



<https://doi.org/10.11646/zootaxa.4317.2.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:3CD420BC-2AED-4166-85F9-CCA0E4403271>

The Wayward Dog: Is the Australian native dog or Dingo a distinct species?

STEPHEN M. JACKSON^{1,2,3,9}, COLIN P. GROVES⁴, PETER J.S. FLEMING^{5,6}, KEN P. APLIN³, MARK D.B. ELDRIDGE⁷, ANTONIO GONZALEZ⁴ & KRISTOFER M. HELGEN⁸

¹*Animal Biosecurity & Food Safety, NSW Department of Primary Industries, Orange, New South Wales 2800, Australia.*

²*School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052.*

³*Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA.*

E-mail: aplin.ken@gmail.com

⁴*School of Archaeology & Anthropology, Australian National University, Canberra, ACT 0200, Australia.*

E: colin.groves@anu.edu.au; antonio.gonzalez@anu.edu.au

⁵*Vertebrate Pest Research Unit, Biosecurity NSW, NSW Department of Primary Industries, Orange, New South Wales 2800, Australia.*

E-mail: peter.fleming@dpi.nsw.gov.au

⁶*School of Environmental & Rural Science, University of New England, Armidale, NSW 2351, Australia.*

⁷*Australian Museum Research Institute, Australian Museum, 1 William St. Sydney, NSW 2010, Australia.*

E-mail: mark.eldridge@austmus.gov.au

⁸*School of Biological Sciences, Environment Institute, and ARC (Australian Research Council) Centre for Australian Biodiversity and Heritage, University of Adelaide, Adelaide, SA 5005, Australia.*

E-mail: kristofer.helgen@adelaide.edu.au

⁹*Corresponding author. E-mail: stephen.jackson@dpi.nsw.gov.au*

Abstract

The taxonomic identity and status of the Australian Dingo has been unsettled and controversial since its initial description in 1792. Since that time it has been referred to by various names including *Canis dingo*, *Canis lupus dingo*, *Canis familiaris* and *Canis familiaris dingo*. Of these names *C. l. dingo* and *C. f. dingo* have been most often used, but it has recently been proposed that the Australian Dingo should be once again recognized as a full species—*Canis dingo*. There is an urgent need to address the instability of the names referring to the Dingo because of the consequences for management and policy. Therefore, the objective of this study was to assess the morphological, genetic, ecological and biological data to determine the taxonomic relationships of the Dingo with the aim of confirming the correct scientific name. The recent proposal for *Canis dingo* as the most appropriate name is not sustainable under zoological nomenclature protocols nor based on the genetic and morphological evidence. Instead we proffer the name *C. familiaris* for all free-ranging dogs, regardless of breed and location throughout the world, including the Australian Dingo. The suggested nomenclature also provides a framework for managing free-ranging dogs including Dingoes, under Australian legislation and policy. The broad principles of nomenclature we discuss here apply to all free-roaming dogs that coexist with their hybrids, including the New Guinea Singing Dog.

Key words: behaviour, Dingo, dog, domesticate, free-roaming dog, genetics, hybridisation, morphology, New Guinea Singing Dog, reproduction, species concept, taxonomy

Introduction

When Europeans came to the Australian continent they encountered dogs in two different contexts—initially as companion animals living with Aboriginal groups resident around the nascent European settlements (Walters 1995), and later as wild animals that roamed through the surrounding bushland and preyed on introduced domestic stock (e.g. Atkinson 1826). It was the wild dog that we now tend to think of as the classic Australian Native Dog or ‘Dingo’ and about which there is ongoing scientific debate regarding its origins, taxonomic status, and conservation values.

An early illustration of a native dog published by Phillip (1789) attracted the attention of several European

zoologists who, in line with practices of the day, used Linnaeus' (1758) new system of binomial nomenclature to coin a variety of names for this newly encountered animal. The two earliest names, both based on the Phillip (1789) illustration, are *Canis antarticus* Kerr, 1792 and *Canis dingo* Meyer, 1793. In subsequent decades additional names were proposed including *Canis familiaris australasiae* Desmarest, 1821; *Canis australiae* Gray, 1826 (a replacement name for *australasiae*); *Canis familiaris novaehollandiae* Voigt, 1831; and *Canis diago* Temminck, 1838 (an apparent incorrect spelling of *dingo*). This plethora of names is quite typical for the early, 'chaotic' phase of zoological description of the Australian fauna and it does not necessarily belie any real diversity of opinion regarding the biological nature of Australian dogs (see Jackson & Groves (2015) for a review of all names).

The specific name *dingo* Meyer, 1793 was widely used for the Australian Dingo until Iredale (1947) noted that *antarticus* Kerr had priority. To avoid potential instability of usage, Tate (1955) applied to the International Commission of Zoological Nomenclature to suppress the name *antarticus*, an action that was supported by Morrison-Scott (1955). After consideration of the issue by the ICZN (1957) the name *Canis antarticus* Kerr, 1792 was suppressed by Opinion 451. Only Troughton (1967) persisted in usage of *antarticus* for the Dingo. Despite its availability, the name *dingo* Meyer, 1793, like all names, is still subject to potential taxonomic revision and can therefore be recognised at species or subspecies rank, or synonymised within another taxon, such as *C. familiaris*, which is proposed here.

The Dingo was accorded species status, as *Canis dingo*, by various early authors including Gould (1859), Kreffit (1866, 1868), Lesèble (1890), and Iredale and Troughton (1934), though Gould (1859) at least clearly believed the Dingo to be recent immigrant that had accompanied Aboriginal peoples "from Northern Asia through the Indian Islands to Australia". Darwin (1868) also speculated that the Dingo had been introduced into Australia by humans, although he conceded that this introduction might have been ancient. This notion of an ancient introduction was further extended by several late nineteenth and early twentieth century authorities including McCoy (1862, 1882), Gregory (1906) and Lucas and Le Souëf (1909), and taken to its zenith by Etheridge (1916) who believed that the Dingo arrived well before Aboriginal Australians, perhaps even during the Pliocene.

The claims for early introduction of the Dingo were systematically reviewed by Wood Jones (1921) who concluded that the Dingo was not indigenous to Australia but rather a relatively recent intrusion that arrived with the assistance of humans. The same conclusion was later expressed by Macintosh (1975). Wood Jones (1921, 1925) and Finlayson (1939) recognised the Dingo as a subspecies of the Domestic Dog, i.e. *Canis familiaris dingo*. From the 1960s this usage came to dominate among both local (e.g. Wakefield 1966; Macintosh 1975; Gollan 1982, 1984; Strahan 1983, 1992; Mahoney & Richardson 1988; Sheldon 1992; Strahan 1992; Vernes *et al.* 2001; Elledge *et al.* 2006) and international authorities, including various workers directly concerned with the evolutionary origins of domestic animals (e.g. Clutton-Brock *et al.* 1976; Corbet & Clutton-Brock 1984; Clutton-Brock *et al.* 1990; Butler *et al.* 2004; Dinets 2015). During the 1990s, following the clarification of the origin of the Domestic Dog from the Gray Wolf, the Dingo was sometimes referred to as a subspecies of the Gray Wolf, i.e. *Canis lupus dingo* (e.g. Corbett 1995; Strahan 1995; Bino 1996; Daniels & Corbett 2003; Wozencraft 2005; Elledge *et al.* 2008; Van Dyck & Strahan 2008; Sillero-Zubiri 2009; Purcell 2010; Stephens *et al.* 2015; Radford *et al.* 2012; Newsome *et al.* 2013a). Interestingly, when Wozencraft (2005) referred to the *dingo* as a subspecies of *lupus* he included "Domestic Dog" in brackets after the name; the name *familiaris*, which he also recognised as a subspecies of *lupus*, was similarly annotated.

Molecular systematics has shed much new light on the origins of the dog and the pattern and process of its domestication. A universally agreed finding is that Domestic Dogs are comparative recent derivatives of the Gray Wolf (*Canis lupus*) (Wayne & Ostrander 1999; Savolainen *et al.* 2002; Pang *et al.* 2009; vonHoldt *et al.* 2010, 2011). While earlier studies provided somewhat conflicting views about when and where domestication took place, the more recent studies based on broad genomic sampling have generated a robust framework for interpreting the evolutionary origin and dispersal history of dog populations through southeast Asia and into Melanesia and Australia (vonHoldt *et al.* 2010, 2011; Oskarsson *et al.* 2012; Sacks *et al.* 2013; Skoglund *et al.* 2015). Through all of this work there is a consistent representation of the Dingo as one of many different lineages within the assemblage of Domestic Dogs, with the implication that it is a domesticate that has become feral following its introduction into Australia. Incidentally, the same finding and interpretation also applies to a wild dog population found in montane habitats of New Guinea—the New Guinea Singing Dog which has been designated taxonomically as *Canis hallstromi* Troughton, 1957 or *Canis familiaris hallstromi*.

Despite this growing certainty as to the evolutionary origin of both the Dingo and the New Guinea Singing Dog, there is an ongoing push to recognize each of these regional wild dog populations as distinct species. This view was championed for the New Guinea Singing Dog by Koler-Matznick (2003, 2007), and more recently for the Dingo by Crowther *et al.* (2014). The latter authors base their case in part on a morphological assessment of Dingo specimens collected during the early colonial period in Australia, on the grounds that these animals are representative of a pure Dingo phenotype prior to hybridization with European Domestic Dogs that commenced soon after the introduction of European Domestic Dogs in 1788. Based on their findings, Crowther *et al.* (2014: 10) justified the recognition of the Dingo as a distinct species on four main grounds: 1) “the ancestry of the Domestic Dog and Dingo is unknown”; 2) “the Dingo was first described as a distinctive wild form and differs from wolves, as well as from New Guinea Singing Dogs and Domestic Dogs, in many behavioural, morphological and molecular characteristics”; 3) Dingoes “are effectively reproductively isolated in undisturbed natural environments”; and 4) “as domesticated forms do not fall into the definition of subspecies, the ICZN has recommended retaining the different specific names for wild and domesticated animals and naming wild ancestors of domesticates using the first available specific name based on a wild population (ICZN 2003)”.

We consider the arguments of Crowther *et al.* (2014) with respect to the Dingo (and incidentally those of Koler-Matznick (2003, 2007) for the New Guinea Singing Dog) to be critically flawed on a number of key points. Accordingly, we reject the suggestion that each of these populations should be treated as a distinct species of canid. Below we address four main points relevant to this argument. Two are matters of principle, namely: 1) the nature of ‘species’ and the basis for their recognition in nature; and 2) the nature of the ICZN rulings and other recommendations in relation to the nomenclature of domestic animals. Two are matters of evidence, namely: 1) the evidence that Dingoes (and New Guinea Singing Dogs) originated as Domestic Dogs; and 2) the nature of the morphological, ecological, behavioural and reproductive differentiation of the Dingo and New Guinea Singing Dogs from other dogs and wolves.

Matters of principle—species and domesticates

The nature of species

When should an isolated or distinctive population be recognised as a distinct species? Is it enough that a population can be distinguished from others by features of morphology or behaviour, or by genetic contrasts, as implied by the approach of Crowther *et al.* (2014)? Or are there more stringent criteria that should be applied? From a biological perspective, this represents the nub of the matter.

The last fifty years or so have seen vigorous debate concerning the nature of species, with at least 26 definitions being proposed (Mayden 1997; Frankham *et al.* 2012). In recent years, much clarity has emerged from the recognition that the profusion of contrasting species concepts and definitions are largely a product of differing emphasis on two major dimensions of the ‘species problem’, namely the historical and operational dimensions (and, within the latter, the significance of population genetics). The historical species dimension emphasizes the discrete evolutionary lineages that in effect are contemporary species (Mayden 1997). de Queiroz (2007) argued that other ‘species concepts’ are criteria of species recognition which arise at different points along the trajectory of a species’ history after its individuation. Operational species concepts are mainly concerned with how species might be recognized through objective methods, and less with their intrinsic meaning (Nixon & Wheeler 1990; Groves 2001; Groves & Grubb 2011). Among these operational criteria, population genetic species concepts stand apart in that they focus attention not only on the observed genetic contrasts but also on the inferred genetic mechanisms that cause lineage divergence and which maintain species as discrete entities (Coyne & Orr 2004; Baker & Bradley 2006).

Although the recent papers of Koler-Matznick (2003, 2007) and Crowther *et al.* (2014) do not explicitly state the species concept followed, both studies have a strong emphasis on the differentiation of each lineage from other dogs and wolves, and on their history of genetic isolation of Dingo and New Guinea Singing Dog from each other and from other canids since their arrival in Australia and New Guinea, respectively. Both also downplay the evidence of hybridization between these ‘native’ dog populations and more recently introduced dog breeds, on the grounds that interspecific hybridization is common among canids and represents a shared primitive characteristic. The general approaches in each case in some respects resemble those of proponents of the Phylogenetic Species

Concept (PSC) which regards any diagnosable population as a potentially distinct species, but differ in that they explicitly extend this criterion to known derivatives of domestic stock. Dinets (2015) also suggested that Crowther *et al.* (2014) used the PSC but raised concern over this species concept by suggesting that it should not be used in vertebrates as it leads to gross taxonomic inflation and has numerous theoretical shortcomings (citing Zachos & Lovari 2013).

Although the PSC approach originated with the context of cladistic approaches to morphological phylogenetics (Cracraft 1983; Nixon & Wheeler 1990), essentially as a definition for terminal entities on a cladogram, it has gained widespread influence on account of its objectivity and broad applicability, and in some quarters, for its lack of reliance on any particular model of speciation (i.e. it is largely free of theory). With increasingly powerful genetic methods it has been maintained that there are issues with the limits of diagnosability under the PSC (Frankham *et al.* 2012).

Accordingly, while some of the present authors have advocated a strict use of the PSC in mammal taxonomy (Groves, 2001, 2004; Groves & Grubb 2011; Jackson & Groves 2015), for several reasons the present issue warrants a nuanced approach. One reason is that the taxonomy of domesticates is qualitatively different from other taxonomic issues, considering the unnatural circumstances of the lineage divergences. Another reason is that much more information is generally available on the genetic relationships and genetic compatibilities of domesticates and their wild progenitors, as well as their breeding systems, morphology and behaviour. Importantly, access to these categories of information allows the identity of domesticates and their feral derivatives to be assessed according to genetic criteria. Such assessment highlights the contrast between the genetic compatibility that exists among all members of a species (with very slight variation in fitness of offspring) and the genetic incompatibilities that sometimes exist between members of different species, such that offspring that result from hybridization have significantly reduced fitness relative to offspring within each of the differentiated gene pools (Baker & Bradley 2006). The degree of genetic incompatibility between populations tends to be related to the amount of genetic divergence that has occurred as a consequence of genetic drift or selection (e.g. Nosil *et al.* 2003; Frankham *et al.* 2011, 2012). There is, incidentally, mounting evidence that genes associated with compatibility are concentrated in certain regions of the genome, most notably on the sex chromosomes (True *et al.* 1996; Tao *et al.* 2003; Geraldès *et al.* 2006; Teeter *et al.* 2008).

The critical information for deciding whether or not the Dingo and Domestic Dogs constitute the same species is whether they are indeed different evolutionary lineages, having regard *inter alia* to the degree of genetic compatibility that exists between these populations (Baker & Bradley 2006; de Queiroz 2007). As will be reviewed below, in the case of the Dingo it is clear that its origin can be traced to within the broader lineage of Domestic Dogs, rather than to a separate lineage. Furthermore, the degree of genetic compatibility between Dingoes and Domestic Dogs has been tested under semi-natural circumstances through the introduction into Australia since European settlement of a variety of Domestic Dog breeds; the outcome of these interactions is reviewed in a later section.

Species identity and nomenclature of domesticates

A domestic animal is different from its wild ancestor. Through extended histories of artificial selective breeding domesticates have undergone changes in morphology, behaviour and reproductive biology, sometimes to a radical extent. Nevertheless, reversing the argument of the previous section, domesticates and their wild ancestors are not different lineages, but that one has been derived from within the other, and unsurprisingly most domesticates remain genetically compatible to a high degree with their wild progenitors. Indeed, in at least some cases, outbreeding with wild stock is encouraged as it appears to enhance offspring fitness through maintenance of genetic diversity (e.g. see Groves *et al.* (1966) on the ass (*Equus asinus*) and, for a very neatly analysed example, French *et al.* (1988) on the Domestic Cat (*Felis catus*)).

Domesticates were among the first suite of animals to be given binomial names by Linnaeus and, in many cases, the name given to the domesticate antedates (or is contemporary with) that given to its wild progenitor (see Corbet & Clutton-Brock 1984 for a summary). Subsequent rationalization of these names has occurred in various ways, including: 1) the maintenance of separate species names for each of the domesticates and their wild progenitor (e.g. *Canis familiaris* and *Canis lupus* for Domestic Dog and Gray Wolf); 2) the referral of domestic and wild version of the same species to a single species, using whichever name has priority (e.g. sections in Wilson & Reeder 1993); 3) the identification of domesticates through use of quotation marks around species names (e.g.

Canis 'familiaris') (Corbet & Clutton-Brock 1984); and 4) the use of special conventions to identify a domesticate, such as Bohlken's (1958, 1961) suggestion of using the wild progenitor's name followed by the domesticate's name, with 'f.' (for 'forma') in between—thus *Canis lupus f. domesticus* for a Domestic Dog; and Dennler de La Tour's (1968) more elaborate proposal that allows for discrimination of wild, semi-domestic, domestic and feral populations through use of the qualifiers '*praefamiliaris*', '*familiaris*' and '*exfamiliaris*', respectively—thus *Canis lupus (exfam.) dingo* for a feral Dingo derived from a Domestic Dog).

As noted by Groves (1995), the third and fourth categories of solutions required usages that do not conform to the International Code of Zoological Nomenclature in the form that it took at that time. Groves (1995) also clearly identified the root cause of the nomenclatural problem—that domesticates are not subspecies of their wild ancestors because they are not geographic isolates and often exist in sympatry with the wild ancestor; and that human intervention is required to maintain reproductive isolation from their ancestral stock. Groves (1995) concluded that domesticates are not in fact natural taxa at all but are more correctly thought of as *parataxa*; as such they fall outside of the scope of the Code.

In 1996 Gentry *et al.* (1996) made application to the ICZN to fix the name for the wild progenitors of 15 domesticates (including 13 mammals, one fish and one invertebrate) as *the earliest available name based on a wild individual or population*. In a number of cases, including the Domestic Horse, this meant by-passing earlier names based on a domesticate (i.e. *Equus caballus* Linnaeus, 1758) for a later name based on a wild individual (*Equus ferus* Boddaert 1785). This application was successful and the consequent rulings were published as Opinion 2027 of the ICZN (2003). In accordance with the underlying principle of taxonomic freedom embodied in the ICZN, the ruling did not dictate whether or not domesticates should be included within wild species or treated as separate entities, nor did it specify how they should be named. These were left open as matters of individual discretion.

To clarify some of these issues for a wider readership, Gentry *et al.* (2004: 649) subsequently made the following recommendations: 1) that “since wild species and their derivatives are recognisable entities, it is desirable to separate them nomenclaturally when distinct names exist”; 2) “that names based on domestic forms be adopted for the corresponding domestic derivatives”; and 3) that “names based on domestic animals apply also to feral populations (i.e. animals living in a self-sustained population after a history of domestication)”. Gentry *et al.* (2004: 650) also noted that “Under Article 17.2 of the Code of Zoological Nomenclature the availability of specific names for domestic animals is not affected even if they are known, or later found to be, of hybrid origin”.

To summarize, while the taxonomic naming of some wild animals has been clarified through recognition of a distinction between these species and their domestic derivatives, the nomenclature of the domestic animals themselves (and of their feral derivatives) remains outside of the scope of the ICZN rulings. In a sense, then, any nomenclatural system for domesticates is equally ‘valid’ and ‘defensible’, or rather none is any more so than any other according to the ICZN. Nonetheless, to avoid the potential chaos of many contrasting usages, it is clearly desirable to fix on some basis for assessing the merits of any particular claim. In our view, the recommendations of Gentry *et al.* (1996) are both firmly rooted in biological reality and eminently sensible, as they engender the least chance of future disruption of established taxonomic usage. Accordingly, we endorse their suggestion that domesticates and their feral derivatives are recognized by species names that differ from those of their wild ancestors, where such names are now or have recently been in common usage; and we further endorse the suggestion of Groves (1995) that these ‘species’ be regarded as *parataxa*, i.e. biological entities of fundamentally different kind to naturally occurring species.

Within this nomenclatural framework, the taxonomic status of the Dingo and New Guinea Singing Dog rests on the answer to two related questions, namely: Are they feral derivatives of a Domestic Dog, with common ancestry to other Domestic Dogs? Or are they derivatives of one or more wild canids, with their occurrence in Australia and New Guinea explained either through natural dispersal or deliberate introduction by people? If the first of these postulates is true, then the Dingo and New Guinea Singing Dog should be treated nomenclaturally as *Canis familiaris*. If the second postulate is true, then these animals would be excluded from *Canis familiaris* and perhaps be treated either as subspecies of a different canid species (if they are each divergent from their wild progenitor), or as separate species in their own right if their wild progenitor is no longer extant.

Matters of evidence—origin of the Dingo and its distinguishing features

The origin of the Dingo

The origin of the Dingo cannot be considered without first understanding the phylogenetic origin and subsequent history of Domestic Dogs in general. There is general agreement from analyses of morphological and palaeontological evidence that Domestic Dogs originated through domestication of the Gray Wolf (e.g. Olsen & Olsen 1977; Clutton-Brock 1995; Germonpré *et al.* 2009, 2015; Ovodov *et al.* 2011; Larsen *et al.* 2012). More uncertainty surrounds the issues of exactly where and when domestication took place, and whether domestication occurred only once with subsequent geographic expansion or on multiple occasions in different geographic foci. Fine-scale interpretations of this kind may simply lie beyond the resolving power of the morphological and/or archaeological evidence.

Molecular approaches offer potential for finer scale resolution of domestication history and, the examination of breeding and selection regimes involved in the domestication process. This evidence is accumulating steadily and growing rapidly in sophistication, hence further refinements of evidence and interpretation can be expected in coming years. Nevertheless, in our view there is enough evidence in hand now to be confident of the main framework of the story. The critical evidence comes from investigation of three contrasting genetic components—the maternally inherited mitochondrial DNA (mtDNA; Vilà *et al.* 1997, 1999; Savolainen *et al.* 2002; Leonard *et al.* 2002; Pang *et al.* 2009; Pilot *et al.* 2010; Druzhkova *et al.* 2013; Thalman *et al.* 2013), the paternally inherited Y-chromosome (Bannasch *et al.* 2005; Sacks *et al.* 2008, 2013; Brown *et al.* 2011; Ding *et al.* 2012), and the biparental autosomal genes and other components of the nuclear genome (Wayne & O'Brien 1987; Lorenzini & Fico 1995; Garcia-Moreno *et al.* 1996; Hedrick *et al.* 1997; Lindblad-Toh *et al.* 2005; Gray *et al.* 2009; vonHoldt *et al.* 2010, 2011; Vaysse *et al.* 2011; Axelsson *et al.* 2013; Wang *et al.* 2013; Freedman *et al.* 2014; Skoglund *et al.* 2015).

At the broadest level, the corpus of genetic studies supports the notion that dogs (including Dingoes) originated from domestication of the Gray Wolf or its immediate ancestor (e.g. Pang *et al.* 2009; Ding *et al.* 2012; Larsen *et al.* 2012; Oskarsson *et al.* 2012; Skoglund *et al.* 2015). Variation in sampling coverage and genetic marker of choice has, not surprisingly, generated somewhat different perspectives in regard to the number and timing of domestication events, and their geographic focus. For example, Vilà *et al.*'s (1997) early analysis of mtDNA sequence variation suggested ancient, multiple origins of dogs from widely dispersed populations of Eurasian wolves; but with progressively more extensive sampling of both wolves and dogs, analysis of the same locus has favoured a quite different scenario—a single, more recent origin of the dog in East Asia (Savolainen *et al.* 2002; Pang *et al.* 2009). Most recently, Pang *et al.* (2009) argued that dogs were domesticated only once, from a Chinese Gray Wolf population, and probably coincident with the earliest experiments in rice cultivation south of the Yangtze River.

Recent genomic-scale analyses have yielded a different, though not incompatible, perspective on dog origins. These findings demonstrate that Domestic Dog genomes are no closer to the extant Chinese population of Gray Wolf than to any other regional wolf population (vonHoldt *et al.* 2010, 2011; Freedman *et al.* 2014). This observation implies either that dogs were domesticated prior to the diversification of present-day Gray Wolf populations or that the wild ancestors of Domestic Dogs are now extinct. If the latter interpretation is correct, one potential candidate is a wolf population of late Pleistocene age recorded from the region of Beringia (Leonard *et al.* 2007). This population was unusually robust and may have been adapted to predation on megafauna which, incidentally, were also targeted by contemporaneous human populations. A necessary corollary of this scenario is that the original East Asian wolf population was subsequently replaced (or heavily introgressed) by the genetically distinct, smaller-bodied wolf that occupies the area today; interestingly, there is mtDNA evidence for a comparable turnover of Gray Wolf populations in Europe during the early Holocene (Pilot *et al.* 2010).

Skoglund *et al.* (2015) tested this dual hypothesis of early dog domestication and lineage replacement among East Asian wolves by sequencing the genome of a 35,000 year old bone of a Siberian wolf. Their results confirm the genetic distinctness of dogs from a clade containing all extant wolves, although some evidence was found of ongoing genetic exchange between certain high latitude dog breeds and locally occurring wolf populations. The genome of the Siberian fossil wolf is closely related to the reconstructed common ancestor of extant dogs and wolves, thereby giving credence to the notion of an early divergence between the dog and wolf clades, probably within the time interval of 27,000–40,000 years ago. Dogs were subsequently maintained as a largely separate gene

pool by human management and subsequently came under increasingly rigorous and diverse selective regimes, while wolves underwent regional differentiation to produce the various regionally distinct sub-clades present in early historic times, some of which survive today. Under this scenario, the observed special mtDNA affinity between dogs and the Chinese wolf might either be due to retention of shared ancestral haplogroups in both lineages (and loss of these haplogroups in other regional wolf populations) or to an early introgression episode involving transfer of mtDNA between the two populations, followed by a selective sweep.

The earliest possible indications of domestication in *Canis lupus* come from Europe and pre-date the Last Glacial Maximum (Germonpré *et al.* 2009, 2015; Ovodov *et al.* 2011), as predicted by the early divergence hypothesis of Skoglund *et al.* (2015). However, uncontested dog remains date from considerably later in time. Two candidates for the earliest dog, both potentially dated to c. 14,000 years ago, are a single jaw fragment from Germany (Koop *et al.* 2000) and specimens from Palegawra in Iraq (Turnbull & Reed 1974; but see Uerpmann (1982) who regarded the age of the Palegawra specimens to be closer to 8,000 years). The earliest uncontested dogs from Southwest Asia are 9,000 years old (Wayne & O'Brien 1987; Goebel 1999) and claims of terminal Pleistocene dogs are based on non-diagnostic material (Leonard *et al.* 2002). The oldest dogs from China are c. 7,500 years old but the presence of dogs in North America in the interval c. 9,000 to 10,000 years ago (Wayne & O'Brien 1987; Grayson 1988; Clutton-Brock 1995) strongly supports their earlier occurrence in East Asia. Leonard *et al.* (2002) used mtDNA sequences to test and refute the alternative possibility that North American dogs were produced through indigenous domestication of American Gray Wolves. Their results support the notion that Domestic Dogs travelled to North America with people, most likely moving along the Beringian corridor in the interval 12,000 to 14,000 years ago (Fiedel 2000; Leonard *et al.* 2002).

The earliest Domestic Dogs were most likely used primarily by mobile hunter gatherer populations for cooperative hunting and camp security and they may not have been very different in appearance from their wild wolf relatives (Gompper 2014). Following the emergence in several parts of the world of more sedentary lifestyles based on animal herding and agriculture, probably starting around 15,000 years ago, Domestic Dogs appears to have come under various new selective regimes, leading to an accelerated phase of phenotypic divergence from wild wolves (Wayne 1993; Vilà *et al.* 1997; Corbett 2006). An interesting observation in this respect is the fact that most dogs show a copy number expansion at the amylase locus (AMY2B) (Axelsson *et al.* 2013), with only two copies usually present in wolves compared with an average 7.4-fold increase in dogs. Amylase locus expansion enhances the capacity of dogs to exploit a starch-rich diet, such as they might be provided with or might access if they fed on refuse from agricultural activity. Notable exceptions to the phenomenon of amylase expansion in dogs are the Dingo, which has two copies of AMY2B, the Basenji, a West African hunting dog, also with two copies, and the Siberian Husky, a breed historically associated with nomadic hunters of the Arctic, which has three to four copies (Axelsson *et al.* 2013; Freedman *et al.* 2014). The Dingo, Basenji and Husky are all widely regarded as 'ancient' breeds, a classification that implies a long history (> 500 years) of separate genetic identity and which distinguishes them from the suite of 'modern' breeds produced by intensive artificial breeding over the past few centuries. The likely antiquity of this adaptation is demonstrated by the occurrence of multiple copies in other 'ancient' breeds (Axelsson *et al.* 2013) including the Saluki (with 29 copies) that originated in the Fertile Crescent where Near East agriculture first flourished, and the New Guinea Singing Dog (with 12 copies) which similarly co-occurs with an early centre of agricultural innovation.

To summarise thus far, the Gray Wolf appears to have been the first animal species to be domesticated by humans. Although some doubt remains as to where and when this happened, it is increasingly likely that domestication commenced more than 20,000 years ago, well before the advent of agriculture and the widespread sedentism of human populations. Although genetic drift and presumably some behavioural and physiological selection began to take effect from the earliest periods, it was not until the advent of sedentary lives that dogs came under more vigorous selection regimes that led to dramatic alteration of their appearance. Nevertheless, due to their long history of close association with people, dogs are now well-differentiated genetically, morphologically and behaviourally from all extant Gray Wolf populations, and they have become a parataxon *sensu* Gentry *et al.* (1996).

Are the Dingo and the New Guinea Singing Dog part of this parataxon? Or are they independently derived from a regional population of Gray Wolves or some other related lineage, perhaps one that is potentially extinct? At one level this question has been convincingly resolved by the genomic-scale studies already discussed. Dingo samples were included in all three of the most comprehensive studies published to date (vonHoldt *et al.* 2010; Freedman *et al.* 2014; Skoglund *et al.* 2015)—in each case Dingoes were found to cluster with the other dogs, albeit with special status as one of the indigenous 'ancient' breeds that are spread across the globe. The New

Guinea Singing Dog was investigated by vonHoldt *et al.* (2010), but it too falls within the cluster that includes all of the other Domestic Dogs. As far as their broad genomic content is concerned the Dingo and the New Guinea Singing Dog were convincingly identified as members of the dog parataxon *Canis familiaris*. In other words, even though they may today exist in a feral state, they were almost certainly derived from a domestic lineage. Support for this proposal was given by Dwer and Minnegal (2016) who concluded that at the time of European colonisation, wild dogs and most, if not all, village dogs of New Guinea comprised a single though heterogeneous gene pool. They also suggested that at this time there is no firm basis from which to assign a unique Linnaean name to dogs that live as wild animals at high altitudes of New Guinea.

A domesticated origin for both of these Australasian ‘feral’ breeds is also strongly suggested by their presumed mode of dispersal and recorded histories of residency. As noted previously, various early naturalists including Gould (1859) and Darwin (1868) all clearly perceived the Dingo as a camp animal that had accompanied people from Asia through the intervening islands to Australia, and this view was later championed by Wood Jones (1921) and Macintosh (1975). To reach Australia through the Southeast Asian archipelago from the Asian mainland involves multiple journeys of at least 50 km over open sea (e.g. over Wallace’s Line), even at the low sea level of glacial maxima (Bellwood 1997). Natural dispersal of a wild dog between Asia and each of Australia and New Guinea is highly improbable, as is human transport of wild dogs as food or some other obscure purpose. Accordingly, the ancestors of the Australian Dingo and the New Guinea Singing Dog almost certainly accompanied people on these long water crossings as domestic animals.

The timing of the introduction of dogs into Australia and New Guinea in the Holocene is relatively well documented, however the exact pathway to Australia is unknown and remains the subject of debate (e.g. Fillios & Taçon 2016). The earliest Dingo remains in the Australian palaeontological and archaeological records date to approximately 3,500 years ago (Table 1) and occurrences of approximately 3,000 yrs BP are reported from south-eastern, South Australia and eastern New South Wales. Given that the fossil occurrences are all in southern Australia, and accepting Gollan’s (1984) argument that a period of 500 years is likely to have elapsed between a Dingo founder population in northern Australia and their widespread appearance as fossils, Corbett (2006) suggested that the Dingo would have arrived in Australia about 4,000 years ago.

TABLE 1. Dates and locations of the earliest records of fossil Dingoes in Australia. Taken from Corbett (2006), after Gollan (1984).

Date (years BP)	Location	Context	Reference
3,450 ± 95	SE Western Australia	Madura Cave	Milham and Thompson 1976
3,230 ± 100	New South Wales	Wombah Midden	Mulvaney 1975
3,170 ± 94	South Australia	Fromm’s Landing	Macintosh 1964
2,980 ± 90	South Australia	Devon Downs	Smith 1980
2,865 ± 57	New South Wales	Capertree 3	Johnson 1979
2,200 ± 96	Western Australia, Nullarbor	Thylacine Hole	Lowry and Merrilees 1969
1,680 ± 100	New South Wales	Burrill Lake	Lampert 1971
1,020 ± 40	South Australia	Mt. Burr	Gollan 1982

The available evidence thus suggests that the Australian Dingo and the New Guinea Singing Dog were introduced into their current geographic areas at least 10,000 years after the effective genetic separation of a Domestic Dog population from the ancestral wolf population.

To explore in greater detail the questions of where the Dingo and New Guinea Singing Dog might have originated, and how they might have come to Australia, it is instructive to turn to the evidence of the two uniparental genetic markers—the maternally inherited mtDNA and the paternally inherited Y chromosome. Each of these markers has proven invaluable for tracing the dispersal and population histories of both humans (Venter *et al.* 2001) and the various animals that have spread around the world in the company of humans, including a range of domesticates and commensals (The Bovine Genome Sequencing and Analysis Consortium *et al.* 2009; Archibald *et al.* 2010; Aplin *et al.* 2011; Suzuki *et al.* 2013).

mtDNA

The first substantial survey of dog mtDNA included four Dingoes (Vilà *et al.* 1997). These produced a single D-loop haplotype (designated A29) that was shared with various breeds of Domestic Dogs. A more comprehensive survey by Savolainen *et al.* (2004) included 211 Dingoes, 2 New Guinea Singing Dogs, and 19 archaeologically provenanced dogs from Polynesia. The Dingo samples yielded 20 distinct D-loop haplotypes, among which haplotype A29 was the most common (see also Sacks *et al.* 2013). Haplotype A29 is embedded within the broader haplotype diversity of Domestic Dogs, rather than being in either a peripheral or basal position, while the remaining 19 haplotypes found in Dingoes all differ from A29 by no more than two base pair substitutions. Other haplotypes derived from A29 include one that is exclusive to the New Guinea Singing Dogs and a few others found in dogs from East Asia (Eastern Siberia, Japan and Indonesia) and Arctic America. The Polynesian dogs yielded two different haplotypes neither of which is closely related to A29. Based on these findings Savolainen *et al.* (2004) drew three main conclusions: firstly, that the Dingo originated from domesticated dogs; secondly, that the Dingo has an East Asian rather than an Indian origin; and thirdly, that the original founder population that reached Australia was very small, possibly even a single pregnant female.

Subsequent analysis of mtDNA from many more Asian dog and wolf samples found the globally highest subclade diversity in East Asia, in particular in the region south of the Yangtze River (Pang *et al.* 2009). Based on this finding and aspects of the haplogroup distributions, Pang *et al.* (2009) inferred that dog domestication occurred only once, most likely in southern China in association with the earliest agricultural communities. Although they did not sequence any additional Dingo or New Guinea Singing Dog samples, their network diagrams (Pang *et al.* 2009: Figure 2b) show haplotype A29 to be peripheral to a predominantly East Asian subclade (group Ac) of Domestic Dog haplotypes. This finding reinforces the conclusion that Dingo and New Guinea Singing Dog mtDNA is the product of mutations that accumulated after the initial domestication of dogs. Of course this does not necessarily imply that other aspects of the Dingo and New Guinea Singing Dog genome are of similarly derived ancestry, since mtDNA introgression into the Dingo from another Domestic Dog population, either before or after initial colonisation of Australia, cannot be ruled out.

Pang *et al.* (2009) noted the apparent discrepancy between their conclusions regarding dog domestication and the archaeological record of Southeast Asia in which dogs make a comparatively late appearance compared with each of Europe and Southwest Asia. They attributed this to archaeological sampling methods and analytical effort.

Y chromosome

The paternally transmitted Y chromosome has received far less attention than mtDNA but nonetheless it provides important, complementary insights into the relationships of the Dingo and New Guinea Singing Dog to wolves and other dogs. Studies to date have focused either on Single Nucleotide Polymorphisms (SNPs; e.g. vonHoldt 2010 2011; Ardalan *et al.* 2012) that generally display a slower mutation rate than the mtDNA D-loop, or on Single Tandem Repeats (STRs or microsatellites: Brown *et al.* 2011) that evolve more rapidly than mtDNA D-loop. The most informative study to date is that of Sacks *et al.* (2013) which integrates the two sources of variation, using SNPs to establish an evolutionary framework and STRs to provide both finer scale detail and a time frame for Dingo and New Guinea Singing Dog introduction and isolation.

The majority of Dingoes and all New Guinea Singing Dogs share Y chromosome haplotype H60, which, while not found elsewhere, belongs to a 'Southeast Asian' clade (Brown *et al.* 2011; Ardalan *et al.* 2012; Sacks *et al.* 2013). A small number of Dingoes possess haplotypes H1 and H3 that occur more widely among Domestic Dogs; these are most likely the product of recent introgression from European dogs. Sacks *et al.* (2013) determined that haplotype H60 is most closely related to haplotype H5 which is recorded thus far in dogs from Taiwan, Cambodia, Japan and Siberia (Ding *et al.* 2011; Sacks *et al.* 2013). By contrast, geographically more proximate dogs from locations such as Bali, Brunei and the Philippines in island Southeast Asia, and from mainland Southeast Asia including Thailand, generally yield more distantly related SNP-defined haplotypes. Analysis of the combined SNP-STR dataset revealed a star-like evolutionary radiation of Y haplotypes among Dingoes, comparable to that observed in the mtDNA. Two of the Y haplotypes found in Dingoes are also present in New Guinea Singing Dogs; to date the latter have not yielded any unique haplotypes defined either by SNPs or combined SNPs-STRs (Sacks *et al.* 2013).

The Y chromosome data thus complement the mtDNA in suggesting a single origin for the Dingo and New

Guinea Singing Dog from within an Asian Domestic Dog stock. The two datasets are also in broad agreement insofar as they identify the Southeast Asian region as the homeland of modern Domestic Dog genetic diversity. Whereas interpretations of mtDNA diversification have postulated an early origin of Domestic Dogs in Southeast Asia, a conclusion that sits uncomfortably with the present lack of archaeological evidence for early dogs in this region, the analysis of the more rapidly evolving Y chromosome STRs suggests a possible three phase evolution of Domestic Dogs—the first phase involving widespread but relatively casual domestication of an ancestral wolf population; the second phase involving more intensive selective breeding of dogs in the context of early agricultural communities in East and Southeast Asia; and the third phase being the westward dispersal of these ‘new style’, more thoroughly domesticated dogs throughout Asia and on to Europe, with ultimate replacement of the more archaic breeds. This model not only accommodates the presence of early Domestic Dogs in the fossil record of Europe and the Middle East but also the genetic patterns observed in both mtDNA and Y chromosomes. It also throws the Dingo and New Guinea Singing Dog under a new spotlight as potential relicts of an early phase of dog evolution that predated the development of the contemporary dog breeds of Island Southeast Asia.

A recent phylogenetic analysis based upon mitochondrial and nuclear DNA suggests there are at least two distinct populations of Dingo in Australia, one in the northwest and the other in the southeast (Cairns & Wilton 2016). This study suggested these lineages split approximately 8300 years before present, outside Australia but within Oceania. A close relationship was also discovered between Dingoes and New Guinea Singing Dogs, which suggests the arrival of the Dingo into Australia occurred via the land bridge between New Guinea and Australia, although seafaring introductions could not be ruled out (Cairns & Wilton 2016). Interestingly, the results of the mitochondrial genome sequences placed New Guinea Singing Dogs closer to the southeast Dingoes than those from the northwest, undermining the prospective separate species status of both the Australian Dingo and New Guinea Singing Dog (Cairns & Wilton 2016).

How different is the Dingo from other dogs?

Our assertion, based on compelling genetic evidence, that the Dingo is a feral Domestic Dog and should be treated as such taxonomically, does not automatically imply that it is of no intrinsic scientific interest or conservation value. To the contrary, if the determination of the Dingo and the New Guinea Singing Dog as populations of an archaic lineage of Southeast Asian Domestic Dog is correct, these populations are of great significance for what they can reveal of the earlier stages of dog domestication. This makes them worthy of conservation in their own right (Fleming *et al.* 2014; Allen *et al.* 2015a; Archer-Lean *et al.* 2015). This same point has been made recently by Clutton-Brock (2015), who makes the case “that this unique dog should be recognised as part of the living history of Australia”; this leads her to follow Crowther *et al.* (2014) in calling it *Canis dingo*, although the context implies that she would regard this as simply a mechanism of highlighting its uniqueness and heritage value, rather than as a taxonomic statement. In this paper, we prefer to separate the issue of the Dingo’s heritage status from the matter of its taxonomic placement.

Morphology

Morphologically the Dingo is said to differ from Domestic Dogs of similar size and stature by having a relatively wider palate, longer rostrum, lower-crowned skull and relatively wider “top ridge” (i.e. the sagittal crest) of the skull (Crowther *et al.* 2014). The Crowther *et al.* (2014) study acknowledged that it was difficult to provide consistent and clear diagnostic features, and their morphological analyses showed considerable overlap between Domestic Dogs and Dingoes for most morphological characters. Morphometric overlap is apparent in all of the provided figures, and this is perhaps not surprising considering that Australian cattle dogs, which are known to have incorporated Dingo genes (Howard 1990), and Australian kelpies, which are suspected to have some Dingo ancestry, were included in the sample of *C. familiaris* (Crowther *et al.* 2014). A study by Gonzalez (2012) found that the Dingo presents clearly identifiable character states including: 1) low cranial height, 2) well developed and characteristically shaped occipital process, 3) large auditory bulla, 4) well developed angular process, and 5) a large diastema between lower premolar 2 (PM₂) and lower premolar 3 (PM₃). In contrast to these observations, Parr *et al.* (2016) showed that the morphology of pure and hybrid Dingoes overlaps greatly so that hybrid animals cannot be reliably distinguished from Dingoes on the basis of cranial metrics. They also found that hybridization

with dog breeds does not bring the Dingo cranial morphology towards that of the wolf. Corbett (1995) discovered dogs, mainly living as pariahs, in Thailand which were intermediate externally and craniodentally between the Dingo and other dogs, to the extent that he dubbed them “Thai dingoes”.

There is considerable variability in the colour of Dingoes but they can have five basic pelage colour combinations that include yellow, brown, ginger/red, black and white (Cairns *et al.* 2011; Crowther *et al.* 2014). In addition to these principal colours the fur on the tip of the tail and each of the four paws is usually white. Some of these colours are common in other breeds of dogs, e.g. basenjis. The vestigial first toes of the hind legs, known as dew claws, are absent in wild canids including wolves and rarely seen in Dingoes. They are commonly present (but not universally so) in large Domestic Dog breeds, and usually reduced or absent in the smaller ones such as poodles and Pekinese (Kadletz 1932; Alberch 1985; Ciucci *et al.* 2003; Corbett 2004). Although in some breeds the hind leg dew claws are maintained through artificial selection (e.g., Great Pyrenees and St. Bernard), in others (e.g. Bernese, Newfoundland) it keeps reappearing in the population despite being consistently selected against (Alberch 1985).

Behaviour

Dingoes were captured and reared as pets by some of the earliest European settlers to live in Australia (Tench 1789). It was noted as early as 1789 by Governor Phillip, who kept a Dingo, that they have much of the manners of a dog but were of a very savage nature and that they neither bark nor growl. Hunter (1793) described how one Dingo reared from a young puppy could not be cured of its savageness—it took every opportunity to snap off the head of a fowl, or worry a pig, and would do it in defiance of correction. He also noted that they are a very good-natured animal when domesticated, but believed them to be impossible to cure of their “savageness”, which all seemed to possess. Wood Jones (1925) suggested that a Dingo pup when reared as a dog is a gentle affectionate and faithful creature, a typical dog at its best, its only drawback being its dismal howl. Dingoes seem unable to bark like most modern Domestic Dog breeds, although they can make various vocalisations, but they are not unique among dogs in this respect as the Basenji typically does not bark.

Since the early European observations, studies of wild and captive Dingoes have revealed that they have a well-developed social structure. Under normal conditions they form stable social groups or ‘packs’ that occupy discrete territories with little overlap between adjacent packs. However, pack structure tends to fragment during drought (Thomson 1992a; Corbett 2008) and during times of plenty when exclusive home ranges are not necessary and defending them is dangerous for individuals (Newsome *et al.* 2013b). In captivity they are typically independent and aloof animals that are challenging to train and domesticate compared with typical Domestic Dogs with a more recent ancestry (Jackson 2003). However, individual Dingoes differ in personality and tractability, which could account for the varying descriptions of the characters of re-domesticated Dingoes. This variability is also expressed in other dogs, where there are general recognisable breed-related temperaments, which are mediated by differences among individuals (McGreevy *et al.* 2013). Studies of feral dogs in Africa and India (e.g. Manor & Saltz 2004; Pal 2001, 2008) showed they have similar behaviours and social structures to free-ranging Dingoes in Australia.

Reproduction

Female Dingoes generally have a single annual breeding season, though males are continuously fertile in most regions (Newsome *et al.* 1973; Catling 1979; Clutton-Brock *et al.* 1990). Most matings take place between March and June with the majority of births occurring between May and August, though there is some variation to this timing due to location and drought (Catling *et al.* 1992; Thompson 1992b). When transferred to the northern hemisphere, Dingoes maintain their pattern of autumn mating and winter whelping, after circadian adjustment (Barker & Macintosh 1979; Kleiman 1968). In contrast to various ancient breeds of dogs, most modern domestic breeds do not have a seasonal pattern of breeding and can breed twice per year with females coming into estrus every seven months on average (Harrop 1960; Christie & Bell 1971; Lord *et al.* 2013). Captive-bred hybrids between a Dingo and a typical Domestic Dog show a breeding pattern similar to that of Domestic Dogs with two breeding seasons that can occur throughout the year (Newsome *et al.* 1973; Catling 1979). By contrast, observations from free-ranging populations of admixed Dingoes and feral Domestic Dogs have revealed a single annual breeding season but with a broader timing of matings and births (Jones & Stevens 1988) and less seasonal change in testis weight.

A pattern of reproduction in which there is only one breeding season per year also occurs in the Gray Wolf (Mech 1970; Zimen 1975) and several other ancient breeds of dogs including the pariah dogs in Thailand (and some other populations in Asia) that reproduce between August and September (Oppenheimer & Oppenheimer 1975; Clutton-Brock *et al.* 1990). Urban free-ranging dogs in West Bengal in India have also been recorded to have only a single breeding cycle with matings being observed from August to January (Pal 2001). The African Basenji (Scott and Fuller, 1965) and the New Guinea Singing Dog (Kleimen 1968; Koler-Matznick *et al.* 2000) also breed once each year.

Hybridization and introgression between Dingoes and Domestic Dogs

As early as 1925 Wood Jones noted that purebred Dingoes were hard to come by as they so freely cross with farm dogs. The use of skull measurements to differentiate pure Dingoes from Domestic Dogs and hybrids was initiated by Macintosh (1975) and further refined by Newsome *et al.* (1980), Newsome and Corbett (1982), and Corbett (1985, 1995). These equations have subsequently been used by various studies throughout Australia (but see criticisms of these approaches by Jones 1990, 2009), often conducted in conjunction with a visual phenotype assessment (e.g. Newsome & Corbett 1985; Jones 1990; Corbett 1995, 2001; Elledge *et al.* 2008; Gonzalez 2012; Crowther *et al.* 2014).

Initial attempts to genetically identify Dingoes from dogs using isozyme markers were not successful (Cole *et al.* 1977). With the development of more sensitive microsatellite markers, it is theoretically possible to distinguish purebred Dingoes from Dingo-dog hybrids and feral dog breeds (Wilton *et al.* 1999; Wilton 2001). However, Daniels and Corbett (2003) and Elledge *et al.* (2006) question the validity of this method because any contemporary 'pure' Dingo is potentially contaminated through some degree of introgression of modern dog genes, since European settlement. Stephens *et al.* (2015) recently documented strong geographic structure in microsatellite profiles of Dingoes and feral dogs across Australia, and made a convincing case that remote parts of central and western Australia support the only 'pure' Dingo populations and that all southern and eastern populations are interbred with modern Domestic Dogs to varying degrees, irrespective of their appearance.

Several studies have endeavoured to assess the concordance of genetic analysis, skull morphology and visual appearance for determining Dingo purity. A study by Elledge *et al.* (2008) found that 70% of animals sampled were assigned the same status by all three methods, 18% the same by genetic and skull methods, 7% by genetic and visual methods; and only 4% by skull and visual methods. Only one animal (or 1%) was given a different status by all three methods. Results of pair-wise comparisons of identification techniques identified a significant relationship between genetic and skull methods, but not between either of these and visual methods. As hybrid animals were more easily identified by visual characters than were Dingoes, they suggested culling obvious hybrids based on visual characteristics, such as sable and patchy coat colours, to slow the process of hybridisation. Another study by Radford *et al.* (2012) compared the use of skull morphology and visual assessment methods for classifying wild canids in south-eastern New South Wales. They found that these two methods did not yield similar results to each other and that skull dimensions had enlarged over time which was attributed to hybridisation.

All studies are in agreement that the prevalence of hybrids is greater in highly populated and longer-settled areas, such as south-east Australia, than in remote areas, such as north and central Australia (Newsome & Corbett 1982 1985; Corbett 1985, 1995; Woodall *et al.* 1996; Stephens *et al.* 2015). The greater proportion of hybrids in south-eastern Australia likely reflects both the longer history of interbreeding and genetic introgression, and the greater probability of contemporary contact that Dingoes, and hybrids, have with modern Domestic Dogs (Newsome & Corbett 1985). The prevalence of Dingo X modern dog hybrids, it has been claimed, has been increasing over time (Corbett 1995, 2001; Elledge *et al.* 2006) resulting in concern that hybridisation is a major threat to the long-term purity of the Dingo (Major 2009; Radford *et al.* 2012).

For the present matter under consideration, the key conclusions are: 1) that Dingoes can and do interbreed freely with other dogs; and 2) that the interbreeding is resulting in the Dingo genome being naturally and progressively introgressed by Domestic Dog genomes.

Discussion

Our review of relevant information on the evolutionary history and biology of the Dingo leads us to two main conclusions. First, that the wild Dingo of Australia is a feral population derived from a domesticated, rather than a wild ancestral population of a domesticated. And second, that irrespective of any morphological or behavioural features that may allow a Dingo to be distinguished from some or all Domestic Dog breeds, it remains genetically and reproductively compatible with modern Domestic Dogs in Australia and is currently in the process of losing its distinctiveness through interbreeding with feral Domestic Dogs and extant hybrids.

The first of these conclusions is certainly valid also for the New Guinea Singing Dog. This population has some commonality of origin with the Dingo, though perhaps with a more complex subsequent history due to contact during late prehistoric times with other breeds of dog carried by Austronesian and other seafarers. Less is known regarding the extent of natural interbreeding between the New Guinea Singing Dog and Domestic Dog breeds; nevertheless, from captive breeding it is clear that there is no genetic incompatibility that would inhibit successful interbreeding and introgression.

Available genetic evidence also points to the Dingo being an ancient breed of dog that probably originated in Southeast Asia and spent much of its early history in this region, presumably as a domestic breed. Sometime around 4,000 years ago, the Dingo was transported to Australia by humans where it continued to be kept as a domestic animal but also became established as a feral population, with regular genetic interchange continuing between the domestic and feral stocks. Subsequently, the ancestral Southeast Asian Dingo stock either interbred with more recently derived Domestic Dog breeds or was replaced without significant admixture. Which of these scenarios is more accurate will become clear as further genetic studies are undertaken, combining the power of modern comparative genomics and refinements in ancient DNA methods to allow prehistoric samples to be included in future analyses.

In light of these conclusions, and taking into account the recommended current practice for taxonomic nomenclature of the domesticateds, as embodied in Opinion 2027 of the ICZN (2003), recent attempts to treat each of the Australian Dingo and the New Guinea Singing Dog as distinct species of canid are clearly unsupported. Dingoes and New Guinea Singing Dogs are feral Domestic Dogs and, as such, they must be treated taxonomically as breeds or varieties of *C. familiaris*. Furthermore, as feral domesticateds, neither variety can be recognised taxonomically as a subspecies, irrespective of whether or not they can be diagnosed by any combination of morphological, behavioural and genetic characters.

Although these conclusions and nomenclatural ramifications deny the Dingo or New Guinea Singing Dog any formal taxonomic status, they do not diminish the importance of either population. The presence of the Dingo on the Australian mainland prior to the advent Europeans is acknowledged in legislation (*Environmental Protection and Biodiversity Conservation Act, 1999*), in which it is considered part of the 'native' biota and hence worthy of conservation. To many Australian Indigenous peoples the Dingo maintains important cultural, spiritual and aesthetic values (Corbett 1995; Smith 2015) and act as companions, protectors and hunting dogs (Balme & O'Connor 2016). Since European settlement, the Dingo has become an icon and many people value seeing a 'pure' Dingo in the wild—this provides economic value to the tourism industry in places such as Fraser Island and in the national parks of the Northern Territory (Fleming *et al.* 2001). In addition, it is possible that Dingoes can suppress introduced Red Foxes (*Vulpes vulpes*) and feral Domestic Cats and thereby be important in the conservation of Australia's mesopredator-threatened fauna and ecosystems (Johnson *et al.* 2007; Ritchie & Johnson 2009; Letnic *et al.* 2009, 2012; Allen *et al.* 2015b), although this suggestion is yet to be supported experimentally (Allen *et al.* 2013). Therefore, irrespective of its taxonomic status, the Dingo maintains an important standing and warrants conservation as Australia's indigenous dog breed or variety (Fleming *et al.* 2001; Corbett 2001; Elledge 2006; Clutton-Brock 2015). Much less is known of the ecological role of the New Guinea Singing Dog, for which even its distribution remains poorly documented.

Conclusion

The Dingo and New Guinea Singing Dog are feral derivatives of ancient breeds of Domestic Dogs that were carried to Australia and New Guinea during prehistoric times by humans. Under Opinion 2027 of the ICZN (2003),

feral derivatives of domesticates cannot be treated as distinct species. Both populations represent ancient breeds or varieties of the Domestic Dog *Canis familiaris* and should be referred to as such. Subspecies designation is not appropriate under current nomenclatural practice.

Denial of formal taxonomic status for the Dingo and New Guinea Singing Dog does not in any way diminish their scientific, ecological and cultural significance. Both varieties of dog are likely representative of an earlier stratum of Domestic Dogs that were later replaced across most of Asia and Europe by novel dog breeds produced in the context of agricultural communities in East and Southeast Asia. As such they are of considerable scientific interest. For the Dingo at least, there are also grounds to believe that the feral population plays a key ecological role that counters some of the negative impacts of other introduced species, notably the Red Fox and feral Domestic Cats.

Conservation of the Dingo (and probably also the New Guinea Singing Dog) as an indigenous variety of dog poses considerable problems. The Dingo genome is already heavily mixed across a large part of its range with genetic components derived from feral European Domestic Dog breeds. Genetic admixture is ongoing across much of the continent and there are no barriers to genetic introgression into even the most remote populations of Dingoes. Culling of feral dogs and obvious 'hybrid' individuals based on external appearance may slow the process but as there is no simple relationship between genetic 'purity' and physical appearance, this is at best a blunt instrument. Captive breeding of 'pure' Dingoes is probably the only way to ensure the long-term survival of the variety. The same conclusion probably also applies for the New Guinea Singing Dog, although the time frame for action may be longer due to the remoteness of some montane populations from human populations and their Domestic Dogs.

References

- Alberch, P. (1985) Developmental constraints: why St. Bernard often have extra digit and poodles never do. *American Naturalist*, 126 (3), 430–433.
<https://doi.org/10.1086/284428>
- Allen, B., Fleming, P.J.S., Allen, L.R., Engeman, R.M., Ballard, G. & Leung, L.K.-P. (2013) As clear as mud: a critical review of the evidence for the ecological role of the Australian dingo. *Biological Conservation*, 159, 158–174.
<https://doi.org/10.1016/j.biocon.2012.12.004>
- Allen, B.L., Higginbottom, K., Bracks, J.H., Davies, N. & Baxter, G.S. (2015a) Balancing dingo conservation with human safety on Fraser Island: the numerical and demographic effects of humane destruction of dingoes. *Australasian Journal of Environmental Management*, 22 (2), 197–215.
<https://doi.org/10.1080/14486563.2014.999134>
- Allen, B.L., Allen, L.R. & Leung, L.K.-P. (2015b) Interactions between two naturalised invasive predators in Australia: are feral cats suppressed by dingoes? *Biological Invasions*, 17, 761–776.
<https://doi.org/10.1007/s10530-014-0767-1>
- Aplin, K.P., Suzuki, H., Chinen, A.A., Chesser, R.T., ten Have, J., Donnellan, S.C., Austin, J., Frost, A., Gonzalez, J.-P., Herbreteau, V., Catzeflis, F., Soubrier, J., Fang, Y.-P., Robins, J., Matisoo-Smith, E., Bastos, A.D.S., Maryanto, I., Sinaga, M.H., Denys, C., Yap, G., Van Den Bussche, R.A., Conroy, C., Rowe, K. & Cooper, A. (2011) Multiple geographic origins of commensalism and complex dispersal history of black rats. *PLoS ONE*, 6 (11), e26357.
<https://doi.org/10.1371/journal.pone.0026357>
- Archer-Lean, C., Wardell-Johnson, A., Conroy, G. & Carter, J. (2015) Representations of the dingo: contextualising iconicity. *Australasian Journal of Environmental Management*, 22 (2), 181–196.
<https://doi.org/10.1080/14486563.2014.985268>
- Archibald, A.L., Cockett, N.E., Dalrymple, B.P., Faraut, T., Kijas, J.W., Maddox, J.F., McEwan, J.C., Oddy, H.V., Raadsma, H.W. & Wade, C. (2010) The sheep genome reference sequence: a work in progress. *Animal Genetics*, 41 (5), 449–453.
<https://doi.org/10.1111/j.1365-2052.2010.02100.x>
- Ardalan, A., Oskarsson, M., Natanaelsson, C., Wilton, A., Ahmadian, A. & Savolainen, P. (2012) Narrow genetic basis for the Australian dingo confirmed through analysis of paternal ancestry. *Genetica*, 140 (1–3), 65–73.
<https://doi.org/10.1007/s10709-012-9658-5>
- Atkinson, J. (1826) *An Account of the State of Agriculture and Grazing in New South Wales*. J Cross, London, 146 pp.
- Axelsson, E., Ratnakumar, A., Arendt, M.-J., Maqbool, K., Webster, M.T., Perloski, M., Liberg, O., Arnemo, J.M., Hedhammar, A. & Lindblad-Toh, K. (2013) The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, 495 (7441), 360–364.
<https://doi.org/10.1038/nature11837>
- Baker, R.J. & Bradley, R.D. (2006) Speciation in mammals and the genetic species concept. *Journal of Mammalogy*, 87 (4),

643–662.

<https://doi.org/10.1644/06-MAMM-F-038R2.1>

- Balme, J. & O'Connor, S. (2016) Dingoes and Aboriginal social organization in Holocene Australia. *Journal of Archaeological Science: Reports*, 7, 775–781.
- Bannasch, D., Bannasch, M., Ryun, J., Famula, T. & Pedersen, N. (2005) Y chromosome haplotype analysis in purebred dogs. *Mammalian Genome*, 16 (4), 273–280.
<https://doi.org/10.1007/s00335-004-2435-8>
- Barker, B.C.W. & Macintosh, A. (1979) The dingo—a review. *Archaeology and Physical Anthropology in Oceania*, 14 (1), 27–53.
- Bellwood, P. (1997) *Prehistory of the Indo-Malaysian Archipelago*. University of Hawaii Press, Honolulu, 384 pp.
- Bino, R. (1996) Notes on behaviour of New Guinea singing dogs (*Canis lupus dingo*). *Science in New Guinea*, 22, 43–47.
- Boddaert, P. (1785) *Elenchus Animalium. Volume I. Sistens Quadrupedia huc usque nota eorumque varietates*. C.R. Hake, Rotterdam, 174 pp.
- Bohlken, H. (1958) Vergleichende Untersuchungen an Wildrindern (Tribus Bovini Simpson, 1945). *Zoologische Jahrbücher. Abteilung für Allgemeine Zoologie und Physiologie der Tiere*, 68, 113–202.
- Bohlken, H. (1961) Der Kouprey, *Bos (Bibos) sauveli* Urbain 1937. *Zeitschrift für Säugetierkunde*, 26, 193–254.
- Brown, S.K., Pedersen, N.C., Jafarishorijeh S., Bannasch, D.L., Ahrens, K.D., Wu, J.T., Okon, M. & Sacks, B.N. (2011) Phylogenetic distinctiveness of Middle Eastern and Southeast Asian village dog Y chromosomes illuminates dog origins. *PLoS ONE*, 6, e28496.
<https://doi.org/10.1371/journal.pone.0028496>
- Butler, J.R.A., du Toit, J.T. & Bingham, J. (2004) Free-ranging Domestic Dogs (*Canis familiaris*) as predators and prey in rural Zimbabwe: threats of competition and disease to large wild carnivores. *Biological Conservation*, 115 (3), 369–378.
[https://doi.org/10.1016/S0006-3207\(03\)00152-6](https://doi.org/10.1016/S0006-3207(03)00152-6)
- Cairns, K.M., Wilton, A.N. & Ballard, J.W.O. (2011) The identification of dingoes in a background of hybrids. In: Urbano, K.V. (Ed.), *Advances in Genetics Research*. Nova Science Publishers, New York, pp. 309–327.
- Cairns, K.M. & Wilton, A.N. (2016) New insights on the history of canids in Oceania based on mitochondrial and nuclear data. *Genetica*, 144, 553–565.
<https://doi.org/10.1007/s10709-016-9924-z>
- Catling, P.C. (1979) Seasonal variation in plasma testosterone and the testis in captive male dingoes, *Canis familiaris dingo*. *Australian Journal of Zoology*, 27 (6), 939–944.
<https://doi.org/10.1071/zo9790939>
- Catling, P.C., Corbett, L.K. & Newsome, A.E. (1992) Reproduction in captive and wild dingoes (*Canis familiaris dingo*). *Wildlife Research*, 19 (2), 195–205.
<https://doi.org/10.1071/WR9920195>
- Christie, D.W. & Bell, E.T. (1971) Some observations on the seasonal incidence and frequency of oestrus in breeding bitches in Britain. *Journal of Small Animal Practice*, 12 (3), 159–167.
<https://doi.org/10.1111/j.1748-5827.1971.tb06213.x>
- Ciucci, P., Lucchini, V., Boitani, L. & Randi, E. (2003) Dewclaws in wolves as evidence of admixed ancestry with dogs. *Canadian Journal of Zoology*, 81 (12), 2077–2081.
<https://doi.org/10.1139/Z03-183>
- Clutton-Brock, J., Corbet, G.B. & Hills, M. (1976) A review of the family Canidae, with a classification by numerical methods. *Bulletin of the British Museum (Natural History), Zoology Series*, 29 (3), 117–199.
<https://doi.org/10.5962/bhl.part.6922>
- Clutton-Brock, J., Corbett, L.K., Harden, B. & Robertshaw, J. (1990) Dingo (*Canis familiaris dingo*). In: Ginsberg, J.R. & Macdonald, D.W. (Eds.), *Foxes, Wolves, Jackals and Dogs: An Action Plan for the Conservation of Canids*. International Union for Conservation of Nature and Natural Resources, Gland, pp. 53–54.
- Clutton-Brock, J. (1995) Origins of the dog: domestication and early history. In: Serpell, J. (Ed.), *Domestic Dog: Its Evolution, Behavior and Interactions with People*. Cambridge University Press, Cambridge, pp. 2–19.
- Clutton-Brock, J. (2015) Naming the scale of nature. In: Behie, A.M. & Oxenham, M.F. (Eds.), *Taxonomic Tapestries: the Threads of Evolutionary, Behavioural and Conservation Research*. Australian National University Press, Canberra, pp.171–182.
- Cole, S.R., Baverstock, P.R. & Green, B. (1977) Lack of genetic differentiation between Domestic Dogs and dingoes at a further 16 loci. *Australian Journal of Experimental Biology and Medical Science*, 55 (2), 229–232.
<https://doi.org/10.1038/icb.1977.17>
- Corbet, G.B. & Clutton-Brock, J. (1984) Appendix: Taxonomy and nomenclature. In: Mason, I.L. (Ed.), *Evolution of Domesticated Animals*. Longman, London, pp. 434–438.
- Corbett, L.K. (1985) Morphological comparisons of Australian and Thai dingoes: a reappraisal of dingo status, distribution and ancestry. *Proceedings of the Ecological Society of Australia*, 13, 277–291.
- Corbett, L. (1995) *The Dingo in Australia and Asia. 1st Edition*. J.B. Books, Marlestone, 200 pp.
- Corbett, L. (2001) The conservation status of the dingo *Canis lupus dingo* in Australia, with particular reference to New South Wales. In: Dickman, C.R. & Lunney, D. (Eds.), *A Symposium on the Dingo*. Royal Zoological Society of New South

- Wales, Sydney, pp. 10–19.
- Corbett, L. (2004) Dingo. In: Sillero-Zubiri, C., Hoffmann, M. & Macdonald, D.W. (Eds.), *Canids: Foxes, Wolves, Jackals and Dogs*. International Union for Conservation of Nature and Natural Resources, Gland, pp. 223–230.
- Corbett, L. (2006) The Australasian Dingo. In: Merrick, J.R., Archer, M., Hickey, G.M. & Lee, M.S.Y. (Eds.), *Evolution and Biogeography in Australia*. Auscipub Pty Ltd., Sydney, pp. 745–751.
- Corbett, L. (2008) Dingo *Canis lupus*. In: Van Dyck, S. & Strahan, R. (Eds.), *The Mammals of Australia*. New Holland, Sydney, pp. 737–739.
- Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, 545 pp.
- Cracraft, J. (1983) Species concepts and speciation analysis. *Current Ornithology*, 1, 159–187.
https://doi.org/10.1007/978-1-4615-6781-3_6
- Crowther, M.S., Fillios, M., Colman, N. & Letnic, M. (2014) An updated description of the Australian dingo (*Canis dingo* Meyer, 1793). *Journal of Zoology*, 293 (3), 192–203.
<https://doi.org/10.1111/jzo.12134>
- Daniels, M.J. & Corbett, L. (2003) Redefining introgressed protected mammals: when is a wildcat a wildcat and a dingo a wild dog? *Wildlife Research*, 30 (3), 213–218.
<https://doi.org/10.1071/WR02045>
- Darwin, C. (1868) *The Variation of Animals and Plants Under Domestication*. 2nd Edition. John Murray, London, 411 pp.
- Dennler de La Tour, G. (1968) Zur Frage der Haustier-Nomenklatur. *Säugetierkundliche Mitteilungen*, 16, 1–20.
- Desmarest, A.G. (1821) *Mammalogie, ou description des espèces de mammifères. Premier Partie, contenant les orders des bimanes, des quadrumanes et des carnassiers*. V. Agasse, Paris, 547 pp.
<https://doi.org/10.5962/bhl.title.59887>
- de Queiroz, K. (2007) Species concepts and species delimitation. *Systematic Biology*, 56 (6), 879–886.
<https://doi.org/10.1080/10635150701701083>
- Ding, Z.-L., Oskarsson, M., Ardalán, A., Angleby, H., Dahlgren, L.-G., Tepeli, C., Kirkness, E., Savolainen, P. & Zhang, Y.-P. (2012) Origins of Domestic Dog in Southern East Asia is supported by analysis of Y-chromosome DNA. *Heredity*, 108 (5), 507–514.
<https://doi.org/10.1038/hdy.2011.114>
- Dinets, V. (2015) The Canis tangle: a systematics overview and taxonomic recommendations. *Vavilovskii Zhurnal Genetiki i Seleksii—Vavilov Journal of Genetics and Breeding*, 19, 286–291.
<https://doi.org/10.18699/VJ15.036>
- Druzhkova, A.S., Thalmann, O., Trifonov, V.A., Leonard, J.A., Vorobieva, N.V., Ovodov, N.D., Graphodatsky, A.S. & Wayne, R.K. (2013) Ancient DNA analysis affirms the canid from Altai as a primitive dog. *PLoS ONE*, 8 (3), e57754.
<https://doi.org/10.1371/journal.pone.0057754>
- Dwyer, P.D. & Minnegal, M. (2016) Wild dogs and village dogs in New Guinea: were they different? *Australian Mammalogy*, 38, 1–11.
<https://doi.org/10.1071/AM15011>
- Elledge, A.E., Leung, L.K.P., Allen, L.R., Firestone, K. & Wilton, A.N. (2006) Assessing the taxonomic status of dingoes *Canis familiaris dingo* for conservation. *Mammal Review*, 36 (2), 142–156.
<https://doi.org/10.1111/j.1365-2907.2006.00086.x>
- Elledge, A.E., Allen, L.R., Carlsson, B.L., Wilton, A.N. & Leung, L.K.P. (2008) An evaluation of genetic analyses, skull morphology and visual appearance for assessing dingo purity: implications for dingo conservation. *Wildlife Research*, 35 (8), 812–820.
<https://doi.org/10.1071/WR07056>
- Etheridge, R. Jr. (1916) The cylindro-conical and cornute stone implements of western New South Wales; The warrigal, or 'Dingo' introduced or indigenous? *Memoirs of the Geological Survey of New South Wales*, Ethnological Series, 2, 1–70.
- Fiedel, S.J. (2000) The peopling of the New World: Present evidence, new theories, and future directions. *Journal of Archaeological Research*, 8 (1), 39–103.
<https://doi.org/10.1023/A:1009400309773>
- Fillios, M.A. & Taçon, P.S.C. (2016) Who let the dogs in? A review of the recent genetic evidence for the introduction of the dingo to Australia and implications for the movement of people. *Journal of Archaeological Science: Reports*, 7, 782–792.
<https://doi.org/10.1016/j.jasrep.2016.03.001>
- Finlayson, H.H. (1939) On mammals from the Lake Eyre Basin. Part IV. The Monodelphia. *Transactions of the Royal Society of South Australia*, 63, 88–118.
- Fleming, P., Corbett, L., Harden, R. & Thompson, P. (2001) *Managing the Impacts of Dingoes and Other Wild Dogs*. Bureau of Rural Sciences, Canberra, 186 pp.
- Fleming, P.J.S., Allen, B.L., Allen, L.R., Ballard, G., Bengsen, A.J., Gentle, M.N., McLeod, L.J., Meek, P.D. & Saunders, G.R. (2014) Management of wild canids in Australia: free-ranging dogs and red foxes. In: Glen, A.S. & Dickman, C.R. (Ed.), *Carnivores of Australia: Past, Present and Future*. CSIRO Publishing, Melbourne, pp. 105–149.
- Frankham, R., Ballou, J.D., Eldridge, M.D.B., Lacy, R.C., Ralls, K., Dudash, M.R. & Fenster, C.B. (2011) Predicting the probability of outbreeding depression. *Conservation Biology*, 25, 465–475.
<https://doi.org/10.1111/j.1523-1739.2011.01662.x>

- Frankham, R., Ballou, J.D., Dudash, M.R., Eldridge, M.D.B., Fenster, C.B., Lacy, R.C., Mendelson III, J.R., Porton, I.J., Ralls, K. & Ryder, O.A. (2012) Implications of different species concepts for conserving biodiversity. *Biological Conservation*, 153, 25–31.
<https://doi.org/10.1016/j.biocon.2012.04.034>
- Freedman, A.H., Gronau, I., Schweizer, R.M., Ortega-Del Vecchyo, D., Han, E., Silva, P.M., Galaverni, M., Fan, Z., Marx, P., Lorente-Galdos, B., Beale, H., Ramirez, O., Hormozdiari, F., Alkan, C., Vilà, C., Squire, K., Geffen, E., Kusak, J., Boyko, A.R., Parker, H.G., Lee, C., Tadiogola, V., Siepel, A., Bustamante, C.D., Harkins, T.T., Nelson, S.F., Ostrander, E.A., Marques-Bonet, T., Wayne, R.K. & Novembre, J. (2014) Genome sequencing highlights the dynamic early history of dogs. *PLoS Genetics*, 10, e1004016.
<https://doi.org/10.1371/journal.pgen.1004016>
- French, D.D., Corbett, L.K. & Easterbee, N. (1988) Morphological discriminants of Scottish wildcats (*Felis silvestris*), domestic cats (*F. catus*) and their hybrids. *Journal of Zoology*, 214, 235–259.
<https://doi.org/10.1111/j.1469-7998.1988.tb04719.x>
- García-Moreno, J., Matocq, M.D., Roy, M.S., Geffen, E. & Wayne, R.K. (1996) Relationships and genetic purity of the endangered Mexican Wolf based in analysis of microsatellite loci. *Conservation Biology*, 10 (2), 376–389.
<https://doi.org/10.1046/j.1523-1739.1996.10020376.x>
- Gentry, A., Clutton-Brock, J. & Groves, C.P. (1996) Case 3010. Proposed conservation of usage of mammal specific names based on wild species which are antedated by or contemporary with those based on domestic animals. *Bulletin of Zoological Nomenclature*, 53, 28–37.
<https://doi.org/10.5962/bhl.part.14102>
- Gentry, A., Clutton-Brock, J. & Groves, C.P. (2004) The naming of wild animal species and their domestic derivatives. *Journal of Archaeological Science*, 31 (5), 645–651.
<https://doi.org/10.1016/j.jas.2003.10.006>
- Geraldes, A., Ferrand, N. & Nachman, M.W. (2006) Contrasting patterns of introgression at X-linked loci across the hybrid zone between subspecies of the European rabbit (*Oryctolagus cuniculus*). *Genetics*, 173 (2), 919–933.
<https://doi.org/10.1534/genetics.105.054106>
- Germonpré, M., Sablin, M.V., Stevens, R.E., Hedges, R.E.M., Hofreiter, M., Stiller, M. & Deprés, V.R. (2009) Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes. *Journal of Archaeological Science*, 36 (2), 473–490.
<https://doi.org/10.1016/j.jas.2008.09.033>
- Germonpré, M., Sablin, M.V., Lázničková-Galetová, M., Deprés, V., Stevens, R.E., Stiller, M. & Hofreiter, M. (2015) Palaeolithic dogs and Pleistocene wolves revisited: a reply to Morey (2014). *Journal of Archaeological Science*, 54, 210–216.
<https://doi.org/10.1016/j.jas.2014.11.035>
- Goebel, T. (1999) Pleistocene human colonization of Siberia and peopling of the Americas: An ecological approach. *Evolutionary Anthropology*, 8 (6), 208–227.
[https://doi.org/10.1002/\(sici\)1520-6505\(1999\)8:6<208::aid-evan2>3.0.co;2-m](https://doi.org/10.1002/(sici)1520-6505(1999)8:6<208::aid-evan2>3.0.co;2-m)
- Gollan, J.K. (1982) *Prehistoric dingo*. Unpublished PhD thesis, Australian National University, Canberra, 463 pp.
- Gompper, M. (2014) The dog-human-wildlife interface: assessing the scope of the problem. In: Gompper, M. (Ed.), *Free-ranging Dogs and Wildlife Conservation*. Oxford University Press, Oxford, pp. 9–54.
- Gonzalez, A. (2012) *The Pariah case: Some comments on the origin and evolution of primitive dogs and on the taxonomy of related species*. PhD Thesis, Australian National University, Canberra, 362 pp.
- Gould, J. (1859 [1845–1863]) *The Mammals of Australia. Vol. III*. The Author, London, 2 pls. [text to pls 51–52]
- Gray, J.E. (1826) Appendix B. Vertebrata. Mammalia. In: King, P.P. (Ed.), *Narrative of a Survey of the Intertropical and Western Coasts of Australia. Performed between the years 1818 and 1822. With an Appendix, containing various subjects relating to hydrography and natural history. Vol. 2*. J. Murray, London, pp. 412–415.
- Gray, M.M., Granka, J., Bustamante, C.D., Sutter, N., Boyko, A., Zhu, L., Ostrander, E.A. & Wayne, R.K. (2009) Linkage disequilibrium and demographic history of wild and domestic canids. *Genetics*, 181 (4), 1493–1505.
<https://doi.org/10.1534/genetics.108.098830>
- Grayson, D.K. (1988) Danger Cave, Last Supper Cave, and Hanging Rock Shelter: The Faunas. *Anthropological Papers of the American Museum Natural History*, 66 (1), 1–130.
- Gregory, J.W. (1906) *The Dead Heart of Australia*. John Murray, London, 371 pp.
- Groves, C.P., Ziccardi, F. & Toschi, A. (1966) *Sull'asino selvatico africano. Ricerche di Zoologia Applicata alla Caccia, Bologna Supplement*, 5, 1–30.
- Groves, C.P. (1995) On the nomenclature of domestic animals. *The Bulletin of Zoological Nomenclature*, 52, 137–141.
<https://doi.org/10.5962/bhl.part.6749>
- Groves, C.P. (2001) *Primate Taxonomy*. Smithsonian Institution, Washington, D.C., 350 pp.
- Groves, C. (2004) The what, why and how of primate taxonomy. *International Journal of Primatology*, 25 (5), 1105–1126.
<https://doi.org/10.1023/b:ijop.0000043354.36778.55>
- Groves, C. & Grubb, P. (2011) *Ungulate Taxonomy*. Johns Hopkins University Press, Baltimore, 317 pp.
- Harrop, A.E. (1960) The physiology of reproduction in the dog and bitch. In: Harrop, A.E. (Ed.), *Reproduction in the Dog*.

- Ballière, Tindall and Cox, London, pp. 64–86.
- Hedrick, P.W., Miller, P.S., Geffen, E. & Wayne, R.K. (1997) Genetic evaluation of the three captive Mexican Wolf lineages. *Zoo Biology*, 16 (1), 47–69.
[https://doi.org/10.1002/\(SICI\)1098-2361](https://doi.org/10.1002/(SICI)1098-2361)
- Howard, A.J. (1990) Hall's heelers. In: Warner, R.M. (Ed.), *Over-Halling the Colony: George Hall Pioneer*. Southwood Press, Sydney, pp. 26–28.
- Hunter, J. (1793) *An Historical Journal of the Transactions at Port Jackson and Norfolk Island, with the Discoveries which have been made in New South Wales and in the Southern Ocean*. J. Stockdale, London, 525 pp.
- International Commission of Zoological Nomenclature (ICZN) (1957) Opinion 451. Use of the plenary powers to secure that the specific name *dingo* Meyer, 1793, as published in the combination *Canis dingo* shall be the oldest available name for the dingo of Australia (Class Mammalia). *Opinions and Declarations Rendered by the International Commission of Zoological Nomenclature*, 15, 329–338.
- International Commission of Zoological Nomenclature (ICZN) (2003) Opinion 2027 (Case 3010). Usage of 17 specific names based on wild species which are predated by or contemporary with those based on domestic animals (Lepidoptera, Osteichthyes, Mammalia). *Bulletin of Zoological Nomenclature*, 60, 81–84.
- Iredale, T. (1947) The scientific name of the dingo. *Proceedings of the Royal Zoological Society of New South Wales*, 67 (1946–1947), 35–36.
- Iredale, T. & Troughton, E. le G. (1934) A check-list of the mammals recorded from Australia. *Memoirs of the Australian Museum*, 6, 1–122.
<https://doi.org/10.3853/j.0067-1967.6.1934.516>
- Jackson, S.M. (2003) Dingoes. In: Jackson, S.M. (Ed.), *Australian Mammals: Biology and Captive Management*. CSIRO Publishing, Melbourne, pp. 381–407.
- Jackson, S.M. & Groves, C.P. (2015) *Taxonomy of Australian Mammals*. CSIRO Publishing, Melbourne, 529 pp.
- Johnson, C.N., Isaac, J.L. & Fisher, D.O. (2007) Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society, Series B Biological Sciences*, 274 (1608), 341–346.
<https://doi.org/10.1098/rspb.2006.3711>
- Johnson, I. (1979) *The getting of data. A case study from the recent industries of Australia*. PhD Thesis, Australian National University, Canberra, 186 pp.
- Jones, E. & Stevens, P.L. (1988) Reproduction in wild canids, *Canis familiaris*, from the eastern highlands of Victoria. *Wildlife Research*, 15 (4), 385–397.
<https://doi.org/10.1071/WR9880385>
- Jones, E. (1990) Physical characteristics and taxonomic status of wild canids *Canis familiaris*, from the eastern highlands of Victoria. *Australian Wildlife Research*, 17 (1), 69–81.
<https://doi.org/10.1071/wr9900069>
- Jones, E. (2009) Hybridisation between the dingo, *Canis lupus dingo*, and the Domestic Dog, *Canis lupus familiaris*, in Victoria: a critical review. *Australian Mammalogy*, 31 (1), 1–7.
<https://doi.org/10.1071/AM08102>
- Kadletz, M. (1932) *Anatomischer Atlas der Extremitätengelenke von Pferd und Hund*. Urban & Schwarzenberg, Berlin, 101 pp.
- Kerr, R. (1792) *The Animal Kingdom, or zoological system, of the celebrated Sir Charles Linnaeus; Class I. Mammalia: containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young; being a translation of that part of the Systema Naturae, as lately published, with great improvements, by Professor Gmelin of Goettingen. Together with numerous additions from more recent zoological writers, and illustrated with copper plates. Vol. I.* J. Murray & R. Faulder, London, 644 pp.
- Kleiman, D.G. (1968) Reproduction in the Canidae. *International Zoo Yearbook*, 8, 3–8.
<https://doi.org/10.1111/j.1748-1090.1968.tb00419.x>
- Koler-Matznick, J., Brisbin, I.L. Jr & McIntyre, J. (2000) The New Guinea singing dog: a living primitive dog. In: Crockford, S.J. (Ed.), *Dogs through time: an archaeological perspective. Proceedings of the 1st ICAZ Symposium on the history of the Domestic Dog*. British Archaeological Press, Oxford, pp. 239–247.
- Koler-Matznick, J., Brisbin, I.L., Feinstein, M. & Bulmer, S. (2003) An updated description of the New Guinea singing dog (*Canis hallstromi*, Troughton 1957). *Journal of Zoology*, 261 (2), 109–118.
<https://doi.org/10.1017/S0952836903004060>
- Koler-Matznick, J., Yates, B.C., Bulmer, S. & Brisbin, I.L. (2007) The New Guinea singing dog: its status and scientific importance. *Australian Mammalogy*, 29 (1), 47–56.
<https://doi.org/10.1071/AM07005>
- Koop, B.F., Burbidge, M., Byun, A., Rink, U. & Crockford, S.J. (2000) Ancient DNA evidence of a separate origin for North American indigenous dogs. In: Crockford, S.J. (Ed.), *Dogs Through Time: An Archaeological Perspective*. British Archaeological Reports, Oxford, pp. 271–285.
- Kreffit, G. (1866) On the vertebrated animals of the lower Murray and Darling: their habits, economy, and geographical distribution. *Transactions of the Philosophical Society of New South Wales*, 1862–1865, 1–33.
- Kreffit, G. (1868) Notes on the fauna of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, 1868, 93–105.
- Lampert, R.J. (1971) *Burrill Lake and Currarong. Terra Australia I*. Australian National University Press, Canberra, 86 pp.

- Larson, G., Karlsson, E.K., Perri, A., Webster, M.T., Ho, S.Y., Peters, J., Stahl, P.W., Piper, P.J., Lingaas, F., Fredholm, M., Comstock, K.E., Modiano, J.F., Schelling, C., Agoulnik, A.I., Leegwater, P.A., Dobney, K., Vigne, J.D., Vilà, C., Andersson, L. & Lindblad-Toh, K. (2012) Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Science*, 109, 8878–8883.
<https://doi.org/10.1073/pnas.1203005109>
- Leonard, J.A., Wayne, R.K., Wheeler, J., Valadez, R., Guillén, S. & Vilà, C. (2002) Ancient DNA evidence for old world origin of new world dogs. *Science*, 298 (5598), 1613–1616.
<https://doi.org/10.1126/science.1076980>
- Leonard, J.A., Vilà, C., Fox-Dobbs, K., Koch, P.L., Wayne, R.K. & Van Valkenburgh, B. (2007) Megafaunal extinctions and the disappearance of a specialised wolf ectomorph. *Current Biology*, 17 (13), 1146–1150.
<https://doi.org/10.1016/j.cub.2007.05.072>
- Lesèble, L. (1890) Les dingos au chenil du Jardin Zoologique d'Acclimatisation. *Revue des Sciences Naturelles Appliquées: Bulletin Bimensuel de la Société National d'Acclimatisation de France*, 37, 681–684.
- Letnic, M., Koch, F., Gordon, C., Crowther, M.S. & Dickman, C.R. (2009) Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society of London, Series B Biological Sciences*, 276 (1671), 3249–3256.
<https://doi.org/10.1098/rspb.2009.0574>
- Letnic, M., Ritchie, E.G. & Dickman, C.R. (2012) Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews*, 87 (2), 390–413.
<https://doi.org/10.1111/j.1469-185X.2011.00203.x>
- Lindblad-Toh, K., Wade, C.M., Mikkelsen, T.S., Karlsson, E.K., Jaffe, D.B., Kamal, M., Clamp, M., Chang, J.L., Kulbokas, E.J., Zody, M.C., Mauceli, E., Xie, X., Breen, M., Wayne, R.K., Ostrander, E.A., Ponting, C.P., Galibert, F., Smith, D.R., deJong, P.J., Kirkness, E., Alvarez, P., Biagi, T., Brockman, W., Butler, J., Chin, C-W., Cook, A., Cuff, J., Daly, M.J., DeCaprio, D., Gnerre, S., Grabherr, M., Kellis, M., Kleber, M., Bardeleben, C., Goodstadt, L., Heger, A., Hitte, C., Kim, L., Koepfli, K.-P., Parker, H.G., Pollinger, J.P., Searle, S.M.J., Sutter, N.B., Thomas, R., Webber, C. & Lander, E.S. (2005) Genome sequence, comparative analysis and haplotype structure of the Domestic Dog. *Nature*, 438 (7069), 803–819.
<https://doi.org/10.1038/nature04338>
- Linnaeus, C. (1758) *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Vol. 1.* Laurentii Salvii, Holmiae, 823 pp.
- Lorenzini, R. & Fico, R. (1995) A genetic investigation of enzyme polymorphisms shared by wolf and dog: suggestions for conservation of the wolf in Italy. *Acta Theriologica*, 40 (Supplement 3), 101–110.
- Lord, K., Feinstein, M., Smith, B. & Coppinger, C. (2013) Variation in reproductive traits of members of the genus *Canis* with special attention to the Domestic Dog (*Canis familiaris*). *Behavioural Processes*, 92, 131–142.
<https://doi.org/10.1016/j.beproc.2012.10.009>
- Lowry, J.W.J. & Merrilees, D. (1969) Age of the desiccated carcass of a thylacine (Marsupialia, Dasyuridae) from Thylacine Hole, Nullarbor Region, Western Australia. *Helictite*, 7 (1), 15–16.
- Lucas, A.H.S. & Le Souëf, W.H.D. (1909) *The Animals of Australia - Mammals, Reptiles, and Amphibians*. Whitcombe & Tombs, Melbourne, 327 pp.
<https://doi.org/10.5962/bhl.title.69495>
- Macintosh, N.W.G. (1964) A 3,000 year old dingo from shelter 6 (Fromm's Landing, South Australia). *Proceedings of the Royal Society of Victoria*, 77, 498–507.
- Macintosh, N.W.G. (1975) The origin of the dingo: an enigma. In: Fox, M.W. (Ed.), *The Wild Canids: Their Systematics, Behavioural Ecology and Evolution*. Van Nostrand Reinhold, New York, pp. 87–106.
- Mahoney, J.A. & Richardson, B.J. (1988) Canidae. In: Walton, D.W. (Ed.), *Zoological Catalogue of Australia. 5. Mammalia*. Australian Government Publishing Service, Canberra, pp. 217–220.
- Major, R. (2009) *Predation and hybridisation by feral dogs (Canis lupus familiaris) - Key threatening process listing*. New South Wales Department of Environment, Climate Change, and Water, Sydney. Available from: <http://www.environment.nsw.gov.au/determinations/feraldogsFD.htm> (accessed 17 July 2017)
- Manor, R. & Saltz, D. (2004) The impact of free-roaming dogs on gazelle kid/female ratio in a fragmented area. *Biological Conservation*, 119 (2), 231–236.
<https://doi.org/10.1016/j.biocon.2003.11.005>
- Mayden, R. (1997) A hierarchy of species concepts: the denouement in the saga of the species problem. In: Oaridge, M.F., Dawah, H.A. & Wilson, M.R. (Eds.), *Species: The Units of Biodiversity*. Chapman & Hall, London, pp. 381–424.
- McCoy, F. (1862) Note on the ancient and recent natural history of Victoria. *Annals and Magazine of Natural History*, Series 3, 9, 137–150.
- McCoy, F. (1882) *Prodromus of the Palaeontology of Victoria; or Figures and Descriptions of Victorian organic remains. Decade VII. Geological Survey of Victoria*. J. Ferres, Melbourne, 30 pp.
- McGreevy, P.D., Georgevsky, D., Carrasco, J., Valenzuela, M., Duffy, D.L. & Serpell, J.A. (2013) Dog behavior co-varies with height, bodyweight and skull shape. *PLoS ONE*, 8 (12), e80529.
<https://doi.org/10.1371/journal.pone.0080529>
- Mech, L.D. (1970) *The Wolf: The Ecology and Behavior of an Endangered Species*. Natural History Press, New York, 384 pp.

- Meyer, F.A.A. (1793) *Systematisch-summarische Uebersicht der neuesten zoologischen Entdeckungen in Neuholland und Afrika: nebst zwey andern zoologischen Abhandlungen*. Dykische Buchhandlung, Leipzig, 178 pp.
<https://doi.org/10.5962/bhl.title.39685>
- Milham, P. & Thompson, P. (1976) Relative antiquity of human occupation and extinct fauna at Madura Cave, southeastern Western Australia. *Mankind*, 10 (3), 175–180.
<https://doi.org/10.1111/j.1835-9310.1976.tb01149.x>
- Morrison-Scott, T.C.S. (1955) Support for Tate's proposed use of the plenary powers to validate the specific name "dingo" Meyer, 1793, as published in the combination "Canis dingo" as the name for the dingo (Class Mammalia). *The Bulletin of Zoological Nomenclature*, 11, 168.
- Mulvaney, D.J. (1975) *The Prehistory of Australia*. Penguin Books, Melbourne, 327 pp.
- Newsome, A.E., Corbett, K.L., Best, L.W. & Green, B. (1973) The dingo. *Australian Meat Research Committee Review*, 14, 1–11.
- Newsome, A.E., Corbett, L.K. & Carpenter, S.M. (1980) The identity of the dingo. I. Morphological discriminants of dingo and dog skulls. *Australian Journal of Zoology*, 28 (4), 615–625.
<https://doi.org/10.1071/ZO9800615>
- Newsome, A.E. & Corbett, L.K. (1982) The identity of the dingo. II. Hybridisation with Domestic Dogs in captivity and in the wild. *Australian Journal of Zoology*, 30 (2), 365–374.
<https://doi.org/10.1071/ZO9820365>
- Newsome, A.E. & Corbett, L.K. (1985) The identity of the dingo. III. The incidence of dingoes, dogs and hybrids and their coat colours in remote and settled regions of Australia. *Australian Journal of Zoology*, 33 (3), 363–375.
<https://doi.org/10.1071/ZO9850363>
- Newsome, T.M., Stephens, D., Ballard, G.-A., Dickman, C.R. & Fleming, P.J.S. (2013a) Genetic profile of dingoes (*Canis lupus dingo*) and free-roaming Domestic Dogs (*C. l. familiaris*) in the Tanami Desert, Australia. *Wildlife Research*, 40 (3), 196–206.
<https://doi.org/10.1071/WR12128>
- Newsome, T.M., Ballard, G.-A., Dickman, C.R., Fleming, P.J.S. & Howden, C. (2013b) Anthropogenic resource subsidies determine space use by Australian arid zone Dingoes: An improved resource selection modelling approach. *PLoS ONE*, 8, e63931.
<https://doi.org/10.1371/journal.pone.0063931>
- Nixon, K.C. & Wheeler, Q.C. (1990) Amplification of the phylogenetic species concept. *Cladistics*, 6 (3), 211–223.
<https://doi.org/10.1111/j.1096-0031.1990.tb00541.x>
- Nosil, P., Crespi, B.J. & Sandoval, C.P. (2003) Reproductive isolation driven by the combined effects of ecological adaptation and reinforcement. *Proceedings of the Royal Society of London, Series B Biological Sciences*, 270 (1527), 1911–1918.
<https://doi.org/10.1098/rspb.2003.2457>
- Olsen, S.J. & Olsen, J.W. (1977) The Chinese wolf, ancestor of New World dogs. *Science*, 197 (4303), 533–535.
<https://doi.org/10.1126/science.197.4303.533>
- Oppenheimer, E.C. & Oppenheimer, J.R. (1975) Certain behavioural features in the pariah dog (*Canis familiaris*) in West Bengal. *Applied Animal Ethology*, 2 (1), 81–92.
[https://doi.org/10.1016/0304-3762\(75\)90067-X](https://doi.org/10.1016/0304-3762(75)90067-X)
- Oskarsson, M.C.R., Klütsch, C.F.C., Boonyaparakob, U., Wilton, A., Tanabe, Y. & Savolainen, P. (2012) Mitochondrial DNA data indicate an introduction through mainland Southeast Asia for Australian dingoes and Polynesian Domestic Dogs. *Proceedings of the Royal Society of London, Series B Biological Sciences*, 279 (1730), 967–974.
<https://doi.org/10.1098/rspb.2011.1395>
- Ovodov, N.D., Crockford, S.J., Kuzmin, Y.V., Higham, T.F.G., Hodgins, G.W.L. & van der Plicht, J. (2011) A 33,000-year-old incipient dog from the Altai Mountains of Siberia: Evidence of the earliest domestication disrupted by the Last Glacial Maximum. *PLoS ONE*, 6 (7), e22821.
<https://doi.org/10.1371/journal.pone.0022821>
- Pal, S.K. (2001) Population ecology of free-ranging urban dogs in West Bengal, India. *Acta Theriologica*, 46 (1), 69–78.
<https://doi.org/10.1007/BF03192418>
- Pal, S.K. (2008) Maturation and development of social behaviour during early ontogeny in free-ranging dog puppies in West Bengal, India. *Applied Animal Behaviour Science*, 111 (1–2), 95–107.
<https://doi.org/10.1016/j.applanim.2007.05.016>
- Pang, J.-F., Klütsch, C., Zou, X.-J., Zhang, A.-B., Luo, L.Y., Angleby, H., Ardalan, A., Ekström, C., Sköllermo, A., Lundeberg, J., Matsumura, S., Leitner, T., Zhang, Y.-P. & Savolainen, P. (2009) mtDNA data indicate a single origin for dogs South of Yangtze River, less than 16,300 years ago, from numerous wolves. *Molecular Biology and Evolution*, 26 (12), 2849–2864.
<https://doi.org/10.1093/molbev/msp195>
- Parr, W.C.H., Wilson, L.A.B., Wroe, S., Colman, N.J., Crowther, M.S. & Letnic, M. (2016) Cranial shape and the modularity of hybridization in dingoes and dogs; hybridization does not spell the end for native morphology. *Evolutionary Biology*, 43, 171–187.
<https://doi.org/10.1007/s11692-016-9371-x>

- Phillip, A. (1789) *The Voyage of Governor Phillip to Botany Bay, with an account of the establishment of the colonies of Port Jackson & Norfolk Island compiled from authentic papers, which have been obtained from the several departments, to which are added the journals of Lieuts. Shortland, Watts, Ball & Capt. Marshall; with an account of their discoveries, embellished with LV copper plates, the maps and charts taken from actual surveys, & the plans and views drawn on the spot, by Capt. Hunter, Lieuts. Shortland, Watts, Dawes, Bradley, Capt. Marshall.* John Stockdale, London, 298 pp.
- Pilot, M., Branicki, W., Jędrzejewski, W., Goszczyński, J., Jędrzejewska, B., Dykyy, I., Shkvyrya, M. & Tsingarska, E. (2010) Phylogenetic history of grey wolves in Europe. *BMC Evolutionary Biology*, 10 (104), 1–11.
<https://doi.org/10.1186/1471-2148-10-104>
- Purcell, B. (2010) *Dingo*. CSIRO Publishing, Melbourne, 166 pp.
- Radford, C.G., Letnic, M., Fillios, M. & Crowther, M.S. (2012) An assessment of the taxonomic status of wild canids in south-eastern New South Wales: phenotypic variation in dingoes. *Australian Journal of Zoology*, 60 (2), 73–80.
<https://doi.org/10.1071/ZO12006>
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12 (9), 982–998.
<https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Sacks, B.N., Bannasch, D.L., Chomel, B.B. & Ernest, H.B. (2008) Coyotes demonstrate how habitat specialization by individuals of a generalist species can diversify populations in a heterogeneous ecoregion. *Molecular Biology and Evolution*, 25 (7), 1384–1394.
<https://doi.org/10.1093/molbev/msn082>
- Sacks, B.N., Brown, S.K., Stephens, D., Pedersen, N.C., Wu, J.-T. & Berry, O. (2013) Y chromosome analysis of dingoes and Southeast Asian village dogs suggests a Neolithic continental expansion from Southeast Asia followed by multiple Austronesian dispersals. *Molecular Biology and Evolution*, 30 (5), 1103–1118.
<https://doi.org/10.1093/molbev/mst027>
- Savolainen, P., Zhang, Y., Luo, J., Lundeberg, J. & Leitner, T. (2002) Genetic evidence for an east Asian origin of Domestic Dogs. *Science*, 298 (5598), 1610–1613.
<https://doi.org/10.1126/science.1073906>
- Savolainen, P., Leitner, T., Wilton, A.N., Matisoo-Smith, E. & Lundeberg, J. (2004) A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences, USA*, 101 (33), 12387–12390.
<https://doi.org/10.1073/pnas.0401814101>
- Scott, J.P. & Fuller, J.L. (1965) *Genetics and Social Behavior of the Dog*. University of Chicago Press, Chicago, 468 pp.
- Sheldon, J. (1992) *Wild Dogs: The Natural History of the Nondomestic Canidae*. Academic Press, Inc, San Diego, 248 pp.
- Sillero-Zubiri, C. (2009) Family Canidae (Dogs). In: Wilson, D.E. & Mittermeier, R.A. (Eds.), *Handbook of the Mammals of the World. Vol. 1. Carnivores*. Lynx Editions, Barcelona, pp. 352–466.
- Skoglund, P., Ersmark, E., Palkopoulou, E. & Dalén, L. (2015) Ancient wolf genome reveals an early divergence of Domestic Dog ancestors and admixture into high-latitude breeds. *Current Biology*, 25 (11), 1515–1519.
<https://doi.org/10.1016/j.cub.2015.04.019>
- Smith, B. (2015) The role of dingoes in Indigenous Australian lifestyle, culture, and spirituality. In: Smith, B. (Ed.), *The dingo debate: origins, behaviour and conservation* CSIRO Publishing, Melbourne, pp. 81–101.
- Smith, M.A. (1980) *Saltbush, Sampling Strategy and Settlement Pattern*. MA Thesis, Australian National University, Canberra, 295 pp. [unpublished]
- Stephens, D., Wilton, A.N., Fleming, P.J.S. & Berry, O. (2015) Death by sex in an Australian icon: a continent-wide survey reveals extensive hybridisation between dingoes and Domestic Dogs. *Molecular Ecology*, 24 (22), 5643–5656.
<https://doi.org/10.1111/mec.13416>
- Strahan, R. (Ed.) (1983) *The Complete Book of Australian Mammals*. Angus and Robertson, Sydney, 530 pp.
- Strahan, R. (1992) *Encyclopedia of Australian Animals: Mammals*. Angus & Robertson, Sydney, 184 pp.
- Strahan, R. (Ed.) (1995) *Mammals of Australia*. Reed Books, Sydney, 756 pp.
- Suzuki, H., Nunome, M., Kinoshita, G., Aplin, K.P., Vogel, P., Kryukov, A.P., Lin, M.-L., Han, S.-H., Maryanto, I., Tsuchiya, K., Ikeda, H., Shiroishi, T., Yonekawa, H. & Moriwaki, K. (2013) Evolutionary and dispersal history of Eurasian house mice *Mus musculus* clarified by more extensive geographic sampling of mitochondrial DNA. *Heredity*, 111 (5), 375–390.
<https://doi.org/10.1038/hdy.2013.60>
- Tao, Y., Chen, S., Hartl, D.L. & Laurie, C.C. (2003) Genetic dissection of hybrid incompatibilities between *Drosophila simulans* and *D. mauritiana*. I. Differential accumulation of hybrid male sterility effects on the X and autosomes. *Genetics*, 164 (4), 1383–1398.
- Tate, G.H.H. (1955) Proposed use of the plenary powers to validate the specific name “dingo” Meyer, 1793, as published in the combination “*Canis dingo*” as the name for the dingo (Class Mammalia). *The Bulletin of Zoological Nomenclature*, 11, 121.
- Teeter, K.C., Payseur, B.A., Harris, L.W., Bakewell, M.A., Thibodeau, L.M., O’Brien, J.E., Krenz, J.G., Sans-Fuentes, M.A., Nachman, M.W. & Tucker, P.K. (2008). Genome-wide patterns of gene flow across a house mouse hybrid zone. *Genome Research*, 18 (1), 67–76.
<https://doi.org/10.1101/gr.6757907>

- Temminck, C.J. (1838) Over de kennis en de verbreiding der zoogdiern van Japan. *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie*, 5, 273–293.
- Tench, W. (1789) *A narrative of the expedition to Botany Bay*. J. Debrett, London, 64 pp. Available from: <http://setis.library.usyd.edu.au/ozlit/pdf/p00039.pdf> (Accessed 1 Sept. 2017)
- Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V.J., Sawyer, S.K., Greenfield, D.L., Germonpré, M.B., Sablin, M.V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.P., Loponte, D.M., Acosta, A.A., Giemsch, L., Schmitz, R.W., Worthington, B., Buikstra, J.E., Druzhkova, A., Graphodatsky, A.S., Ovodov, N.D., Wahlberg, N., Freedman, A.H., Schweizer, R.M., Koepfli, K.P., Leonard, J.A., Meyer, M., Krause, J., Pääbo, S., Green, R.E. & Wayne, R.K. (2013) Complete mitochondrial genomes of ancient canids suggest a European origin of Domestic Dogs. *Science*, 342 (6160), 871–874.
<https://doi.org/10.1126/science.1243650>
- The Bovine Genome Sequencing Analysis Consortium, Elsik, C.G., Tellam, R.L. & Worley, K.C. (2009) The Genome Sequence of Taurine Cattle: A Window to Ruminant Biology and Evolution. *Science*, 324 (5926), 522–528.
<https://doi.org/10.1126/science.1169588>
- Thompson, P.C. (1992a) The behavioural ecology of dingoes in north-western Australia. IV. Social and spatial organisation, and movements. *Wildlife Research*, 19 (5), 543–564.
<https://doi.org/10.1071/WR9920543>
- Thompson, P.C. (1992b) The behavioural ecology of dingoes in North-Western Australia. II. Activity patterns, breeding season, and pup rearing. *Wildlife Research*, 19, 519–530.
<https://doi.org/10.1071/WR9920519>
- Troughton, E. le G. (1957) A new native dog from the Papuan highlands. *Proceedings of the Royal Zoological Society of New South Wales*, 76 (1955–1956), 93–94.
- Troughton, E. le G. (1967) *Furred Animals of Australia*. 9th Edition. Angus and Robertson, Sydney, 314 pp.
- True, J.R., Weir, B.S. & Laurie, C.C. (1996) A genome-wide survey of hybrid incompatibility factors by the introgression of marked segments of *Drosophila mauritiana* chromosomes into *Drosophila simulans*. *Genetics*, 142 (3), 819–837.
- Turnbull, P.F. & Reed, C.A. (1974) The fauna of the terminal Pleistocene of Palegawra Cave, a Zarazian occupational site in northeastern Iraq. *Fieldiana Anthropology*, 63, 81–146.
- Uerpmann, H.-P. (1982) Faunal remains from Shams ed-Din Tannira, a Halafian Site in Northern Syria. *Berytus Archaeological Studies (supplement)*, 30, 3–52.
- Vaysse, A., Ratnakumar, A., Derrien, T., Axelsson, E., Rosengren Pielberg, G., Sigurdsson, S., Fall, T., Seppälä, E.H., Hansen, M.S., Lawley, C.T., Karlsson, E.K., The LUPA Consortium, Bannasch, D., Vilà, C., Lohi, H., Galibert, F., Fredholm, M., Häggström, J., Hedhammar, A., André, C., Lindblad-Toh, K., Hitte, C. & Webster, M.T. (2011) Identification of genomic regions associated with phenotypic variation between dog breeds using selection mapping. *PLoS Genetics*, 7 (10), e1002316.
<https://doi.org/10.1371/journal.pgen.1002316>
- Van Dyck, S. & Strahan, R. (2008) *The Mammals of Australia*. 3rd Edition. Reed New Holland, Sydney, 887 pp.
- Venter, J.C., Adams, M.D., Myers, E.W., Li, P.W., Mural, R.J., Sutton, G.G., Smith, H.O., Yandell, M., Evans, C.A., Holt, R.A., Gocayne, J.D., Amanatides, P., Ballew, R.M., Huson, D.H., Wortman, J.R., Zhang, Q., Kodira, C.D., Zheng, X.H., Chen, L., Skupski, M., Subramanian, G., Thomas, P.D., Zhang, J., Gabor Miklos, G.L., Nelson, C., Broder, S., Clark, A.G., Nadeau, J., McKusick, V.A., Zinder, N., Levine, A.J., Roberts, R.J., Simon, M., Slayman, C., Hunkapiller, M., Bolanos, R., Delcher, A., Dew, I., Fasulo, D., Flanigan, M., Florea, L., Halpern, A., Hannenhalli, S., Kravitz, S., Levy, S., Mobarry, C., Reinert, K., Remington, K., Abu-Threideh, J., Beasley, E., Biddick, K., Bonazzi, V., Brandon, R., Cargill, M., Chandramouliswaran, I., Charlab, R., Chaturvedi, K., Deng, Z., Di Francesco, V., Dunn, P., Eilbeck, K., Evangelista, C., Gabrielian, A.E., Gan, W., Ge, W., Gong, F., Gu, Z., Guan, P., Heiman, T.J., Higgins, M.E., Ji, R.R., Ke, Z., Ketchum, K.A., Lai, Z., Lei, Y., Li, Z., Li, J., Liang, Y., Lin, X., Lu, F., Merkulov, G.V., Milshina, N., Moore, H.M., Naik, A.K., Narayan, V.A., Neelam, B., Nusskern, D., Rusch, D.B., Salzberg, S., Shao, W., Shue, B., Sun, J., Wang, Z., Wang, A., Wang, X., Wang, J., Wei, M., Wides, R., Xiao, C., Yan, C., Yao, A., Ye, J., Zhan, M., Zhang, W., Zhang, H., Zhao, Q., Zheng, L., Zhong, F., Zhong, W., Zhu, S., Zhao, S., Gilbert, D., Baumhueter, S., Spier, G., Carter, C., Cravchik, A., Woodage, T., Ali, F., An, H., Awe, A., Baldwin, D., Baden, H., Barnstead, M., Barrow, I., Beeson, K., Busam, D., Carver, A., Center, A., Cheng, M.L., Curry, L., Danaher, S., Davenport, L., Desilets, R., Dietz, S., Dodson, K., Doup, L., Ferreira, S., Garg, N., Gluecksmann, A., Hart, B., Haynes, J., Haynes, C., Heiner, C., Hladun, S., Hostin, D., Houck, J., Howland, T., Ibegwam, C., Johnson, J., Kalush, F., Kline, L., Koduru, S., Love, A., Mann, F., May, D., McCawley, S., McIntosh, T., McMullen, I., Moy, M., Moy, L., Murphy, B., Nelson, K., Pfannkoch, C., Pratts, E., Puri, V., Qureshi, H., Reardon, M., Rodriguez, R., Rogers, Y.H., Romblad, D., Ruhfel, B., Scott, R., Sitter, C., Smallwood, M., Stewart, E., Strong, R., Suh, E., Thomas, R., Tint, N.N., Tse, S., Vech, C., Wang, G., Wetter, J., Williams, S., Williams, M., Windsor, S., Winn-Deen, E., Wolfe, K., Zaveri, J., Zaveri, K., Abril, J.F., Guigo, R., Campbell, M.J., Sjolander, K.V., Karlak, B., Kejariwal, A., Mi, H., Lazareva, B., Hatton, T., Narechania, A., Diemer, K., Muruganujan, A., Guo, N., Sato, S., Bafna, V., Istrail, S., Lippert, R., Schwartz, R., Walenz, B., Yoosheph, S., Allen, D., Basu, A., Baxendale, J., Blick, L., Caminha, M., Carnes-Stine, J., Caulk, P., Chiang, Y.H., Coyne, M., Dahlke, C., Mays, A., Dombroski, M., Donnelly, M., Ely, D., Esparham, S., Fosler, C., Gire, H., Glanowski, S., Glasser, K., Glodek, A., Gorokhov, M., Graham, K., Gropman, B., Harris, M., Heil, J., Henderson, S., Hoover, J., Jennings, D., Jordan, C., Jordan, J., Kasha, J., Kagan, L., Kraft, C., Levitsky, A., Lewis, M., Liu, X., Lopez, J.,

- Ma, D., Majoros, W., McDaniel, J., Murphy, S., Newman, M., Nguyen, T., Nguyen, N., Nodell, M., Pan, S., Peck, J., Peterson, M., Rowe, W., Sanders, R., Scott, J., Simpson, M., Smith, T., Sprague, A., Stockwell, T., Turner, R., Venter, E., Wang, M., Wen, M., Wu, D., Wu, M., Xia, A., Zandieh, A. & Zhu, X. (2001) The Sequence of the Human Genome. *Science*, 291 (5507), 1304–1351.
<https://doi.org/10.1126/science.1058040>
- Vernes, K., Dennis, A. & Winter, J. (2001) Mammalian diet and broad hunting strategy of the dingo (*Canis familiaris dingo*) in the wet tropical rainforests of northeastern Australia. *Biotropica*, 33 (2), 339–345.
[https://doi.org/10.1646/0006-3606\(2001\)033\[0339:mdabhs\]2.0.co;2](https://doi.org/10.1646/0006-3606(2001)033[0339:mdabhs]2.0.co;2)
- Vilà, C.P., Savolainen, P., Maldonado, J.E., Amorim, I.R., Rice, J.E., Honeycutt, R.L., Crandall, K.A., Lundenberg, J. & Wayne, R.K. (1997) Multiple and ancient origins of the Domestic Dog. *Science*, 276 (5319), 1687–1689.
<https://doi.org/10.1126/science.276.5319.1687>
- Vilà, C., Amorim, I.R., Leonard, J.A., Posada, D., Castroviejo, J., Petrucci-Fonseca, F., Crandall, K.A., Ellegren, H. & Wayne, R.K. (1999) Mitochondrial DNA phylogeography and population history of the grey wolf *Canis lupus*. *Molecular Ecology*, 8 (12), 2089–2103.
<https://doi.org/10.1046/j.1365-294x.1999.00825.x>
- Voigt, F.S. (1831) *G. Cuvier, Das Thierreich, geordnet nach seiner organisation : Als grundlage der naturgeschichte der thiere und einleitung in die vergleichende anatomie. Vol. 1.* Brockhaus, Leipzig, 974 pp.
- vonHoldt, B.M., Pollinger, J.P., Lohmueller, K.E., Han, E., Parker, H.G., Quignon, P., Degenhardt, J.D., Boyko, A.R., Earl, D.A., Auton, A., Reynolds, A., Bryc, K., Brisbin, A., Knowles, J.C., Mosher, D.S., Spady, T.C., Elkahoul, A., Geffen, E., Pilot, M., Jedrzejewski, W., Greco, C., Randi, E., Bannasch, D., Wilton, A., Shearman, J., Musiani, M., Cargill, M., Jones, P.G., Qian, Z., Huang, W., Ding, Z.-L., Zhang, Y.-P., Bustamante, C.D., Ostrander, E.A., Novembre, J. & Wayne, R.K. (2010) Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature*, 464 (7290), 898–903.
<https://doi.org/10.1038/nature08837>
- vonHoldt, B.M., Pollinger, J.P., Earl, D.A., Knowles, J.C., Boyko, A.R., Parker, H., Geffen, E., Pilot, M., Jedrzejewski, W., Jedrzejewska, B., Sidorovich, V., Greco, C., Randi, E., Musiani, M., Kays, R., Bustamante, C.D., Ostrander, E.A., Novembre, J. & Wayne, R.K. (2011) A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. *Genome Research*, 21 (8), 1294–1305.
<https://doi.org/10.1101/gr.116301.110>
- Wakefield, N.A. (1966) Mammals of the Blandowski Expedition to north western Victoria, 1856-57. *Proceedings of the Royal Society of Victoria*, 79 (2), 371–379.
- Walters, B. (1995) *The Company of Dingoes: Two Decades with our Native Dog*. Australian Native Dog Conservation Society, Bargo, NSW, 109 pp.
- Wang, G.-D., Zhai, W.W., Yang, H.-C., Fan, R.-X., Cao, X., Zhong, L., Wang, L., Liu, F., Wu, H., Cheng, L.G., Poyarkov, A.D., Poyarkov, N.A., Tang, S.S., Zhao, W.M., Gao, Y., Lv, X.M., Irwin, D.M., Savolainen, P., Wu, C.I. & Zhang, Y.P. (2013) The genomics of selection in dogs and the parallel evolution between dogs and humans. *Nature Communications*, 4 (1860), 1–9.
<https://doi.org/10.1038/ncomms2814>
- Wayne, R.K. (1993) Molecular evolution of the dog family. *Trends in Genetics*, 9 (6), 218–224.
[https://doi.org/10.1016/0168-9525\(93\)90122-x](https://doi.org/10.1016/0168-9525(93)90122-x)
- Wayne, R.K. & O'Brien, S.J. (1987) Allozyme divergence within the Canidae. *Systematic Zoology*, 36 (4), 339–355.
<https://doi.org/10.2307/2413399>
- Wayne, R.K. & Ostrander, E.A. (1999) Origin, genetic diversity, and genome structure of the Domestic Dog. *Bioessays*, 21 (3), 247–257.
[https://doi.org/10.1002/\(sici\)1521-1878\(199903\)21:3<247::aid-bies9>3.0.co;2-z](https://doi.org/10.1002/(sici)1521-1878(199903)21:3<247::aid-bies9>3.0.co;2-z)
- Wilson, D.E. & Reeder, D.M. (1993) *Mammal Species of the World - A Taxonomic and Geographic Reference*. Smithsonian Institution Press, Washington D.C., 1206 pp.
- Wilton, A.N., Steward, D.J. & Zafiris, K. (1999) Microsatellite variation in the Australian dingo. *Journal of Heredity*, 90 (1), 108–111.
<https://doi.org/10.1093/jhered/90.1.108>
- Wilton, A.N. (2001) DNA methods of assessing dingo purity. In: Dickman C.R. & Lunney, D. (Eds.), *A Symposium on the Dingo*. Royal Zoological Society of New South Wales, Sydney, pp. 49–56.
<https://doi.org/10.7882/fs.2001.008>
- Wood Jones, F.W. (1921) The status of the dingo. *Transactions of the Royal Society of South Australia*, 45, 254–263.
- Wood-Jones, F. (1925) *The Mammals of South Australia. Part III. The Monodelphia*. R.E.E. Rogers Government Printers, Adelaide, 458 pp.
- Woodall, P.F., Pavlov, P. & Twyford, K.L. (1996) Dingoes in Queensland, Australia: skull dimensions and the identity of wild canids. *Wildlife Research*, 23 (5), 581–587.
<https://doi.org/10.1071/WR9960581>
- Wozencraft, W.C. (2005) Order Carnivora. In: Wilson, D.E. & Reeder, D.A. (Eds.), *Mammal Species of the World. A Taxonomic and Geographic Reference. 3rd Edition*. Johns Hopkins University Press, Baltimore, pp. 532–628.

- Zachos, F.E. & Lovari, S. (2013) Taxonomic inflation and the poverty of the Phylogenetic Species Concept—a reply to Gippoliti and Groves. *Hystrix. Italian Journal of Mammalogy*, 24, 142–144.
- Zimen, E. (1975) Social dynamics of the wolf pack. In: Fox, M.W. (Ed.), *The Wild Canids: Their Systematics, Behavioral Ecology and Evolution*. Robert E. Krieger Publishing Co., Florida, pp. 336–362.