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The Dogma of Dingoes—Taxonomic status of the dingo: A reply to Smith *et al*.

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Abstract

Adopting the name *Canis dingo* for the Dingo to explicitly denote a species-level taxon separate from other canids was suggested by Crowther *et al.* (2014) as a means to eliminate taxonomic instability and contention. However, Jackson *et al.* (2017), using standard taxonomic and nomenclatural approaches and principles, called instead for continued use of the nomen *C. familiaris* for all domestic dogs and their derivatives, including the Dingo. (This name, *C. familiaris*, is applied to all dogs that derive from the domesticated version of the Gray Wolf, *Canis lupus*, based on nomenclatural convention.) The primary reasons for this call by Jackson *et al.* (2017) were: (1) a lack of evidence to show that recognizing multiple species amongst the dog, including the Dingo and New Guinea Singing Dog, was necessary taxonomically, and (2) the principle of nomenclatural priority (the name *familiaris* Linnaeus, 1758, antedates *dingo* Meyer, 1793). Overwhelming current evidence from archaeology and genomics indicates that the Dingo is of recent origin in Australia and shares immediate ancestry with other domestic dogs as evidenced by patterns of genetic and morphological variation. Accordingly, for Smith *et al.* (2019) to recognise *Canis dingo* as a distinct species, the onus was on them to overturn current interpretations of available archaeological, genomic, and morphological datasets and instead show that Dingoes have a deeply divergent evolutionary history that distinguishes them from other named forms of *Canis* (including *C. lupus* and its domesticated version, *C. familiaris*). A recent paper by Koepfli *et al.* (2015) demonstrates exactly how this can be done in a compelling way within the genus *Canis*—by demonstrating deep evolutionary divergence between taxa, on the order of hundreds of thousands of years, using data from multiple genetic systems. Smith *et al.* (2019) have not done this; instead they have misrepresented the content and conclusions of Jackson *et al.* (2017), and contributed extraneous arguments that are not relevant to taxonomic decisions. Here we dissect Smith *et al.* (2019), identifying misrepresentations, to show that ecological, behavioural and morphological evidence is insufficient to recognise Dingoes as a separate species

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from other domestic dogs. We reiterate: the correct binomial name for the taxon derived from Gray Wolves (*C. lupus*) by passive and active domestication, including Dingoes and other domestic dogs, is *Canis familiaris*. We are strongly sympathetic to arguments about the historical, ecological, cultural, or other significance of the Dingo, but these are issues that will have to be considered outside of the more narrow scope of taxonomy and nomenclature.

Key words: Dingo, Canis familiaris, dogs, taxonomy, nomenclature

Introduction

The taxonomic and nomenclatural status of the Australian native dog, the Dingo, have been the subject of much debate, and this has increased over the last few years. Dingoes were usually referred to as either *Canis lupus dingo* or *C. familiaris dingo* during the 1990s and 2000s, though other names, such as *C. familiaris* and *C. dingo* were also (rarely) used. A paper by Crowther *et al.* (2014) re-ignited debate when it firmly proposed to recognise the Dingo as a distinct species, i.e. *C. dingo*. Concern over this taxonomy was raised by Jackson and Groves (2015) and Jackson *et al.* (2017), who highlighted errors in the proposal and suggested that, based on available evidence, the Dingo should be recognised as an ancient lineage of domestic dog, *C. familiaris*.

Smith *et al.* (2019) have responded to again advocate for the recognition of the Dingo as *Canis dingo*. For the Dingo to be accepted as a separate species within the Canidae, as per Smith *et al.* (2019) and Crowther *et al.* (2014), would require that these proponents demonstrate: a) that the animal has a sufficiently independent evolutionary history from other canids to be credited as a specific-level taxon (i.e. information that is relevant to modern taxonomic decisions); and b) that the nomen *dingo* is best applicable in this case (i.e. information that is relevant to nomenclatural designations). Smith *et al.* (2019) have failed on both counts. This is especially because Smith *et al.* (2019) do not demonstrate a clear understanding of the distinct spheres involved in: (1) decisions about nomenclatural availability (the province of the ICZN, based on a set of 'legalistic' rules and adjudications), versus (2) decisions about taxonomic arrangements (the province of practicing taxonomists, based, at least in the modern sense, on evidence reflecting the evolutionary history of organisms themselves). That said, a confusing aspect of nomenclatural usage arises because these two rather different spheres merge where conventions about binomial names for wild species and their domesticated offshoots are concerned, a point we review again below.

Smith *et al.* (2019) also argue that the Australian Dingo is: (1) a geographically isolated (allopatric) species from all other *Canis*, and is genetically, phenotypically, ecologically, and behaviourally distinct; and (2) the Dingo appears largely devoid of many of the signs of domestication, including surviving largely as a wild animal in Australia for millennia. Here we address each suggestion and highlight the problems involved in these assertions, with the aim of confirming that the Dingo should be recognised as derived from the domestic dog, i.e. *C. familiaris*.

Names

The suggestion by Smith *et al.* (2019) that "any changes to the current nomen of the Dingo (currently *Canis dingo* Meyer, 1793), must therefore offer a strong, evidence-based argument in favour of it being recognised as a subspecies of *Canis lupus* Linnaeus, 1758, or as *Canis familiaris* Linnaeus, 1758" is a misrepresentation of current nomenclature and nomenclatural practice. Until the name combination *Canis dingo* was firmly encouraged by Crowther *et al.* (2014), this name was not in common usage and had not been for some 20 years as names such as *Canis familiaris dingo* or *Canis lupus dingo* were the most commonly used names for Dingoes. Indeed, a review of 387 papers that used scientific names (Kreplins *et al.* 2018) indicated the most commonly used names were: those including a domestic dog ancestry—*Canis familiaris*, *Canis familiaris dingo*, *Canis lupus domesticus* and *C. l. familiaris* (169); those referring to a wolf ancestry, as *Canis lupus* and *Canis lupus dingo* (154), with only 64 referring to the Dingo as a distinct species (*Canis dingo*), most of which were published since 2014. Therefore, it could be argued that the attempt to elevate the Dingo to species rank as *Canis dingo* has added further nomenclatural instability.

Smith *et al.* (2019) suggest that ICZN (2003) "recommends that domesticates (generally, and not specific to the case of the Dingo) not be named as subspecies, and instead recommends retaining different species names for wild and domestic forms. It recommends naming wild ancestors of domesticates with the first available name based on a wild population." However, these authors failed to recognise that Case 3010 of the ICZN (Gentry *et al.* 1996) specifically includes the name *dingo* within *familiaris*. This position was reiterated by Gentry *et al.* (2004).

Overall, we feel that Smith *et al.* (2019) generally misunderstand the purpose of this recommendation by the ICZN, which in our view is to denote domesticated and wild-type versions of the same taxonomic lineage, such as *C. familiaris* and *C. lupus*, by separate binomial names simply for ease of communication. The purpose of this is to make it more straightforward in nomenclatural terms to identify the animals in question, but this does not serve to argue that they are indeed separate species in a true taxonomic sense. This is a nomenclatural convention, not a taxonomic decision. Most mammalogists do not in fact view the wolf as distinct at the species level from dogs or Dingoes, despite this "rule-of-thumb" nomenclatural recommendation that different binomial names be employed (e.g. Wozencraft 2005). This is often misunderstood. It might be considered analogous to traditional designations of wild-type versus lab-derived versions of organisms in experimental biology—a matter of parlance, or communicative ease, not one that actually indicates any taxonomic distinction or decision in an evolutionary sense.

Smith *et al.* (2019) state that in "1957 there was a successful application to the International Commission of Zoological Nomenclature (ICZN, also referred to as 'the Commission') to suppress the name *C. antarticus* officially in favour of *C. dingo* because the latter name was in common usage (ICZN 1957). This decision by the Commission was a nomenclatural action (protecting the epithet *dingo* against a senior synonym), and subsequently, the Commission has not taken a stand on the nomenclature or taxonomic status of the Dingo." This is highly misleading because, as stated by Jackson *et al.* (2017), the decision of the ICZN (1957) only made the commonly used name *dingo* Meyer, 1793 available for usage and suppressed the name *antarticus* Kerr, 1792 as it was then considered to be an overlooked but older name. Therefore 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* (Jackson *et al.* 2017). The subsequent literature clearly reflects this as various combinations have since been used since 1957 including *Canis familiaris*, *Canis familiaris dingo*, *Canis lupus dingo* and *Canis dingo*. In short, this point is not relevant. It shows further indications of stark confusion by Smith *et al.* (2019) about the very different conceptual spaces encoded by nomenclatural legalities, species concepts, and practical decision making about species boundaries, respectively.

Smith *et al.* (2019) are also confused when they suggest that as a result of the ICZN (1957) decision they "take this to mean that no Case has been brought forward to the Code offering positive evidentiary argument in favour of demoting it to a subspecies of *C. lupus* Linnaeus, 1758 or *C. familiaris* Linnaeus, 1758. To this day, there has been no proposed or grounded change to the original ICZN listing." This is because the ICZN case related only to the names *antarticus* and *dingo*. This is not relevant in any way to taxonomic decisions about whether the Dingo is a distinct species. Of course, the ICZN regulates the availability of names, not their taxonomic operationalization.

Smith *et al.* (2019) also refer to the name *C. familiaris dingo* Blumenbach, 1780, as cited in Wood Jones (1925), but this appears to perpetuate an error. An inspection of Blumenbach revealed the genus *Canis* was included within volume 1 (published in 1779, Volume 2 was published in 1780) but did not reveal the name *familiaris dingo*. This is consistent with references to, and specimens of, the Dingo not reaching Europe until after the First Fleet arrived in Australia in 1788. Indeed the first published record of the name 'Dingo' appears to be from Tench (1789). Therefore, the reference to *C. familiaris dingo* Blumenbach (1780 [=1779]) by Wood Jones (1925) appears to be an error and not used by any other authors until it was incorrectly revived by Smith *et al.* (2019). Nonetheless, if Blumenbach, 1780 [= 1779] had included the name *C. familiaris dingo*, it is obvious that the authors of Opinion 451 were not aware of it when they published ICZN (1957). If the ICZN were aware of such a publication there would have been no need to suppress the name *antarticus* as *dingo* Blumenbach, 1780 [= 1779] would have been recognised as the oldest available name and therefore already have precedence. This too has absolutely no bearing on what name should be used for the Dingo in any operational sense involving evidence-based taxonomic decision-making.

The objective of Jackson *et al.* (2017) was not to apply the biological species concept *sensu stricto* to the Dingo but to summarize taxonomic history and opinions to determine which nomen was available and currently used for Dingoes and other wild dogs in Australia. This was done and the salient points are reiterated above. Given the misunderstanding and consequent misrepresentation of taxonomic processes in Smith *et al.* (2019), "the effective burden of the argument" actually lies with them to show why the current designation (i.e. *C. familiaris,* Jackson & Groves 2015; Jackson *et al.* 2017) requires revision.

Species concepts

The assertion by Smith *et al.* (2019) that Jackson *et al.* (2017) applied a strict version of the Biological Species Concept (BSC) is incorrect and misleading. The strict BSC has few if any modern proponents, as it has become increasingly clear that many widely recognised species boundaries are leaky to gene flow (Mallet 2008; Frankham *et al.* 2012; del Hoyo & Collar 2014; Coats *et al.* 2018). Instead a relaxed version of the BSC, which allows for occasional gene flow between species remains widely used (Frankham *et al.* 2012; del Hoyo & Collar 2014). This highlights that many distinct species maintain occasional gene flow but still retain clearly separate identities (e.g. Gray Wolves, *C. lupus* and Coyotes, *C. latrans*) as opposed to the merging of gene pools and loss of separate identities as observed between Dingoes and modern dogs. Concerns with the application of the Phylogenetic Species Concept (PSC) as recommended by Smith *et al.* (2019), which emphasises diagnosability, have previously been outlined (e.g. Frankham *et al.* 2012, 2017; Jackson *et al.* 2017; Zachos *et al.* 2013). For example, the deployment of high resolution genetic markers enables many populations within a species to be clearly diagnosable, but this does not mean each is a separate species (e.g. Eldridge *et al.* 2017; Johnson *et al.* 2018). In any case, the various species concepts in modern usage generally involve different ways of identifying "separately evolving lineages" which are identified operationally by various kinds of evidence that may include a combination of reciprocal monophyly, deep genetic divergence, reduced reproductive compatibility, morphological discontinuity, and so forth (de Queiroz 2007). In modern mammal taxonomy, identifying and classifying distinct mammal species involves demonstrating deep and largely independent evolutionary histories that usually involve genetic distinctions maintained over hundreds of thousands or millions of years (e.g. Baker and Bradley 2006).

Recognised domestic dog breeds, including the Dingo, may be diagnosable using genetic and/or morphological criteria, but an understanding of these lineage's shallow evolutionary histories does not allow them to be recognised as separate species by criteria in general use by twenty-first century mammalogical taxonomists. We hope that Smith *et al.* (2019) can evaluate comparative sources of evidence that are used to recognise overlooked species in mammalian carnivores—two recent examples are papers by Helgen *et al.* (2013) and Koepfli *et al.* (2015), which use data from nuclear and mitochondrial genomes, among other datasets, to show concordant evidence for identifying deep evolutionary lineages that were previously overlooked in taxonomic and nomenclatural practice. The latter study shows exactly how a potentially contentious question involving species boundaries in *Canis* can be reconciled with many different sources of evidence. Arguments about the putative species-level status for the Dingo falter instantly given the recent time involved in the putative separation from closely related lineages.

A geographically isolated (allopatric) species from all other *Canis*

Smith *et al.* (2019) argue that the Dingo should be considered distinct taxonomically because it was geographically isolated (i.e. allopatric) in Australia relative to all other species of *Canis* prior to the arrival of modern dogs in 1788. This is problematic, because allopatry is of itself not a good criterion for taxonomic decisions regarding species status. Of course, most mammal species demonstrate allopatric populations, with many being distributed across various continents, archipelagos, and islands, for example. Again, the recent arrival of the Dingo and its demonstrated genetic relationship with other domestic dogs suggest that the Dingo was neither present long enough in Australia, nor ever sufficiently isolated, to come even close to the amount of time in terms of evolutionary divergence that modern taxonomists would require to consider its candidacy as a distinct mammal species. Further, the statement by Smith *et al.* (2019) that the Dingo may have arrived into Australia up to 10,000 years ago is highly misleading. Various published palaeontological and archaeological records date the Dingo's arrival to a maximum of approximately 3,500 years ago and most genetic studies suggest their arrival was approximately 5,000 years ago (see Fillios & Taçon 2016; Jackson *et al.* 2017 for review). The most recent paleontological studies by Balme *et al.* (2018) dated bones from Madura Cave on the Nullarbor Plain in southern Australia to approximately 3250 years of age. These authors suggested that this is the oldest reliable date for the Dingo in Australia and in their view this date is very likely close to the time of first arrival of this species as they suggested it spread extremely rapidly throughout mainland Australia after its arrival. Finally, the Dingo in Australia may not have been geographically isolated since its introduction as there is evidence of multiple introductions over the last ~4,000 years with an unknown time span between them (Cairns *et al.* 2017).

Genetically distinct

When deploying high resolution genetic markers, it would be expected that many breeds of domestic dog, including Dingoes, may be genetically diagnosable, since each represents a distinct population. Each of these has an origin and history that reflects its movement and breeding by humans. Obviously, this does not mean that each breed or population should be regarded as distinct species, as genomic data should be interpreted conservatively when used to delineate species (Coates *et al.* 2018). That there are some genetic differences between Dingoes and other domestic dog breeds is unremarkable, especially given that dingoes have potentially been isolated in Australia for at least 3,000 generations: more than enough time for founder effects and genetic drift alone to produce differences in allele frequencies (potentially of no adaptive consequence). However, Smith *et al.* (2019) have failed to demonstrate that the Dingo is sufficiently genetically distinct from all other domestic dog breeds and Gray Wolves to be regarded as a separate species.

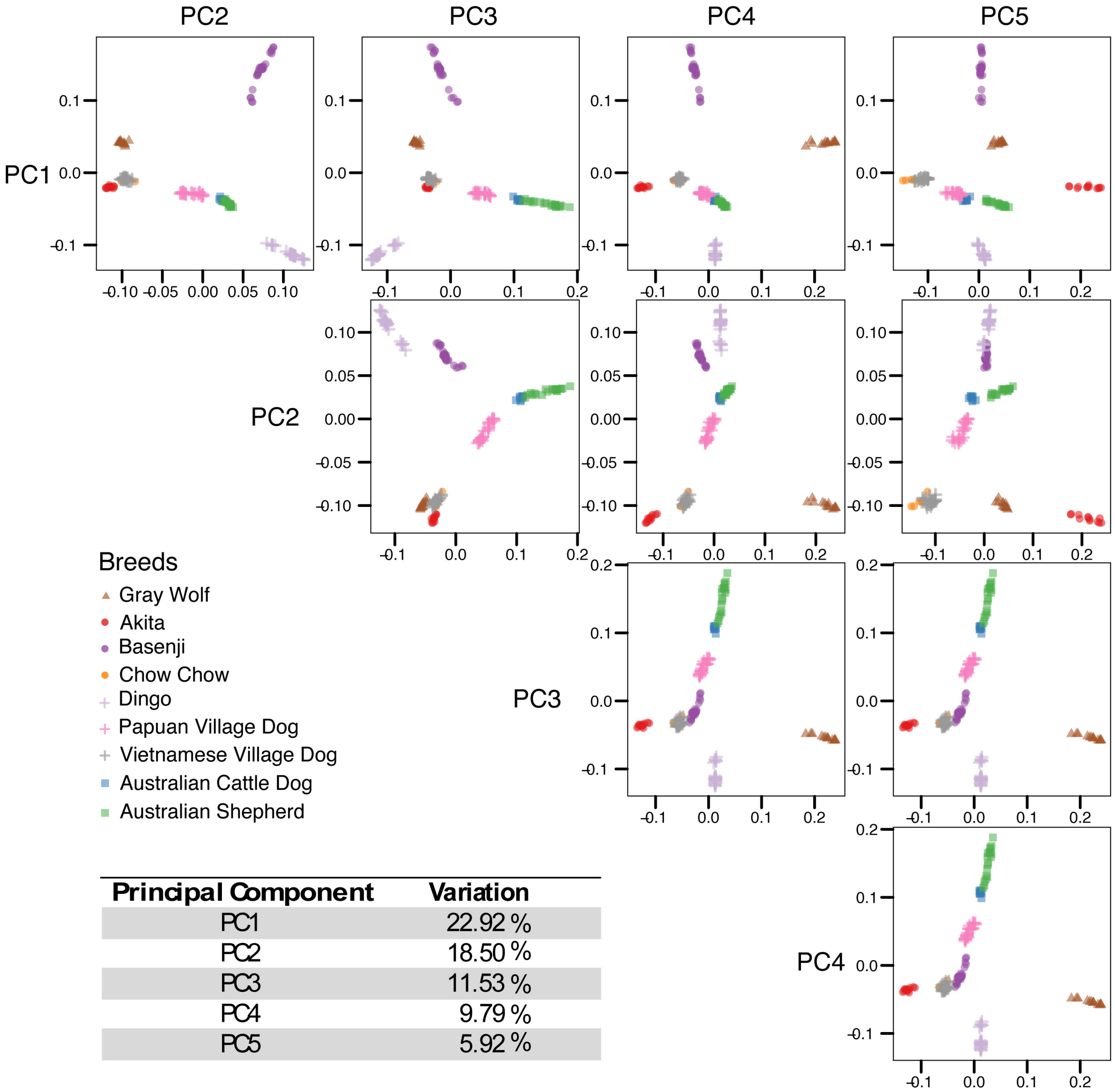
Most canid genetics papers that include Dingoes place them firmly within a domestic dog clade (e.g. Freedman *et al.* 2014; Skoglund *et al.* 2015; vonHoldt *et al.* 2010). A consistent pattern in recent genetic and genomic studies comparing most breeds of domestic dogs and Gray Wolves has been the placement of the Dingo within a group containing other Asian domestic dogs including the New Guinea Singing Dog, Chow Chow, Akita, Tibetan Mastiff, Chinese Indigenous Dog, Chinese Shar-pai, as well as the Alaskan malamute, Siberian husky and basenji (termed ancient breeds) (vonHoldt *et al.* 2010; Wang *et al.* 2013, 2016). Other genetic studies have consistently resolved a close relationship between Dingoes and Asian domestic dogs (e.g. Oskarsson *et al.* 2012: Sacks *et al.* 2013; Savolainen *et al.* 2004). In this context, the use of principal component analyses (PCAs) by Smith *et al.* (2019: Figure 3) to conclude that Dingoes "form a discrete population divergent from modern domestic dogs and wolves" is a problematic interpretation. It is not clear from their Figure 3 if other ancient domestic dog breeds were included and the analysis does not include the full diversity that is present within Gray Wolves (see Von Holdt *et al.* 2010). Here we recreate a scenario similar to Figure 3 in Smith *et al.* (2019) where we plot the first five principal components as a function of each other (**Figure 1**); this helps demonstrate how these kinds of visualizations depend entirely on which components are contrasted; single plots can be presented to support particular arguments. In another published comparison, Freedman *et al.* (2014) contrasted six principal components, summarizing genomic data for three Gray Wolves from different regions, a Dingo, a basenji, a boxer and a Golden Jackal (*C. aureus*), resulting in different groupings in each. In one plot the Dingo is grouped with both the boxer and basenji, in another plot it is more closely aligned with the Gray Wolves and the Golden Jackal than with the other two dogs, and in the third plot it is substantially isolated compared to all other samples. However, looking closely at Freedman *et al.* (2014), their PC1 versus PC2 plot shows the greatest distances between boxer, basenji, and all other samples including the Golden Jackal. This is an artefact of PCA known as the "uneven sampling bias" (e.g. McVean 2009), resulting in a sample size-driven distortion of the projection. Arguments based on visual summaries of genomic data as simplified by contrasting principal components must be interpreted with great care.

Study of uniparentally inheritated genetic data shows that Dingoes fall well within domestic dog diversity. For instance, results from vonHoldt *et al.* (2010), Skoglund *et al.* (2015), and Cairns *et al.* (2016, 2017) show that dingo mitochondrial and Y-chromosome lineages are nested within domestic dogs. The same result is corroborated using whole-genome data (Freedman *et al.* 2014, Skoglund *et al.* 2015), and genome-wide Single Nucleotide Polymorphisms (SNPs) data which we use here to demonstrate an ancestry reflecting drift sharing (shared history) and splits (**Figure 2**). In contrast, Smith *et al.* (2019: Figure 4) seem to conclude that Dingoes and New Guinea Singing Dogs form a separate lineage. This figure is based on low-resolution data, and it has been revisited by Freedman *et al.* (2016), showing that the split bottleneck between Gray Wolves and domestic dogs happened approximately 15kya, a domestication bottleneck that Dingoes, New Guinea Singing Dogs, and domestic dogs have all been subject to (Freedman *et al.* 2014).

The amylase 2B locus (AMY2B) is often referred to in the context of the timing of domestication of dogs in relation to the agrarian revolution and natural selection of dogs that could better digest a starchy, grain-supplemented diet (Fillios & Taçon 2016; Ollivier *et al.* 2016). Smith *et al.* (2019) emphasise that Dingoes only have two copies of the AMY2B locus as a point of distinction from other dogs. However, this characteristic is not unique to Dingoes because standard poodles also have only two copies and Siberian husky have only three to four copies (Freedman *et al.* 2014; Botigué *et al.* 2017). Two copies are common in other ancient dog samples (Ollivier *et al.* 2016), Gray Wolves, some Golden Jackals and foxes, and the Coyote (Botigué *et al.* 2017). This compares to other domestic dogs, with apparently longer history with agriculture, that have 10-20 copies (Freedman *et al.*

2014; Botigué *et al.* 2017). Therefore, this genetic character is not a point of differentiation of Dingoes from other dogs or, indeed, any canids.

The arguments of Smith *et al.* (2019) that the frequency of Dingo-dog hybridisation is overstated in other studies (e.g. Stephens *et al.* 2015) are erroneous and misleading. The genetic testing of Stephens *et al.* (2015) was undertaken in isolation from knowledge of phenotype or appearance of the sampled animals. Comparisons of samples from "southeast Australia to those in the northwest" only looked at the microsatellites of the tissues provided. The goals of Stephens *et al.* (2015) and Wilton *et al.* (1999) were, in fact, to determine the genetic makeup of free-roaming dog populations across Australia, rather than establishing the distribution of admixture or populations "devoid of modern dog ancestry" as Smith *et al.* stated. There was therefore no bias in the research question asked, nor in the sampling. Contrary to Smith *et al.* 's (2019) claims, most sampling was done in areas of low human activity as in Western Australia where most of the samples came from or across the complete regional distribution of free-ranging dogs, as in Victoria (Fig 1 of Stephens *et al.* 2015 and Fig 2 in Cairns *et al.* 2017).



Principal Component	Variation
PC1	22.92 %
PC2	18.50 %
PC3	11.53 %
PC4	9.79 %
PC5	5.92 %

FIGURE 1. Principal component analysis of 14 Gray Wolves, 40 Village dogs, 40 ancient dog breeds (Akita, Basenji, Chow Chow), 29 modern Australian dog breeds (Cattle dog and Australian Shepherd) from Shannon *et al.* (2015), and 23 Dingoes from Cairns *et al.* (2018). We filtered the data from the different studies to include only breeds of interest, and we kept shared SNPs using PLINK v1.90b5 (Chang *et al.* 2015). PC analysis was conducted using PLINK. Variation explained by the first five principal components was computed based on the eigenvalues of the first 20 components.

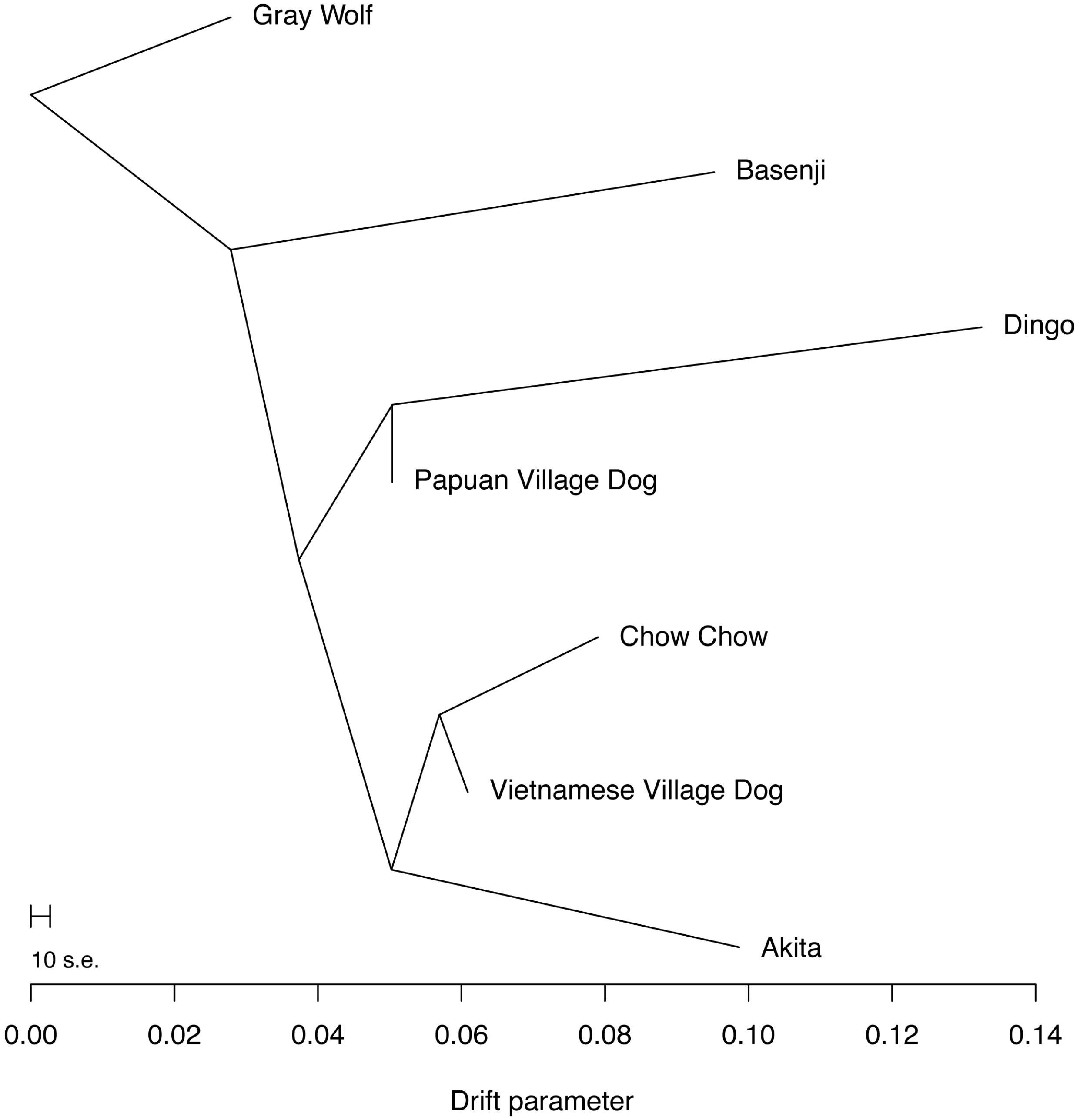


FIGURE 2. Maximum likelihood tree of Gray Wolves, Dingoes, village dogs and ancient dog breeds. We used PLINK to filter the merged dataset created for Fig. 1, and we used TreeMix v. 1.13 (Pickrell *et al.* 2012) to generate a maximum likelihood tree modelling shared ancestry and splits with no migration edges.

Phenotypically distinct

All breeds of domestic dog are, arguably, phenotypically distinct, but each breed is not and should not be regarded as a distinct species. The Australian National Kennel Council has a breed standard in relation to the characteristics and temperament of the Dingo (Australian National Kennel Council 2009) and other domestic dog breeds. That there are some morphological differences between Dingoes and other domestic dog breeds is unremarkable and Smith *et al.* have failed to demonstrate that the Dingo is sufficiently morphologically distinct from other domestic dog breeds and wolves to be regarded as a separate species.

The morphological differences identified by Smith *et al.* (2019) are not points of differentiation of the Dingo from the full spectrum or morphological variation in *C. familiaris*. Rather, the arguments of Smith *et al.* (2019)

place the Dingo's phenotype firmly within the range of domestic dogs for each of the cited characteristics. For example, all dogs have precaudal (or supracaudal) glands, as do many other mammals. Nearly all dogs have smaller heads than Gray Wolves and morphological diminution is often a product of domestication (Clutton-Brock 2017). Although many dog breeds are dolichocephalic (long-nosed) like wolves, most dogs have different cranial shapes to wolves. All dogs have either elongated faces (e.g. greyhounds) or paedomorphic skulls, whether extremely so like the brachycephalic (short-nosed) types or moderately so like mesaticephalic types (Georgevsky *et al.* 2014; Carrasco *et al.* 2014). The ratio of head width to head length (cephalic index) is highly variable among dogs (Georgevsky *et al.* 2014), even sometimes between sexes (Carrasco *et al.* 2014). Pure Dingoes do not "have a longer muzzle than domestic dogs", being mid-range (i.e. mesaticephalic to dolichocephalic) between extreme brachycephalic breeds like pugs and bulldogs, and dolichocephalic breeds like greyhounds (Georgevsky *et al.* 2014). Likewise, the fact that Dingoes have larger brain size to body size ratio than modern dogs does not differentiate them from other dogs, but rather correlates with supposed lesser impacts of anthropogenic selection compared to modern breeds. The ratio is expected because smaller relative brain size is associated with greater anthropogenic selection (Saetre *et al.* 2004). Modern dogs are further removed, through extensive recent selection (e.g. Coppinger & Schneider 1995), from wolves than ancient breeds like Dingoes, and so have smaller brain sizes (Wayne 1986).

Smith *et al.* (2019) also highlight numerous problems relating to separating Dingoes from modern domestic dogs morphologically. The 12 graphs on cranial morphology in Crowther *et al.* (2014), cited by Smith *et al.* (2019), showed a complete overlap in skull dimensions between the Dingo and dog skulls they measured. Even within Dingoes there is evidence of morphological separation between north-western and south-eastern populations (Colman 2015).

The Dingo's inner-ear shape was suggested as a point of differentiation by Smith *et al.* (2019), citing Schweizer *et al.* (2017). However, this argument is not supported by the reference cited, which suggests there was no significant difference between prehistoric and modern dogs, or between wolves and modern dogs, and "Dingoes reflect the mean shape in the context of variation in the sample" (Schweizer *et al.* 2017). These authors also suggest that this mirrors the condition of feral forms in other organs, in which there is an incomplete return to ancestral characteristics. Another of the suggested features of differentiation by Smith *et al.* (2019) is that the "Dingo's body is longer than its height". However, we observe that this can also be said of various other breeds of dogs including the corgi or dachshund.

Smith *et al.* (2019) suggest via their Figure 1 that the typical phenotype of a Dingo is the classical ginger coloured dog. This is unsurprising because the ginger colouration is dominant (Corbett 2001). However, Dingoes can be white, black and white, sable or black and tan in colour (e.g. Corbett 2001; Elledge *et al.* 2006; Fleming *et al.* 2014), which supports the contention that the Dingo is a mixed dog with possible multiple introductions (e.g. Cairns & Wilton 2016; Cairns *et al.* 2017) and that they were not isolated from further introductions after they first arrived in Australia. These observations clearly highlight that the Dingo is not consistent in its phenotype, and undermines the notion that the Dingo was geographically isolated after its arrival in Australia (see above).

Ecologically distinct

Ecological distinctiveness is not necessarily a helpful criterion for taxonomic decisions about species boundaries; populations within most widely distributed species frequently have distinct ecologies throughout their distributions. Nonetheless, the roles of dogs in ecosystems are various (Doherty *et al.* 2017; Fleming *et al.* 2014), and adaptable generalists like Dingoes (e.g. Davis *et al.* 2015; Corbett 2001) can play different roles in different contexts (Fleming *et al.* 2017). The roles and importance of the Dingo in Australian ecosystems remains contested (e.g. Arthur *et al.* 2012; Fleming *et al.* 2012; Allen *et al.* 2013; Johnson & Ritchie 2013; Newsome *et al.* 2017). This state of uncertainty will remain until studies provide stronger inference (Ford & Goheen 2015; Allen *et al.* 2017a, b) and the genetic composition of study populations is assessed simultaneously with their ecology (e.g. Claridge *et al.* 2009). All of this has no relevance for questions about the Dingo's taxonomic distinction.

Behaviourally distinct

Arguments about the behaviour of dogs are not especially helpful in taxonomic decisions about the Dingo's species status. Many breeds of domestic dog, including the Dingo, are behaviourally quite distinct and their morphology reflects their different recent histories, including selection pressures for certain behaviours (Duffy *et al.* 2008; McGreevy *et al.* 2013). For example, livestock herding dogs have behaviours toward domestic prey animals that are diametrically opposed to livestock guarding breeds such as marremas, Grand Pyreneans and karabash types (Coppinger & Coppinger 1993; Coppinger & Schneider 1995). Importantly (from these citations), there is a relationship between skull morphology and a breed's purpose, with dogs bred for similar purposes having similar cephalic indices (Georgevsky *et al.* 2014). It should therefore be no surprise that Dingoes have different skulls to Great Danes, pugs and trufflers. The claim that dogs don't howl (Smith *et al.* 2019) is unsupported (Cohen & Fox 1976; Faragó *et al.* 2014) and having varied vocalisations is not a unique characteristic of Dingoes because basenjis are also "barkless", with a howl-like vocal repertoire (Basenji Club of New South Wales 2000).

Devoid or largely devoid of many of the signs of domestication, including surviving largely as a wild animal in Australia for millennia

While the history and progression of dog domestication is of scientific interest, this criterion has no relevance in assessing the species status of the Dingo. Current evidence indicates that all domestic dogs, including Dingoes, were derived by passive and active domestications from wolves on more than one occasion (Pang *et al.* 2009; Frantz *et al.* 2016) across Eurasia (Freedman *et al.* 2014; Thalmann *et al.* 2013; vonHoldt *et al.* 2010). That Dingoes and other dogs were formed by domestication from wolves is not in dispute (Skoglund *et al.* 2015) and that some populations of Dingoes later became feral and "survived as a wild animal" is immaterial to taxonomic or nomenclatural arguments.

Nonetheless, the argument that Dingoes were not a domestic animal in Australia appears difficult to sustain. As acknowledged by Smith *et al.* (2019), the Dingo is unusual in that, in its relationship with Aboriginals, it may be considered neither wild nor domesticated as defined by Dobney and Larson (2006). Alternatively, one could consider them both feral and domesticated, depending on the closeness or distance of their association with people, and indigenous languages had different words and phrases for the Dingo in those different associations (e.g. Troy & Troy 1994). Available historical information suggests the Australian Dingo was clearly an integral part of many Aboriginal communities and had an intricate relationship with them. For example, George Caley, while exploring west of the Cow Pastures on the Nepean River in the Sydney Basin of New South Wales, met with an indigenous party near present day Mount Hunter (34°04'16" S; 150°38'12" E) on 12th February 1804. The party, led by Cannabygal, had never seen a European person and had "a large domesticated native dog with them" (Caley's diary quoted in Lee 1925, p. 138). Likewise, Allan Cunningham accompanying King on the "Mermaid" observed "three native dogs of a red colour" accompanying a group of Tiwi Islanders near St Asaph's Bay, Melville Island (11°20'22" S; 130°23'37"E) on 16th May 1818 (Cunningham's diary quoted in Lee 1925, p. 387).

Later reports showed that Dingoes were bred and reared as pets by Aboriginal Australians and multiple animals slept with their owners (Meggitt 1965; Hamilton 1972; Lumholtz 1889; McIntosh 1975). They were given individual names and in at least some locations such as tropical northern Queensland and central Australia they were groomed of fleas and given great affection, including caressing them (Lumholtz 1889; Berndt & Berndt 1942; Hamilton 1972). Though it appears that Dingoes were owned by both men and women in central Australia, and at least some other locations, the Aboriginal women were known to carry dogs around their waist like babies with the fore paws and nose being grasped in one hand, while the hind paws and tail are in the other (White 1915), and even breast-feed pups (Krefft 1862; Berndt & Berndt 1942; Hamilton 1972). Pups were even rubbed with ochre to protect them against spirits in both central and south east Australia (Krefft 1862; Hamilton 1972). When Gerard Krefft (1862) travelled along the Lower Murray and Darling Rivers he noted that "of their dogs the natives are almost as fond as of their children. Woman do not hesitate to suckle pups". Such was the status of Dingoes, that upon their death they appear to have been the only animals that were given a formal burial in a record from Arnhem Land (Gunn *et al.* 2010; Meehan *et al.* 1999). Therefore, it seems difficult to deny that Dingoes were under some form of domestication by Aboriginal people.

Conservation implications

The suggestion by Smith *et al.* (2019) that the recognition of the Dingo as a distinct species would "likely aid in the conservation and management of the Dingo" is a dangerous consideration. Taxonomy and nomenclature should be based on evidence about evolutionary distinctness and accepted use of ICZN protocols, respectively, and not adjusted for conservation convenience or outcome. In all likelihood, the applied nomen will have little influence on the management or conservation of the Dingo. The management of free-roaming dogs in Australia is complex and falls under various legislation that acknowledges their multiplicity of status. However, the various State biosecurity acts mostly take precedence over conservation acts, and definitions of wild dogs under those acts and associated regulations and control orders incorporate Dingoes specifically (see Appendix D in National Project Steering Committee [NWDAP 2014] for a list of legislation pertaining to free-roaming dogs across Australia). Recent reviews of the Dingo's conservation status suggest the Dingo is not currently threatened (Woinarski *et al.* 2014; Allen *et al.* 2017c). Allen *et al.* (2017c) provide a roadmap for practical conservation of Dingoes in Australia that applies regardless of nomenclature.

Conclusion

Smith *et al.* (2019) demonstrate manifold misunderstandings about taxonomy and nomenclature and provided various arguments that are extraneous to taxonomy. Smith *et al.* (2019) failed to provide sufficient evidence to differentiate the Dingo from other domestic dogs at the species level, which in a modern taxonomic framework would involve demonstrating a separate evolutionary history dating back hundreds of thousands to millions of years. Current evidence instead demonstrates the very close relationship between the Dingo and other domestic dogs, and the lack of any identifiable species boundary between the Dingo and domestic dogs in a modern taxonomic sense. By convention and Opinion (Gentry *et al.* 1996; ICZN 2003), domesticates of a wild progenitor must be referred to by their own binomen. In this case, the binomen for the species domesticated from Gray Wolves, including Dingoes, New Guinea Singing Dogs, and other domestic dogs, is *Canis familiaris* (Jackson *et al.* 2017). There are many reasons to appreciate the Dingo and to recognise its importance in Australian culture, heritage, and ecology. However, these considerations need to be made outside of any special status attributable to modern taxonomic distinction, or nomenclatural standing.

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