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The *Canis* tangle: a systematics overview and taxonomic recommendations

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Despite high research interest, the systematics and taxonomy of mammalian genus *Canis* are among the most convoluted and controversial: species boundaries are blurred and incongruent with any existing species concept, while genetic differences between species are low. I provide an overview of existing controversies, the most recent findings, and taxonomic possibilities, and recommend the most practical and well-substantiated solutions. The genus boundaries have to be changed, with two African jackals (*C. adustus* & *C. mesomelas*) moved to a separate genus *Lupulella*. The systematic status of taxa occurring in eastern North America has caused much argument; most recent data indicate that Algonquin (*C. lycaon lycaon*) and Red (*C. l. rufus* and recently exterminated subspecies) Wolves originate from ancient hybridization and should be considered a separate species, while two other populations are of more recent hybrid origin. The systematic position, intraspecific classification, origin and taxonomy of Dog (*C. familiaris*) are particularly controversial. It has been alternatively classified as a subspecies of Gray Wolf (*C. lupus*), a subspecies of Dingo (*C. dingo*), or a full species (*C. familiaris*) with Dingo as a subspecies. Analysis of available data shows that Dog should be classified as a full species with four subspecies, since its origin from a common ancestor with modern Gray Wolf has likely predated its domestication (contrary to the most popular view), and interbreeding between Dog and Gray Wolf in the wild is limited. It is possible that never-domesticated Dog populations have survived in southeastern Asia until very recently, or even exist today.

Key words: wolf; dog; jackal; coyote; dingo; domestication; history; phylogeny; systematic; taxonomy.

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Собачий узел: систематический обзор рода *Canis* и предложения по таксономии

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Несмотря на значительное внимание исследователей, систематика и таксономия млекопитающих рода *Canis* относятся к наиболее спорным и запутанным. Многие таксоны, входящие в этот род, не соответствуют ни одной из существующих концепций вида, а генетические различия между видами малы. Обзор существующих противоречий, новейших данных и таксономических альтернатив позволяет рекомендовать наиболее обоснованные и практически целесообразные решения таксономических проблем. Границы рода подлежат пересмотру: два вида африканских шакалов (*C. adustus* и *C. mesomelas*) должны быть выделены в отдельный род *Lupulella*. Систематическое положение представителей рода, обитающих на востоке Северной Америки, вызывало ожесточенные дискуссии. Последние данные подтверждают видовую самостоятельность и древнее гибридное происхождение волков алгонкинского (*C. lycaon lycaon*) и рыжего (*C. l. rufus* и недавно истребленных подвидов), а также недавнее гибридное происхождение двух других популяций. Особенно противоречивы систематическое положение, внутривидовая классификация, происхождение и таксономия собаки. Ее классифицируют как подвид или группу подвидов серого волка (*C. lupus*), подвид динго (*C. dingo*) или, наоборот, как самостоятельный вид (*C. familiaris*) с динго в качестве подвида. Анализ имеющихся данных показывает, что собака должна классифицироваться как самостоятельный вид с четырьмя подвидами, поскольку ее происхождение от общего с современным серым волком предка, вопреки распространенному мнению, предшествовало доместикации, а способность к гибридизации с серым волком в природе ограничена. Возможно, что первично популяции собак существовали в Юго-Восточной Азии до недавнего времени или даже существуют до сих пор.

Ключевые слова: волк; собака; шакал; койот; динго; одомашнивание; история; филогения; систематика; таксономия.

Carnivores of genus *Canis* are among the best-studied mammals (Nowak, 1999). The bibliography on their phylogeny is so extensive that its sheer volume can make it difficult to keep perspective, as illustrated by persistent misconceptions criticized by Koler-Matznick (2002), so it appears that a concise overview of the subject and the most recent developments in the area is needed. Despite all the research attention, the systematics of *Canis* still present numerous challenges due largely to high genetic similarity between taxa and to the ability of many species to produce fertile hybrids, and sometimes hybrid swarms, in the wild (Lindblad-Toh et al., 2005; Way, 2013). In addition, the genus includes the world's oldest domesticated species that has diversified, hybridized with many wild species, and evolved into a number of secondarily wild taxa, thus greatly complicating the taxonomic problems. (I will use the term «secondarily wild» for populations completely independent of human presence, and the term «feral» for populations that are human commensals at least to some extent.) These complications mean that the taxonomy of the genus cannot be adequately sorted out using any one of widely used species concepts, and a compromise approach is the most practical. Below is an overview of the systematics of extant *Canis* spp., with a list of major controversies and proposed taxonomic solutions.

Wolves, jackals and coyotes

Traditionally, seven primarily wild extant species of *Canis* have been recognized (Nowak, 1999); recently an eighth species is sometimes added (see below). A few more species, closely related to Gray Wolf and differing mostly in size and the degree of hypercarnivory, have gone extinct since 100 kya (Mech, Boitani, 2003). Below is the list of extant species, with brief accounts of distribution and taxonomic controversies.

Striped Jackal (*C. adustus* Sundevall 1847) and **Black-backed Jackal** (*C. mesomelas* Schreber 1775). Striped Jackal has a continuous range across the savanna zone of Africa from Mauritania to Ethiopia and south to KwaZulu-Natal, and although seven subspecies have been described, their validity is highly questionable (Sillero-Zubiri, 2009); only the animals from the Horn of Africa are highly distinctive phenotypically (pers. obs.). Black-backed Jackal has disjunct distribution, with two distinctive subspecies inhabiting eastern and southern Africa, respectively (Walton, Joly, 2003).

These two closely related (but widely sympatric) species have recently been found to be outside the clade that includes other *Canis* taxa, Dhole (*Cuon alpinus*), and African Wild Dog (*Lycaon pictus*) (Wayne, O'Braien, 1987; Lindblad-Toh et al., 2005). This means that they should be placed in a separate genus, for which the name *Lupulella* Hilzheimer 1906 is available (Walton, Joly, 2003), or, alternatively, that *Cuon* and *Lycaon* should be subsumed into *Canis*, as proposed many times for *Cuon* (Wayne et al., 1997; Vila et al., 1999), but never for *Lycaon*. Since African Wild Dog has very distinctive morphology (including dentition) and behavior (Sillero-Zubiri, 2009), the optimal solution seems to separate the two jackals into *Lupulella*, maintain *Lycaon* as a separate genus, but merge *Cuon* into *Canis*. Accidentally, Dhole has been reported to hybridize with one of *Canis* species in the wild, although only once (Pocock, 1941), while African Wild Dog is not known to hybridize with any other species even

in captivity (Sillero-Zubiri et al., 2004). All species of *Canis*, *Cuon* and *Lycaon* share the same chromosome number: $2n = 78$ (Wayne, 1993).

Simien Wolf (*C. simensis* Rüppell 1835). This distinctively marked species is a highly localized and critically endangered endemic of Ethiopian Highlands. There are two weakly differentiated subspecies, separated by the Rift Valley (Sillero-Zubiri, 2009). This species has been known as Ethiopian Wolf, but since now it is known that Gray Wolf also occurs in Ethiopia (see below), the name «Simien Wolf» is preferable as less ambiguous.

Golden Jackal (*C. aureus* Linnaeus 1758). Historically inhabiting the Balkan Peninsula, Africa south to Senegal and Tanzania, and southern Asia from Turkey and Russia's Black Sea coast to Sri Lanka and Myanmar, this species is currently expanding and has reached Italy, Austria, Vietnam and Malawi (Dinets, Rotshild, 1997; Sillero-Zubiri, 2009). A dozen subspecies have been described, but their validity is doubtful and the species is remarkably uniform phenotypically throughout its range (Sillero-Zubiri, 2009; also pers. obs.).

Coyote (*C. latrans* Say 1823). Historically interior Alaska, western Canada, western USA, Mexico, and Central America south to Honduras (Young, Jackson, 1978); in the last 300 years has colonized most of Alaska, Central America south to Panama, and eastern North America (Sillero-Zubiri, 2009). Coyotes in eastern USA and adjacent parts of Canada have some genes of the following three species, are somewhat wolf-like in appearance, and are known as «Eastern Coyotes» (a taxon never formally described). Within the historical range, nineteen subspecies have been described, but the variation between them is largely clinal (Young, Jackson, 1978), and the validity of many subspecies is highly questionable (Sillero-Zubiri, 2009).

Gray Wolf (*C. lupus* Linnaeus 1758). Historically northern and western North America south to Mexico (where recently extirpated), Eurasia except the tropical rainforest zone, and many islands such as Britain (where also extirpated) and Greenland (Sillero-Zubiri, 2009). The distinctive form *lupaster* of Egypt and Libya has been alternatively assigned to this species and *C. aureus*; recent studies have found that it belongs to the present species and occurs around the periphery of the Sahara and south to Senegal and Ethiopia (Gaubert et al., 2012). In Simien National Park of Ethiopia *C. l. lupaster* is sympatric with as many as four other *Canis* species, including all three jackals and the Simien Wolf, although the latter is altitudinally separated to some extent (pers. obs.). Other highly distinctive subspecies are known from Japan (extinct) (Walker, 2005), Italy (Randi et al., 2000), Haida Gwaii (Weckworth et al., 2010), and India (Aggarwal et al., 2007). Over 35 subspecies have been described (Sillero-Zubiri, 2009); the actual number is still highly controversial. Australian Dingo is often listed as *C. l. dingo*, while the domestic dog is often called *C. l. familiaris*, but this is not the optimal taxonomy, as discussed below.

Red Wolf (*C. rufus* Audubon & Bachman 1851) and **Algonquin Wolf** (*C. lycaon* Schreber 1775) are two forms from eastern North America; the latter is also known as Eastern Timber Wolf. Red Wolf historically inhabited the southeastern USA, was exterminated in the wild, and has recently been reintroduced in North Carolina (there is also a small, inten-

sively managed population on an offshore island in Florida); of the three described subspecies, only the nominate is extant (Nowak, 2002). Algonquin Wolf inhabits a relatively small area centered on Algonquin Provincial Park, Canada (Dinets, 2015). The status of these two forms has been a matter of intense controversy; they have been considered one or two independently evolved species (Wilson et al., 2004; Chambers et al., 2012), hybrid swarms (Wayne, 1991; Koblmuller et al., 2009), or subspecies of Gray Wolf (Lawrence, Bossert, 1975). The most recent data (Way, 2013) suggest that both forms result from ancient hybridization events between Gray Wolf and Coyote, with the share of wolf heritage higher in Algonquin Wolf and lower in Red Wolf. It is unclear if these two forms form a monophyletic lineage (Wilson et al., 2004) or have evolved independently from each other (Chambers et al., 2012).

All North American canids interbreed in the wild, although direct interbreeding between Gray Wolf and Coyote is extremely limited, and genetic exchange between these two forms occurs with Algonquin Wolf as a «conduit» (Way, 2013). Wolves inhabiting much of Great Lakes area have been recently found to be hybrids between Gray and Algonquin Wolves, while Coyotes inhabiting coastal areas from New Jersey to Nova Scotia are hybrids between Eastern Coyote and Algonquin Wolf (Way, 2013). Despite all this ongoing hybridization on all sides, Algonquin Wolves in the core part of their range maintain genetic and phenotypical distinctiveness (Rutledge et al., 2010), supporting the view that they deserve the status of full species (jointly with Red Wolf or separately). The existence of mammalian species of hybrid origin is now a well-known and universally recognized fact (Lavrenchenko, 2014), so the ancient hybrid origin of Algonquin and Red Wolves should not preclude their recognition as a full species or two. As they are very similar in appearance and behavior (Way, 2013; also pers. obs.), pending more data it seems reasonable to consider Algonquin Wolf a subspecies of Red Wolf. Since *C. lycaon* has a priority, the proper name for the only surviving subspecies of Red Wolf should be *C. lycaon rufus*, while Algonquin Wolf should be called *C. lycaon lycaon*.

Dog: history and controversies

Dog (*C. familiaris* Linnaeus 1758), originally described from a domestic European specimen, has occurred in association with humans on all continents (except the Antarctic) prior to European contact (Nowak, 1999). Feral populations exist in many areas, and some of them have become secondarily wild and independent of humans. Three of these have been scientifically described: Dingo of Australia (as *C. lupus dingo* Meyer, 1793), Singing Dog of New Guinea (as *Canis hallstromi* Troughton 1957), and Tengger Dog of Java (as *C. f. var. tenggerana* Kohlbrugge 1896). Feral populations of tropical Asia (the so-called Pariah Dog) are remarkably similar to Dingo and Singing Dog in appearance, and are included in species *C. dingo* in some classifications, such as Corbett (1995). It has been shown that a secondarily wild population known as Carolina Dog has originated from an ancient introduction of pariah-like dogs to North America (van Asch et al., 2013).

Due to the recent trend to name domestic animals as subspecies of their wild ancestors, Dog is sometimes called *C. lupus familiaris* or *C. l. dingo*, but this is wrong for reasons

mentioned below. Unfortunately many popular sources have followed this trend. Recently it's been proposed that Australian Dingo should be considered a full species *C. dingo* (Crowther et al., 2014), but the authors used Phylogenetic Species Concept which should not be used in vertebrates as it leads to gross taxonomic inflation and has numerous theoretical shortcomings (Zachos, Lovari, 2013).

Dog is known to hybridize in the wild and produce fully fertile hybrids with all *Canis* species except Striped and Black-backed Jackals, especially where the wild species is close to extinction (Lindblad-Toh et al., 2005). In parts of northern Eurasia, populations of Gray Wolf-Dog hybrids have become a serious problem for wildlife management and public safety (Dinets, Rotshild, 1998). There is ample evidence of Gray Wolf-Dog hybridization in ancient and modern times, with gene flow in both directions (Von Holdt et al., 2010; Galibert et al., 2011; Klütsch et al., 2011; Wayne, 2012). In some areas of the Arctic, crossing domestic Dogs with Gray Wolves is traditionally practiced (Dinets, Rotshild, 1998); such hybrids are still kept as pets in many Western countries (Willems, 1994/1995). However, there is conspicuous paucity of records of Gray Wolf-Dog hybrids from the Middle East, lowland India and China, even though local wolves often inhabit the vicinity of human settlements and are similar in size to feral Dogs (Koler-Matznick, 2002). Even in areas where Dogs are regularly cross-bred with Gray Wolves, gene flow in either direction can be very limited (Aghbolaghi et al., 2014) or at least restricted (Kopaliani et al., 2014). Where normal wolf pack structure is still maintained, wolves regularly hunt dogs, often preferring them to any other prey (Dinets, Rotshild, 1997). It appears that Gray Wolf-Dog hybridization, although possible and occasionally occurring, is strongly suppressed in the wild.

Originally, it was suggested that Golden Jackal and/or Coyote had played a part in Dog's origins (Darwin, 1859), but that theory is now largely rejected based on genetic evidence (Koler-Matznick, 2002). Gray Wolf is now generally believed to be the sole ancestor, although, as discussed below, this view might be overly simplistic.

When and where was Dog domesticated? The results of various studies contradict each other. The place of origin has been claimed to be the Middle East (Gray et al., 2011; Wayne, 2012), Europe (Wayne, 2012; Thalmann et al., 2013), and southeastern Asia (Savolainen et al., 2002; Ardalan et al., 2011; Ding et al., 2011). The time estimates vary from hundreds of thousands of years (Vila et al., 1997) to less than 10 kya (Thalmann et al., 2013). Notably, the oldest estimates are of the gray Wolf-Dog split, not domestication per se.

The oldest Dog remains associated with human settlements are the 36 kya Goyet specimen of Belgium and the 33 kya specimen from Razboinichya Cave in Altai Mountains (Ovodov et al., 2011), but these old specimens do not appear related to extant Dogs (Ovodov et al., 2011). Moreover, they are strangely rare. Dog remains become much more common at archeological sites around 14 kya (Ovodov et al., 2011).

The differences between Dog and Gray Wolf are larger than between any domestic animal and its wild ancestor. Dog has 30 % smaller relative brain size, noticeable differences in dentition, adaptations to an omnivorous diet in their digestive tract, and numerous other anatomical differences; even its gait

and tracks are different. There are very significant behavioral differences: for example, Dogs can't feed their puppies by regurgitating food (Dinets, Rotshild, 1998; Koler-Matznick, 2002).

Experiments on Red Fox (*Vulpes vulpes*) have shown that many of those differences can be reproduced simply by selection for friendliness to humans. By using this method over 30–40 generation of foxes, D. Belyaev produced animals with Dog-like tails, floppy ears, irregular coloration, early sexual maturity and many neotenic behavioral traits (see Trut, 1999, for English summary). However, some of the differences between Dog and Gray Wolf probably needed a very long time to evolve.

The “domesticated wolf” theory has serious problems. Some features of Dog anatomy, particularly brain structure, resemble Golden Jackal and Coyote, but not Gray Wolf (Darwin, 1859). Although the most primitive Dog breeds and the oldest feral populations all look somewhat similar, they do not particularly resemble Gray Wolf, having typical Dog anatomy and mostly reddish or yellowish coloration (Dinets, Rotshild, 1998). In fact, as many explorers have noticed (see, for example, Sykes, 1831), they can look remarkably similar to Dhole; such Dhole-like Pariah Dogs can be seen, for example, around some Tibetan monasteries (pers. obs.). And, most interestingly, Pariah Dog of Asia hardly ever hybridizes with sympatric Gray Wolf, despite the fact that both forms coexist in very close proximity and are similar in size (Koler-Matznick, 2002, also pers. obs.).

A much better explanation for all known facts is that Dog has existed in Asia as a wild animal prior to the arrival of modern-type humans and subsequent domestication. This idea has been well substantiated by Wayne, Ostrander (1999). In a little-noticed publication, Koler-Matznick (2002) provides an extensive summary of abundant evidence showing that the ancestor of Dog was not Gray Wolf *sensu stricto*, but a closely related, smaller extinct canid. The author suggests *Canis (lupus) variabilis*, an extinct wolf that occurred in present-day China 100–200 kya, as the most likely candidate, and notices that since it was sympatric with *C. lupus sensu stricto* in time and space, it was already a separate species. Although the specifics are uncertain, the idea that Dog has split from its common ancestor with modern Gray Wolf prior to its domestication is supported by virtually all recent data. The rarity of Dog remains at Pleistocene archeological sites indicates that it was hunted as a wild animal, rather than present at those settlements as commensal or domestic animal. Druzhkova et al. (2013) found that the unique haplotype of the Razboinichya Cave dog is more closely related to modern dogs and prehistoric New World canids than it is to contemporary wolves. It appears that wild Dog has been domesticated independently in southeastern Asia (Ding et al., 2011) and in the area stretching from Europe to Altai Mountains (Thalman et al., 2013).

Extreme differences in morphology, physiology and behavior between Dog and Gray Wolf, as well as abundant data indicating that the split between the two taxa has occurred prior to Dog's domestication, and the fact that they are partially reproductively isolated in the wild, make it impossible to consider them conspecific, so the proper scientific name for Dog is *Canis familiaris*. It appears that four subspecies should be recognized.

Western Dog (*C. f. familiaris* Linnaeus 1758) includes most domestic dogs of the Holarctic, and almost all domestic breeds (see cladograms in von Holdt et al., 2010, and in Larson et al., 2012). This subspecies probably originated from domestication events in Europe and adjacent areas. Dogs in the northern parts of Asia and North America are heavily influenced by hybridization with Gray Wolf, while in Asia there is a broad zone of introgression with the next subspecies. Feral Western Dogs do not reverse to Dingo-like appearance over time (Barnett, 1986, also pers. obs.). There are countless commensal and feral populations, but the only ones known for sure to be secondarily wild are those on four islands in the Galapagos, now eradicated on Isabela, Floreana and San Cristobal and replaced by feral and commensal Dogs on Santa Cruz (Barnett, 1986; Reponen et al., 2014).

Pariah Dog (*C. f. indica* Sykes 1831). Exists as commensal and feral populations over much of tropical Asia and on islands as far as New Guinea (Miklouho-Maclay, 1882) and historically Polynesia, including Hawaii and New Zealand (Oskarsson et al., 2012). Pre-Colombian American breeds, Canaan breed of the Middle East, and some (but not all) native African and East Asian breeds also belong to this subspecies (Boyko et al., 2009; von Holdt et al., 2010; Larson et al., 2012). Feral Dogs of this subspecies reverse to Dingo-like rather than Gray Wolf-like appearance (Dinets, Rotshild, 1998). The only known secondarily wild population in the Americas, the Carolina Dog, might be extinct, although it was still present at Savannah River Site in South Carolina in 2007 (Dinets, 2015). Another wild (presumably secondarily) population, described from mountains of Java as *C. f. var. tetengerana* Kohlbrugge 1896, also appears to be extinct (Kohlbrugge, 1901). It could conceivably represent a relict population of primarily wild *C. familiaris*, but, although three specimens have been submitted to Leyden Museum of Natural History (Jentink, 1897), they have not been studied recently (S. van der Mije, pers. comm.). Other primarily wild populations of *C. familiaris* might still exist in remote areas of Southeast Asia or adjacent islands, although no wild (primarily or secondarily) Dogs exist in Indochina (Francis, 2008).

Singing Dog (*C. f. hallstromi* Troughton 1957). A secondarily wild subspecies endemic to New Guinea highlands. It has numerous morphological, physiological and behavioral differences from all other dogs, and has split from other lineages thousands of years ago (Koler-Matznick, 2003; von Holdt et al., 2010). Unfortunately, it might be on the verge of extinction in the wild (Koler-Matznick et al., 2007).

Dingo (*C. f. dingo* Meyer, 1793). A secondarily wild subspecies inhabiting Australia and a few offshore islands. It shares many similarities with Pariah Dog, but is larger and heavier, and has consistent differences in morphology and behavior from all other Dogs (Fleming et al., 2001; Crowther et al., 2014). Mainland Australian Dingoes now increasingly show signs of hybridization with *C. f. familiaris*, but the ones on Frazer Island are thought to be unaffected by hybridization (Corbett, 1995), although this is disputed (Woodall et al., 1996).

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Conflict of interests

The author declares no conflicts of interest.

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