

# Center for Academic Research & Training in Anthropogeny (CARTA) Domestication and Human Evolution

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Chairs:

*Terrence Deacon,* UC Berkeley *Robert Kluender,* UC San Diego This CARTA symposium is made possible by: *The G. Harold and Leila Y. Mathers Charitable Foundation* 

## ABSTRACTS

### The Transformation of Wolf to Dog: History, Traits, and Genetics Robert Wayne, UCLA

The dog may be our most diverse and remarkable living invention. The diversity of dogs in size and proportion exceeds that of the entire carnivore order, including more than 270 species. Functional diversity is also impressive, with specific dog breeds having enhanced sensory, locomotor and cognitive abilities. However, perhaps the most meaningful attribute of dogs is their eagerness to do useful work for humans. These tasks are as varied as their form, including guarding, rescue, warfare, hunting, herding, transport and companionship, mirroring the functions of individuals in human society. Consequently, understanding the historical development of this parallel will enlighten study of human evolution. I present a historical perspective on dog evolution, as probing the context of first domestication is essential to predicting the effect of historical contingency on subsequent evolution. The timing and context of dog domestication is controversial with various analyses supporting China, the Middle East or Europe as centers of origination from gray wolves. Similarly, the timing varies from less than 10.000 to as much as 100.000 years ago. I present data that suggests past analysis are flawed as they make the implicit assumption of origin from an ancestor closely related to modern wolves followed by limited back-crossing. Our results of mitochondrial DNA from ancient wolves and dogs, and recent analysis of complete nuclear genome sequencing, instead suggest an origin from a now extinct form of European wolves more than 20,000 years ago which is followed by persistent interbreeding with wolves. These findings place domestication at a time and place when humans were migratory hunter-gatherers and suggest that a unique domestication scenario applies to the dog, the only large carnivore ever domesticated.

## *Fox Domestication and Genetics of Complex Behaviors* **Anna Kukekova**, University of Illinois at Urbana-Champaign

Domestication as a special form of evolution offers valuable insight into how genomic variation contributes to complex differences in behavioral and morphological phenotypes. The genetics-centered view of domestication is supported by experimental selection of farm-bred foxes (Vulpes vulpes) that began at the Russian Institute of Cytology and Genetics in the 1950s. Selection of foxes, separately, for tame and for aggressive behavior, has yielded two strains with markedly different, genetically determined behavioral phenotypes. Tame-strain foxes communicate with humans in a positive manner and are eager to establish human contact. Foxes from the aggressive strain are aggressive to humans and difficult to handle. Although selected solely for behavior, changes in physiology, morphology, and appearance with significant parallels to characteristics of the domestic dog were observed in tame-strain foxes. These fox strains provide a rich resource for investigating the genetics of complex social behaviors. Although the focus of our work is on the genetics of domestication in the silver fox, there is a broader context. In particular, one expectation of the silver fox research is that it will be synergistic with studies in other species, including humans, to yield a more comprehensive understanding of the molecular mechanisms and evolution of a wider range of social interactive behaviors.

## Craniofacial Feminization in Canine and Human Evolution Robert Franciscus, University of Iowa

Anatomically modern humans are recognized in the fossil record primarily by retraction and diminution of the facial skeleton compared to pre-modern "archaic" humans. Several explanatory models for this facial "gracilization" shift have been proposed, all of which have theoretical or empirical shortcomings. The last 200,000 years of human cultural evolution have also witnessed initially ephemeral occurrences of innovation, planning depth, and abstract and symbolic thought (i.e., "behavioral modernity") which became persistent sometime after 80,000 years ago. A promising model for the advent of facial diminution argues that anatomically modern humans represent a 'self-domesticated' species where selection for increased social tolerance led to growth and developmental alterations producing craniofacial "feminization," which itself results in a phenotypic signal of reduced aggressiveness. A higher level of social tolerance was likely a necessary prerequisite to increased human population densities, and/or extended cooperative social networks among relatively small groups leading

to persistent behavioral modernity. A consideration of key parallel craniofacial changes occurring during both the archaic-to-modern human and wolf-to-dog evolutionary transitions, considered in light of previous experimental work in other animal models (especially domesticated foxes), provides key insights and support for the modern human 'self-domestication' model.

#### *The Domesticated Brain* **Terrence Deacon**, UC Berkeley

The brains of domestic animals tend to share a number of traits in common. Perhaps the most common trait is relative reduction of overall brain size in domestic as compared to wild ancestors, though this is not always present with domestication, and is often complicated by changes in overall body size. Reduction of size is not uniformly represented in all brain structures and tends to disproportionately affect a fairly consistent set of structures. These tend to be telencephalic structures and disproportionately affect olfactory and limbic structures across a diverse group of domesticated mammals. These changes may reflect selection that affects social and sexual behaviors that are maladaptive in domestic conditions and eliminated by selective breeding or are simply no longer of reproductive value and have degenerated due to relaxed selection. The signature pattern of specific brain structure changes can in this way provide evidence to distinguish between these two processes associated with domestication understood broadly.

#### *Neotenous Gene Expression in the Developing Human Brain* **Philipp Khaitovich**, CAS-MPG Partner Institute for Computational Biology

Human evolution has resulted in a species that possesses an apparently unique set of phenotypic capabilities. In our laboratory, we search for molecular features specific to humans, through integrative analysis of genetic, transcriptomic and metabolomic data measured in modern and archaic humans, as well as closely related mammalian species: chimpanzees, macaques and mice. Following this approach, we have identified human-specific delay in timing of neocortical synaptogenesis as one of molecular mechanisms that potentially underlie the evolution of the human phenotype.

## The Domestication Syndrome and Neural Crest Cells: A Unifying Hypothesis Tecumseh Fitch, University of Vienna

Charles Darwin was the first to notice that all of the mammals domesticated by man show an unusual suite of traits not found in their wild forebears. These include changes in pigmentation (e.g. white spots), short snouts, smaller teeth, and floppy ears. My colleagues Adam Wilkins and Richard Wrangham and I have suggested that the origin of this odd collection of phenotypic variants lies in their embryological origins in the neural crest. The neural crest is a transitory embryonic tissue that, early in development, gives rise to a very diverse set of tissues and organs including pigment cells (melanocytes), bones, muscles and connective tissues in the head, and the adrenal gland. By our hypothesis, selection for tameness during early stages of domestication led to delayed maturation and reduced output of the adrenal component of the "fight or flight" response, via reduced neural crest input. This led, as an unselected byproduct, to other neural crest-derived tissues also being reduced, including melanocytes, the bones of the face, the precursors of teeth and cartilages of the ears. Our hypothesis thus accounts, via a unified selective force and single developmental mechanism, for an otherwise puzzling hodge-podge of traits that have been recognized, but gone unexplained, since Darwin.

#### Domestication and Vocal Behavior in Finches Kazuo Okanoya, The University of Tokyo

Bengalese finches (BFs) are a domesticated strain of wild white-rumped munias (WRMs) imported from China to Japan 250 years ago. BF songs are composed of multiple chunks. Each chunk is a combination of 2-4 song notes. Chunks are arranged in a syntactic rule. We studied how and why BFs sing such complex songs. We found the following facts. 1). WRMs sing simpler songs. 2). There is high learning specificity in WRMs but not in BFs. 3). BFs have larger brain structures related with song than WRMs. BFs also have higher level of plasticityrelated gene expressions in the brain than WRMs. 4). Both BF and WRM females prefer complex songs as measured by the degree of reproductive effort they provide. Males with complex songs are more physically fit than males with simpler songs. These results promoted sexual selection scenario of song complexity in BFs: Song complexity evolved because it served as a sexy signal for females.

We further examined factors related with domestication. We examined songs of WRMs in subpopulations of Taiwan. Where there is a sympatric species to WRMs, songs were simpler. This leads to a hypothesis that in the wild, songs needed to be simple to secure species identification, but under domestication, this constraint was set free. We also examined socio-emotional indexes including the corticosterone level, the degree of aggression, and the response to a novel stimulus. All indices suggested that WRMs have higher levels of stress and social shyness, which should be adaptive under natural environment, but could be limiting opportunities for learning

complex songs.

Thus, evolution of song complexity involves not only factors related with sexual selection and species identification, but also socio-emotional factors due to domestication. It is tempting to think about a scenario of language evolution in humans based on sexual selection and self-domestication.

#### *Did Homo sapiens Self-Domesticate?* **Richard Wrangham**, Harvard University

"Self-domestication" here refers to the evolution of a reduced propensity for reactive aggression (compared to an immediate ancestor), without the active involvement of another species. Animal species that have been domesticated by humans all have low reactive aggression and also tend to share a suite of behavioral, physiological and anatomical symptoms (the "Domestication Syndrome"). This suggests that in self-domesticated species, a parallel set of features should be found (the "Self-Domestication Syndrome, SDS"), which I illustrate with evidence for bonobos compared to chimpanzees. In humans, evidence of self-domestication comes from a low propensity for reactive aggression and an anatomy indicative of a SDS. I show that the communal sanctions practiced by hunter-gatherers, which depend on proactive aggression, provide a leading candidate mechanism selecting against high levels of reactive aggression. I therefore propose that human self-domestication is an ironic consequence of a particularly well-developed facility for proactive aggression. I conclude that humans indeed self-domesticated, providing a critical underpinning for inter-individual tolerance and cooperation.