The Origin of the Dog Revisited

Janice Koler-Matznick
5265 Old Stage Road, Central Point, OR 97502 U.S.A.
jkoler@ccountry.com

Abstract

The most widely accepted hypothesis of the origin of the dog, *Canis familiaris*, is that the dog is a domesticated gray wolf, *Canis lupus*. This paper reviews the evidence for this conclusion, finds many unanswered questions and conceptual gaps in the wolf origin hypothesis, and explores the alternative hypothesis that the most likely ancestor of the domestic dog was a medium-size, generalist canid.

Introduction

Currently, there is a general consensus that the sole ancestral species of the domestic dog, *Canis familiaris* L. 1758, is the gray wolf, *Canis lupus* L. 1758 (Coppinger & Smith 1983; Clutton-Brock 1984, 1995; Olsen 1985; Wayne 1986; Tchernov & Horowitz 1991; Morey 1992; Wilson and Reeder 1993; Cohn 1997; Vilà *et al.*1997; Budiansky 1999; Crockford 2000; Coppinger & Coppinger 2001). However, there is at least one competing hypothesis that is equally plausible, yet has not been given adequate evaluation in the published literature. The dog origin alternatives are: (1) an origin from golden jackal (*Canis aureus*) (Lorenz 1954); (2) an origin from hybrids of wild canids (Darwin 1875; Clutton-Brock 1977; Brisbin 1997); or (3) an origin from a wild *Canis* other than jackal or *C. lupus* (Epstein 1971; Zeuner 1963; Fox 1973; Manwell & Baker 1983). Jackal ancestry of the domestic dog (hereafter DD) can be dismissed due to the large genetic distance separating the two (Wayne & O'Brien, 1987; Wayne *et al.*, 1991a). Although a hybrid origin (*e.g.*, *Canis simensis* or *Cuon alpinus* with small subspecies of *C. lupus*), suggested by several authors to account for the sudden shift from wolf to primitive dog morphology, cannot be ruled out, currently no direct evidence supports this hypothesis. In this paper, I review selected behavioral, morphological, molecular, and fossil information relative to the competing hypotheses of wolf origin and wild canid origin. Appendix I provides my working definitions of terms with variable meanings.

Discussion

Behavior

Many hypothesize that the wolf was pre-adapted for domestication as it is one of the rare pack-living canids. Gregarious social structure facilitates domestication because humans manage domesticants through social domination (Clutton-Brock 1981, 1994, 1995; Olsen 1985; Hemmer 1990). However, wolf behavior has significant differences from the behavior of domesticated non-predatory species. Unlike most gregarious non-carnivore species, wolves are able to survive as individuals independent of the group and within the pack have diverse roles (Mech 1970; Sullivan 1978). With careful conditioning using modern methods, wolves can be tamed (Crisler 1958; Klinghammer & Goodman 1985), but not trained to follow commands reliably. Although they respect limits on inter-individual conduct, wolves resist human direction of their activities and

inhibition training (Frank & Frank 1983; Klinghammer & Goodman 1985; Coppinger & Coppinger 2001). This is why there are no wolf acts in circuses. In a stable wolf pack, usually only the dominant pair reproduces. Therefore, wolves have a biological imperative to move up in the hierarchy (Mech 1970), making sexually mature captive wolves dangerous (Fox 1971; Klinghammer & Goodman 1985).

Group social organization is not an invariable pre-requisite to domestication. Hamilton-Smith (1839) reported that South American indigenous people tamed a fox, *Dusicyon culpaeus*, which bred in captivity and was used as a hunting aid. Thus, domestication of a non-pack canid is possible. Another domesticated carnivore, the non-gregarious cat, *Felis sylvestris*, adapts well to group living (Clutton-Brock 1981).

The lack of wolf-like pack forming behavior in DDs is sometimes ascribed to their retention of the behavior of immature wolves before integration into the pack (Coppinger and Schneider 1995). However, many DDs reside amiably in groups, and the response of primitive dogs to group confinement is variable (Scott & Fuller 1965; Corbett 1995; Koler-Matznick, Brisbin & Feinstein 2001). The DD's variable social tolerance and absence of hierarchical pack formation could also be due to natural (niche related) or artificial selection for neotenous behavior compared to a non-pack-forming ancestor, or to selective emphasis on gregariousness within a variable ancestral social repertoire. Monogamous pair social structure with temporary family groups is the most common pattern in canids (Kleiman 1967; Ewer 1973; Kleiman & Brady 1978). Therefore, the lack of long-term hierarchical pack formation in the DD is what would be expected if the ancestors of DDs was not a wolf, but rather a more typical canid.

The statement "Man domesticated the wolf," implying human proactive effort, appears in most speculations about DD origin. Vilà *et al*. (1997) conclude that the DD may have originated from tamed wolves 135,000 YBP, when *Homo sapiens* was a young species (Wolpoff & Caspari 1996). This hypothesis has conceptual gaps. The question of how humans created a domesticated wolf between 15,000 YBP, the oldest estimate from the fossil record for DD (Clutton-Brock 1995), and 135,000 YBP, the highest estimate for separation of DD/wolf from mtDNA (Vilà *et al.* 1997), is rarely addressed.

Further, the reasons for wolf domestication need to be analyzed in the context of human cultural evolution. The value of domesticating such an animal is generally assumed to be to assist with large game hunting or to act as guards (*e.g*., Clutton-Brock 1977, 1995; Olsen 1985; Wayne 1986; Cohn 1997). Wolves hunt large prey cooperatively, thus some propose wolves easily adapt to hunting as human partners (Olsen 1985; Clutton-Brock 1999). The time of separation of DD and wolf is estimated to be between 76,799 YBP to 135,000 YBP from mtDNA (Okumura *et a*l. 1996; Vilà *et al.*1997). At that time, humans had only clubs, axes, spears and knives (Gowlett 1993). With these tools, stealth and ambush are used to secure large prey. Wolves are extremely difficult to condition to reliably inhibit inherent behavior (Fox 1973; Frank & Frank 1983, 1987). They instinctively chase large prey, and thus would hinder humans hunting cursorial game, rather than assist. Wolves are also extremely food-possessive (Klinghammer & Goodman 1985; Goodman & Klinghammer 1990; Koler-Matznick personal observation). If hungry tamed wolves did secure prey, humans would have to fight them for it.

Dingoes provide a modern example of tamed wild canids as hunting aids (Hayden 1975). The Aboriginies used dingoes to locate small prey that goes to ground or trees, but

prevented dingoes from following when hunting kangaroos because the dingoes chased them off (Meggitt 1965). If tamed wild canids are not useful aids for hunting cursorial game and smaller canids are as proficient at locating smaller prey, there is no reason to keep large wolves in domestication.

Humans could be easily kleptoparasitic on small to medium-sized proto-dogs that hunted independently of humans. Indian pariah dogs occasionally hunt deer. Humans encourage this. Pariah dogs (11 – 16 kg) usually range only near villages, so their prey is readily confiscated (Fox 1984; Corbet & Hill 1992). Smaller prey brought back by pariah dog dams for their pups may also be confiscated (Bulmer 1976). Modern humans have sometimes followed the inoffensive Indian dhole (*Cuon alpinus*) (10 – 20kg), a pack hunter, to appropriate its kills (Stewart 1993). Confiscating prey from wolves would be more risky.

The assumption that tamed wolves would be effective guards is not supported by behavioral studies. All wild canids, including dingoes and NGSDs, make poor guards (Manwell & Baker 1984; Koler-Matznick personal observation). They will not physically defend even their own offspring if their personal survival is threatened. Wolf alerting behaviors would notify humans danger was in the area, but alerting behavior is performed equally well by smaller canids such as aboriginal dogs (Coe 1994) and NGSDs (Koler-Matznick personal observation).

Knowledge of innate modern wolf behavior indicates that early humans would have been wolf prey. In contemporary India, wolves prey upon children (Mech 1996; Kumar 2001). Before the development of long-range weapons and persecution by agricultural/pastoral peoples, wolves would have been bolder. Fearless wolves that associate man with food may injure humans (Mech 1998). For their safety, pre-modern humans would have instilled wolves with fear. However, prior to the domestication of livestock, the presence of non-threatening jackal-size canid scavengers could have safely been tolerated. If the DD ancestor was a small canid frequently encountered waiting for scraps at kill sites, through familiarity they may also have been permitted around camps for cleanup duty.

Wolves require substantial amounts of high-protein food and have extended adolescent periods of up to two years during which they must be supported while learning to hunt large game cooperatively (Crisler 1958; Mech 1970). The smaller, more precocious canids, such as dingoes, are independent before one year (Ginsberg & Macdonald 1990). Dingoes commensal with Aboriginal hunter-gatherer groups are fed scraps, otherwise fending for themselves in the game-depleted areas around camps. Meggitt (1965) notes that tame dingoes could be distinguished from wild specimens due to their poor condition. Wolves in similar circumstances would be more nutritionally compromised. Even if they could eventually train wolves to hunt large prey in accord with human techniques, it is unlikely that pre-modern humans would provide the substantial amount of care-taking needed to support wolves through maturation.

The earliest proto-DD/human association was without doubt voluntary. Individually tamed wild "pets" kept within the species' natural environment, if not confined, at maturity usually join their wild conspecifics. Early Holocene humans had no means of keeping canids confined. Many authors answer the question "Why did wolves choose to become commensal?" by hypothesizing that wolves were attracted by camp refuse (*e.g.,* Coppinger & Smith 1983; Tchernov & Horowitz 1991; Budiansky 1999;

Crockford 2000; Coppinger & Coppinger 2001). That hypothesis is unconvincing, especially before 12,000 YBP, the date usually proposed for the founding of permanent settlements. Depending upon the area, season and the size of the group, nomadic hunter-gatherers may use almost all the nutritious portions of any carcass (Blumenschine & Marean 1993; Jones 1993; Oliver 1993), so camps frequently generate little nutritious refuse that would support wolves (Brain 1967; Davis 1987; Jones 1993). While wolves are opportunistic scavengers (Brisbin 1977; Boitani 1983), there would not have been enough nutrition available at campsites to support a breeding population of wolves on its way to domestication. Given the paucity of dependable, nutritious waste, without a compelling reason (*e.g.* local prey base crash) it would be highly unusual for a large predator to make a niche shift to refuse-scavenger. No such compelling reason has been offered.

Failure to investigate primitive dogs has resulted in spurious reasoning from modern, highly derived DDs. The wolf, largest of the living canids, becomes annually reproductive at two years (Ginsberg & Macdonald 1990). Most modern DDs become sexually mature before one year of age and average two reproductive cycles yearly. The wolf-to-dog hypothesis assumes that, in the pariah niche, faster sexual maturity and increased fecundity were strongly favored, so wolves rapidly became smaller with bi-annual reproductive cycles not entrained to the environment (Clutton-Brock 1995; Coppinger & Coppinger 2001). However, ancient pariah and primitive dogs have annual reproductive cycles entrained to the environment (Coe 1994; Corbett 1995; Pal, Gosh & Roy 1998; Koler-Matznick, Brisbin & MacIntyre 2000), and, like similar-sized wild canids, come into first estrus at about one year old (Ginsberg & Macdonald 1990).

The specialized wolf is an unlikely candidate for the behavioral flexibility required to adapt to the pariah niche. Most wild animals that have adapted to anthropocentric environments are generalists: *e.g.,* raccoon (*Procyon lotor*); opossum (*Didelphis virginianus*); rat (*Rattus norvegicus*, *Rattus rattus*); and mouse (*Mus domesticus*, *Mus musculus*). Wolves have never been reported as voluntary commensals, whereas generalist canids, including coyote and red fox (*Vulpes vulpes*) readily reproduce in metropolitan areas (Gier 1975; Kleiman & Brady 1978) and golden jackals scavenging around human settlements can become a nuisance and subject to eradication (Harrison & Bates 1991).

Morphology

Primitive dogs have typical *Canis* conformation (Fig. 1). Dog characters that differ from wolves are generally attributed to artificial selection, but these analyses typically begin with the assumption dogs are descended from wolves. Most authors conclude that, compared to wolves, adult DDs have relatively reduced rostrums, elevated frontals, wider palates, broader craniums, and smaller teeth (Hildebrand1954; Clutton-Brock, Corbet & Hills 1976; Olsen 1985; Wayne 1986; Hemmer 1990; Morey 1990). Others point out that these traits vary, with overlap between and variation within the two species (Crockford 1999; Harrison 1973). Because wolf cubs have similar relative skull proportions as DDs (Wayne 1986), this is considered evidence that the DD is a neotenic wolf due to conscious or unconscious artificial selection for juvenile appearance, or to a pleiotropic effect of selection for juvenile behavior (Clutton-Brock 1977; Belyaev 1979; Wayne 1986; Coppinger and Schneider 1995). Body size reduction from wolf to early

Figure 1. A young male New Guinea singing dog from the North American captive population illustrates typical primitive dog morphology. Photo credit: Photosynthesis Studio.

DDs is attributed to niche selection (*e.g*. Olsen 1985; Morey 1992;Coppinger & Coppinger 2001). For example, Morey (1992:199) says: "Results [of a comparison of morphology of early DDs to morphological change in *C. lupus* during ontogeny]…are consistent with a hypothesis that early domestic dogs are evolutionary paedomorphs, products of strong selection for ontogenetically channeled size reduction and alterations of reproductive timing associated with the new domestic way of life."

Wayne (1986) compares DD skull morphology to wild canid species and concludes that the DD is closer in skull morphology to the other canids in his study (*Canis latrans*, *Canis aureus*, *Canis adustus*, *Canis mesomelas*, *Cuon alpinus*, *Lycaon pictus*), than to the wolf. Unlike previous authors (*e.g*., Stockhaus 1965), Wayne (1986) also concludes that his DD samples did not have significant relative shortening of the rostrum compared to wolves. The previously reported reduced rostrum length of DD's, assumed to be a secondary effect of captivity or of neoteny (Stockhaus 1965; Olsen 1985; Clutton-Brock 1984), is thus called into question.

Although no discussion of a functional reason for the dog's elevated frontals was located, Endo *et al*. (1997) show that the Japanese wolf (*Canis hodophilax*), with typical low frontals, had sinuses less developed in the dorso-ventral direction compared to the

Akita dog, which had elevated frontals. Endo *et al*. (1997) suggest that the smaller frontal sinus may have an influence on respiratory function.

Dahr (1942) concludes that the shape of the DD brain case is closer to the coyote than the wolf, and most closely resembles the coyote when the DD is between jackal and wolf size. Manwell and Baker (1983) review Dahr's findings and additional dental data for DDs, wolves, and jackals, and conclude that the DD most closely approaches wild *Canis* parameters at body sizes below that of any living subspecies of wolf. They hypothesize the DD ancestor was probably within the range of 13.6 – 20.5 kg. This is about the size of dingoes and considerably smaller than the 27 - 54 kg given for living wolves (Mech 1970).

Dog dentition is relatively less robust than the wolf's (Olsen 1985; Hemmer 1990). This is attributed to relaxation of selection when wolves became commensal scavengers or to artificial selection (Olsen 1985; Clutton-Brock 1995). Kieser and Groeneveld (1992) compared the mandibulodental measurements of jackals (*Canis adustus*, *C. mesomelas*) and Cape foxes (*Vulpes chama*) to equivalently-sized DDs. They found that the canines of the other canids tended to be slightly smaller and their second molars larger compared to DDs. Otherwise, the proportions were essentially the same in all species. They conclude: "...the teeth of canids appear to have evolved in concert with one another and relatively independently of differences in dimorphism, size or functional demands" (*ibid,* p. 423). If correct, this calls into question the assumption that dog teeth are relatively small due to recent selection, suggesting the possibility that dog dentition is plesiomorphic from a progenitor smaller than the wolf.

Some diagnostic dog characters have no evident connection to paedomorphism. Of these, two are mandibular. The dog's coronoid apex has a posteriorly directed curve not present in wolves, except some *C. l. chanco* and *C. l. pallipes* (Olsen 1985; Hemmer 1990). The presence of this character in *C. l. chanco* is cited by Olsen (1985) as evidence that the dog may have descended from this subspecies. Neither Olsen (1985) nor Hemmer (1990) mention possible dog introgression as a source of this variation. The ventral edge of the dog horizontal ramus has a convex curve not present in *C. lupus* (Olsen 1985; Clutton-Brock 1995). No discussion of possible significance of the difference in the dog mandible shape was found in the literature. However, Biknevicius and Van Valkenburgh (1997) note that the horizontal ramus of bone-processing predators is thicker dorso-ventrally at the point caudal to the site of bone processing. Perhaps this thickening of the dog ramus was a functional niche adaptation in the dog ancestor.

The bullae of DDs are relatively smaller and flatter than those of wolves (Harrison 1973; Clutton-Brock, Corbet & Hill 1976; Nowak 1979; Olsen 1985; Wayne 1986), a difference attributed to relaxed selection under domestication. Presumably, the bullae became smaller because DDs did not need the wolf's acute hearing. Bullae function as air chambers behind the tympanic membrane, damping the chain of auditory ossicles. According to Ewer (1973), bulla shapes facilitate increased resonance effects and sensitivity to specific frequencies. Differently constructed bullae are sensitive to different frequencies, but shape and size may not be correlated with general acuity. No references to studies of comparative auditory acuity of wild *Canis* species and DDs were located. Those carnivores with highly inflated bullae are predators that need to hear high frequency sounds, whereas the bullae of largely nonpredaceous omnivores, such as bears (Ursidae), are relatively small (Ewer 1973). Without evidence of selective forces

directing change from wolf to dog conformation, the parsimonious explanation for the observed differences is that the bullae retain ancestral shape.

There are additional characters separating DDs and wolves that are rarely mentioned in the literature. Atkins and Dillon (1971) describe the superficial brain morphology of jackals (*C. mesomelas*, *C. aureus*), coyotes, wolves (*C. lupus*, *C. rufus*), and DDs. They conclude that the cerebellum of the DD most closely approximates the coyote, which is closely allied with the jackals, and that wolves show numerous brain traits distinct from the other species. Wolves also have serological and biochemical traits distinct from DDs (Leone and Wiens 1956; Lauer, Kuyt & Baker 1969).

A trend toward neoteny, if indeed that is present in the dog, is a recognized mode of adaptive evolution (Gould 1977). There is no reason to attribute neotenic traits to artificial selection. The most parsimonious explanation for the different morphological characters of dogs and wolves is that the DD ancestor was adapted to a different niche than the wolf.

Fossils

A problem for the wolf-origin hypothesis is the absence of fossils intermediate between wolves and the small early DDs of 9,000 - 14,000 YBP (Olsen 1985; Benecke 1987). Vilà, *et al.* (1997) explain this by speculating that proto-DDs showed little size change before permanent settlements, an argument incompatible with the hypothesis of strong selection for size reduction when wolves entered the scavenger niche. A few fossil canid skulls have been classified as tamed wolves or wolf-to-dog transitional forms because of their relatively reduced rostrum lengths and large, crowded teeth (Ovodov 1998), characters present in some wolves (Clutton-Brock 1995; Clutton-Brock, Kitchener & Lynch 1994) and possibly attributable to dog introgression.

Pei (1934) and Olsen (1985) describe one possible candidate for the ancestral dog, *Canis lupus variabilis*. Along with *C. l. pallipes*, B. Lawrence (1967) mentions *C. l. variabilis* as a possible dog ancestor. This canid was found at Choukoudian, China, in layers dating 200,000 YBP - 500,000 YBP, associated with *Homo erectus* or *H. sapiens* artifacts, and in the layer predating *Homo* evidence (Kahlke & Chow 1961). Pei (1934) suggests the fossil Chinese canid specimens previously named *Canis chihliensis* (Zdansky 1925; Teilhard de Chardin & Piveteau 1930) should be *C. l. variabilis*. *C. l. variabilis* is also known from Lantian in Saanxi Provence (Hu & Qi 1978), so it had a wide range in time and space. At the time Pei wrote*, C. lupus variabilis* was four times more common than "true" *C. lupus* at Choukoudian. Pei (1934) describes this diminutive "wolf" as exhibiting variation in size and tooth adaptations, stating that it's skull differs from the typical wolf in much smaller size (about 175.0 mm total length for a large *C. l. variabilis* specimen), with a more slender muzzle and weak or absent sagittal crests. In addition, the lower border of some *C. variabilis* mandibles is "…strongly convex as in the dog…" (Pei 1934:15). The one trait aligning *C. l. variabilis* with wolves is relatively large carnassial teeth (P^1 20.4 – 23.0 mm; M_1 22.0 – 24 mm). Pei concludes: (1934:17): "Although no sharp line can be traced between the above described *Canis* and a true *lupus*, the marked differences found in the size, and in the cranial characters, seem to be sufficient for creating, at least, a new variety, *Canis lupus variabilis*, for the Choukoudian . . . small wolf."

The conspecific status of *C. l. variabilis*, a presumably extinct but diagnostically distinct canid sympatric through time and space, with *C. lupus*, is open to question. Pei (1934) states that he adopted a new *C. lupus* sub-specific designation for this Choukoutien canid chiefly for stratigraphical convenience. Olsen's justification for naming this canid *C. lupus* is that he felt the assignment to this category was inadequate, but that it is always better to assign to a general category if there is not enough material to be more specific (S. J. Olsen, personal communication 1996). However, *C. lupus* is a defined species, not a "general category." Additional *C. l. variabilis* finds were made after Pei's publication where they were designated as "common." So, they remained distinct from sympatric *C. lupus* for tens of thousands of years over a large geographic range (Olsen 1985). Designation of *C. l. variabilis* as simply *Canis variabilis*, or retention of the earlier *C. chihliensis* designation, may have significantly altered inference concerning the origin of the dog.

Some authors comment on the resemblance of the oldest European DD finds to the dingo (*e.g*., Dahr 1942; Degerbøl 1961). Higham, Kijngam & Manly (1980) examined dog skulls from Ban Chiang, Thailand, and determined that those dated 3,900 YBP are nearly identical to the living dingo-like pariah dogs of the area. Australian dingo skulls from about 3, 900 YBP are also essentially identical to modern dingo skulls (Gollan 1982). Although he offers no evidence, Corbett (1995) hypothesizes that several races of ancient dingo-like pariah dogs are domesticated dingoes. Today, these ancinet pariahs are being genetically mixed with, and in some areas swamped by, imported European and Asian DDs (Meggitt 1958; Titcomb 1969; Corbett 1995). But the dingo morphotype apparently was very widespread before recent artificial selection for variable DD morphotypes. It is also the morphotype that predominates in long-term free-ranging, free-breeding modern DD populations after many generations (Brisbin 1977, 1997). Such populations never assume wolf morphology.

Molecular Evidence

According to Wayne, Van Valkenburgh and O'Brien (1991), Nei's genetic distance between dog and wolf, based on one-dimensional allozyme electrophoresis, is 0.042. This is slightly greater than the 0.030 reported for leopard (*Panthera pardus*) and jaguar (*Panthera onca*). Nei's genetic distances among bear species from single-copy DNA hybridization are slightly lower than the dog and wolf's (Wayne,Van Valkenburgh & O'Brien 1991), yet they have not been declared the same species because of the relatively small genetic/molecular distance.

The available mtDNA evidence is interpreted as indicating that the dog and wolf could have separated about 76,000 to 135,000 YBP (Tsuda *et a*l.1997; Vilà *et al*. 1997). Vilà *et al*. (1997) found only one mtDNA haplotype shared by wolves and DDs, 25 types specific to dogs and 26 to wolves. Six of the unique dog types inter-grade with wolf types on relatedness diagrams (Vilà, *et al*. 1997). Tsuda *et al*. (1997) also found that dog haplotypes, while different, inter-graded with wolves in a neighbor-joining analysis. From this statistically close relationship of mtDNA types, both Vilà *et al*. (1997) and Tsuda *et al*. (1997) conclude that the wolf is the DD's ancestor. However, in Vilà *et al*. (1997) 19 dog types (including primitive dogs') grouped together separately from wolves, indicating they are monophyletic. The maximum within-dog divergence given is 12 substitutions, the divergence between wolves/dogs as 12 substitutions and between dogs

and coyote/jackal as 20 substitutions and two insertions. Thus, in mtDNA, dogs are more distantly related to jackals/coyotes than to wolves. The mtDNA of *C. l. pallipes* and *C. l. arabs*, the wolves closest to primitive dog size and morphology so often proposed as the DD ancestor (*e.g*., Gollan 1982; Corbett 1995), are no closer to DD types than *other C. lupus* (Vilà *et al*. 1997). No study found compared dog mtDNA to *Canis simensis* or *Cuon alpinus*.

The mtDNA studies cited above conclude that the DD is a wolf without addressing the inherent limitations and assumptions of such studies. MtDNA is essentially a single locus marker, inherited in a clonal fashion, and is only effective at estimating maternal lineage relationships. The inclusion of nuclear DNA in analyses would be more meaningful and might lend clarity to the heterogeneity observed in the mtDNA phylogenetic trees. Cronin (1993: 343) shows that a relatedness tree based on mtDNA sequence divergence may not be the same as a phylogenetic tree, because recently differentiated groups will often share a considerable amount of incompletely sorted genetic characteristics. Incomplete lineage sorting is common among closely related species with a recent common ancestor. Wayne and Ostrander (1999) emphasize that, while molecular genetic data seem to support the origin of dogs from wolves, dogs may have descended from a now extinct species of canid whose closest living relative was the wolf.

Due to descent from a common ancestor, several species have populations with mtDNA closer in sequence to another species than to conspecific populations (Carr *et al*. 1986; Cronin, Vyse & Cameron 1988; Avise, Ankey & Nelson 1990; Cronin *et al.* 1991). There are also examples of introgressions of mtDNA between species, which could be misinterpreted as evidence of conspecific status if analyzed without regard to other diagnostic characteristics (Avise 1986; Cronin 1993).

Wolves and DDs have been sympatric for thousands to tens of thousands of years, yet only one mtDNA type is shared. Although occasional hybridization may have taken place in some areas, panmixia has not occurred despite the fact that until the last few hundred years most dogs free-ranged, breeding at will (Clutton-Brock 1981; Boitani 1983; Boitani *et al*. 1995; Nowak 1995; Randi & Lucchini 2002). For example, Indian pariah dogs are about the same size as the Indian wolf (*C. l. pallipes*), one of the candidates for the dog's "ancestral wolf" (Olsen 1985; Hemmer 1990; Corbett 1995), their estrus seasons coincide, the wolf population today is small and fragmented, yet they are not known to hybridize (Oppenheimer & Oppenheimer 1975; Shahi 1983; Pal, Gosh & Roy 1998). If dogs and- wolves did not have relatively effective behavioral barriers to interbreeding, they would share most if not all of their mtDNA types. Therefore, the dog and wolf seem to meet the criteria of the Biological Species Concept (O'Brien and Mayr 1991).

The shared or very similar mtDNA types are not necessarily of wolf origin. Crockford (2000) hypothesizes that the similarity of dog/wolf mtDNA could be due to genetic introgression of dog into the wolf population. Koop *et al*. (2000) found some pre-contact Northwest American aboriginal dogs had mtDNA types closer to North American wolves than to other DDs, concluding that these DDs may have originated from local wolves. Crockford (2000) instead hypothesizes that perhaps these mtDNA haplotypes are similar due to essentially rare unidirectional feral female dog to male wolf hybridization occurring for so long that extant wolf populations have dog mtDNA.

Contemporary wild wolf/dog hybrids have been collected in Alaska (B. Yates, personal communication 2001), Vancouver Island, B.C., Canada (Koop *et al*. 2000), Italy (Randi & Lucchini 2002) and are known from the archaeological record (Walker & Frison 1982). Vilà and Wayne (1999) suggest that, because of reproductive timing differences, the direction of wolf/dog hybridization was probably female wolves to male dogs (implying the shared mtDNA types are wolf). They overlook reports that show male wolves do breed with female dogs (Gottelli *et al*. 1994) and coyotes (Wayne *et al*. 1991), and the offspring incorporated into the wolf population. Given the unpredictable behavior of wolf hybrids and the difficulty of keeping F1 hybrids confined (Gloyd 1992; Hope 1994; Marx 1994; Steinhart 1995) it is unlikely that prehistorically and in the recent past, hybrids would have successfully integrated into the DD population. Crockford (2000) points out that the genetic integrity of specimens used to represent wolves in most DNA studies are not clearly defined, and concludes that the use of contemporary wolves, or those from archaeological contexts, in comparative studies of mtDNA with DDs may be misleading due to the possibility of long-standing introgressive hybridization with dogs.

Conclusion

Manwell and Baker (1983) suggest that research on the origin of the dog had been constrained by "disciplinary dogmatism": the strong, authoritative and oft-repeated assertion that humans domesticated the dog from a gray wolf. They (1983:221) conclude that although they cannot rule out a wolf origin, the most likely hypothesis is "…the currently unpopular idea of the origin of the dog from a wild *Canis familiaris*." Since 1983, dogmatism about the origin of the DD has only increased, to the point that Wilson & Reeder (1993) felt confident [accepting Wozencraft's] renaming *C. familiaris* as *C. lupus familiaris* without discussion.

The morphological and molecular evidence discussed here, combined with a consideration of plausible human and canid behavior, suggests that the hypothesis that humans created the dog by purposefully domesticating the wolf is unlikely. The hypothesis that wolves were voluntary commensals, and that wolf morphology rapidly changed after adopting a pariah scavenger niche, is not supported by any evidence. Dogs have several diagnostic morphological characters that are possibly plesiomorphic and not by-products of artificial selection. The wolf and dog seem to be clearly separated but closely related, universally sympatric species with effective reproductive isolation. Thus, the current fashion of placing *C. familiaris* in synonymy with *C. lupus* is not supported.

The lack of agreed-upon dog fossils from before 15,000 YBP has been used as evidence for the recent origin of the dog from the wolf. However, Olsen (1985) notes there are many small Pleistocene "wolves" in the fossil record of Eurasia that need more careful consideration.

The hypothesis that fits the available evidence most parsimoniously is that the first DDs descended from a species of medium-sized generalist canid, a "wild *C. familiaris*," that voluntarily adopted the pariah niche and remained commensal for an extensive period before some populations became truly domesticated. If the inertia created by the wolf-origin dogma can be overcome, and the problem considered without preconceptions, perhaps investigation of possible functional origins of the morphological differences between dogs and wolves, expanded nuclear DNA studies and re-evaluation

of the canid archaeological and fossil record will answer some of the unresolved questions concerning our most ancient domesticant.

References

Atkins, D. L. and L. S. Dillon, 1971. Evolution of the cerebellum in the genus *Canis*. Journal of Mammalogy 52(1): 96 -107.

Avise, J. C. 1986. Mitochondrial DNA and the evolutionary genetics of higher animals. Philosphical Transactions Royal Society London [Biology] 312: 325 - 342.

Avise, J. C., C. D. Ankey and W. S. Nelson. 1990. Mitochondrial gene trees and the evolutionary relationship of mallard and black ducks. Evolution 44: 109 - 119.

Belyaev, D. K. 1979. Destabilizing selection as a factor in domestication. Journal of Heredity 70: 301 - 308.

Benecke, N. 1987. Studies of early dog remains from northern Europe. Journal of Archaeological Science 14: 31 - 49.

Biknevicius, A. and B. Van Valkenburgh. 1997. Design for killing: craniodental adaptations of predators. In Carnivore behavior, ecology, and evolution. 393 – 428, ed. J. L. Gittleman. Cornell University Press, Ithaca, NY.

Blumenschine, R. J. and C. W. Marean. 1993. A carnivore's view of archaeological bone assemblages. In From Bones to Behavior: ethnoarchaeological and experimental contributions to the interpretation of faunal remains. 273 – 300, ed. J. Hudson. Center for Archaeological Investigations Occasional Paper No. 21. Southern Illinois University, Carbondale.

Boitani, L. 1983. Wolf and dog competition in Italy. Acta Zoologica Fennica 174: 259 - 264.

Boitani, L., F. Francisci, P. Ciucci & G. Andreoli. 1995. Population biology and ecology of feral dogs in central Italy. In The Domestic Dog: its evolution, behaviour and interactions with people. 217 – 244, ed. J. Serpell, Cambridge University Press, Cambridge, UK.

Brain, C. K. 1967. Hottentot food remains and their bearing upon the interpretation of fossil bone assemblages. Scientific papers of the Namib Desert Research Insitutue 32: 1 – 11.

Brisbin, I, L. Jr. 1977. The pariah: Its ecology and importance to the origin, development and study of purebred dogs. Purebred Dogs: American Kennel Gazette 94: 22 - 29.

Brisbin, I. L. Jr. 1997. Primitive dogs, their ecology and behavior: Unique opportunities

to study the early development of the human-canine bond. Journal American Veterinary Medical Association 210(8): 1122-1126.

Budiansky, S. 1999. The covenant of the wild: why animals chose domestication. Yale Univ. Press, New Haven.

Bulmer, R. 1976. Selectivity in hunting and in disposal of animal bone by the Kalam of the New Guinea Highlands. In Problems in economic and social archaeology. 169 – 186. eds. G. de G. Sieveking, I. H. Longworth and K. E. Wilson. Duckworth, London.

Carr, S. M., S. W. Ballinger, J. N. Deer, L. H. Blankenship, and J. W. Bickham. 1986. Mitochondrial DNA analysis of hybridization between sympatric white-tailed deer and mule deer in west Texas. Proceedings National Academy of Sciences 83(9): 576 - 580.

Clutton-Brock, J. 1977. Man-made dogs. Science 197:1340-1342.

Clutton-Brock, J. 1981. Domesticated animals from early times. British Museum (Natural History)/Heinemann, London.

Clutton-Brock, J. 1984. Dog. In Evolution of domestic animals. 198 – 211, ed. I. Mason. Longman, London.

Clutton-Brock, J. 1994. The unnatural world: behavioral aspects of humans and animals in the process of domestication. In Animals and human society: changing perspectives. 23 – 35, eds. A. Manning & J. Serpell. Routledge, London.

Clutton-Brock, J. 1995. Origins of the Dog: domestication and early history. In The domestic dog: its evolution, behaviour and interactions with people. 7 – 20, ed. J. Serpell. Cambridge University Press, NY.

Clutton-Brock, J. 1999. A natural history of domesticated animals. Cambridge University Press, Cambridge.

Clutton-Brock, J., G. B. Corbet and M. Hills. 1976. A review of the family Canidae with a classification by numerical methods. Bulletin British Museum (Natural History) Zoology 29: 117 B 119.

Clutton-Brock, J., A. C. Kitchener & J. M. Lynch. 1994. Changes in the skull morphology of the Arctic wolf, *Canis lupus arctos*, during the twentieth century. Journal of Zoology 233: 19 - 36.

Coe, S. 1994. The basenji, out of Africa to you. Doral Publishers, Wilsonville, Oregon, USA.

Cohn, J. 1997 How wild wolves became domestic dogs. BioScience 47: 725 B728.

Coppinger, R. and L. Coppinger. 2001. Dogs: a startling new understanding of canine origin, behavior and evolution. Scribner, NY.

Coppinger, R. P. and C. K. Smith. 1983. The domestication of evolution. Environmental Conservation 10(4): 283 – 292

Coppinger, R. and R. Schneider. 1995. Evolution of working dogs. In The domestic dog: its evolution, behaviour and interactions with people. 21 –47. ed. J. Serpell. Cambridge University Press, Cambridge, UK.

Corbet, G. B. and J. E. Hill. 1992. The Mammals of the Indomalayan Region: a systematic review. Oxford University Press, Oxford.

Corbett, L. 1995. The dingo in Australia and Asia. Cornell Univ. Press, NY.

Crisler, L. 1958. Arctic wild. Harper and Brothers, New York.

Crockford, S.J. 2000. A commentary on dog evolution: regional variation, breed development and hybridization with wolves. In Dogs through time: an archaeological perspective. 295 – 312, ed. S. J. Crockford. BAR International Series 889. Archaeopress, Oxford.

Cronin, M. A. 1993. Mitochondrial DNA in wildlife taxonomy and conservation biology: cautionary notes. Wildlife Society Bulletin 21: 339 - 448.

Cronin, M. A., E. R. Vyse and D. G. Cameron. 1988. Genetic relationships between mule deer and white-tailed deer in Montana. Journal Wildlife Management 52: 320-328.

Cronin, M. A., S. C. Amstrup, G. Garner and E. R. Vyse. 1991. Intra- and interspecific mitochondrial DNA variation in North American bears (*Ursus*). Canadian Journal of Zoology 69: 2,985 – 2,992.

Dahr, E. 1942. Arkiv for zoologie (Stockholm). 33A: 1 – 56. (Cited in Manwell and Baker 1983.)

Darwin, C. 1875. The variation of animals and plants under domestication. 2nd. ed. Vol. 1. John Murray, London.

Davis, S. J. 1987. The archaeology of animals. Yale University Press, New Haven.

Degerbøl, M. 1961. On a find of a preboreal domestic dog from Starr Carr, Yorkshire, with remarks on other Mesolithic dogs. Proceedings Prehistorical Society 27: 35 - 55.

Endo, H., I. Obara, T. Yoshida, M. Kurohmaru, Y. Hayashi, and N. Suzuki. 1997. Osteometrical and CT examination of the Japanese wolf skull. Journal of Veterinary Medical Science 59(7): 531-538.

Epstein, H. 1971. The origin of the domestic animals of Africa. Vol. 1, Africana Publishing Corp., N.Y.

Ewer, R. F. 1973. The carnivores. Cornell University Press, Ithaca, NY.

Fox, M. W. 1971. Behavior of wolves, dogs and related Canids. Robert E. Krieger Publishing Company, Malabar, Florida, USA.

Fox, M. W. 1973. Origin of the dog and effects of domestication. American Kennel Club Gazette 90(7): 33 -35.

Fox, M. W. 1984. The whistling hunters: field studies of the Asiatic wild dog (*Cuon alpinus*). State University of New York Press, NY.

Frank, F. and M. Frank. 1983. Inhibition training in wolves and dogs. Behavioural Processes 8: 363 B 377.

Frank, F. and M. Frank. 1987. The University of Michigan canine information-processing project (1979-1981). In Man and wolf. 143 – 167, ed. H. Frank. Dr. W. Junk Publishers, Dordrecht, the Netherlands.

Gier, H. T. 1975. Ecology and behavior of the coyote (*Canis latrans*). In The wild canids: their systematics, behavioral ecology and evolution. 247-262, ed. M. Fox. Van Nostrand Reinhold, NY.

Ginsberg, J. R. and D. W. Macdonald. 1990. Foxes, wolves, jackals, and dogs: an action plan for the conservation of canids. IUCN/SSC Canid Specialist Group/Wolf Specialist Group, Oxford.

Gloyd, J. S. 1992. Wolf hybrids: A Biological time bomb? Journal of the American Veterinary Medical Association 210: 381-382.

Gollan, K. 1982. The prehistoric dingo. Ph.D. thesis. Australian National University, Canberra.

Goodman, P. A. and E. Klinghammer. 1990. Wolf ethogram. Ethology Series Number 3, revised. North American Wildlife Park Foundation, Battle Ground, Indiana, USA.

Gottelli, D., C. Sillero-Zubiri, G. D. Applebaum, M.S. Roy, D. J. Girman, J. Garcia-Moreno, E. Ostrander and R. K. Wayne. 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf. Molecular Ecology 3: 301-312.

Gould, S. J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, Massachusetts, USA.

Gowlett, J. A. J. 1993. Ascent to civilization: an archaeology of early humans. 2nd ed. McGraw-Hill, Inc., NY.

Hamilton-Smith, C. 1839. Dogs. Vol. 1. In Naturalists Library. ed. W. Jardine. Lizars, Edinburgh.

Harrison, D. L. 1973. Some comparative features of the skulls of wolves (*Canis lupus* Linn.) and pariah dogs (*Canis familiaris* Linn.) from the Arabian peninsula and neighboring lands. Bonner Zoologische Beiter, Herausgeber, Zooloisches Forschungsintitut und Museum Alexander Koenig, Bonner (24): 185 – 191.

Harrison, D. L. and P. J. J. Bates. 1991. The mammals of Arabia. 2nd ed. Harrison Zoological Museum Publication,

Hayden, B. 1975. Dingoes: pets or producers? Mankind 8: 287 – 295.

Hemmer, H. 1990. Domestication: the decline of environmental appreciation. Cambridge Univ. Press., NY.

Higham, C. F. W., A. Kijngam and B. F. J. Manly. 1980. An analysis of prehistoric canid remains from Thailand. Journal of Archaeological Science 7: 149-165.

Hildebrand, M. 1954. Comparative morphology of the body skeleton in recent canidae. University of California Press, Berkeley.

Hope, J. 1994. Wolves and wolf hybrids as pets are big business - but a bad idea. Smithsonian 25(3): 40 - 43.

Hu, C. & T. Qi. 1978. Gongwangling Pleistocene mammalian fauna of Lantian, Shaanxi. Paleontologia Sinica, Whole Series no. 155, New Series C no. 21, 64 pages. Bejing. (Cited in S. Olsen 1985)

Jones, K. T. 1993. The archaeological structure of a short-term camp. In From bones to behavior: ethnoarchaeological and experimental contributions to the interpretation of faunal remains. 101- 114, ed. J. Hudson. Center for Archaeological Investigations. Occasional Paper No. 21. Southern Illinois University, Carbondale.

Kahlke, H. D. & B.- S. Chow. 1961. A summary of stratigraphical and paleontological observations in the lower layers of Choukoutien, Locality 1 and on the chronological position of the site (in Chinese). Vertebrata PalAsiatica, 3: 212-240. (Cited in Olsen 1985.)

Kieser, J. A. and H. T. Groeneveld. 1992. Comparative morphology of the

mandibulodental complex in wild and domestic canids. Journal of Anatomy 180: 419-424.

Kleiman, D. G. 1967. Some aspects of social behavior in the Canidae. American Zoologist 7: 365 - 372.

Kleiman, D. G. & C. A. Brady. 1978. Coyote behavior in the context of recent canid research: problems and perspectives. In Coyotes: biology, behavior and management 163 – 188, ed. **M.(arc)** Bekoff. Academic Press, NY.

Klinghammer, E. and P. A. Goodman. 1985. The management and socialization of captive wolves (*Canis lupus*) at Wolf Park. North American Wildlife Park Foundation, Battle Ground, Indiana, USA.

Koler-Matznick, J., I. L. Brisbin, Jr. & J. MacIntyre. 2000. The New Guinea singing dog: A living primitive dog. In Dogs through time: an archaeological perspective. 239-247, ed. S. J. Crockford. BAR International Series 889. Archaeopress, Oxford.

Koler-Matznick, J., I. L. Brisbin, Jr. & M. Feinstein. 2001. An ethogram of the New Guinea singing dog (*Canis hallstromi*). New Guinea Singing Dog Conservation Society, Central Point, Oregon, USA.

Koop, B. F., M. Burbidge, A. Byun, U. Rink & S. J. Crockford. 2000. Ancient DNA evidence of a separate origin for North American indigenous dogs. In Dogs through time: an archaeological perspective. 271 – 286, ed. S. J. Crockford. BAR International Series 889. Archaeopress, Oxford.

Kumar, S. 2001. Wolves in India: compensation policies complicate wolf depredation conflicts. International Wolf. 1(3): 8 – 9.

Lauer, B. H., E. Kuyt and B. E. Baker. 1969. Arctic wolf (*Canis lupus arctos*) and husky milk: gross composition and fatty acid constitution. Canadian Journal of Zoology 47: 99 – 102.

Lawrence, B. 1967. Early domestic dogs. Zeitschrift für Säugetierkunde 32: 44 – 59.

Leone, C. A. and A. L. Wiens. 1956. Comparative serology of carnivores. Journal of Mammalogy 37:11 – 23.

Lorenz, K. 1954. Man meets dog. Methuen, London.

Macintosh, N.W.G. 1975. The origin of the dingo: an enigma. In The wild canids: their systematics, behavioral ecology and evolution. 87 – 106, ed. M. Fox.
Van Nostrand Reinhold, NY.

Manwell, C. & C. M. A. Baker. 1983. Origin of the dog: from wolf or wild *Canis*

familiaris? Speculations in Science and Technology 6 (3): 213-224.

Manwell, C. and C. M. Baker. 1984. Domestication of the dog: hunter, food, bed-warmer, or emotional object? Zeitschrift für Tierzüchtung und Züchtunsbiologie – Journal of Animal Breeding and Genetics 101 (4): 241-256 1984

Marx, D. 1994. Wolf hybrids: to own or not to own? Dog World 79: 42 - 45.

Mech, L. D. 1970. The wolf: ecology and behavior of an endangered species. Doubleday, NY.

Mech, L. D. 1996. Wolves and 'child lifting' in India. International Wolf 6(4): 16.

Mech, L. D. 1998. Who's afraid of the big bad wolf? International Wolf 8(1): 8 – 11.

Meggitt, M. J. 1958. The Enga of the New Guinea highlands: some preliminary observations. Oceania 28(4): 253 - 330.

Meggitt, M. J. 1965. The association between Australian aboriginies and dingoes. In Man, culture and animals. 7 – 26, eds. A. Leeds and A. P. Vayda. American Association for the Advancement of Science, Washington, DC.

Morey, D. F. 1990. Cranial allometry and the evolution of the domestic dog. Ph. D. **T**hesis. University of Tennessee, Knoxville, USA.

Morey, D. F. 1992. Size, shape and development in the evolution of the domestic dog. Journal of Archaeological Science 19: 181 - 204.

Nowak, R. M. 1979. North American Quaternary *Canis*. Monograph 6. Museum of Natural History, University of Kansas, Lawrence, Kansas, USA.

Nowak, R. M. 1995. Hybridization: the double-edged threat. Canid News 3: 2-6.

O'Brien, S. J. and E. Mayr. 1991. Bureaucratic mischief: recognizing endangered species and subspecies. Science 251: 1187-1188.

Okumura, N., N. Nakano, N. Ishiguro, A. Matsui and M. Sahara. 1996. Intra- and interbreed genetic variations of mitochondrial DNA major non-coding regions in Japanese native dog breeds (*Canis familiaris*). Animal Genetics 27:397-405.

Oliver, J. S. 1993. Carcass processing by the Hadza: bone breakage from butchery consumption. In From bones to behavior: ethnoarchaeological and experimental contributions to the interpretation of faunal remains. 200 – 227, ed. J. Hudson. Center for Archaeological Investigations Occasional Paper No. 21, Southern Illinois University at Carbondale, USA.

Olsen, S. J. 1985. Origins of the domestic dog: the fossil record. Univ. of Arizona Press, Tucson, USA.

Oppenheimer, E. & R. Oppenheimer. 1975. Certain behavioral features in the pariah dog (*Canis familiaris*) in west Bengal. Applied Animal Ethology 2: 81 - 92.

Ovodov, N. D. 1998. The ancient dog of Siberia. Abstract. 223. Final program and abstracts. 8th International Congress of the International Council for Archaeozoology (Becky Wigen, Chair, Organizing Committee). University of Victoria, Canada.

Pal, S. K., B. Gosh and S. Roy. 1998. Agonistic behaviour of free-ranging dogs (*Canis familiaris*) in relation to season, sex and age. Applied Animal Behaviour Science 59: 331-348.

Pei, W. C. 1934. The carnivora from locality 1 of Choukoutien. Palaeontologia Sinica, Series C, vol. 8, Fascicle 1, Geological Survey of China, Bejing.

Randi, E. and V. Lucchini. 2002. Detecting rare introgression of domestic dog genes into wild wolf (*Canis lupus*) populations by Bayesian admixture analyses of microsatellite variation. Conservation Genetics 3(1): 29 – 43.

Scott, J. P. and J. Fuller. 1965. Genetics and the social behavior of dogs. University of Chicago Press, Chicago.

Shahi, S. P. 1983. Status of the gray wolf in India. Acta Zoologica Fennica 174: 283-286.

Steinhart, P. 1995. The company of wolves. Vintage Books, New York.

Stewart, P. 1993. Mapping the dhole. Canid News 1: 18-21.

Stockhaus, K. 1965. Metrische Untersuchungen an Schudlen von Wolfen und Hunden, Zeitschrift fur Zoologishe Systematik und Evolutionsforschung 3: 157 B 258.

Sullivan, J. O. 1978. Variability in the wolf, a group hunter. In Wolf and man: evolution in parallel. 31 – 40. eds. R. L. Hall. and H. S. Sharp. Academic Press, NY.

Tchernov, E. and L. K. Horowitz. 1991. Body size diminution under domestication: unconscious selection in primeval domesticants. Journal of Anthropological Archaeology 10: 54 – 75.

Teilhard de Chardin, P. and J. Piveteau. 1930. Les mammifères fossiles de Nihowan (Chine). Annales de Paleontologie, T. XIX, Paris. (Cited in Pei 1934)

Titcomb, M. 1969. Dog and man in the ancient pacific with special attention to Hawaii. Bernice P. Bishop Museum Special Publication 59. Honolulu, Hawaii, USA.

Tsuda, K., Y. Kikkawa, H. Yonekawa and Y. Tanabe. 1997. Extensive interbreeding occurred among multiple matriarchal ancestors during the domestication of dogs: Evidence from inter- and intraspecies polymorphisms in the D-loop region of mitochondrial DNA between dogs and wolves. Genes, Genetics and Systematics 72: 229 - 238.

Vilà,C., P. Savolainen, J. E. Maldonado, I. R. Amorim, J. E. Rice, R. L. Honeycutt, K. A. Crandall, J. Ludeburg, R. K. Wayne. 1997. Multiple and Ancient Origins of the Dog. Science 276: 1687-1689.

Vilà, C. and R. K. Wayne. 1999. Hybridization between wolves and dogs. Conservation Biology 13 (1): 195-198.

Walker, D. N. & G. C. Frison. 1982. Studies on Amerindian dogs, 3: prehistoric wolf/dog hybrids from the Northwestern plains. Journal of Archaeological Science 9: 125 - 172.

Wayne, R. K. 1986. Cranial morphology of domestic and wild canids: the influence of development on morphological change. Journal of Morphology 187: 301 - 319.

Wayne. R. K. and S. J. O'Brien. 1987. Allozyme divergence within the Canidae. Systematic Zoology 36: 339-355.

Wayne, R. K., B. Van Valkenburgh and S. J. O'Brien. 1991. Molecular distance and divergence time in carnivores and primates. Molecular & Biological Evolution 8(3): 297-319.

Wayne, R. K., N. Lehman, M. W. Allard and R. Honeycutt. 1991. Mitochondrial DNA variability of the gray wolf: genetic consequences of population decline and habitat fragmentation. Conservation Biology 6(4): 559 – 569.

Wayne, R. K. and E. A. Ostrander. 1999. Origin, genetic diversity, and genomic structure of the domestic dog. BioEssays 21: 247-257.

Wilson , D. E. & D. M. Reeder. 1993. Mammal species of the world: a taxonomic and geographic reference. Smithsonian Inst. Press, Washington, DC.

Wolpoff, M. and R. Caspari, 1997. Race and human evolution. Simon & Schuster, NY.

Zdansky, O. 1925. Quartäre Carnivoren aus Nord-China. Palaeontologia Sinica Series C, Vol. II, Fascicle 2, pp. 1 – 38. (Cited in Pei 1934)

Zeuner, F. E. 1963. A history of domesticated animals. Harper and Row, NY.

Appendix I.

Aboriginal dogs: Autochthonous ancient races of DDs associated with indigenous cultures.

Dog: Canids that are not wolves, jackals, or foxes: namely *Canis familiaris*, *Canis dingo* (Australian dingo), *Canis hallstromi* (New Guinea singing dog).

Domesticated dog: A population whose reproduction has been under human control for many generations, with artificial selection.

Pariah dogs: Free-ranging, free-breeding semi-domesticated dogs commensal with humans: scavenger ecological niche.

Primitive dogs: Populations that approximate wild *Canis* morphology, with no derived characters such as pendant ears, and which have not, as far as is known, been subjected to controlled breeding. Examples: dingo, New Guinea singing dog.

Proto-domestic dogs: Tamed wild canids utilizing commensal scavenger niche.

Wild dogs: Populations mainly utilizing predator niche, subsisting without any dependency upon humans or human wastes.

Wolf: gray wolf, *Canis lupus*.