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- Letters

Man and His Dog

The contention of Carles Vilà *et al.* (Reports, [13 June, p. 1687](#)) that analysis of mitochondrial DNA (mtDNA) shows divergence of the domestic dog (*Canis lupus familiaris*) from the wolf (*C. lupus*) more than 100,000 years ago is not supported by the fossil record ([1](#)). In addition, basing the dog's molecular clock on substitution rates of wolves and coyotes may be inappropriate. As the report's senior author Robert Wayne notes in Virginia Morell's Research News article ([13 June, p. 1687](#)), mtDNA sequences have notoriously high and uneven rates of change. Moreover, the rate of evolutionary change in wolves and coyotes may have varied substantially from that of dogs because of differing selective pressures and generational turnover. Initial effects of domestication include physiological as well as morphological changes (2, 3). Wolves and coyotes mature later than do dogs and usually enter estrus only once a year. Dogs normally have larger litters, commonly reproduce twice annually, and, through their association with people, have a higher pup survival rate.

Vilà *et al.* also suggest that domestication of the dog was a rare event and required special skill. Belyaev (2) produced similar changes in silver foxes (*Vulpes vulpes*) by selecting and breeding only those individuals showing submissive tendencies toward humans. He brought about these changes in about 20 fox generations, within his own lifetime, not in 100,000 years. The foxes exhibited modified reproduction (with two annual estrous cycles), barking behavior, drooping ears, and altered coloration. The process involved destabilization of the endocrine system and was accomplished through selective breeding for docility.

These patterns of change in canids might parallel humanity's own "domestication" through a transition to an agrarian lifestyle. Development of large, permanent, agriculture-based societies probably facilitated both behavioral modifications and extension of reproductive activity. This process, occurring approximately 5000 to 12,000 years ago, was associated with the domestication of a number of mammalian species, of which the dog is thought to have been the first. It is unlikely that dog domestication could have occurred much earlier, because human societies would not then have been capable of keeping dogs separate from wolves and thus maintaining a purportedly different genetic content (reproductive isolation). Separation would have been especially difficult if the two species were then morphologically identical, as suggested by Vilà *et al.* If the data presented by Vilà *et al.* are accurate, however, another interpretation might be that the unique genetic markers of dogs are a carryover from a now-vanished or as-yet-unsampled wolf population. Indeed, wolves and humans were sympatric 100,000 years ago, but these "mitochondrial Lassies" were probably not dogs, but wolves.

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Morell's Research News article commenting on the report by Vilà *et al.* agrees with previous behavioral genetics and archaeological research which indicates that dogs were domesticated from wolves, probably a Middle Eastern middle-sized variety. This social invention proved so useful that it spread to other human populations throughout the world, so that when European explorers in the 18th and 19th centuries finally mapped the world, they found dogs wherever people existed (1).

Some questions remain unanswered. Although Vila *et al.* surveyed 69 breeds, they included only one, the Mexican hairless, from the two American continents. While most of the Amerind dogs have become extinct, some still remain. These breeds could have interbred with the coyote, *C. latrans*.

Also, new dog populations may still be discovered in the Old World, as in the case of the Malaysian Telomian dog discovered by Elliot in 1965 (2). These animals have chromosomes identical with those of European breeds, but little work has been published about their DNA (3).

Current reevaluation of the phylogenetics of another group, namely humans, indicates that mtDNA does not constitute the exclusive key to understanding the ancestry of the hominids; it plays instead a role complementary to that of paleontology (4). Part of the difficulty in drawing conclusions from the DNA research may arise from a lack of discernment between gene genealogies and individual genealogies (5).

In addition, recent suggestions by Van Berkorn (6) indicate that mtDNA findings may be affected as much by population dynamics involving infectious diseases (through Wright's bottleneck effect) as by evolutionary branching.

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Response: Federoff and Nowak raise four main points. First, they point out that an ancient origin of the domesticated dog (about 135,000 years ago) is not supported by the fossil record. This was, of course, the point of our report: We believe that the fossil record may never support an ancient origin of the dog because the original domesticated dog (on the basis of genetic criteria) may have had the morphology of a wolf.

Second, they suggest that the molecular clock assumption may be inappropriate. Unlike many researchers who invoke a molecular clock, we actually tested this assumption and found it to be valid, that is, the region of mtDNA sequenced from dogs, wolves, and coyotes evolves at equal rates of substitution [see note (19) in our report]. Further, it is not obvious how differences in the estrous cycle would cause differences in the rates of evolution in the control region of the mitochondrial genome.

Third, Federoff and Nowak argue that we overstated our contention that domestication was a rare event that required special skill. They support this by citing a reference to a study selecting for different behavior over 20 generations in foxes. Our contention that this was a rare event was not based on the ability to enforce a selective breeding program, but on the data showing that only a few clades of dogs evolved from wolves. If domestication were a common event, dog and wolf haplotypes would be mixed to a much greater extent than they are. The vast majority of dog haplotypes are found in a single clade, which indicates that domestication was a rare event.

Last, Federoff and Nowak argue that early hunter-gatherer societies were not “capable” of keeping dogs separate from wolves. However, recent hunter-gatherer societies (for example, Plains Indian and Eskimos) managed to keep their dogs distinct from wolves, and today, where feral dogs and wolves overlap, interbreeding has had little impact on the gene pools of the wild or domestic populations (1). Moreover, all species in the genus *Canis* can interbreed, but they rarely do so when their ranges overlap. There are potentially many ecological and behavioral reasons why dogs and wolves would not interbreed that do not require active interference by humans.

J. P. Scott *et al.* raise four issues of varying relevance to our conclusions. First, they suggest that DNA could be analyzed from additional Native American dog breeds that possibly could have hybridized with coyotes, and second, that DNA of the ancient Malaysian Telomian dog discovered by the authors should be analyzed. We would be interested in analyzing DNA from both dog types, but do not see (nor is it explained) how such analysis would challenge our results.

We agree with the third point that mtDNA should complement paleontological studies. In fact, with regard to dog domestication, the genetic and archaeological data might reveal complementary information. The genetic data provide information concerning the date that dogs were first genetically isolated from wolves, whereas the archaeological remains document when dogs first changed dramatically in morphology. This morphological change, beginning about 14,000 years ago, may in turn reflect a greater diversity of functions that dogs fulfilled with the transition to an agrarian lifestyle.

Finally, we agree that gene trees may not exactly correspond with species or population trees. However, the unexpected result in our study is that the majority of dog sequences coalesce to a

single common ancestor far removed from any sequences in living gray wolf populations. Consequently, paraphyletic or polyphyletic relationships of DNA sequences do not bias origination times. Moreover, to estimate origination times, we conservatively use sequence divergence values within the monophyletic dog clade rather than divergence values between that clade and wolves.

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