

Population Genetics

The dog that came in from the cold

GM Acland and EA Ostrander

Heredity (2003) 90, 201–202. doi:10.1038/sj.hdy.6800224

‘Wild Dog crawled into the Cave and laid his head on the Woman’s lap...And the Woman said, “His name is not Wild Dog any more, but the First Friend,” Rudyard Kipling *‘Just So Stories’*.

The dog, beloved as humankind’s most faithful companion, descends from the wild gray wolf, but how this happened has been a matter of conjecture, controversy and confusion. Two recent publications in *Science* move our understanding forward from *‘Just So Stories’* to address key questions in the field. With their studies of dog mitochondrial DNA, Savolainen *et al* (2002) and Leonard *et al* (2002) effectively address how and when dogs and wolves diverged.

Savolainen and colleagues looked at sequence variations within 582 base pairs (bp) of mtDNA in 654 domestic dogs worldwide. Over 95% of the sequences clustered into one of three clades, A, B and C, found throughout Eurasia at similar frequencies. They conclude that dog populations represent a single gene pool, and argue for a simultaneous origin in East Asia about 15 000 years ago for clades A and B, and possibly clade C. They also suggest that while clades B and C derive from a single wolf female line, clade A appears to have originated from several wolf haplotypes.

Leonard and her co-workers examined 452 bp of mtDNA from 37 dogs deposited in precolumbian archeologi-

cal sites in Mexico, Peru, and Bolivia, and from Alaskan dogs buried before Europeans arrived. These data were compared to sequences from 67 diverse modern dog breeds, and from wolves from 30 locations worldwide. The authors conclude that about five major founding lineages came to North America when humans colonized the New World 12 000–14 000 years ago, and that ancient American and Eurasian domestic dogs share a common origin from Old World Grey Wolves (Figure 1). They argue further that the large diversity of mtDNA lineages observed in dogs colonizing the New World implies a large, well-mixed ancestral population of Eurasian dogs.

Together these studies extend and confirm prior data, establishing that the divergence of dogs from wolves stems from at least five different maternal wolf lineages. ‘At least’ is an important caveat as there may have been many more female wolf founders than is apparent from the mitochondrial data. Maternal lineages halt whenever a generation produces only sons, and are thus sensitive to both population bottlenecks and selective breeding that



Figure 1 The American Grey Wolf (*Canis lupus lupus*). This animal differs significantly in appearance from the smaller, shortcoated, middle eastern and Asian wolves (*C. l. pallipes*, *C. l. arabs*, *C. l. chanco*) that probably represent more closely the type of wolf contributing to dog ancestry.

emphasizes the contribution of males versus females.

The calculated date of dog/wolf divergence depends on a choice of assumptions and analytic methods, with estimates ranging from as long ago as 40–100 000 years to as recently as 12–15 000 years. A key issue is whether some clades represent different founders, or radiation from a single founder. This divergence date corresponds, however, not to the beginning of domestication as it is generally conceived, but to the time that the first wild dogs became adapted to the ecological niche created by humans.

Of course, the mitochondrial view of the dog's female ancestors might suggest a very different story from that yet to be revealed by analyses of the paternally inherited Y chromosome or biparentally inherited autosomes. A high-density SNP map of the canine Y chromosome would provide a powerful resource for better understanding the relationship of modern dog breeds to their wolf ancestors.

Regardless of their reliance on mitochondrial data alone, the proposed dates are well supported by archaeological records. During the last Ice Age wolves were widespread throughout Europe and Asia, and modern humans had arrived in the Levant, Southern Europe, and Western Asia. In this period, 40 000–12 000 years before the present day, there is little or no evidence for cooperation between canids and humans, and essentially no archeological evidence for the presence of dogs (Zeuner, 1963; Olsen, 1985; Clutton-Brock, 1995, 1999). The end of the Ice Age marks the first archeological evidence for close coexistence of canids and humans. Small canid skeletons, variously and controversially identified, occur in association with humans from 6 to 12 000 years before present (ybp) in Europe (Olsen, 1985; Clutton-Brock, 1995, 1999), the Middle East (Olsen, 1985; Clutton-Brock, 1995, 1999), and

China (Olsen, 1985). Whatever their true identity, these canids clearly had sociological significance to humans, as evidenced in some examples by their deliberate coburial with humans (Davis and Valla, 1978). The first indisputable evidence of the modern dog appears in the Late Neolithic period in China (Olsen, 1985), about 5000 ybp, associated with the commencement of rice agronomy, and in the wide range of distinct dog types recognized in Babylonian, Assyrian, and Egyptian records (Zeuner, 1963) from 2500 to 4500 ybp.

But how did the gene pool of ancient wolves lead to the phenotypic diversity of modern dog breeds? Some of the variation in traits such as body size and proportion might represent adaptations to specific environments and food resources. Less obvious is the basis for the extreme variation, exemplified by comparison of a chihuahua and mastiff, or a bulldog and saluki. Similarly, the range of characteristic behavioral traits associated with different dog breeds is hardly predictable from those of their wolf ancestors. Each of these traits must have been inherent in the wolf gene pool; understanding how they emerged in the dog remains a great and fascinating challenge.

The recent announcement by the National Advisory Council for Human Genome Research, that sequencing the canine genome has been given high priority (<http://www.nih.gov/news/pr/sep2002/nhgri-12.htm>), assures the resources needed to dissect the genetic basis of simple and complex canine traits. The integration of meiotic linkage, RH and comparative maps of the dog genome has provided tools for navigating dog chromosomes and exploiting comparative data from human and mouse genomes (Breen *et al*, 2001). The emerging canine BAC and EST maps provide further support for mapping and positional cloning efforts.

Still to be considered is how dense the SNP map of the dog genome should be,

and which breeds such a map should encompass. The Canine Genome White Paper submitted by the Whitehead Center for Genome Research and the Canine Genomics Scientific community proposes, in addition to a 6 × dog sequence, that one million sequence reads be devoted to the analysis of genomic diversity across 10 major dog breeds. The selection of those breeds will be the key for determining what phenotypic and behavioral traits will be initially accessible for mapping studies. As canine genomic sequence becomes available, it will enhance our ability to track the steps that transformed the wild wolf into the diverse species that is now man's favored companion, and hold up a new mirror to the simultaneous evolution of the dog's companion, *Homo sapiens*.

'This, O Beloved of mine, ends the first part of the tale!'

Rudyard Kipling 'Just So Stories' ■

Elaine A Ostrander is at the Divisions of Human Biology and Clinical Research, Fred Hutchinson Cancer Research Center, D4-100 Seattle, WA 98109-1024, USA.

e-mails: gma2@cornell.edu and eostrand@fhcrc.org

GM Acland is at the Center for Canine Genetics and Reproduction, James A Baker Institute for Animal Health, College of Veterinary Medicine, Cornell University, Ithaca, NY, 14853 USA.

Savolainen P, Zhang YP, Luo J, Lundeberg J, Leitner T (2002). *Science* **298**: 1610–1613.

Leonard JA, Wayne RK, Wheeler J, Valadez R, Guillen S, Vila C (2002). *Science* **298**: 1613–1616.

Clutton-Brock J (1995). Origins of the dog: domestication and early history. In: Serpell J (ed) *The Domestic Dog its Evolution, Behaviour and Interactions with people*, Cambridge University Press: Cambridge, pp 7–20.

Clutton-Brock J (1999). *A Natural History of Domesticated Mammals*. Cambridge University Press: Cambridge.

Olsen SJ (1985). *Origins of the Domestic Dog*. University of Arizona Press: Tucson, Arizona.

Zeuner FE (1963). *A History of Domesticated Animals*. Harper & Row: New York.

Davis SJM, Valla FR (1978). *Nature* **276**: 608–610.

Breen M, Jouquand S, Renier C, Mellersh CS, Hitte C, Holmes NG *et al* (2001). *Genome Res* **11**: 1784–1795.