Article

Taxonomic status of the Australian dingo: the case for *Canis dingo* Meyer, 1793

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Abstract

The taxonomic status and systematic nomenclature of the Australian dingo remain contentious, resulting in decades of inconsistent applications in the scientific literature and in policy. Prompted by a recent publication calling for dingoes to be considered taxonomically as domestic dogs (Jackson *et al.* 2017, *Zootaxa* 4317, 201-224), we review the issues of the taxonomy applied to canids, and summarise the main differences between dingoes and other canids. We conclude that (1) the Australian dingo is 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. The case of defining dingo taxonomy provides a quintessential example of the disagreements between species concepts (e.g., biological, phylogenetic, ecological, morphological). Applying the biological species concept *sensu stricto* to the dingo as suggested by Jackson *et al.* (2017) and consistently across the Canidae would lead to an aggregation of all *Canis* populations, implying for example that dogs and wolves are the same species. Such an aggregation would have substantial implications for taxonomic clarity, biological research, and wildlife conservation. 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, and a successful application to the International Commission for Zoological Nomenclature - neither of which can be adequately supported. Although there are many species concepts, the sum of the evidence presented in this paper affirms the classification of the dingo as a distinct taxon, namely *Canis dingo*.

Key words: dingo, dog, canid, Canidae, domestication, hybridisation, nomenclature, species concept, taxonomy

Introduction

The dingo (Order Carnivora: Family Canidae: Genus *Canis*) occurs over much of mainland Australia but is absent from the island of Tasmania. It was the only representative of its genus, and the largest non-human terrestrial eutherian in Australia since its arrival *circa* 5 to 10 thousand years before present (ka), until the arrival of the Europeans in the late 18th Century (Johnson 2006; Smith & Savolainen 2015). The dingo has possibly the most ambiguous taxonomic identity of any Australian mammal, and its accepted scientific name has varied over time.

Over the past few decades, there has been inconsistent use of nomenclature for dingoes, varying primarily between *Canis lupus dingo*, *C. dingo*, and *C. familiaris dingo*, and several papers have attempted to resolve the issue. Some authors argue that the dingo should be considered a separate species and subsequently claim that the nomen *C. dingo* is more appropriate (e.g., Crowther *et al.* 2014; Clutton-Brock 2015; Smith 2015a). Others have called for the dingo to be considered alongside dogs as *C. familiaris*, and not warranting designation as a subspecies (Jackson & Groves 2015; Allen *et al.* 2017; Jackson *et al.* 2017; also see general reviews of the genus *Canis* such as van Gelder 1978 and Dinets 2015). Although scientific agreement can be difficult (a task made inherently more difficult due to the contentious nature of both taxonomy and nomenclature), a concerted effort is needed to apply an approach for the dingo that is consistent at least with the taxonomic and nomenclatural approach applied to other canids. We apply this approach to respond to Jackson *et al.* (2017) who most recently proposed that dingoes are a domestic dog (*C. familiaris*), to reaffirm that dingoes are dingoes (*C. dingo*).

Taxonomic background

The dingo was first named *C. familiaris dingo* Blumenbach, 1780; and shortly after *C. antarticus* Kerr, 1792 and *C. dingo* Meyer, 1793. The two latter names were based on a rudimentary drawing and brief description included in the journal of Australia's first colonial governor, Arthur Phillip (Mazell & Phillip 1789). For a comprehensive taxonomic history of the dingo see Jackson *et al.* (2017). In 1957 there was a successful application to the International Commission of Zoological Nomenclature (ICZN, hereafter referred to as 'the Commision') 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. We 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.

The contemporary use of *C. familiaris dingo* began with Newsome *et al.* (1972), and appears to have increased after the identification of 'dingo like' canids from studies that suggested a lack of morphological separation between dingoes and Asian village dogs (Corbett 1985, 2001a). In the 1990s, the dingo began to be referred to as *C. lupus dingo* as part of a larger shift to classify dogs as *C. lupus familiaris* (Corbett 2001a), and this trinomial remains in many publications as well as on the latest International Union for Conservation of Nature Red List of Threatened Species (iucnredlist.org) (Corbett 2008).

Species concepts and delimitation

At least 32 species concepts have been applied in attempts to provide accurate and consistent allocation of biological populations (Zachos 2016). Although these can be somewhat reduced to fewer distinct species concepts (Mayr & Ashlock 1991), the plurality of species concepts prohibits us from addressing all possible ways the dingo could be treated taxonomically relative to other *Canis* populations. We can, however, contrast the two most commonly applied species concepts to the dingo: the biological (*sensu* Mayr 1942, 1963) and the phylogenetic species concepts (*sensu* Eldredge & Cracraft 1980; Cracraft 1983; Groves *et al*. 2017).

Biological species concept and hybridisation. Applying the biological species concept to the dingo and consistently across canids, with its emphasis on the reproductive isolation and 'zygostructure' (*sensu* Jolly 2001) of populations, would result in demotion of the biological population to a subspecies (or sub-subspecies) of a single, effectively globally distributed, polytypic species of *Canis*. It has been established that *Canis* species, where parapatric or kept in captivity (grey wolf [*C. lupus*], red wolf [*C. rufus*], eastern wolf [*C. lycaon*], coyote [*C. latrans*], Ethiopian wolf [*C. simensis*], golden jackal [*C. aureus*], dingo [*C. dingo*], and domestic dog [*C. familiaris*]), are capable of interspecific hybridisation resulting in viable, fertile offspring (e.g., dingoes and wolves; Lockyear 1932). This has complicated the genetic relationships within the species complex and the taxonomy of the group (Ardalan *et al.* 2011; Klütsch *et al.* 2011; Hindrikson *et al.* 2012; vonHoldt *et al.* 2013). In particular, North American canids (wolf species and coyotes) readily hybridise and there is evidence of historic introgression by domestic dogs in both wolves and coyotes. Several canid populations share ancestries from two or three species (vonHoldt *et al.* 2011; vonHoldt *et al.* 2016). For example, analyses of genome-wide nuclear data indicate that, since the first origin of dogs, there has been substantial admixture between dogs and wolves throughout history, leading to approximately 10% genetic admixture of wolf in dog and *vice versa* in populations across Eurasia (vonHoldt *et al.* 2010; Shannon *et al.* 2015; Wang *et al.* 2016; Fan *et al.* 2016; Botigué *et al.* 2017).

Hybridisation between dingoes and domestic dogs has been the subject of several studies. An Australia-wide study looking at the extent and spatial pattern of dingo–domestic dog admixture (Stephens 2011; Stephens *et al*. 2015) indicated that in regional/remote areas, most dingoes have retained their dingo ancestry, and that those that have dog ancestry have only a small percentage of dog genes. Overall, 46% of dingo samples were classified as having no dog ancestry. The southeast of Australia had the highest proportion of dingo-dog admixture, with only 1–4% of tested animals showing no dog-like genetic markers. This is not surprising given the density of human settlement and the location of the best land for agriculture in the southeast—factors that have been flagged as strong predictors of dingo-domestic dog admixture (Newsome & Corbett 1985; Woodall *et al.* 1996). The incidence of hybridisation has seemingly changed little over the past few decades (e.g., Newsome & Corbett 1985, using skull morphology); however, high proportions of dingoes with no dog ancestry were found in other parts of Australia, particularly in central Australia (only 13% showing evidence of dog ancestry), and in Western Australia (41% with dog ancestry). There are three reasons why the frequency of dingo–domestic dog hybrids might be overstated; (1) Current DNA testing methods (i.e., Stephens *et al.* 2015 or Wilton 2001) were designed without knowledge of the geographical, phenotypic, and genetic variation within dingoes (Cairns & Wilton 2016, Cairns *et al.* 2017). Thus, when comparing dingoes in southeast Australia to those in the northwest, they might appear different, and so could be falsely labelled as having dog ancestry. (2) Most studies of the genetic integrity of dingo populations have been done with the goal of establishing the distribution of dingo–domestic dog admixture, rather than of populations devoid of any dog ancestry. That is, samples used for genetic studies (e.g., Stephens *et al.* 2015) are biased towards animals collected (killed) from areas with high human activity and artificially abundant food

resources. As a result, samples do not always reflect dingoes that do not encounter dogs. (3) There are some behavioural barriers that hinder hybridisation in canids (Hinton *et al.* 2018). It is difficult for a feral domestic dog to integrate and compete with a large dingo population that has a stable pack structure (Corbett 2001b). As is the case for wolf hybridisation with other *Canis* species (Vilà & Wayne 1999), behavioural and physiological differences make mating difficult, and hybrid offspring can exhibit lower fitness in the wild. For these reasons, Vilà and Wayne (1999) argued that hybridisation is not a major management concern, and that natural selection will help ensure that the behavioural sequences necessary for survival and reproduction are maintained and passed onto subsequent generations (Jones 1990).

Research on dingo-domestic dog hybridisation raises the question of how the biological population of dingoes is delimited. The proposed definition of a dingo by Smith and Savolainen (2015) excludes all dingoes that have dog ancestry (as well as free-living domestic dogs with modern domestic ancestry, such as a pet dog that has escaped a farm, a hunting dog abandoned in the bush, or a village dog). However, given that most wild dingo–dog hybrids have a higher proportion of dingo ancestry than domestic dog ancestry (Stephens *et al.* 2015), and in the wild hybrids express a 'dingo identity' in morphology (Parr *et al.* 2016), ecology (Glen 2010), and seasonality (Cursino *et al.* 2017), not all hybrids should be completely excluded from modern definitions of the dingo. Instead, considering vonHoldt *et al.*'s (2017) suggestion of a 10-20% threshold of genomic admixture (e.g., between coyotes and wolves), we concur that an adjustment might be needed to the existing definition of dingoes to include those with at least 75% dingo genetic identity (Glen 2010; Purcell 2010; Parr *et al.* 2016).

The genus *Canis* is not alone in presenting challenges to maintaining biologically meaningful 'units' of analysis under strict application of the biological species concept because of increasing documentation of hybridisation between previously recognised species. A diverse literature has highlighted the regularity of interspecific and intergeneric hybridisation across major taxonomic groups, from carnivores to cetartiodactyls, and plants to primates (Knobloch 1972; Groves 1997; Jolly *et al.* 1997; Allendorf *et al.* 2001; Jolly, 2001, 2003; Detwiler et al. 2005; Mallet, 2005; Halbert & Derr 2007; Lecis *et al.* 2006; Garnett & Christidis, 2007; Jolly *et al.* 2011; Li *et al.* 2016; Zachos 2016; Groves *et al.* 2017). This increasing documentation of hybridisation challenges traditional taxonomic classification and biological research, and complicates the management and conservation of wild species (particularly through domestic genetic introgression; Halbert & Derr 2007; Hertwig *et al.* 2009; Hindrikson *et al.* 2012; vonHoldt & Driscoll 2016; Kumar *et al.* 2017). For taxonomy, it highlights the difficulty of a universal definition for a species that can be applied across all biological populations (Zachos 2016 and references therein). For biological research, it results in uneven application of species concepts to delimit populations under analysis, leading to artificial aggregations or delineations that amplify or obscure natural variation or meaningful relationships (Jolly 2001, 2003; Zachos, 2016). In wildlife conservation and management, using a particular species concept can substantially influence government policy, funding allocations, and management strategies (Detwiler *et al.* 2005; Garnett & Christidis 2007; Zachos, 2016; Groves *et al.* 2017). Hybridisation and resulting introgression could be viewed as an important source of genetic variation and adaptation, rather than a threat to species 'purity'. Because species delimitation is done *post factum*, hybridisation can be viewed simply as a part of evolutionary processes that occur during and after speciation events (Li *et al.* 2016; Zachos 2016).

Phylogenetic species concept. Biologists working across taxonomic groups have developed other species concepts to define and delimit biological variability beyond focus on reproductive limitations (zygostructure) and towards the distribution of heritable characters (genetic, phenotypic; phenostructure; *sensu* Jolly 2001, 2003) on the species-concept continuum (see also Zachos 2016). Included within the more phenostructure-oriented species concepts is the phylogenetic species concept (*sensu* Groves *et al.* 2017), which emphasises diagnosable characters and unique character-state combinations, and delimits species as "... the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983: p. 170). Although receiving strong support and increasingly applied (e.g., Groves & Grubb 2011; Groves 2014; Groves *et al.* 2017), the phylogenetic species concept is not without criticism, particularly when viewed as using inconsistent criteria or artificially inflating species numbers by elevating populations or historic subspecies to the taxonomic rank of species (Garnett & Christidis 2007; Zachos 2016).

The treatment of the dingo as a separate species is supported by application of the phylogenetic species concept (or other species concepts, like the cohesion species concept; Templeton 1989) and considering the unique genetic and phenotypic characters and character states relative to other species of *Canis* outlined in this paper.

While applying the biological species concept or other species delimitations with more weight on zygostructure could be used to argue for a particular subspecific status for the dingo, we note that doing so (1) discounts the genetic, phenotypic and behavioural data outlined below that delimit the dingo relative to other *Canis* species, (2) ignores the allopatry of dingoes prior to the European introduction of domestic dogs, with anthropogenic-origin hybridisation and potentially still mediated by anthropogenic factors, (3) means consistent application of the biological species concept would require the global consolidation of many Canid populations (for example, *Canis* is currently divided as species or subspecies of wolves, coyotes, jackals, and domestic dogs) into a single polytypic species that collapses substantial genetic and phenotypic variability, and (4) positions dingoes as demographically exchangeable with domestic dogs and/or other wild canid populations and expressing the same ranges, abilities, and adaptive niche. The effective burden of the argument is not in supporting the positive case for maintaining the current nomen *C. dingo* listed with the ICZN, but rather why this current designation requires revision.

Need for more integrative approaches to canid taxonomy. While Jackson *et al.* (2017) are free to follow a strict interpretation of the biological species concept, there are implications to applying the concept consistently to wild canids-namely, translating substantial interspecific variability into intraspecific variability and eliminating the utility of having meaningful population 'units' within biology, ethology, and ecology. Taking a broader, more integrative approach that focuses on evidence emerging from distinct fields such as morphology, genetics and behaviour, allows for a better species delimitation (Dayrat 2005; Padial *et al.* 2010; Schlick-Steiner *et al.* 2010). Integrative taxonomy can, for instance, help distinguish cryptic taxa (e.g., Goodman *et al.* 2009) or in the case of taxa such as *Canis*, help delineate species even without reproductive isolation. Thus, following the integrative approach, we discuss the extent of the similarities and differences between dingoes and dogs on a suite of traits: genetics, morphology, behaviour and ecology. Based on the evidence, we argue that if two populations are different enough in these characteristics, they warrant separate designation, irrespective of potential genetic compatibility.

Differentiating dingoes from other canids

Jackson *et al.* (2017) focus on the apparent "... degree of genetic compatibility that exists" (p. 204) between dingoes and domestic dogs, and argue that because dingoes (1) share a genetic continuum with dogs and can readily hybridise with dogs, (2) were assumed to have been introduced to the Australian continent by humans, and (3) overlap morphologically with dogs, that dingoes should be classified as a breed of domestic dog. This mirrors the global confusion and discussion about the naming of species where there are wild and domestic derivatives (see later section). Indeed, these arguments do not adequately reflect the complexity of the issue of distinguishing canids, and do not sufficiently account for the uniqueness of the dingo. Below we outline additional reasons why dingoes can and should be differentiated from domestic dogs.

Phenotypic comparisons

General appearance. The average adult dingo weighs approximately 15 kg, stands 55 cm at the shoulder and measures 123 cm from nose to tail tip (Corbett 2001a; Smith 2015a). Smith (2015b) outlined several features considered typical (or hallmarks) of the pure dingo that can be used to distinguish dingoes from most breeds of dog because they are not common features of domestic dogs (see Sanchez-Villagra *et al.* 2016). For example, the dingo's body is longer than its height; the ribcage is long and extends to the rear; the head is the widest part of its body (i.e., it has a narrow chest and does not extend below the elbow); the skull is high behind the ears, and the ears are positioned forward of the occiput; the eyes are slanted, almond–shaped and obliquely placed; and the tail is typically carried low, does not curl over the back, and a precaudal scent gland is positioned on the tail. For an example of a 'typical' dingo phenotype refer to Fig. 1.

Coat colour (e.g., a uniform coat colour, white markings) can provide some indication of difference between pure and hybrid dog–dingoes (Newsome & Corbett 1985; Jones 1990; Corbett 2001a,b). Colours that indicate hybridisation (domestic dog heritage) are brindle, patchy colours, spots, and saddle patterns (e.g., German shepherds), which are controlled by modern mutations likely tied to domestication and artificial selection, and would not be present in a 'pure' dingo with no modern dog ancestry (Cairns *et al.* 2011; Smith 2015a). There is a

general perception, both in the scientific literature and the lay public more generally, that dingoes are uniformly yellow (or ginger) with white markings at the extremities. However, while this is often the case, old skins show that other pelage colourations also existed in remote areas in the 19th Century, including animals that were black with brown extremities, animals with dark dorsal fur (sable colouration), and white (Crowther *et al.* 2014). The variation in pelage makes it difficult to distinguish dingoes from those hybridised with domestic dogs with any confidence. Overall, phenotypic comparison with the domestic dog is difficult (Elledge *et al.* 2006, 2008; Newsome *et al.* 2013), particularly given the extreme variability in dog phenotypes (Crowther *et al.* 2014; Drake & Klingenberg 2010). Thus, there is often overlap across breeds of dogs and wild canids (Crowther *et al.* 2014; Smith *et al.* 2018).

FIGURE 1. An example of a typical dingo phenotype. Photograph depicts a male from K'gari-Fraser Island (Queensland) by John Williams.

Cranial morphology. Morphological separation of the dingo from other canids has long been documented (Zeuner 1963; Epstein 1971; Macintosh 1975; Barker & Macintosh 1979). Dingoes generally have smaller skulls than wolves (e.g., the skull length of dingoes is approximately 15% smaller than the relatively small Indian wolf *C. lupus pallipes*) and have different cranial (Gollan 1982; Corbett 2001a; Crowther *et al.* 2014; Parr *et al.* 2016; Geiger *et al.* 2017) and inner-ear shapes (Schweizer *et al.* 2017). Compared with wolves, dingoes also have a paedomorphic skull shape, characterised by a shorter, broader face (Geiger *et al.* 2017). In addition, dingoes show clear separation in cranial morphology from the village dogs of Thailand and Indonesia (Gollan 1982; Corbett 1985; Gonzalez 2012). Dingoes also differ morphologically from New Guinea singing dogs (*C. hallstromi*) by their smaller relative zygomatic width (Koler–Matznick *et al.* 2003; Crowther *et al.* 2014).

Compared with domestic dogs, 'pure' dingoes have a longer muzzle (Newsome *et al.* 1980; Newsome & Corbett, 1982), larger canine and carnassial teeth, with canine teeth slightly longer and more slender, larger auditory bullae (Newsome *et al.* 1980; Newsome & Corbett 1982; Corbett 2001a), larger brain/body size (Smith *et al.* 2018), and a flatter cranium with larger nuchal (Newsome *et al.* 1980; Newsome & Corbett 1982; Geiger *et al.* 2017) and sagittal crests (Gollan 1984; Jones 1990). The dingo's inner-ear shape is more like wolves than that in many dog breeds (Schweizer *et al.* 2017). However, morphological separation of dingoes from domestic dogs remains a problem for the following reasons:

1   There is more morphological variation in cranial shape within the domestic dog than there is among all species within the whole Carnivora (Drake & Klingenberg 2010);

2   Dingoes and dingo–dog hybrids can be difficult to separate morphologically (Newsome & Corbett 1982; Jones 1990; Elledge *et al.* 2008; Newsome *et al.* 2013; Parr *et al.* 2016);

3   Morphological and molecular separation of dingoes and domestic dogs are based on post–European contact animals, or those that were captive (Newsome *et al* 1980; Newsome & Corbett, 1982; Elledge *et al.* 2006, 2008; Wilton *et al.* 1999; Wilton, 2001); hence, samples could have contained pedigrees showing introgression;

4   Some dog breeds, particularly the Australian cattle dog, show evidence of past dingo hybridisation (Arnstein *et al.* 1964), potentially causing difficulties in providing clear and consistent diagnostic features that separate dingoes from dogs in the past (Newsome *et al.* 1980);

5   Dingoes exhibit morphological variation through space and time, mostly in size (Corbett 2001a,b; Radford *et al.* 2012; Claridge *et al.* 2014; Colman 2015);

6   There is genetic evidence for at least two sub-populations of the dingo, possibly the result of multiple introductions into Australia (Cairns & Wilton 2016; Cairns *et al.* 2017). These sub-populations also show some evidence of morphological separation (Colman 2015), thus further clouding possible diagnostic features between dingoes and dogs.

Crowther *et al.* (2014) recognised these difficulties in providing reliable morphological diagnostic features to separate dingoes from domestic dogs. Hence, they defined dingoes not by using absolute separation of characters in bivariate and principal components plots, but by defining dingoes as a tight cluster within the variation of domestic dogs. Parr *et al.* (2016) also showed a tight clustering of dingoes within a broader spread of feral and domestic dogs in whole cranial morphology. Despite overlap, dingoes have relatively larger palatal widths, longer rostra, shorter skull heights, and wider temporal ridges of the skull (Crowther *et al.* 2014) compared to domestic dogs. Furthermore, dingo skulls do not display any of the more extreme modifications or changes caused by domestication (and high incidence of inbreeding this entails) such as more rounded and forward pointing eyes, shortening of muzzle, and subsequent overcrowding of teeth, reduction in size of the sagittal and nuchal crests, and reduced tympanic bulla (Jones 1990) (Fig. 2).
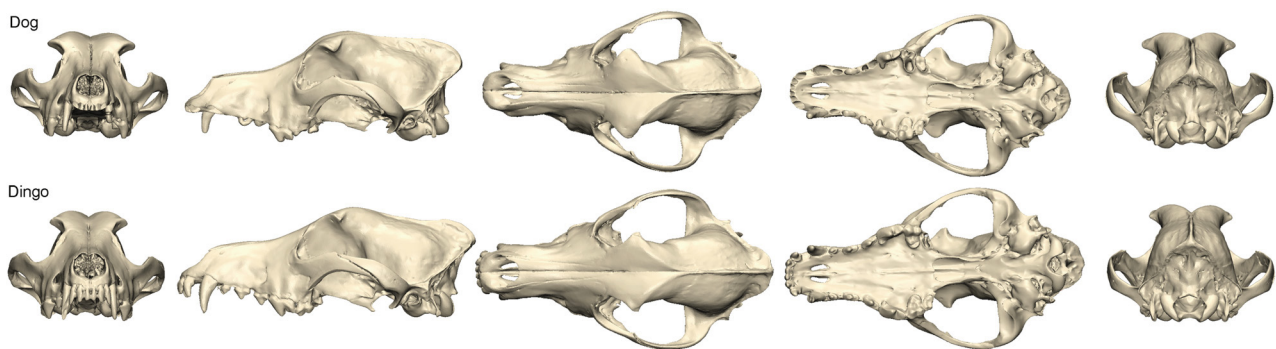

FIGURE 2. Cranial 3-D reconstructions of a dingo (bottom) and a free-ranging dog (top), highlighting the differences in cranial morphology mentioned in the text. The dog cranium has been scaled to match the length of the dingo cranium to facilitate the comparison of feature shape. The dingo (male) was collected from Minburra Station in South Australia. The dog (female, 14.5 kg) was collected in 1981 from the Victorian Highlands (Evan Jones Collection).

Crowther *et al.* (2014) also tackled the problem of uncertainty in relation to dingo ancestry by using pre–European contact specimens, as well as specimens from parts of pre–1900 Australia where European settlement was sparse. While hybridisation could have played a part in producing patterns of coat colouration (Newsome & Corbett 1985; Cairns *et al.* 2011; Crowther *et al.* 2014), it appears to have contributed little to altering the cranial shape of dingoes. Parr *et al.* (2016) used a 3-D geometric-morphometric approach to quantify the overall cranial (osteological) morphology of dingoes, domestic dogs, and dingo dog–hybrids. They used dingoes and dingo–dog hybrids that had been bred for experimental studies (Catling *et al.* 1992; Newsome & Corbett 1982), as well as a selection of domestic and feral (wild–caught) dogs. Dingoes and dingo–dog hybrids formed tight clusters within the canid morphospace, and were statistically indistinguishable, while domestic dogs were widely spread across the

morphospace. This might be in part because domestic dogs are selectively bred to fix sometimes extreme phenotypic traits, which are often genetically recessive, leading to more homozygous recessive fixation in the genome. Wild dingoes experience natural selection on a wider gene pool, which maintains dominant trait phenotypes and heterozygous genotypes (Parr *et al.* 2016).

Most of the world's dogs live semi-autonomous mutualistic relationships with humans (Barnett & Rudd 1983; Gompper 2014). In this most common condition, the dog phenotype does share some generic traits with dingoes. However, this phenotype is much more variable than the dingo phenotype — i.e., they can still exhibit flopped ears, spotty/patchy coat — depending on the ancestry of the domestic dog breed. Village dogs in Southeast Asia can share superficial phenotypic similarity to dingoes, but are distinguishable from dingoes on a range of morphological, phenotypic, and genetic variables (Corbett 1985; Gonzalez 2012; Cairns & Wilton 2016).

Jackson *et al.* (2017) made note of Parr *et al.'s* (2016) observation 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" (p. 210–211). While this is partially true, it requires qualification because what Parr *et al.* (2016) had in fact shown was that dingoes and dingo-dog hybrids could not be differentiated based on a morphometric analysis of the *overall* cranial shape. This included testing the landmarks used by Newsome *et al.* (1980), Newsome & Corbett (1982) and Corbett (2001a,b) that could not differentiate the cranial shapes of dingoes and hybrids. However, these findings do not exclude the dingo from having unique morphology in particular regions of the cranium.

Further, Parr *et al.* (2016) did not show that hybridisation changes the shape of descendant animals, but rather that over successive generations of hybridisation events (i.e., F1 = dingo × breed dog, F2 = dingo × F1, F3 = dingo × F2, etc. …), the hybrids express dingo morphology. This is explained through the dingo line essentially representing a 'wild type' genetic lineage, at least compared to breed dogs, which are frequently back–crossed to 'fix' desirable (at least to humans) phenotypic traits. In other words, the 'breed dogs' represent narrower, often recessive, genotypes, whose phenotypes are not expressed after the F2 generation of hybrids with the 'wild type' dingoes. This supports the assertion of Parr *et al.* (2016) that admixture between dingoes and dogs does not preclude native dingo morphology.

Genetic origins and identity

Genetic studies show that the Australian dingo fits within the phylogeny of *Canis* and is most closely related to dogs in the southern part of East Asia (Savolainen *et al.* 2004; vonHoldt *et al.* 2010; Oskarsson *et al.* 2011; Ardalan *et al.* 2012; Sacks *et al.* 2013; Wang *et al.* 2016; Cairns & Wilton 2016). This is in agreement with morphological analyses based on measurements taken of dingo, wolf, and dog skulls (Gollan 1982). Although descended from a dog-like ancestor, according to a variety of genetic markers dingoes are genetically distinct from modern dogs, including Asian village dogs, and share some genetic signatures with Asian wolves (Savolainen *et al.* 2004; vonHoldt *et al.* 2010; Sacks *et al.* 2013; Freedman *et al.* 2014; Cairns & Wilton 2016; Wang 2016, Zhang *et al.* 2018). Mitochondrial and Y–chromosome data indicate that dingoes are closely related to Southeast Asian dogs (Savolainen *et al.* 2004; Oskarsson *et al.* 2011; Ardalan *et al.* 2012; Sacks *et al.* 2013).

There is a range of genetic markers that can distinguish dingoes from domestic dogs, including mitochondrial and Y–chromosome markers (Savolainen *et al.* 2004; vonHoldt *et al.* 2010, Oskarsson *et al.* 2011; Ardalan *et al.* 2012; Sacks *et al.* 2013; Cairns & Wilton, 2016; Cairns *et al.* 2017), as well as microsatellites and nuclear single nucleotide polymorphisms (SNPs). Since the 1990s, microsatellite–based DNA testing has been used to distinguish dingoes, dingoes with dog ancestry, and feral domestic dogs. Originally based on 14 microsatellites, 23 markers (including two insertion–deletion [indel] markers) are now used (Wilton *et al.* 1999; Wilton 2001; Elledge *et al.* 2008; Newsome *et al.* 2013; Stephens *et al.* 2015). These markers were chosen because of differences in allele distributions between a reference population of dingoes and a reference population of mixed-breed dogs (Wilton *et al.* 1999; Wilton 2001).

A major criticism of these microsatellite–based methods for distinguishing dingoes from dingoes with some domestic dog ancestry is the lack of a pre–European reference sample (Crowther *et al.* 2014). Instead, the dingo reference sample consisted of a set of dingoes kept by sanctuaries, zoos, or specimen collections that fitted an undefined phenotypic description of dingoes provided by 'experts'. This was the case because at the time of the

studies there was no formal description of the physical characteristics on which to base the dingo (Corbett 2001b; Wilton 2001; Elledge *et al.* 2008) until Crowther *et al.* (2014) provided one based on the physical characteristics of 18th and 19th Century dingo specimens.

Still, the early genetic research found that the reference dingo and domestic dog populations are genetically distinct, and suggested that introgression of dog genes in the reference dingo population was low (Wilton *et al.* 1999; Wilton 2001, Zhang *et al*. 2018). Advances in technology have improved the original method by applying Bayesian clustering, reducing the reliance on a small, pre–defined dingo or domestic dog reference sample (Stephens 2011; Stephens *et al*. 2015). Modelling now infers dingo ancestry using a predefined reference population, but also allows comparison between hundreds (or thousands) of already genotyped dingoes and dingoes with some dog ancestry. However, the currently used 23 markers give limited coverage of the genome, so future tests should ideally incorporate early or pre–European dingo samples and higher-density genetic sampling to monitor introgression.

Today, based on the recent exceptional advances in DNA technology, sequencing of the entire nuclear genome and analysis using genome-wide high density SNP panels offer powerful tools for distinguishing dingoes from other canids (vonHoldt *et al.* 2010; Freedman *et al.* 2014; Cairns 2015). These analyses show that dingoes are a highly divergent, ancient dog lineage (vonHoldt *et al.* 2010; Freedman *et al.* 2014; Cairns & Wilton 2016; Wang *et al*. 2016, Zhang *et al*. 2018). For example, principal component analysis based on whole-genome SNPs distinguishes dingoes from other canid populations: village dogs and modern breed dogs, as well as wolves (Fig. 3). These data indicate that dingoes (and New Guinea singing dogs) form a discrete population divergent from modern domestic dogs and wolves (Fig. 4).
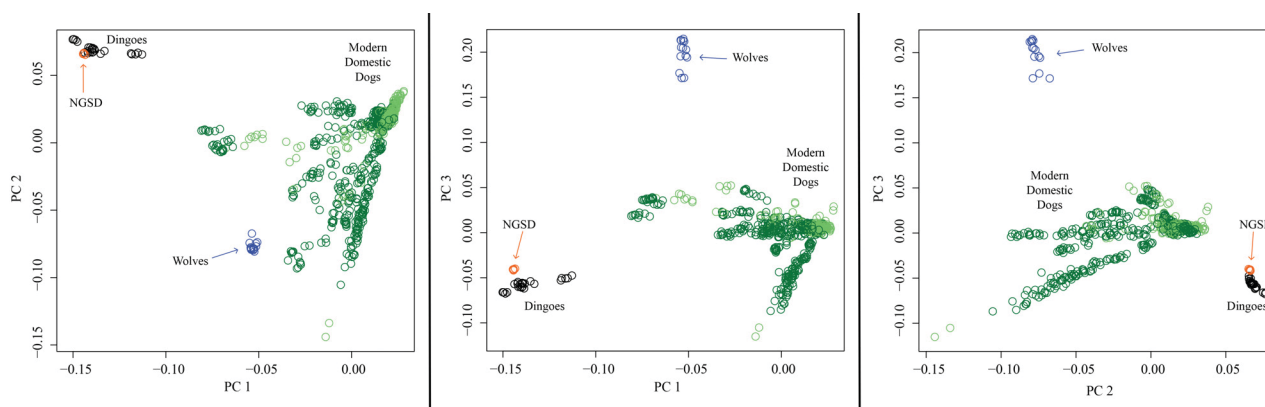

FIGURE 3. Genetic variation among dingoes, New Guinea singing dogs, wolves and modern domestic dogs based on genome-wide single-nucleotide polymorphism (SNP) data expressed using principal components analysis (PCA) representing 841 dogs (green), 24 dingoes (black), 5 New Guinea singing dogs (orange), 14 wolves (blue). Within the dogs there were 292 breed dogs (light green) and 549 village dogs (dark green). We genotyped each of these canid samples using the Illumina CanineHD 170 SNP chip (data from Cairns 2015 and Shannon *et al.* 2015). We analysed genotype data in PLINK 1.9 (Chang *et al.* 2015) by merging the datasets and removing SNPs that were missing in more than 10% of samples. The total remaining SNP markers were 166,019. We did the PCA in PLINK 1.9 and visualised the results using R (v 3.2.1). PC1 accounts for 49.2% of variation, PC2 accounts for 20.7% of variation and PC3 accounts for 10.8% of variation ($\sigma_{PC1}^2 + \sigma_{PC2}^2 + \sigma_{PC3}^2 = 80.7\%$).

Early studies that used genetic methods to investigate the origin of the dingo asserted that Australian dingoes formed a homogenous population, probably as a result of a single immigration event (Savolainen *et al.* 2014). However, Cairns and Wilton (2016) used whole mitochondrial genomes and observed that there are two phylogenetically distinct mitochondrial lineages ('southeastern' and 'northwestern') in dingoes. These two lineages have a geographically subdivided distribution, where one is almost restricted to southeastern Australia (southeastern) and the other to the remaining parts of Australia (central; north and west; northwestern). Although less distinctly, Y–chromosome data also show evidence of geographical structure (Ardalan *et al.* 2012; Sacks *et al.* 2013; Cairns *et al.* 2017) and suggest that the dingo could have originated from at least two migrations, forming two basic populations that subsequently experienced sex-biased admixture, with males being more mobile than females. The ultimate geographic origin of the male and female lineages is yet to be fully resolved, but the fact that one each of the mitochondrial and Y-chromosomal lineages are shared with New Guinea singing dogs indicates

that some of the migrations might have occurred via the land bridge between New Guinea and Australia (completely disconnected by around ~ 7 ka; Torgersen *et al*. 1988) — with or without human intervention (Cairns & Wilton 2016; Cairns *et al*. 2017).

Currently, there are two to three genetic subpopulations of dingo: south-eastern, north-western, and K'gari-Fraser Island (Cairns & Wilton 2016; Cairns *et al*. 2017). Present–day dingoes exhibit some morphological and size variation across the continent that approximately matches environmental gradients and genetic subdivisions (Colman 2015), leading to so-called 'alpine', 'desert', and 'tropical' types of dingo. Yet, when comparing genetic markers, mitochondrial and Y-chromosome DNA, microsatellites and genome-wide sequence and SNP data, collectively dingoes are identified as a distinct population that is divergent from all kinds of domestic dog as well as wild canids.
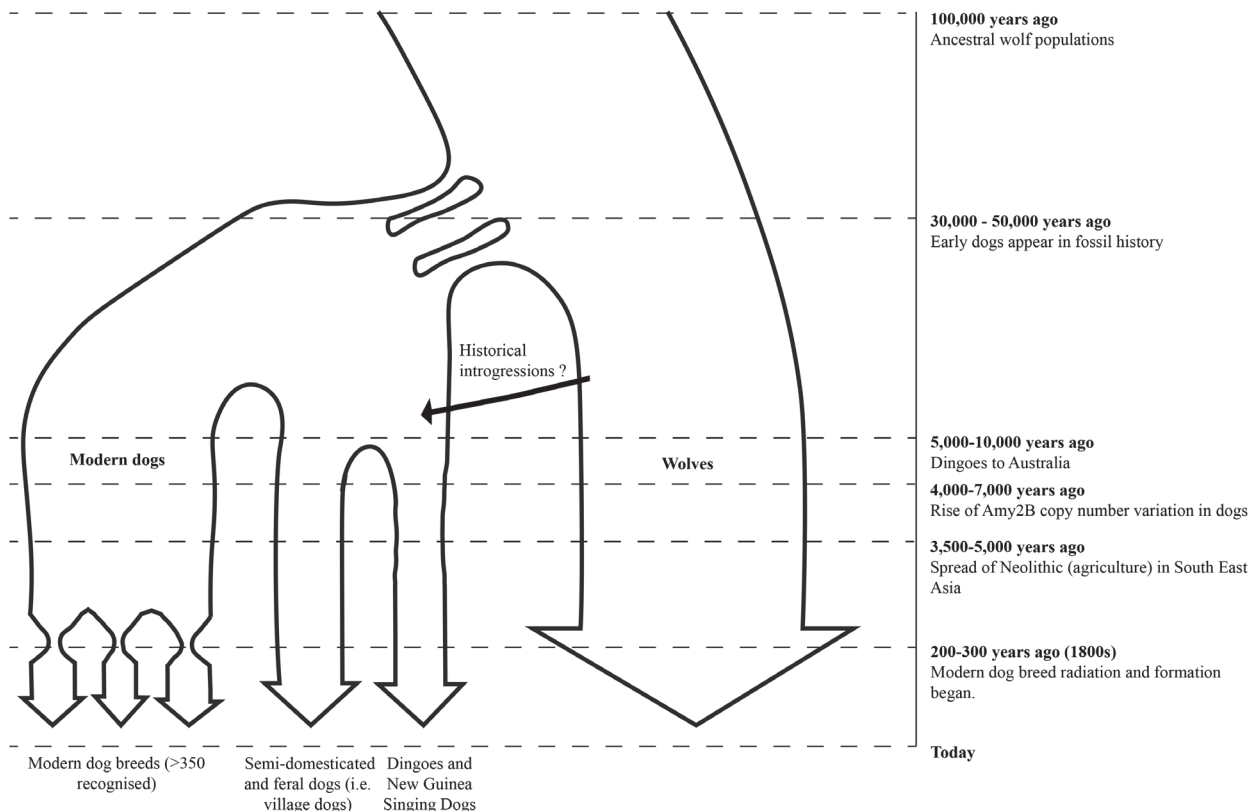

FIGURE 4. A summary of the evolutionary relationships among wolves, dingoes and modern domestic dogs. This figure is a synthesis of the various dog-origin models from vonHoldt *et al*. (2010), Cairns & Wilton (2016) and vonHoldt & Driscoll (2016). Dingoes and other ancient lineages of dog such as New Guinea singing dogs form a distinct lineage separate from modern domestic dogs which have undergone successive generations of artificial selection.

Behavioural comparisons

Reproduction. Reproductive seasonality clearly differentiates dingoes from the more recently evolved domestic dog groups that rely on anthropogenic food sources (Lord *et al*. 2013). Like all wild canids, male and female dingoes follow a seasonal reproductive pattern (one litter per year), that is related to, but not completely determined by, photoperiod (Lord *et al*. 2013; Smith 2015a, Cursino *et al*. 2017). For dingoes, the breeding season typically occurs in the autumn (February–June), with whelping occurring in the winter (June–August) (Catling 1979; Catling *et al*. 1992; Thomson 1992a; Jones & Stevens 1988; Catling *et al*. 1992; Smith 2015a). Dingoes are capable of reproducing in their first year during productive seasons, and particularly when social groups break down (Wallach *et al*. 2009), but most do not bear pups until they are two years old (Breckwoldt 1988; Catling *et al*. 1992; Jones & Stevens 1988). Oestrus is variable, occurring between one and four years of age (Jones & Stevens 1988). In contrast, domestic dogs and village dogs can reproduce twice a year (at any time/season of the year), generally

coming into oestrus every 6–9 months (Boitani *et al.* 2006, Majumder & Bhadra 2015). In some cases, village dogs breed only once a year, although the mating period is long (up to 5 months) compared to wild canids (Pal 2001, 2011). Studies of village dogs indicate that male and female dogs breed in their first year (Boitani *et al.* 1995); however, this can vary depending on size of the dog (Lord *et al.* 2013).

Territorial behaviour and social organisation. In general, dingoes exhibit the same territorial and pack behaviours that have been described for other wild canids, some of which are not common in the domestic dog groups. In most cases, a family or social group of dingoes can maintain a distinct territory or territories within a home range and is usually loyal to this site from year to year (Thomson 1992a,b; Corbett 2001a). Groups typically contain a dominant or primary breeding male and female pair (the parents) and their offspring of various ages, with pack sizes ranging between three and 12 individuals; unrelated animals are rarely allowed to join a pack (Thomson 1992a; Corbett 2001a). In comparison, feral/village dogs tend to live in large groups, but in most situations do not form distinct social groups or pair bonds, or defined territories, and they depend on anthropogenic food (subsidies) rather than wild prey (Berman & Dunbar 1983; Pal *et al.* 1999; Boitani *et al.* 2006). Village and pariah dog communities are, however, highly variable, with disparity in the degree of social behaviour observed across various study sites (Cafazzo *et al.* 2010).

Vocal communication. Barking occurs in all *Canis* species, although differences exist across subspecies. Dingoes bark in threat contexts (e.g., close-range agonistic interactions and upon approach by unfamiliar humans), and as part of howl choruses (Déaux & Clarke 2013). However, dingoes do not bark in affiliative interactions, even when excitation is high, such as during playful interactions (Byosiere *et al.* 2018). This contrasts with domestic dogs, which bark in seemingly all situations, during agonistic interactions, when alarmed, at feeding times, or when they are socially isolated (Feddersen–Petersen 2000; Yin & McCowan 2004; Lord *et al.* 2009). Importantly, barking is commonly reported in play contexts and is an important signal for mediating play interactions (Bekoff 1972; Yin & McCowan 2004; Horowitz 2009; Smuts 2014). Another difference between dingoes and most dog breeds is that dingoes produce howls as a means of defending their territories (Corbett 2001a). While some dog breeds can and do howl (e.g., Siberian huskies), most do not (Bradshaw & Nott 1995), and the function it serves is unknown. Importantly, village dogs in Italy and India use barking in territorial defence against conspecifics, but do not howl (Boitani & Ciucci 1995; Pal 2015). Thus, while most communicative behaviours are highly conserved across the *Canis* genus, there are important differences between dingoes and dogs.

Cognition. Despite the close relationship between wolves and dogs, dingoes differ in their approaches to solving problems. As with wolves (e.g., Frank 1980; Frank & Frank 1985, 1987), dingoes are more adept at non–social problem solving than domestic dogs. For example, Smith and Litchfield (2010) showed that dingoes completed a spatial problem-solving task far more successfully than dogs (Pongrácz *et al.* 2001, 2005, 2008), exhibiting shorter latencies and fewer errors, as well as no signs of frustration or confusion. Further, like wolves (Fox, 1971; Frank 1980; Mech 1991), dingoes have exhibited complex problem-solving behaviours such as tool use in captivity (Smith *et al.* 2012), and have been documented responding to the death of a conspecific in a wild population in a manner previously only observed in other recognisably sapient species such as primates, some cetaceans, and elephants (Appleby *et al.* 2013). Miklósi *et al.* (2003) concluded that one of the main differences between dog and wolf behaviour is the dog's willingness to engage in mutual eye contact with humans, and to use looking as a method of communication. That is, even after intensive socialisation, wolves appear uninterested in human communicative signals or engaging in communicative interactions with humans (Miklósi 2007). Johnston *et al.* (2017) investigated the preference of dingoes to make eye contact with humans. In contrast to wolves (Nagasawa *et al.* 2015), dingoes initiated eye contact with humans, but did so for a shorter time than dogs, and they tended to avoid prolonged eye contact (Johnston *et al.* 2017). Agreeing with Smith and Litchfield (2013), dingoes are not as motivated as dogs to initiate or seek eye contact with humans, or to maintain it. Johnston *et al.* (2017) suggested that dingoes might have developed some motivation to initiate eye contact with people early interactions, but did not develop the desire to maintain this contact as this occurred at a later stage of dog domestication.

The dingo's unique ecological niche

The dingo can be delimited as a unique species across several other species concepts, particularly because it is not demographically exchangeable (following the cohesion species concept; Templeton 1989) with any other canid

populations. In other words, dingoes do not display the same ranges and abilities of tolerance in all relevant ecological variables, and thus occupy a niche that cannot be readily occupied by other closely related populations (Templeton 1989; Zachos 2016; Groves *et al.* 2017). The role that the dingo plays in the Australian landscape is unique, and cannot be readily replaced or fulfilled by a dog: dingoes perform a functional role as an apex predator (Glen *et al.* 2007; Letnic *et al.* 2012), and dingoes can and do cause trophic cascades by suppressing the abundance of prey and/or mesopredators (Johnson *et al.* 2007, Letnic *et al.* 2009, Moseby *et al.* 2012, Newsome *et al.* 2015).

Globally there are few reports of truly feral dogs (Reponen *et al.* 2014), and in most instances feral dogs exist as commensals that scavenge and hunt close to human settlements (Gompper 2014). Indeed, support for the idea that dogs rarely go truly wild is evidenced by the rarity of feral dogs in the Australian island state of Tasmania where dingoes never occurred, despite the presence and opportunity to escape of similar dog breeds to those on mainland Australia (Tasmanian Farmers & Graziers Association 2013).

We are unaware of any sustainable, truly feral populations of domestic dogs in Australia (i.e., populations living away from human settlements and without some form of anthropogenic assistance). Thus, of the domestic dogs that interbreed with dingoes, most are likely to be free-roaming but still supported in some way by anthropogenic means. This process of hybridisation is ongoing (Stephens *et al.* 2015), but the morphology of hybrids is similar to dingoes (Parr *et al.* 2016; see also morphology section), so the ecological role of dingoes with some domestic dog ancestry is unlikely to differ markedly to that of dingoes. Indeed, much research examining the role of dingoes as apex predators has been done in areas where hybridisation rates are high (Claridge & Hunt 2008, Letnic *et al.* 2012, Colman *et al.* 2014, Stephens *et al.* 2015).

The dingo as a 'domesticate'

In all, there are several graduations of canid groups that are distinguishable in terms of their evolutionary histories and lifestyle. Domestic dogs in particular are widely variable across a variety of characteristics due to extensive artificial selection. The domestic dog group encompasses: (1) modern breeds of dogs, with breed standards from the Victorian era subject to strict breeding control (*C. familiaris*); (2) traditional dog breeds that have been subject to some degree of intentional breeding (*C. familiaris*); and (3) feral, village, and pariah dogs that live relatively autonomously beside human communities but rely on anthropogenic resources (*C. familiaris*). These three dog groups all live in more or less close relationships with humans. The rest of the world's *Canis* spp. are wild and living independently of humans, or are highly capable of doing so. We include the dingo and New Guinea singing dog as representatives of this latter group of species.

Genetic analysis indicates that all of the graduations just described come from the same dog lineage because they share some common alleles. But this simply tells us that dingoes share ancestry with dogs (i.e., from a lineage that excludes wolves); it does not conclusively demonstrate that dingoes are themselves domestic dogs, nor does it indicate the degree of domestication. For example, there is still uncertainty in relation to the timing of the lineage — or, more specifically, the point at which early dog-like canids became 'domestic dogs'. The timing of when these dog alleles were 'fixed' matters to the status of the dingo, particularly whether the dingo split 'before' dogs became true domesticates (i.e., living with humans and under intense artificial selection). In the dog lineage, investigations of the AMY2B locus in dingoes compared to modern domestic dogs show that dingoes split from dogs prior to the rise of agriculture and strict selective breeding (Fig. 4; Freedman *et al.* 2014; Arendt *et al.* 2016). As such, wolves and dingoes digest starch less efficiently than modern dogs because they carry only two copies of AMY2B compared to the normally 10-20 copies that modern dogs carry. Modern dogs are thought to have accumulated these extra copies of AMY2B as an adaption to the starch-rich diet of humans after the rise and spread of agriculture (Axelsson *et al.* 2013).

Although the dingo is a member of an ancient 'dog' lineage, diverging some 5–10 ka before present and well before agriculture and the diversification of modern dogs, we know little about these ancestral canids. Indeed, it is also uncertain what the wild ancestor of the dingo was, because dingoes do not sit within any extant wolf clade. Dingoes do bear a resemblance to village dogs in Asia, but can be easily distinguished by their DNA (Savolainen *et al.* 2004; Oskarsson *et al.* 2011; Sacks *et al.* 2013; Cairns & Wilton 2016, Zhang *et al.* 2018), as well as their morphology (e.g., larger size and cranial measurements; Corbett 1985), behaviour and lifestyle, consistent with limited domestication. In the following sections, we explore other independent lines of evidence that suggest the dingo and its ancestors were never truly domesticated.

SMITH *ET AL.*

Geographic origins and their translocation

Most genetic models suggest that dogs in Southeast Asia and Polynesia migrated commensally with humans, but the timing of these events is debated (Pang *et al.* 2009; vonHoldt *et al.* 2010; Sacks *et al.* 2013; Wang *et al.* 2013; Shannon *et al.* 2015; Cairns & Wilton 2016, Fillios & Taçon 2016, Frantz *et al.* 2016; Wang *et al.* 2016). The oldest fossil evidence of dingoes sets a minimum arrival date of 3.5 ka (Balme *et al.* 2018; Macintosh 1964; Smith & Savolainen 2015). Dating based on control region mitochondrial data has suggested an arrival of up to 5,000 years (Savolainen *et al.* 2004). Molecular dating based on entire mitochondrial genomes suggests that the dingo's ancestors diverged in Asia and could have arrived in Australia between 6 to 10 ka (Oskarsson *et al.* 2011; Cairns & Wilton 2016; Cairns *et al.* 2017).

The geography of Sahul (Australia and New Guinea) during the Late Pleistocene and Early Holocene and its subsequent separation when sea levels began to rise following the Last Glacial Maximum supports the hypothesised date of arrival provided by genetic analysis (see Smith & Savolainen 2015). For example, the island of Tasmania, where there are no traces of dingoes (either contemporary, archaeologically or palaeontologically; Jones 1970), was separated from the Australian mainland about 10-14 ka (Mulvaney & Kamminga 1999; Lambeck & Chappell 2001), and New Guinea was completely cut off from the mainland around 7 ka (Torgersen *et al*. 1988). While it remains plausible, it is unlikely (see discussions by Wallace 1893, Wood Jones 1921, and Smith & Savolainen 2015) that dingoes travelled to Australia without human intervention. Importantly, after their arrival in Australia, dingoes appear to have been isolated from all other canid (dog or wolf) lineages outside of Australia until the arrival of Europeans in 1788 (Savolainen *et al.* 2004; Oskarsson *et al.* 2011; Sacks *et al.* 2013; Cairns & Wilton 2016; Fillios & Taçon 2016; Cairns *et al.* 2017).

As argued by Fillios and Taçon (2016) and Cairns and Wilton (2016), it is unlikely that dingoes were brought to Australia as part of a Neolithic cultural expansion, because there were no other Neolithic cultural markers (pig, chickens, agriculture) brought to Australia. Instead, dingoes likely came as an earlier radiation of dogs, presumably associated with human hunter–gatherers, reaching Australia on one or more occasions (and possibly even without human intervention). This is consistent with Y-chromosome modelling that indicates dingoes are an older radiation than dogs found on the islands of Southeast Asia (Sacks *et al.* 2013; Zhang *et al.* (2018).

However, the translocation of animals is not a requirement of, or a fundamental hallmark of domestication. There are many cases where wild animals were historically transported by humans. For example, around the same time that the dingo was thought to have arrived in Australia, wild species such as rusa deer (*Rusa timorensis*), long-tailed macaques (*Macaca fascicularis*), and various civets (*Paradoxurus hermaphroditus*, *Viverra tangalunga* and *Viverricula indica*), cuscuses (*Phalanger orientalis* and *Spilocuscus maculatus*), wallabies *(Thylogale browni, T. brunii, Dorcopsis muelleri* and *Notamacropus agilis*) and cassowaries (*Casuarius casuarius* and *C. bennetti*) were all translocated around the islands of Wallacea and do not show evidence of domestication (Heinsohn 2003). Likewise, more recent introductions into Australia such as the European rabbit (*Oryctolagus cuniculus*) or the red fox (*Vulpes vulpes*) do not render them domesticated.

The Channel Island fox (*Urocyon littoralis*) highlights an example whereby speciation occurred over a short time frame as a direct result of human intervention. In this instance, grey foxes (*U. cinereoargenteus*) were taken to the islands by people during the Holocene (< 10 ka). Bottlenecking has resulted in sufficient morphological and genetic divergence for them to be considered to be a unique species separate from grey foxes, with distinct subspecies on each island (Stains 1975; Gilbert *et al.* 1990; Collins 1993; Rick *et al.* 2009; Funk *et al.* 2016). Strangely, Stains (1975), who recognised that Channel Island fox populations resulted from human intervention and considered them a separate species, also simultaneously argued that dingoes should be recognised as *C. familiaris* for the same reason. This yet again highlights the inconsistency that can arise in trying to classify canids.

Interactions with humans and domestication

Likewise, living close to humans does not automatically imply domestication. A diverse multitude of urban and rural wildlife species live close to humans globally, yet such sympatric relationships do not automatically result in domestication (see Luniak 2004). In relation to the dingo, this relates to before and after their arrival in Australia, although we understand little regarding the former. For example, we do not know whether humans at this time were actively selecting for (or against) particular traits or what transpired that might have led to canid divergence.

The presence of dingoes in both palaeontological and archaeological contexts dating > 3,500 years suggests that upon arrival in Australia, dingoes existed in both wild and commensal situations (Smith & Litchfield 2009). However, there is no evidence that dingoes were exposed to domestication or selection pressure by Aboriginal peoples (Meggitt 1965; Macintosh 1975; Manwell & Baker 1984; Smith & Litchfield 2009). This is presumed to be because: (1) dingoes bred in natural environments, and were taken from the den as puppies — once they reached sexual maturity, they returned to the wild; (2) there are behavioural barriers to training, breeding, and containing dingoes; and (3) Aboriginal lifestyles did not easily facilitate the domestication process (e.g., minimal infrastructure and high nomadism). Arguably, a tame dingo (one that tolerates the presence of people and is not aggressive) provided the perceived necessary benefits from the relationship, without requiring any selective pressure on the local dingo population (Smith & Litchfield 2009). Again, there are many historical examples of relationships between tame wild animals and humans.

The Aboriginal-dingo relationship more broadly, as well as instances where dingoes lived in close contact with humans, fail to meet the criteria for domestication. Using established criteria, Smith and Litchfield (2009) determined that although the relationship between some dingoes and Aboriginal people appears to meet the 'cultural criteria' for domestication (where an animal becomes incorporated into the social structure of a human community and is an object of ownership, inheritance, purchase, or exchange; Clutton–Brock 1995), it does not meet the 'biological criteria' (where there has been natural selection in response to the human community and environment, and artificial selection for economic, cultural, and aesthetic reasons; Clutton–Brock 1995). That is, there is no conclusive evidence that there was any active or inadvertent selective breeding of dingoes. According to the five stages of domestication outlined by Zeuner (1963), dingoes living in close contact with humans only meets stage one (where animals maintain a loose contact with humans, but breed freely without human intervention). Similarly, according to Dobney and Larson's (2006) summary of the types of relationships between humans and animals, the Aboriginal–dingo relationship is one that is neither wild nor domesticated, falling outside the more rigid definitions of domestication. Thus, since the dingo arrived on the Australian continent, it has developed a truly unique history as a geographically isolated, free–ranging wild canid living under the influence of natural selection and free from intensive human selective pressure or admixture with other canids.

We therefore argue that having lived in Australia as free-living populations for > 5,000 years almost exclusively under the forces of natural selection nullifies any notion of the dingo as a domestic animal, if indeed it could ever have been considered one. This isolation across time and geography between dingoes and the modern dog phylogeny has led to a dog-dingo evolutionary split, with each taxon evolving into separate populations.

Taxonomic status of wild and domestic species

Following the lack of clear evidence of domestication of the dingo, the prior argument by Jackson *et al.* (2017) regarding the status of subspecies with regard to the International Code of Zoological Nomenclature ('the Code') becomes moot. To clarify, they contended that domesticated forms cannot be recognised as subspecies under the Code (ICZN 2003) because they fail to correspond to the current 'concept of subspecies', following discussion in Groves (1995). Yet, nowhere in the Code is there a taxonomic definition (biological, genetic, phylogenetic or evolutionary) of any of the nomenclatural ranks; 'subspecies' is simply a term that designates a nomenclatural rank below species. This lack of a definition of subspecies in nomenclature is because concepts and definitions of taxonomic categories are a matter of taxonomy, not of nomenclature. The category of 'parataxon' to which Jackson *et al.* (2017) referred the use of the rank subspecies for the dingo is misapplied to the dingo, because the term was introduced to designate a taxonomic category comprising incomplete parts of animals that cannot be referred to whole animals, and not for taxa of ranks below species that do not correspond to our current understanding of subspecies (Moore & Sylvester-Bradley 1957).

The Code (ICZN 2003) recommends that domesticates (generally, and not specific to the case of the dingo) not be named as sub-species, 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. For this reason, Crowther *et al.* (2014, p.10) argued that "... because the ancestry of the dogs and dingoes is unknown, and because the dingo was first described as a distinctive wild form and differs from wolves, New Guinea singing dogs and domestic dogs in many behavioural, morphological and molecular characteristics, and they are effectively

reproductively isolated in undisturbed natural environments and thus like *C. hallstromi* can be considered a distinct taxon." We agree, and reiterate the point that in regard to domesticates not being considered subspecies, this only matters in cases concerning domesticates, which we demonstrate does not apply to dingoes.

Conclusion

The dingo has a distinct and unique evolutionary lineage. It is a member of an ancient 'dog' lineage, diverging some 5,000–10,000 years before present, and prior to intense agriculture and the diversification of modern dogs. The dingo is geographically isolated from all other species of *Canis*, and admixture has only been possible because of recent human activity. Restrictions in breeding behaviour between dingoes and domestic dogs are also apparent (e.g., female dingo to male domestic dog breeding bias).

Further evidence in support of dingoes being considered a 'wild type' capable of surviving in the absence of human intervention and under natural selection, is exemplified by the consistent reversion of hybrids to a morphologically and phenotypically dingo-like canid throughout the Australian mainland and on several islands. In Tasmania, where dingoes have never been present, a lack of established populations of wild-living domestic dogs, commensurate with those of the many mainland dingo populations, including those in similar habitats, suggests that successful 'feralisation' of domestic dogs is severely hampered.

As we have shown, the dingo is distinguishable as a discrete taxon of wild *Canis* across a broad spectrum of ecological, behavioural, morphological, and molecular characteristics. Collectively, this evidence allows the dingo to be differentiated from modern domestic dogs, feral domestic dogs, Asian village dogs and wolves. Simultaneously, little evidence exists to support the notion that any of these other canids are interchangeable with dingoes, despite the fact that they can all successfully interbreed. There is no historical evidence of domestication once the dingo arrived in Australia, and the degree of domestication prior to arrival is uncertain and likely to be minimal compared to modern domestic dogs.

Further, we have argued that dingoes have survived in Australia for millennia, subject to the rigours of natural selection, thriving in all terrestrial habitats, and largely in the absence of human intervention or aid. This serves as a fitting testament to their status as a wild, Australian animal. Even if allowance is given to a nebulous and distant past involving some degree of domestication, to label the dingo as nothing more than a 'feral domestic dog', expunges their unique, long and quintessentially wild history.

We acknowledge that defining various species in the genus *Canis* is problematic — particularly due to the many competing ways in which species can be defined (Clutton-Brock 2015; Zachos, 2016). There will always be debate between so-called 'lumpers' and 'splitters'. The underlying logic and adherence to the biological species concept *sensu stricto* consistently across the Canidae dictates that if you choose to lump dingoes and dogs together (as Jackson *et al.* 2017 suggested), then you must also lump dogs and wolves and, in fact, all canids that are capable of interbreeding and producing viable offspring. Yet, nobody argues that wolves and dogs are alike to the point of interchangeability. It is our evidence-based position that dingoes, wolves, and dogs are all readily distinguishable from one another. Indeed, few would argue that a dingo living in the Tanami Desert independently of humans is anything but a dingo, nor that a dingo in a zoo exhibit, or on K'gari-Fraser Island, could be replaced by a domestic dog. All canids share similarities, but their differences are also many and marked. Thus, it makes more scientific sense for the dingo to be considered separately from wolves and domestic dogs, while acknowledging that they all occupy the same species complex more broadly.

Given the problems with the biological species concept, and especially its application to canids, using diagnosable criteria within lineages following the phylogenetic species concept is more a practical and sensible solution. Of course, one is free to follow the biological species concept and thus subsume all canids, but by following other more comprehensive and integrative approaches, the sum of the evidence reveals multiple unique and distinguishable taxa, including in the dingo. Using this approach we have presented scientifically valid arguments to support the ongoing recognition of the dingo as a distinct taxon. As the dingo is currently listed with the ICZN as *Canis dingo* Meyer, 1793, we assert that this nomen is appropriate. Widespread acceptance of this approach to classifying dingoes will reduce unnecessary tensions resulting from multiple and conflicting definitions of species, and likely aid in the conservation and management of the dingo.

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Conflict of interest

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