and the
extent of the variation in the ancient wolf populations is
often not well studied. Musil (2000) and Davis (1981) fur-
ther mention the impact of sexual dimorphism on size
measurements. Since female wolves are on average smaller
than male wolves, this fact may add to the difficulties in
distinguishing between wolves and early dogs. It is in fact
often impossible to find out from a few bones, if the canid
was a female or a male. Further, Musil (2000) writes that all
potential dog characteristics (reduced body size, shorter
snout and facial parts of the skull, crowded teeth, reduced
brain volume) can develop within a few generations in wild
wolves kept in captivity. Finally, other authors (Davis and
Valla, 1978; Davis, 1981; Dayan, 1994) discuss the prob-
lematic use of body size and associated measurements from
a different perspective. Temperature rose at the end of the
Pleistocene, resulting in a decrease in body size of wolves
and other species around 10 000–12 000 years BP (Davis,
1981). Domestication itself is also characterised by
decrease in body size, possibly because of selection of
smaller individuals in the ancestral population (giving
easier handling, and more specimens in a confined space)
and/or insufficient food supply (Davis, 1981). Thus, with
two possible causes for small body size in canids, the dis-
tinction between small wolves and early dogs gets even
more complicated. Olsen and Olsen (1977) point out that
Chinese wolves (but not larger wolf subspecies) share a
morphological feature with dogs ‘the turned-back apex of
the coronoid process of the ascending ramus’, giving an
indication that dogs originated from Chinese wolves. A few
studies by Jing (2008) and others (Underhill, 1997; Jin and
Xu, 1992) pushes the earliest record for domestic dog to
10 000 years before present in North China. However,
relatively little archaeological work has been performed
and the soil in many regions of South China is acidic.

<table>
<thead>
<tr>
<th>Place</th>
<th>Potential date</th>
<th>Remarks</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bonn-Oberkassel (Germany)</td>
<td>~14 000 BP</td>
<td>Subadult specimen; wolf-sized specimen (Deguilloux et al., 2009)</td>
<td>Nobis (1979); Street (2002)</td>
</tr>
<tr>
<td>Hayonim Terrace (northern Israel)</td>
<td>~11 500 BP</td>
<td>Two fairly complete canid remains</td>
<td>Tchernov and Valla (1997)</td>
</tr>
<tr>
<td>Eliseevichi I (Russia)</td>
<td>13 000–17 000 BP</td>
<td>Canid cranium; wolf-sized specimen (Deguilloux et al., 2009)</td>
<td>Sablin and Khlopachev (2002)</td>
</tr>
<tr>
<td>Kesslerloch cave (Switzerland)</td>
<td>14 100–14 600 BP</td>
<td>Skull fragment includes a large part of the right maxilla and a small portion of the zygomaticum and the palatinum; adult</td>
<td>Napierala and Uerpmann (2010)</td>
</tr>
<tr>
<td>Goyet (Belgium)</td>
<td>31 680 ± 250 BP</td>
<td>A ‘fossil large canid’</td>
<td>Germonpré et al. (2009)</td>
</tr>
<tr>
<td>northern Israeli sites of Ein Mallaha (Eynan) and Hayonim terrace (Israel)</td>
<td>11 310–12 310 BP</td>
<td>Three canid finds, consisting of a diminutive carnassial and mandible, and a canid puppy skeleton buried with a human</td>
<td>Davis and Valla (1978)</td>
</tr>
<tr>
<td>Kniegrotte Cave, Teufelsbrücke Cave, and Oelknitz (Germany)</td>
<td>Kniegrotte: 12 230 ± 90 BP; 13 585 ± 165 BP; Teufelsbrücke: 12 300 ± 85–13 025 ± 85; Oelknitz: 10 990 ± 85–12 545 ± 80 BP</td>
<td>Several canid remains</td>
<td>Musil (2000)</td>
</tr>
</tbody>
</table>

Note: BP = before present.
result, many dog remains may have been incorrectly assigned to *Canis lupus* instead to *Canis familiaris* (Jing Y, personal communication). Further excavations in South China may shed light on the earliest domestication history of dogs in this region.

To conclude, the archaeological record is very difficult to interpret and there is considerable controversy about the authenticity of many of the earliest findings proposed to be dog. However, from around 10 000 years ago, the archaeological findings of dogs and especially burials (Morey, 2006) become numerous and an established relationship between humans and dogs seems unambiguous. Therefore, the archaeological record shows that domestic dogs existed 10 000 years ago, and this implies that the domestication event might have been a few thousand years earlier. However, where and when exactly the dog was domesticated remains unclear based on the archaeological record alone.

### Genetical Studies

Another way to tackle the domestication history of the dog and other domesticates, is the use of genetical markers, such as mitochondrial deoxyribonucleic acid (mtDNA; Table 2). This marker has been widely used to study domestication (e.g. pig: Larson *et al.*, 2010; horse: Lei *et al.*, 2009; dog: Savolainen *et al.*, 2002; Pang *et al.*, 2009).

In principal, these analyses involve comparing mtDNA haplotypes among all dogs and possibly also wolves, worldwide. If all dog populations have a similar set of haplotypes, this would indicate a single common origin of all dog populations, and the geographical region with the most complete set of haplotypes would be considered the likely origin. Derived populations would have only a subset of all haplotypes since some haplotypes would have been lost as dog spread all over the world. If instead dog populations throughout the world would have largely

<table>
<thead>
<tr>
<th>Marker/type of study</th>
<th>Inheritance</th>
<th>Properties/advantages</th>
<th>Disadvantages</th>
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</thead>
<tbody>
<tr>
<td>mtDNA</td>
<td>Maternal</td>
<td>High copy number; therefore usable for all kind of tissues including ancient/low-quality DNA material</td>
<td>Can be poor estimator of total genomic diversity, because limited to one locus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Highly variable (≈10 x higher than nuclear genome)</td>
<td>No information about nuclear and paternal variation (mtDNA is an extra-nuclear genetic marker)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Haploid; phylogenetic analysis is relatively straightforward (Bruford <em>et al.</em>, 2003)</td>
<td>Low diversity</td>
</tr>
<tr>
<td>Y-chromosome</td>
<td>Paternal</td>
<td>Haploid; analysis of haplotypes straightforward</td>
<td>Have to be recovered from a representative sample of the population, otherwise ascertainment bias can affect analysis severely (Albrechtsen <em>et al.</em>, 2010)</td>
</tr>
<tr>
<td>SNP</td>
<td>Autosomal/biparental</td>
<td>Next-generation sequencing makes it possible to recover a high number of SNPs in the genome</td>
<td></td>
</tr>
<tr>
<td>SNP</td>
<td>Autosomal/biparental</td>
<td>Gives information about nuclear genome</td>
<td></td>
</tr>
<tr>
<td>Modern DNA studies</td>
<td>NA</td>
<td>High sample numbers</td>
<td>Past events such as replacement of lineages may be hard to detect</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Thereby, giving a detailed picture of today’s genetic variation and reconstruction of past events possible to a certain degree</td>
<td></td>
</tr>
<tr>
<td>aDNA</td>
<td>NA</td>
<td>Additional estimates about original genetic diversity</td>
<td>Often few samples</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May give temporal change of genetic diversity estimates (e.g. identification of hybridisation and/or local domestication leading to partial or total replacement of lineages)</td>
<td>Error-prone due to high contamination risk (Malmström <em>et al.</em>, 2005; Linderholm <em>et al.</em>, 2008) and low-quality DNA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High conservation variability of DNA among geographical locations and different body parts</td>
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nonoverlapping gene pools, then this would indicate several origins from different wolf populations.

The most comprehensive study based on mtDNA to date, including 1543 dogs from all over Eurasia and Africa (Figure 3 and Figure 4; Pang et al., 2009), is the only genetic study with a global sampling of mostly nonbreed dogs. This study indicates that all dogs worldwide have a single origin from Southeast Asia, South of the Yangtze River (Figure 4b), less than 16000 years ago. The study focused on dogs only, because it is unclear to date, if the contemporary wolf populations are representative for the wolf populations at the time of domestication.

It showed that almost 100% of dogs in all regions share haplogroups A, B and C (Figure 3a and Figure 4a), indicating a single geographical origin. Genetic variation is clearly highest South of the Yangtze River in China (Figure 3b and Figure 4b). Outside this region, all other regions (Africa, Europe, Middle East and even North China) show only a subset of genetic diversity in terms of unique haplotypes and haplogroups (Figure 3b and Figure 4b). For example, all 10 principal subhaplogroups of haplogroups A, B and C among dogs are found only South of Yangtze River, but in China North of Yangtze River only 7 haplogroups are found, in SW Asia and Africa 5, and in Europe 4. This indicates that the full set of 10 haplogroups originated South of Yangtze River and when dogs migrated to other parts of the world, only a subset of the subhaplogroups was spread. Importantly, dogs worldwide have the same subset of haplogroups, indicating a scenario that includes an expansion from a single region of origin. The improved sampling (in comparison to earlier studies by Vilà et al., 1997 and Savolainen et al., 2002) and analysis of whole mtDNA genomes refined molecular dating for the dog origin which is now more in agreement with archaeological data (e.g. Jing, 2008; Davis and Valla, 1978; Street, 2002) than older estimates by Vilà et al. (1997). Further, the data suggest that a high number of female wolves (~50 or more) were domesticated, for the first time giving some insight into the earliest stages of dog domestication.

Savolainen et al. (2004) investigated the origins of the dingo (Figure 5), a feral dog living in Australia, as an example for an early migration from the centre of domestication in Southeast Asia. In their study, 211 Australian dingoes sampled in all states of Australia were sequenced for the mtDNA control region and compared to sequences from 676 dogs from all continents and 38 Eurasian wolves (Savolainen et al., 2002). All sequences among dingoes were either identical to or differing by a single substitution from one mtDNA haplotype, called A29. This haplotype was found in more than 50% of all sampled dingoes and is otherwise found only among dogs in Southeast Asia, Siberia and Arctic America. Of 19, 18 other identified haplotypes were found in dingoes only, indicating that these haplotypes derived from the central A29 haplotype. Based on the mean genetic distance of these derived dingo sequences to A29, the arrival of the dingo in Australia was calculated to 5000 YBP which is roughly in congruence with the archaeological record. This study suggests that dingoes originate from domestic dogs in Southeast Asia, that they had a very small founder population, and have lived largely isolated from other dog populations for several thousand years. Interestingly, the New Guinea Singing dog (NGSD), another wild dog living in the New Guinea highlands, share mtDNA haplotype A29 with the dingo and dogs from Southeast Asia, and also some alleles of another genetical marker, the Dog leucocyte antigen class II (Runstadler et al., 2006) as well as some morphological and behavioural characteristics (Koler-Matznick et al., 2003). Therefore, it seems likely that these two populations have a common origin from a migration of early domestic dogs from Southeast Asia.

At least three events of subsequent local dog–wolf hybridisation are also indicated by mtDNA data, one each in Japan (forming haplogroup F), Middle East (haplogroup d2) and Scandinavia (haplogroup d1; Klütsch et al., 2011). These minor subhaplogroups consist of one or only a few haplotypes and are found only regionally which is why dog–wolf hybridisation is their most likely source. Additionally, there is one possible hybridisation event identified in North America by Koop et al. (2000). In their phylogenetic tree, sequences of ‘ancient’ (a couple of hundred years old) samples of the North American Tahltan dog and Wool dog clustered with a wolf sample from Yukon in a separate group, indicating a close phylogenetic relationship between the two indigenous dog types and the North American wolf. Therefore, the authors concluded that a separate local domestication might have occurred in North America. However, hybridisation of Old World dogs with a New World wolf is a more probable scenario, considering that no evidence for a separate domestication has been found in North American archaeological sites (Koop et al., 2000) and that in genetical analyses of ancient and modern dog samples, Leonard et al. (2002) found that all New World dogs have an origin from Old World wolves.

Importantly, hybridisation is not part of de novo domestication, but may nevertheless contribute to the gene pool of both species. Hybridisation between dogs and wolves as an intentional act by humans is part of the domestication history of dogs, but still not domestication de novo. The distinction between hybridisation and domestication might be challenging in different areas of research and ancient DNA (aDNA) analysis may help to establish original genetic diversity in both wolves and dogs at a given locality before hybridisation. Thus, aDNA may give more detailed insights into temporal local changes, including hybridisation and/or local domestication events.

Notably, these studies of modern and ancient dogs do not imply that there have been no additional attempts somewhere in the world to breed wolves in captivity, and ultimately domesticate them. However, if this is the case, they have not contributed to the mtDNA gene pool of modern dogs, possibly because the population went extinct at some point of time. Additionally, mtDNA displays only the maternal side of the story and other markers, such as the Y-chromosome (paternally inherited; Natanaelsson et al., 2006) and autosomal SNPs are needed to complement the picture.
Figure 3 Genetic relationships between the mtDNA CR sequences (582 bp). (a) Phylogenetic tree for dog (unlabeled), wolf (filled square) and coyote (Coy) haplotypes. The six main phylogenetic haplogroups (A–F) of dog haplotypes, discussed in the text, are indicated. Note the close relation between dog and wolf, compared to coyote (the closest wild relative of wolf), clearly indicating that dogs originate from wolf. (b) Minimum spanning networks showing the relationships between the haplotypes in dog haplogroup A, B and C, and the representation in different geographical regions. The haplotypes are symbolised by circles (coloured or white), and are separated by one mutational step; black dots are hypothetical intermediates. Fourteen virtually universally occurring haplotypes (‘Universal Types’: UTs) are indicated with bold lining. The representation of haplotypes in the geographical regions is shown by the colour and size of the circles. A coloured circle indicates the presence of the haplotype (blue for haplotypes shared with other regions and orange for haplotypes unique to the region); white denotes nonrepresented haplotypes. The size of the circle is proportional to the frequency of the haplotype in the region. Note the difference in representation between the eastern (East Asia) and western (West: Europe, SW Asia and Africa) parts of the Old World, and that Asia South of Yangtze River (ASY) is the only subregion with virtually complete representation in all parts across the networks. (c) The 10 principal subhaplogroups in haplogroups A, B and C (six for haplogroup A, two each for B and C), identified by analysis of the entire mtDNA genomes for the samples indicated by colour. Haplogroup A: subclade a1 orange, a2 green, a3 red (upper part of network), a4 red (lower part of network), a5 blue and a6 yellow. B: subclade b1 orange and b2 green. C: subclade c1 green and c2 orange. See geographical representation of the 10 subhaplogroups in Figure 4, compare also with Figure 3b. Reproduced from Pang et al. (2009) with permission from Oxford University Press.
Geographical Origin of the Domestic Dog

(a)

(b)
To conclude, mtDNA gives a very distinct indication that dogs originated in a single region, Southern East Asia, 10,000–16,000 years ago, and that the population is based on a founder population of at least 50 wolf females and some subsequent regional hybridisation events.

Genome-wide SNP Data

A recent study by vonHoldt et al. (2010) aimed at determining the primary centre of dog domestication by a genome-wide SNP survey of pure-bred dogs (mainly from Europe/the United States; 66/85 breeds) and wolves from Europe, the Middle East and North/Central China. They found highest haplotype sharing between modern dogs and wolves from the Middle East, and therefore suggested the ‘Middle East as a primary source of genetic variation in the dog’ (vonHoldt et al., 2010). This clearly contradicts the comprehensive studies of mtDNA discussed earlier, which suggest that dogs were domesticated in Southeast Asia. However, the SNP study suffers a similar bias as the archaeological record, namely a lack of representative samples, for both dogs and wolves, from many parts of the world, and especially from southern East Asia. Clearly, the lack of samples from southern East Asia may explain the discrepancy between the results of vonHoldt et al. (2010) and those of Pang et al. (2009). Actually, if dogs originated in southern East Asia, this could not have been detected by this study, since no wolves from southern East Asia were analysed. Furthermore, the source for SNPs used for the analyses was almost exclusively European breed dogs, and not a single dog or wolf from southern East Asia was included. Therefore, the SNPs were recovered from only a small part of the total gene pool of dogs. As a result, the SNPs used are likely to suffer a phenomenon called ascertainment bias (e.g. Morin et al., 2004; Albrechtsen et al., 2010) and hence are not suitable for an objective comparison of genetic diversity in dogs and wolves worldwide. To reconcile the results of the different genetic studies, it is vital to recall that mtDNA data indicated regional hybridisations of dogs and wolves, one of them in the Middle East. Hence, there is a possibility that the signal picked up by the SNP survey of vonHoldt et al. (2010) may result from dog–wolf admixture rather than ancestry of dogs in Southwest Asia. Autosomal (e.g. SNP) markers are undoubtedly an important tool for future investigations, but studies of the origins of dogs must be based on samples with practically complete geographical coverage.

Ancient DNA Studies

To study early domestication history and migration routes from southern East Asia in more detail, it would be crucial to look at ancient DNA of early dog and early wolf remains and compare these with contemporary samples.
For example, this may show whether the earliest dogs universally had the same mix of haplogroups A, B and C as found among today’s dogs. This is imperative also because today’s wolf population represents only a fraction of the wolf population that existed in the past. Consequently, genetic diversity is probably reduced and not representative of earlier wolf populations and in many regions the wolf populations are completely exterminated (Gao, 2006). Also, because there is increasing evidence of recent hybridisation between dogs and wolves in the wild (Wronski and Macaser, 2008; Anderson et al., 2009; Iacolina et al., 2010), analysis of ancient wolf samples may be necessary for reconstructing the original genetic diversity in prehistoric wolves. Likewise, unresolved issues such as the origin of haplogroup D, including subhaplogroups d1 (mainly found in Scandinavia; Klütisch et al., 2011) and d2 (only found in the Middle East and along the Mediterranean Sea; Pang et al., 2009; Klütisch et al., 2011) could be tackled by ancient DNA approaches. So far, neither contemporary wolves nor historical/ancient dog and wolf samples were found to carry haplotypes from these subhaplogroups (Flagstad et al., 2003; Malmström et al., 2008).

In order to determine the origin of North American dogs, Leonard et al. (2002) analysed mtDNA for 24 pre-European dogs collected from archaeological sites in Alaska, Mexico, Peru and Bolivia. With this approach, the problem that modern European dogs might have contributed to the gene pool of modern New World dogs was avoided. These sequences were compared to sequence data of modern wolves and dogs. This showed that native American dogs originate from multiple Old World dog lineages (haplogroups A, B and C), indicating that all ancient and modern dogs worldwide have a common origin from Old World wolf ancestors.

Additional ancient DNA studies of dogs have focused on local comparisons of ancient and wolf samples in Europe. Deguilloux et al. (2009) retrieved three haplotypes, all belonging to the previously identified haplogroup C (Vila et al., 1997; Savolainen et al., 2002; Pang et al., 2009), from one location (Villeneuve–Tolosane) in Southeast France from the Middle Neolithic (6000–5800 YBP). In a study of 24 ancient dog samples from Sweden (Malmström et al., 2008), including dogs from Neolithic (~5300–4500 YBP) and Medieval sites (~1000–500 YBP), haplogroups A and C were found. Finally, Verginelli et al. (2005) analysed five Italian prehistoric canid remains. Two dog samples from the Eneolithic and the Bronze age (from 4110±40 YBP to 3040±40 YBP) had haplotypes from haplogroups A and C, in agreement with the findings of Malmström et al. (2008) and Deguilloux et al. (2009). The other three canids could not be definitely identified as dogs or wolves. Two samples from around 10000 YBP had haplogroup A and B haplotypes, and the third from around 15000 YBP a haplotype from haplogroup C. Therefore, ancient DNA studies suggest that in the Middle Neolithic, haplogroups A and C were well established in European as well as North American dogs. Remarkably, clade B haplotypes are under-represented (only one canid each in Verginelli et al., 2005; Leonard et al., 2002). Whether this under-representation of clade B haplotypes in ancient samples is caused by sample bias or mirrors a real pattern warrants investigation of a larger number of ancient DNA materials. Nevertheless, the most important finding is that ancient and modern dogs carry the same three major haplogroups A, B and C, confirming a genetic continuity through time. Hence, DNA data in ancient and modern dogs do not support the hypothesis of lineage replacement, that is, ancient European and American dogs having a different genetic makeup (different haplogroups) than modern European/American dogs.

Conclusion
Recent mtDNA studies of modern dog samples indicate a single origin of dogs in southern East Asia, 10000–16000 years ago, and ancient mtDNA studies showing a similar mix of haplogroups A, B and C as modern dogs do not contradict these findings. The mtDNA data also indicate that at least 50 and potentially hundreds of wolves were domesticated. Two other lines of evidence, the archaeological record and the genome-wide SNP data set by von-Holdt et al. (2010), have mostly indicated that either the Middle East and/or Europe might have been geographical regions of dog origins. However, both datasets are geographically biased, having no or only a few samples from southern East Asia. Therefore, if the dog origin is in southern East Asia, this would have gone undetected by these studies.

Although the details of the earliest dog domestication history are not yet completely clear, recent studies have established a plausible scenario. Further studies of geographically comprehensive modern sample collections as well as key archaeological specimens, using additional genetic markers, for example Y-chromosome sequence and autosomal SNPs, promises a precise picture of how the domestic dog originated and subsequently spread around the world. See also: Ancient DNA: Phylogenetic Applications; Ancient DNA: Recovery and Analysis; Chromosome Y; History of Scientific Agriculture: Animals; Microsatellite Instability; Microsatellites; Mitochondrial DNA Polymorphisms; Mitochondrial Genome; Single Nucleotide Polymorphism (SNP); Y Chromosome

References


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Further Reading


