Taxonomy of the Dingo: It's an ancient dog

Stephen M. Jackson[1,2,3,4,*], Peter J.S. Fleming[5,6], Mark D.B. Eldridge[4], Michael Archer[2], Sandy Ingleby[4], Rebecca N. Johnson[4,7], Kristofer M. Helgen[4,8]

[1]Biosecurity NSW, NSW Department of Primary Industries, 161 Kite Street, Orange, New South Wales 2800, Australia.

[2]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia.

[3]Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, United States of America.

[4] Australian Museum Research Institute, Australian Museum, 1 William Street, Sydney, New South Wales 2010, Australia.

[5] Vertebrate Pest Research Unit, Biosecurity NSW, NSW Department of Primary Industries, 1447 Forest Road, Orange, New South Wales 2800, Australia.

[6]Ecosystem Management, School of Environmental and Rural Science, University of New England, Armidale, New South Wales 2351, Australia.

[7]National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, United States of America.

[8] ARC (Australian Research Council) Centre for Australian Biodiversity and Heritage, University of New South Wales, Sydney, New South Wales 2052, Australia.

[*] Corresponding author: E: stephen.jackson@dpi.nsw.gov.au

ABSTRACT

Taxonomy is the science of the classification of living things and comprises two main processes, defining taxa and naming them. In relation to the taxonomy of the Dingo, the scientific name has been unstable for many years. It has been referred to as *Canis familiaris, Canis familiaris dingo, Canis lupus familiaris, Canis lupus dingo* or *Canis dingo*. The nomenclature, however, has become even more unstable in recent years with advocacy for the name *Canis dingo* by some authors in spite of a lack of morphological differentiation or interfertility between Dingo and Domestic Dog hybrids. As a result, there is a need to review the taxonomy of the Dingo with the aim of confirming its correct scientific name in order to promote stability. Using the most widely accepted species concepts, we reviewed the taxonomy of the Dingo by objectively dissecting each of the proposed arguments for recognising the Dingo as a distinct species. We conclude that the most appropriate taxonomic name to use for the Dingo is *Canis familiaris*, and that this binomial is the appropriate taxonomic name for all ancient and modern dog breeds, their hybrids and wild-living derivatives. It is important to highlight that correct taxonomy is an important part of on-ground conservation and management of wildlife. However, the taxonomy used as a basis for management decisions needs to be based on a consistent and evidence-based scientific approach and not other factors.

Key words: taxonomy, dingo, dog, *Canis*, morphology, ecology, genetics.

DOI: https://doi.org/10.7882/AZ.2020.049

Introduction

Taxonomy is the theoretical study of classification including its principles, procedures and rules. It comprises two main parts including classification (identification of taxa) and naming of those taxa (nomenclature). Taxonomy has its modern origins a century prior to evolutionary theory as articulated by Darwin (1859), when Linnaeus (1758) published his Systema Naturae in which he developed the binomial system of nomenclature (i.e. a two-word system of naming: genus and species). Importantly the taxonomic system reflects or is intended to reflect the evolutionary relationships of species. Animals that have more recent common ancestry will be genetically, and in most cases morphologically, more similar to each other than either is to more distantly related animals. This network of deduced relationships should ideally be reflected in their classification. An important principle for the practice of taxonomy is to optimise, as much as possible, nomenclatural stability of the scientific names used for species and the groups to which they belong (ICZN 1999).

Within Canidae, the appropriate scientific name of the Dingo has been uncertain for many years. There have been five different binomials/trinomials used with varying frequency (Allen *et al.* 2011; Kreplins *et al.* 2019). These include: *Canis familiaris* Linnaeus, 1758; *Canis lupus familiaris* Linnaeus, 1758; *Canis familiaris dingo* Meyer, 1793; *Canis lupus dingo* Meyer, 1793; and *Canis dingo* Meyer, 1793. Of these five, the name *Canis dingo* had widely fallen into disuse (Jackson *et al.* 2019; Kreplins *et al.* 2019), until its advocated use by Crowther *et al.* (2014). Although Crowther *et al.* (2014) did not explicitly state the rank at which the taxonomic name Dingo should be placed, it is apparent from subsequent publications that they intended it to be recognised as a distinct species, i.e. *Canis dingo* (Smith 2015; Smith *et al.* 2019). Since 2014 there has been increasing instability because the name *Canis dingo* has continued to be promoted by some authors in spite of the fact that this binomial has been reviewed and consistently rejected by numerous taxonomists (including the IUCN Canid Specialist Group) with *dingo* being regarded to be a junior synonym of *familiaris* (Jackson & Groves 2015; Jackson *et al.* 2017, 2019; Alvares *et al.* 2019).

In reference to the taxonomic status of the Dingo, the International Commission of Zoological Nomenclature has published two opinions relevant to the taxonomic status of the Dingo. These include:

Opinion 451 – This publication suppressed the older name *Canis antarticus* [sic] Kerr, 1792 and made the younger name '*dingo*' available for usage (ICZN 1957). As discussed by Jackson *et al.* (2017, 2019), the availability of the name '*dingo*' does not mean its use as a specific name is obligatory because it remains subject to taxonomic revision and can be recognised as a synonym of another species-level taxon.

Opinion 2027 (Case 3010) (ICZN, 2003) – This publication reviewed 17 specific scientific names based on wild species that are pre-dated by, or contemporary with, those based on domestic animals. This publication lists the Grey Wolf (*Canis lupus* Linnaeus, 1758) and its domestic derivative the Dog (*Canis familiaris* Linnaeus, 1758). It also explicitly places the name Dingo in brackets after the name Dog to provide a clear indication that the Dingo was considered to be a Dog. In addition, the Opinion confirmed that Linnaeus' binomial, e.g. *Canis familiaris*, should be retained for the 17 domestic animals and their wild-living (sensu Darwin 1859) derivatives as a matter of nomenclatural procedure. This arrangement was reiterated by Gentry (2004).

Smith *et al.* (2019) offered a view different to the IUCN and ICZN and instead proposed that the Dingo should be recognised as a distinct species because it is "… geographically isolated, genetically distinct, phenotypically distinct, ecologically distinct, behaviourally distinct, and devoid of many of the signs of domestication". The first four of these arguments can be related to speciation and species concepts while the last two are not relevant to the recognition of species and will not be discussed further. All have previously been considered and found to be unsupported, based on standard procedures and criteria applied in taxonomy (Jackson *et al.* 2019). The aim of this review is to further evaluate the first four arguments to determine their validity, and to outline what would be required for taxonomists to consider the Dingo to be a separate species.

A fundamental issue undermining the case brought by Smith *et al.* (2019) is their focus on arguing for the Australian population of the Dingo to be a distinct species. The species distinction of the Australian Dingo remains untenable while 'Dingo'-like canids (the presumed progenitor population of the Australian Dingo) still exist in South East Asia, such as Pariah dogs and other ancient breeds of Asian dogs (vonHoldt *et al.* 2010). Authors such as Corbett (2001) and Sillero-Zubiri (2009) regard these South-East Asian and Australian dog populations as the same taxon (i.e. *Canis lupus dingo*) [sic], that is they are all Dingoes. This makes biological sense given their recent shared ancestry and no clear argument against this arrangement has yet been made. No proposal to make the Australian Dingo a separate species can be supported until this issue is addressed.

Geographical isolation of the Dingo

The use of allopatry to recognize the Dingo as a distinct species is highly problematic and not a sound criterion for taxonomic decisions. This is because allopatry does not necessarily equate to speciation as the many current mammal species with allopatric populations, across various continents, archipelagos and islands demonstrate (e.g., Wilson & Reeder 2005; Van Dyck & Strahan 2008).

It is generally accepted that the Dingo was introduced into Australia by humans (e.g. Wood Jones 1921; Macintosh 1975; Filios & Taçon 2016). The fossil record consistently suggests the Dingo arrived in Australia less than 3,500 years ago (Corbett 2006). Fossil Dingoes from approximately 3,250 years ago discovered in Madura Cave on the Nullarbor Plain provide the oldest reliable date for the Dingo in Australia (Balme *et al.* 2018). These authors also suggest that this date is very likely close to the time of first arrival of Dingoes because it probably spread rapidly throughout mainland Australia after its arrival. Other fossil records suggest the earliest date may be 3,450 years ago (Corbett 2006, Smith & Savolainen 2015). These findings are consistent with the archaeological evidence of Greig *et al*. (2018) who proposed that dogs were introduced to the islands of Oceania, via island Southeast Asia, around 3,300 years ago and were tied to human expansion. They also suggested that as a result of their genetic analysis of archaeological dog specimens, from mainland and island Southeast Asia and the Pacific, that there were at least three dog dispersal events into the region in addition to the introduction of Dingoes to Australia (Greig *et al*. 2018). These archaeological studies are also supported by genetic studies using mitochondrial DNA that indicate that the Australian Dingo, New Guinea Singing Dog and ancient Polynesian dogs are all recently descended from East Asian dogs (Savolainen *et al*. 2004). Interestingly the results of Cairns *et al*. (2017) suggested a closer relationship between southeast Australian Dingoes and the New Guinea Singing Dog than to the northwest Australian Dingoes.

Some molecular studies have suggested that Dingoes were introduced to Australia earlier than their occurrence in the fossil record. These estimations include ~4,600-5,400 or 4,600-10,800 BP (Savolainen *et al*. 2004) and 4,600–18,300 years BP (Oskarsson *et al*. 2012) based on a small (<600 bp) section of one mtDNA gene. Using whole mtDNA genomes (~16,000 bp) Cairns and Wilton (2016) identified two divergent mtDNA lineages within Australian Dingoes and estimated that they diverged ~8,300 (range 5,700-11,700) years BP, most likely outside Australia and prior to their independent introduction to Australia. More robustly, Freedman *et al*. (2014) using data from whole genomes (10 million SNPs) estimated that the Dingo diverged from other ancient dog breeds 12,800 years BP (range 11,800-13,700). This divergence would have had to occur prior to the Dingo's introduction to Australia. Most of these dates should be treated with some caution given that mtDNA effectively represents a single locus, the uncertainty surrounding the mutation rates and calibration points used, as well as the widespread introgression of modern Domestic Dog DNA into Australian Dingo populations and the often limited sampling of the progenitor South-East Asian population.

Suggestions that the Dingo arrived in Australia up to 10,000 years ago, or longer, (Smith *et al*. 2019) are unlikely and unsupported by the fossil evidence. Despite there being many fossil deposits known from around the continent that are older than 3,500 ybp, none of them contain the remains of Dingoes. In addition, if the Dingo had been in Australia longer it would also be expected to occur in modern or archaeological records of offshore islands including Kangaroo Island and Tasmania where the land bridges broke down approximately 8,900 and 12,000 years BP respectively (Lambeck & Chappell 2001; Haoucher *et al*. 2014; Bowdler 2015).

Not only is the introduction of the Dingo into Australia very recent but it also appears that it is unlikely to have been isolated since its initial introduction because there is evidence of at least two introductions over the last ~4,000 years with an unknown time span between them (Cairns & Wilton 2016; Cairns *et al*. 2017). This highlights that the Dingo does not appear to have been completely isolated since its first introduction into Australia.

The Dingo's introduction to Australia is not exceptional. Numerous animals have been translocated by people throughout Wallacea, New Guinea and other nearby islands over the last 20,000 years or more. For example, the Northern Common Cuscus (*Phalanger orientalis*) is thought to have been introduced to New Ireland in the Bismarck Archipelago approximately 23,500 to 20,000 ago in the Late Pleistocene (Flannery & White 1991; Spriggs 1997; Summerhayes 2007; Heinsohn 2003, 2010). Similarly, the New Guinean Pademelon (*Thylogale browni*) appears to have been introduced to New Ireland around 8400 to 7000 BP (Flannery & White 1991; Spriggs 1997; Summerhayes 2007). Many of these populations have some amount of morphological and genetic distinction. Yet none of these or many other species that have been translocated to different islands by humans during this period have been thought to be, or recognised as, distinct species.

This level of recent differentiation, involving populations established or isolated for no more than tens of thousands of years, is not generally recognised as taxonomically relevant in mammalogy. There are thousands of island mammal populations globally (and hundreds just within Australia) that have been allopatric since the Last Glacial Maximam (a longer time period than the Dingo has been in Australia) and have not evolved into different species (Abbott & Burbidge 1995; Wilson & Reeder 2005; Van Dyck & Strahan 2008). This is because speciation is not a simple linear process that flows rapidly or inevitably from isolation. Populations isolated in similar environments commonly do not develop partial or total reproductive isolation from each other (i.e. speciate) even over long periods of time (Frankham *et al*. 2011). Speciation events are typically associated with adaptation to novel environmental components and/or chromosome changes over variable periods of time (Frankham *et al*. 2011). For example, the North American and Eurasian populations of Grey Wolves have been isolated since the Last Glacial Maximam (LGM) but are still regarded to be the same species. Similarly, in the Australian context, the evolution of endemic island mammal species has only resulted in a handful of taxa that are overwhelmingly associated with long-isolated (millions of years) oceanic islands (e.g. Christmas Island, Lord Howe Island) and not the recently separated land-bridge islands that only became isolated from the mainland at the end of the LGM (10-15K YBP) (Van Dyck & Strahan 2008). Most Australian mammal species now found only on land-bridge islands (e.g. Tasmanian Devil *Sarcophilus harrisii*, Long-tailed Mouse *Pseudomys higginsi*) have become so as a result of their extinction from the mainland (Van Dyck & Strahan 2008) and not in situ island evolution.

Globally there are a few cases where relatively recent island populations of canids have been recognised as distinct species. The Dwarf California Channel Islands Fox

(*Urocyon littoralis*) and the extinct Falkland Islands Wolf (*Dusicyon australis*) are two currently-recognised island endemic canids that are only shallowly differentiated from mainland relatives. The timing of the arrival of these two taxa to their respective islands has been estimated to be 7,000-16,000 year ago (Hofman *et al.* 2015) and 16,000 years ago (8,000–31,000) (Austin *et al.* 2012) respectively. However, these relatively new insights (i.e. Austin *et al.* 2012; Hofman *et al.* 2015) into the recent origin of these isolated populations means their taxonomic status as distinct species is now in doubt. *Dusicyon australis* is probably in fact conspecific with its mainland relative, often called *Dusicyon avus*, which became extinct in southern South America in the Holocene. These congeners are genetically and morphologically similar and have been traditionally recognised as closely related mainland and island counterparts (Austin *et al.* 2012). The "Falkland Islands" Wolf, in other words, was likely in fact the last surviving population of a formerly widespread species that likely evolved principally in mainland South America, rather than being an island endemic per se (this is an extinction trajectory that will be familiar to Australian mammalogists!).

Genetic studies have also shown that *Urocyon littoralis* is less distinctive compared to mainland Gray Foxes (*U. cinereoargenteus*) than various mainland populations of *U. cinereoargenteus* are to one another, and island foxes are even suspected to have arrived throughout the Channel Islands by human transport (Hofman *et al.* 2015). Thus, the Dwarf California Channel Islands Fox is a recently isolated island population of a single widespread species that occurs broadly across the American continents from northern North America to South America, rather than a distinct species. Similarly, recent taxonomic reviews of the other Carnivora widespread on islands in the Americas—the raccoons of the Bahamas ("*Procyon maynardi*"), Guadeloupe ("*P. minor*"), Barbados ("*P. gloveralleni*"), the Tres Marias Islands ("*P. insularis*"), and Cozumel ("*P. pygmaeus*")—have now shown that all of these putative species are very recently isolated, and in many cases human transported, island populations of the very widespread Common Raccoon (*P. lotor*) (Helgen and Wilson 2002, 2003, 2005; Louppe *et al.* 2020). One other similar situation is the Cozumel Island Coati, which was traditionally classified as a distinctive island endemic, *Nasua nelsoni*, but it is now regarded as a population (not necessarily even a subspecies) of the widespread White-nosed Coati (*N. narica*) following genetic studies (e.g. Nigenda-Morales *et al.* 2019). All of these formerly recognized island carnivores were originally classified as distinct species mainly because they were isolated island populations that differ in minor ways, mainly in body size, from their mainland congeners. To summarize: similar to the case of the insular raccoons and coati, "island" canid taxa often traditionally accorded taxonomic status (i.e. prior to genetic evidence of their relationships and level of divergence being available)—the Falkland Islands Wolf, the Island Gray Fox, and the Dingo—are now understood to be recently established variants of more widespread mainland lineages, and as such it is increasingly recognised they do not or may not deserve taxonomic recognition.

Genetic distinction of the Dingo

Within animal populations there is a spectrum of genetic differentiation ranging from between individuals within a population, through populations within a species to differentiation between species within a genus. It is expected that at the level of species there should be a major break in the distribution of genetic diversity, that differentiates each species from others in the genus. The suggestion by authors, including Crowther *et al.* (2014) and Smith *et al.* (2019), that the Dingo is genetically distinct is not surprising given the current use of high-resolution genetic markers that enable most populations within a species to be distinguishable. This does not mean each diagnosed population is a separate species. For example, Koala (*Phascolarctos cinereus*) populations are genetically differentiable across their distribution with high resolution genetic markers yet only a single species, with no subspecies, is recognised (Neaves *et al.* 2016; Johnson *et al.* 2018). Similarly, Abrolhos Island populations of Tammar Wallabies (*Notamacropus eugenii*), are readily genetically distinguishable from southwest Western Australian mainland populations after over 10,000 years of isolation but are still considered a single species (Eldridge *et al.* 2017). The ability of modern high-resolution genetic markers to distinguish most populations within species, and indeed often family groups within populations, should not be used as the basis for spurious taxonomic splitting of what are otherwise demonstrably single species (Frankham *et al.* 2012). The use of diagnosable phylogenetic species concepts is well known to result in over-splitting and if applied in the current context would result in all diagnosable dog breeds being considered separate species – which would be biologically and taxonomically unsustainable and unmeaningful.(Frankham *et al.* 2012).

In modern mammal taxonomy, identifying and classifying distinct mammal species involves demonstrating deep and largely independent evolutionary histories that usually involve genetic distinctions acquired over hundreds of thousands or millions of years (e.g. Baker and Bradley 2006). However, when the phylogenetic position of the Dingo is compared with wolves and other canids, it is clear that the phylogenetic position of the Dingo fits solidly within a group containing ancient Asian dog breeds (vonHoldt *et al.* 2010).

VonHoldt *et al.* (2010) investigated the domestication of the dog from the wild wolf using genetic differences. This large-scale study used more than 48,000 single nucleotide polymorphisms in the genome from 912 dogs of 85 modern breeds of modern and ancient dog breeds, and 225 grey wolves. VonHoldt *et al.* (2010) showed that when the Dingo is considered in context with other dog breeds it clearly sits within the group containing the Shar-Pei, Akita, Chow Chow and New Guinea Singing Dog. These results were subsequently supported by the research of Wang *et al.* (2013, 2016). Genetically, the Dingo is no more distinct than any other ancient dog breed and so does not warrant recognition as a separate species.

The fact that dingoes readily interbreed and hybridise with domestic dogs, leading to widespread introgression between them (e.g. Stephens *et al.* 2015; Cairns *et al.* 2017), also undermines the suggestion that the Dingo should be recognised as a distinct species. Effective reproductive isolation remains the gold standard for establishing species status under the most widely used species concepts, although it is now recognised that occasional hybridisation and introgression is common between good species, including amongst canid species which nevertheless maintain their separate identities.

Morphological distinction of the Dingo

Dingoes are not consistently, readily or robustly morphologically distinguishable from other ancient or modern dogs. Their body, skull and dentition are similar to those of other dogs. The cephalic indices and other cranial features demonstrate that Dingo skull morphology falls within the range for dogs as a whole. We agree with Smith *et al.* (2019) that the morphological separation of Dingoes from domestic dogs remains problematic. This is because there is:

- Large morphological variation in cranial shape within domestic dogs.
- Dingoes also exhibit morphological variation through space and time.
- Dingoes and dingo–dog hybrids can be difficult to separate morphologically (Parr *et al.* 2016).
- Efforts to distinguish Dingoes and domestic dogs on the basis of morphology have been based on examination of skulls that post-date European contact (e.g. Crowther *et al.* 2014); hence any of these could be the result of cross-breeding rather than pure dingoes.
- Similarly, some dog breeds, particularly the Australian cattle dog, show evidence of previous hybridisation with Dingoes.
- There is evidence for at least two sub-populations of Dingoes in Australia, possibly the result of multiple introductions (Cairns & Wilton 2016; Cairns *et al.* 2017). These sub-populations also show some evidence of morphological separation (Colman 2015), thus further obscuring efforts to characterise and distinguish the skulls of Dingoes from those of other dogs.

Even if the Dingo could be distinguished consistently on the basis of cranial morphology, as some other breeds of dogs can be distinguished (e.g., Chihuahuas, Pugs, and Great Danes), it does not change the Dingo's ancestry. It is unsurprising that artificial selection for morphological variation among modern dogs should give rise to a wide variety of diverse morphologies (Georgevsky *et al.* 2014, Jackson *et al.* 2019). Nor is it surprising that Dingoes, which have been isolated from intensive anthropogenic selection and introgression of modern dog genes until recent times, should be relatively consistent and likely similar to those that were first introduced.

As an ancient dog breed the dingo has not been highly modified by anthropomorphic selection and so is morphologically similar to some other ancient breeds of dogs and to free-living dogs throughout much of the world, including dogs found in India, Japan, Philippines, Thailand, Malaysia, Singapore, Indonesia and New Guinea (e.g. Corbett 2001; Koler-Matznick *et al.* 2003; Smith & Savolainen 2015; Fillios & Taçon 2016, McIntyre *et al.* 2020).

The ecological distinction of the Dingo

In regard to the suggestion that the Dingo is ecologically distinct, the ecology of an animal is not typically a criterion used for distinguishing species. Species of most widespread mammalian carnivores (e.g. canids, big cats, bears, toothed whales) often have populations that are ecologically and/or behaviourally distinct from other populations. In any case, no substantial ecological difference, as such, has been demonstrated between Dingoes and other dogs (Crowther *et al.* 2020) or even most other canids. Dingoes and other free-roaming dogs are generalist, opportunistic predators and scavengers (Ritchie *et al.* 2014; Fleming *et al.* 2017) that have adapted their foraging behaviours and diets to fit the opportunities of their specific environments (Thomson 1992; Corbett 2001; Purcell 2010). In this same context, free-roaming dogs are similar to Coyotes (*Canis latrans*) in that they are all highly adaptable to a wide range of environments with ecological behaviours tailored to suit. While some Coyote populations are ecologically distinct from others, this does not mean that they should be regarded as different species.

Dingoes and hybrids with modern dogs fill many roles across Australia, ranging from scavengers to preferential predators of common macropodids (Corbett 2001; Fleming *et al.* 2001; Vernes *et al.* 2001; Doherty *et al.* 2019). For example, Dingoes readily become commensal when artificial resources are provided when there are natural environmental deficits and in so doing they can become focused on scavenging anthropogenic food waste (e.g. Newsome *et al.* 2014a; 2014b). Feral, free-roaming modern dogs sometimes fulfil a similar commensal role, and interact in the wild with Dingoes and hybrids (Gabriele-Rivet *et al.* 2019; Sparkes *et al.* 2014, 2016).

There are often greater ecological differences between Dingo populations than there are between co-occurring dingoes and Red Fox (*Vulpes vulpes*) or feral Cat (*Felis catus*) populations, which can have highly overlapping diets (Allen *et al.* 2012; Fleming *et al.* 2012). Such highly overlapping diets means they eat the same things and therefore have shared ecological roles. None of these studies suggests that 'different ecology' should be a criterion for distinguishing species.

As a result of the issues discussed above, it is difficult to functionally differentiate Dingoes, wild-living modern dogs and hybrids (Claridge & Hunt 2008; Crowther *et al.* 2021). Therefore, until animals can be reliably distinguished in the field, and functional differences can be demonstrated, all wild living canids in Australia should be inclusively labelled and managed as 'wild dogs' (Fleming *et al.*, 2001; Allen *et al.* 2011).

Conclusion

Our review of taxonomic criteria suitable for distinguishing the Dingo from other dogs confirms the view that dingoes inhabiting Australia should not be recognised as a distinct species of canid, but rather should be recognised as an ancient breed of domestic dog with the scientific name *Canis familiaris*. When aiming to distinguish the Dingo as a breed distinct from other ancient or modern breeds of dog, we recommend authors use: *Canis familiaris* (Dingo). Our review also demonstrates that the literature does not support the proposal by Smith *et al.* (2019) that because the Dingo is geographically isolated, genetically distinct, phenotypically distinct, or ecologically distinct it should be regarded as a separate species. In contrast, the literature is very clear that:

1. Australian dingoes have not been geographically isolated for any great length of time, and that populations of other species geographically isolated for longer are still recognised as the same species;

2. though the Australian Dingo can be genetically distinguished from other dogs, so can all other dog breeds, populations and subpopulations. Recent genetic divergence or distinctiveness of dog breeds reflects their recent population history and is not grounds for recognising a distinct species (or inventing a new species);

3. the phenotypes expressed by the Dingo in Australia are very common across free-roaming dog populations on most continents and also sit firmly within the normal phenotypical range of other dogs; and

4. not only are dingoes not ecologically distinct, but ecological distinctiveness is often highly variable within species.

Smith and colleagues' (2019) claims to the contrary are inconsistent with published data and do not provide a rational basis for establishing species distinction. This position is supported by Opinion 3010 of the ICZN (Gentry *et al.* 1996; ICZN 2003) and sustained during recent review by the IUCN Canid Specialist Group (Alvarez *et al.* 2019), which places the Dingo with the domestic dog. Consequently, the Dingo is ineligible for consideration on the IUCN Red List of Threatened Species and has been recently removed from that list (see www.iucnredlist.org).

Though the correct scientific name of the Dingo is *Canis familiaris*, this in no way diminishes its iconic status or conservation value, or impedes on-ground Dingo conservation actions (Allen *et al.* 2017, 2021; Fleming *et al.* 2021). While we are sympathetic to the need to protect the important ecosystem function provided by this population of wild dogs in Australia, changing their taxonomic designation is not an appropriate way of doing this.

For the Dingo to be recognised as a separate species or subspecies would require that Opinion 3010 of the ICZN (Gentry *et al.* 1996; ICZN 2003) be rescinded or countermanded by a new Opinion. In addition, for the Dingo to be regarded as a separate species would require one or more of the following:

i. new evidence of effective reproductive isolation of the Dingo from related canids

ii. new genetic evidence that showed the Dingo does not cluster within the diversity represented by domestic dog breeds

iii. new evidence that the Dingo was an independently derived evolutionary lineage that was more distinct from domestic dog breeds, than these breeds are from each other

iv. In addition, the relationship of the Australian Dingo population with other 'Dingo' populations in mainland and island South-East Asia including New Guinea (Singing Dog) would need to be clarified.

Acknowledgements

We thank: Danielle Stephens for detailed discussions about the genetics of free-roaming dogs in Australia; Bernie Dominiak who reviewed an earlier version of this manuscript; the organisers of the Royal Zoological Society of NSW Dingo Dilemma Forum for the opportunity to present our case; and an anonymous referee, Ben Allen and Dan Lunney who provided valuable comments on the manuscript.

References

Abbott, I. and Burbidge, A. 1995. The occurrence of mammal species on the islands of Australia: A summary of existing knowledge. CALMScience 1: 259 324.

Allen, B.L., Engeman, R.M. and Allen, L.R. 2011. Wild dogma II: The role and implications of wild dogma for wild dog management in Australia. Current Zoology 57: 737-740.

Allen, B.L., Fleming, P.J.S., Hayward, M., Allen, L.R., Engeman, R.M., Ballard, G. and Leung, L.K-P. 2012. Top-predators as biodiversity regulators: contemporary issues affecting knowledge and management of dingoes in Australia. In 'Biodiversity enrichment in a diverse world.' Ed. GA Lameed. Vol. Chapter 4 pp. 85-132. (InTech Publishing: Rijeka, Croatia)

Allen, B.L., Allen, L.R., Ballard, G., Jackson, S.M. and Fleming, P.J.S. 2017. A roadmap to meaningful dingo conservation. Canid Biology & Conservation 20: 45-56.

Allen, B. L., Allen, L. R., Graham, M. and Buckman, M. 2021. Elucidating dingoes' ecological roles: contributions from the Pelorus Island feral goat biocontrol project. *Australian Zoologist* (in press.)

Alvares, F., Bogdanowicz, W., Campbell, L.A.D., Godinho, R., Hatlauf, J., Jhala, Y.V., Kitchener, A.C., Koepfli, K.P., Krofel, M., Moehlman, P.D., Senn, H., Sillero-Zubiri, C., Viranta, S. and Werhahn, G. 2019. Old World *Canis* spp. with taxonomic ambiguity: Workshop conclusions and recommendations. CIBIO, Vairão, Portugal, May 2019. http://www.canids.org/Old_world_canis_taxonomy_workshop.pdf.

Austin, J.J., Soubrier, J., Prevosti, F.J., Prates, L., Trejo, V., Mena, F. and Cooper, A. 2012. The origins of the enigmatic Falkland Islands wolf. *Nature Communications* **4**: 1552. http://dx.doi.10.1038/ncomms2570

Baker, R.J. and Bradley, R.D. 2006. Speciation in mammals and the genetic species concept. *Journal of Mammalogy* **87**: 643-662.http://dx.doi.10.1644/06-MAMM-F-038R2.1

Balme, J., O'Connor, S. and Fallon, S. 2018. New dates on dingo bones from Madura Cave provide oldest firm evidence for arrival of the species in Australia. *Nature Scientific Reports* **8**: 9933. http://dx.doi.org/10.1038/s41598-018-28324-x

Bowdler, S. 2015. The Bass Strait islands revisited. *Quaternary International* **385**: 206-218. http://dx.doi.org/10.1016/j.quaint.2014.07.047

Cairns, K.M. and Wilton, A.N. 2016. New insights on the history of canids in Oceania based on mitochondrial and nuclear data. *Genetica* **144**: 553–565. http://dx.doi.org/10.1007/s10709-016-9924-z

Cairns, K.M., Brown, S.K., Sacks, B.N. and Ballard, J.W.O. 2017. Conservation implications for dingoes from the maternal and paternal genome: multiple populations, dog introgression and demography. *Ecology and Evolution* **7**: 9787-9807. http://dx.doi.org/10.1002/ece3.3487

Cairns, K.M., Shannon, L.M., Kolner-Matznick, J., Ballard, J.W.O. and Boyko, A.R. 2018. Elucidating biogeographical patterns in Australian native canids using genome wide SNPs. *PLoS ONE* **13**(6): e0198754. https://doi.org/10.1371/journal.pone.0198754

Claridge, A. and Hunt, R. 2008. Evaluating the role of the Dingo as a trophic regulator: Additional practical suggestions. *Ecological Management & Restoration* 9: 116–119. http://dx.doi:10.1111/j.1442-8903.2008.00402.x

Colman, N.J. 2015. Morphological variation and ecological interactions of Australia's apex predator – the dingo (*Canis dingo*). PhD thesis. University of Western Sydney, Sydney.

Corbett, L.K. 2001. The Dingo in Australia and Asia. Second Edition. JB Books Australia, Marleston.

Corbett, L. 2006. The Australasian Dingo. In: Merrick, J.R., Archer, M., Hickey, G.M. and Lee, M.S.Y. (Eds.), *Evolution and Biogeography in Australia*. Auscipub Pty Ltd., Sydney, pp. 745–751.

Crowther, M.S., Cairns, K.M., van Eeden, L.M. and Letnic, M. 2021. Introgression does not influence the positive ecological and functional role of dingo populations. *Australian Zoologist* **41**: 338-346. https://doi.org/10.7882/AZ.2020.016

Crowther, M.S., Fillios, M., Colman, N. and Letnic, M. 2014. An updated description of the Australian dingo (*Canis dingo* Meyer, 1793). *Journal of Zoology* **293**: 192–203. http://dx.doi.org/10.1111/jzo.12134

Cursino, M.S., Harriott, L., Allen, B.L., Gentle, M. and Leung, L.K.-P. 2017. Do female dingo–dog hybrids breed like dingoes or dogs? *Australian Journal of Zoology* **65**: 112-119. http://dx.doi.org/10.1071/ZO17005

Darwin, C. 1859. *On the origin of species by means of natural selection or, the preservation of favoured races in the struggle for life*. John Murray, London.

Doherty, T.S., Davis, N.E., Dickman, C.R., Forsyth, D.M., Letnic, M., Nimmo, D.G., Palmer, R., Ritchie, E.G., Benshemesh, J., Edwards, G., Lawrence, J., Lumsden, L., Pascoe, C., Sharp, A., Stokeld, D., Myers, C., Story, G., Story, P., Triggs, B., Venosta, M., Wysong, M. and Newsome, T.M. 2019. Continental patterns in the diet of a top predator: Australia's dingo. *Mammal Review* **49**: 31-44. http://doi.org/10.1111/mam.12139

Dugatkin, L.A. and Trut, L. 2017. *How to Tame a Fox (and build a dog): Visionary Scientists and a Siberian Tale of Jump-started Evolution*. The University of Chicago Press: Chicago.

Dugatkin, L.A. 2018. The silver fox domestication experiment. *Evolution: Education and Outreach* **11**(16): 1-5.

Eldridge, M.D.B., Miller, E.J., Neaves, L.E., Zenger, K.R. and Herbert. C.A. 2017. Extensive genetic differentiation detected within a model marsupial, the tammar wallaby (*Notamacropus eugenii*). *PLoS ONE* **12**(3): e0172777. https://doi.org/10.1371/journal.pone.0172777

Fillios, M. and Taçon, P. 2016. Who let the dogs in? A review of the recent genetic evidence for the introduction of the dingo to Australia and implications for the movement of people. *Journal of Archaeological Science: Reports* **7**: 782–792. https://doi.org/10.1016/j.jasrep.2016.03.001

Flannery, T.F. and White, J.P. 1991. Animal Translocation: Zoogeography of New Ireland Mammals. *National Geographic Research and Exploration* **7**: 96-113.

Fleming, P., Corbett, L., Harden B. and Thomson P. 2001. Managing the impacts of dingoes and other wild dogs. Bureau of Rural Sciences: Canberra.

Fleming, P.J.S., Allen, B.L. and Ballard, G. 2012. Seven considerations about dingoes as biodiversity engineers: the socioecological niches of dogs in Australia. *Australian Mammalogy* **34**: 119-131.

Fleming, P.J.S., Nolan, H., Jackson, S.M., Ballard, G-A., Bengsen, A., Brown, W.Y., Meek, P.D., Mifsud, G., Pal, S.K. and Sparkes, J. 2017. Roles for the Canidae in food webs reviewed: Where do they fit? *Food Webs* **12**: 14-34. http://dx.doi.org/10.1016/j.fooweb.2017.03.001

Fleming, P.J.S., Ballard, G. and Cutter, N. 2021. There is no Dingo dilemma: legislation facilitates culling, containment and conservation of Dingoes in New South Wales. *Australian Zoologist* in press.

Frankham, R., Ballou, J.D., Eldridge, M.D.B., Lacy, R.C., Ralls, K., Dudash, M.R. and Fenster, C.B. 2011. Predicting the probability of outbreeding depression. *Conservation Biology* **25**: 465-75. http://doi.org/10.1016/j.biocon.2012.04.034

Frankham, R., Ballou, J.D., Dudash, M.R., Eldridge, M.D.B., Fenster, C.B., Lay, R.C., Mendelson II, J,R., Porton, I.J., Ralls, K. and Ryder, O.A. 2012. Implications of different species concepts for conserving biodiversity. *Biological Conservation* **153**: 25-31. http://dx.doi.org/10.1016/j.biocon.2012.04.034

Gabriele-Rivet, V., Arsenault, J., Wilhelm, B., Brookes, V.J., Newsome, T.M. and Ward M.P. 2019. A scoping review of dingo and wild-living dog ecology and biology in Australia to inform parameterisation for disease spread modelling. *Frontiers in Veterinary Science* **6**: 47. https://doi.org/10.3389/fvets.2019.00047

Gentry, A., Clutton-Brock, J. and Groves, C.P. 1996. Case 3010. Proposed conservation of usage of mammal specific names based on wild species which are antedated by or contemporary with those based on domestic animals. *Bulletin of Zoological Nomenclature* **53**: 28–37. https://doi.org/10.5962/bhl.part.14102

Gentry, A., Clutton-Brock, J. and Groves, C.P. 2004. The naming of wild animal species and their domestic derivatives. *Journal of Archaeological Science* **31**: 645–651. https://doi.org/10.1016/j.jas.2003.10.006

Georgevsky, D., Carrasco, J.J., Valenzuela, M. and McGreevy, P.D. 2014. Domestic dog skull diversity across breeds, breed groupings, and genetic clusters. *Journal of Veterinary Behavior* **9**: 228-234. https://doi.org/10.1016/j.jveb.2014.04.007

Greig, K., Gosling, A., Collins, C.J., Boocock, J., McDonald, K., Addison, D.J., Allen, M.S., David, B., Gibbs, M., Higham, C.F.W., Liu, F., McNiven, I.J., O'Connor, S., Tsang, C.H., Walter, R. and Matisoo-Smith, E. 2018. Complex history of dog (*Canis familiaris*) origins and translocations in the Pacific revealed by ancient mitogenomes. *Scientific Reports* **8**(9130): 1-9. https://doi.org/10.1038/s41598-018-27363-8

Haouchar, D., Haile, J., McDowell, M.C., Murray, D.C., White, N.E., Allcock, R.J.N., Phillips, M,J., Prideaux, G.J. and Bunce, M. 2014. Thorough assessment of DNA preservation from fossil bone and sediments excavated from a late Pleistocene-Holocene cave deposit on Kangaroo Island, South Australia. *Quaternary Science Reviews* **84**: 56-64. http://dx.doi.org/10.1016/j.quascirev.2013.11.007

Heinsohn, T. 2003. Animal translocation: long-term human influences on the vertebrate zoogeography of Australasia (natural dispersal versus ethnophoresy). *Australian Zoologist* **32**: 351-376. https://doi.org/10.7882/AZ.2002.014

Heinsohn, T. 2010. Marsupials as introduced species: Long-term anthropogenic expansion of the marsupial frontier and its implications for zoogeographic interpretation. Pp. 133-176, in S. Haberle, J. Stevenson and M. Prebble (eds.) *Altered Ecologies: Fire, Climate and human influence on terrestrial landscapes.* Australian National University Press, Canberra.

Helgen, K.M., and Wilson, D.E. 2002. The history of the raccoons of the West Indies. *Journal of the Barbados Museum and Historical Society* **48**: 1-11.

Helgen, K.M., and Wilson, D.E. 2003. Taxonomic status and conservation relevance of the raccoons (*Procyon* spp.) of the West Indies. *Journal of Zoology (London)* **259**: 69-76.

Helgen, K.M., and Wilson, D.E. 2005. A systematic and zoogeographic overview of the raccoons of Mexico and Central America. Pp. 221-236 in, V. Sanchez-Cordero and R.A. Medellin (eds.), Contribuciones Mastozoológicas: en Homenaje a Bernardo Villa, Instituto de Biologia e Instituto de Ecologia, UNAM, Mexico City, Mexico.

Helgen, K.M., Maldonado, J.E., Wilson, D.E. and Buckner, S.D. 2008. Molecular confirmation of the origin and invasive status of West Indian raccoons. *Journal of Mammalogy* **89**: 282-291.

Hofman, C.A., Rick, T.C., Hawkins, M.T.R., Funk, W.C., Ralls, K., Boser, C.L., Collins, P.W., King, J.L., Morrison, S.A., Newsome, S.D., Sillett, T.S., Fleischer, R.C. and Maldonado, J.E. 2015. Mitochondrial genomes suggest rapid evolution of dwarf California Channel Islands Foxes (*Urocyon littoralis*). *PLoS ONE* **10**(2): e0118240. https://doi.org/10.1371/journal.pone.0118240

International Commission of Zoological Nomenclature (ICZN) 1957. Opinion 451. Use of the plenary powers to secure that the specific name *dingo* Meyer, 1793, as published in the combination *Canis dingo* shall be the oldest available name for the dingo of Australia (Class Mammalia). Opinions and Declarations Rendered by the *International Commission of Zoological Nomenclature* **15**: 329–338.

International Commission on Zoological Nomenclature (ICZN) 1999. *International Code of Zoological Nomenclature.* International Trust for Zoological Nomenclature and the British Museum of Natural History, London. Fourth Edition.

International Commission on Zoological Nomenclature (ICZN) 2003. Opinion 2027 (Case 3010). Usage of 17 specific names based on wild species which are predated by or contemporary with those based on domestic animals (Lepidoptera, Osteichthyes, Mammalia). *Bulletin of Zoological Nomenclature* **60**: 81-84.

Jackson, S.M. and Groves, C.P. 2015. *Taxonomy of Australian Mammals*. CSIRO Publishing, Melbourne, 529 pp.

Jackson, S.M., Groves, C.P., Fleming, P.J., Aplin, K.P., Eldridge, M.D., Gonzalez, A. and Helgen, K.M. 2017. The wayward dog: Is the Australian native dog or dingo a distinct species? *Zootaxa* **4317**: 201–224. http://dx.doi.org/10.11646/zootaxa.4317.2.1

Jackson, S.M., Fleming, P.J.S., Eldridge, M.D.B., Ingleby, S., Flannery, T.F., Johnson, R.N., Cooper, S.J.B., Mitchell, K.J., Souili, Y., Cooper, A., Wilson, D.E. and Helgen, K.M. 2019. The dogma of dingoes - Taxonomic status of the dingo: A reply to Smith *et al. Zootaxa* **4564**: 198–212. https://doi.org/10.11646/zootaxa.4564.1.7

Johnson, R.N., O'Meilly, D., Chen, Z., Etherington, G.J., Ho, S.Y.W., Nash, W.J., Grueber, C.E., Cheng, Y., Whittington, C., Dennison, S., Peel, E., Haerty, W., O'Neill, R.J., Colgan, D., Russell, T.L., Alquezar-Planas, D.E., Attenbrow, V., Bragg, J.G., Brandies, P.A., Chong, A.Y.-Y., Deakin, J.E., Di Palma, F., Duda, Z., Eldridge, M.D.B., Ewart, K.M., Hogg, C.J., Frankham, G.J., Georges, A., Gillett, A.K., Govendir, M., Greenwood, A.D., Hayakawa, T., Helgen, K.M., Hobbs, M., Holleley, C.E., Heider, T.N., Jones, E.A., King, A., Madden, D., Graves, J.A.M., Morris, K.M., Neaves, L.E., Patel, H.R., Polkinghorne, A., Renfree, M.B., Robin, C., Salinas, R., Tsangaras, K., Waters, P.D., Waters, S.A., Wright, B., Wilkins, M.R., Timms, P. and Belov, K. 2018. Adaptation and conservation insights from the koala genome. *Nature Genetics* **50**: 1102-1111. https://doi.org/10.1038/s41588-018-0153-5

Kerr, R. 1792. *The Animal Kingdom, or zoological system, of the celebrated Sir Charles Linnaeus; Class1. Mammalia: containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young; being a translation of that part of the Systema Naturae, as lately published, with great improvements, by Professor Gmelin of Goettingen. Together with numerous additions from more recent zoological writers, and illustrated with copper plates*. Vol. 1. J. Murray & R. Faulder, London, 644 pp.

Koler-Matznick, J., Brisbin, I.L., Feinstein, M. and Bulmer, S. 2003. An updated description of the New Guinea singing dog (*Canis hallstromi,* Troughton 1957). *Journal of Zoology* **261**: 109–118.

Kreplins, T., Gaynor, A., Kennedy, M., Baudains, C., Adams, P. and Fleming, T. 2019. What to call a dog? A review of the common names for Australian free-ranging dogs. *Pacific Conservation Biology* **25**: 124-134. https://doi.org/10.1071/PC18018

Lambeck, K. and Chappell, J. 2001. Sea level change through the last glacial cycle. *Science* **292**(5517): 679-686.

Lee, K.E., Seddon, J.M., Johnston, S., FitzGibbon, S.I., Carrick, F., Melzer, A., Bercovitch, F. and Ellis, W. 2013. Genetic diversity in natural and introduced island populations of koalas in Queensland. *Australian Journal of Zoology* **60**: 303-310. https://doi.org/10.1071/ZO12075

Linnaeus, C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. *Editio decima, reformata*. **Vol**. 1. Laurentii Salvii, Holmiae, 823 pp.

Louppe, V., Baron, J., Pons, J.-M. and Veron, G. 2020. New insights on the geographical origins of the Caribbean raccoons. *Journal of Zoological Systematics and Evolutionary Research*. In press. https://doi: 10.1111/jzs.12382

Macintosh, N.W.G. 1975. The origin of the dingo: an enigma. In: Fox, M.W. (Ed.) *The Wild Canids: Their Systematics, Behavioural Ecology and Evolution*. Van Nostrand Reinhold Co., New York, Pp. 87-106.

McIntyre, J.K., Wolf, L.L., Sacks, B.N., Koibur, J. and Brisbin Jr, I.L. 2020. A population of free-living highland wild dogs in Indonesian Papua. *Australian Mammalogy* **42**: 160-166.

Meyer, F.A.A. 1793. *Systematisch-summarische Uebersicht der neuesten zoologischen Entdeckungen in Neuholland und Afrika: nebst zwey andern zoologischen Abhandlungen*. Dykische Buchhandlung, Leipzig, 178 pp. https://doi.org/10.5962/bhl.title.39685

Neaves, L.E., Frankham, G.J., Dennison, S., FitzGibbon, S., Flannagan, C., Gillett, A., Hynes, E., Handasyde, K., Helgen, K.M. and Tsangaras, K. 2016. Phylogeography of the koala (*Phascolarctos cinereus*), and harmonising data to inform conservation. *PLoS ONE* **11**(9): e0162207. https://doi.org/10.1371/journal.pone.0162207

Newsome, T.M., Ballard, G.-A., Crowther, M.S., Fleming, P.J. and Dickman, C.R. 2014a. Dietary niche overlap of free-roaming dingoes and domestic dogs: the role of human-provided food. *Journal of Mammalogy* **95**: 392-403. http://dx.doi.org/10.1644/13-MAMM-A-145.1

Newsome, T.M., Ballard, G.-A., Fleming, P.J.S., van de Ven, R., Story, G.L. and Dickman, C.R. 2014b. Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia* **175**: 139-150. http://dx.doi.org/10.1007/s00442-014-2889-7

Nigenda-Morales, S.F., Gompper, M.E., Valenzuela-Galván, D., Lay, A.R., Kapheim, K.M., Hass, C., Booth-Binczik, S.D., Binczik, G.A., Hirsch, B.T., McColgin, M., Koprowski, J.L., McFadden, K., Wayne, R.K. and Koepfli, K.-P. 2019. Phylogeographic and diversification patterns of the white-nosed coati (*Nasua narica*): Evidence for south-to-north colonization of North America. *Molecular Phylogenetics and Evolution* **131**: 149-163. https://doi.org/10.1016/j.ympev.2018.11.011

Oskarsson, M.C.R., Klütsch, C.F.C., Boonyaprakob, U., Wilton, A., Tanabe, Y. and Savolainen, P. 2012. Mitochondrial DNA data indicate an introduction through Mainland Southeast Asia for Australian dingoes and Polynesian domestic dogs. *Proceedings of the Royal Society B: Biological Sciences,* **279**, 967-974. https://doi.org/10.1098/rspb.2011.1395

Parr, W. C. H., Wilson, L. A. B., Wroe, S., Colman, N. J., Crowther, M. S. and Letnic, M. 2016. Cranial shape and the modularity of hybridization in dingoes and dogs; hybridization does not spell the end for native morphology. *Evolutionary Biology* **43**: 171-187. doi: 10.1007/s11692-016-9371-x.

Purcell, B. 2010. *Dingo*. CSIRO Publishing, Canberra.

Ritchie, E.G., Dickman, C.R., Letnic, M. and Vanak, A.B. 2014. Dogs as predators and trophic regulators. Pp. 55-68, in, (Ed. M.E. Gompper), *Free-ranging dogs and wildlife conservation*. (Oxford University Press: Oxford)

Savolainen, P., Leitner, T., Wilton, A. N., Matisoo-Smith, E. and Lundeberg, J. 2004. A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 12387-12390. https://doi.org/10.1073/pnas.0401814101

Sillero-Zubiri, C. 2009. Family Canidae (Dogs). Pp. 352-446, in D.E. Wilson and R.A. Mittermeier (eds.) *Handbook of the Mammals of the World*. Volume 1. Carnivores. Lynx Edicions, Barcelona.

Smith, B. 2015. Characteristics of the Australian Dingo (*Canis dingo* Meyer, 1793). Pp. 1-23, in, (Ed. B. Smith), *The dingo debate: Origins, behaviour and conservation.* CSIRO Publishing, Melbourne.

Smith, B. and Savolainen, P. 2015. The origin and ancestry of the dingo. Pp. 55-79, in B. Smith (ed.) *The dingo debate: Origins, behaviour and conservation.* CSIRO Publishing, Melbourne.

Smith, B.P., Cairns, K.M., Adams, J.W., Newsome, T.M., Fillios, M., Déaux, E.C., Parr, W.C.H., Letnic, M., Van Eeden, L.M., Appleby, R.G., Bradshaw, C.J.A., Savolainen, P., Ritchie, E.G., Nimmo, D.G., Archer-Lean, C., Greenville, A.C., Dickman, C.R., Watson, L., Moseby, K.E., Doherty, T.S., Wallach, A.D., Morrant, D.S. and Crowther, M.S. 2019. Taxonomic status of the Australian dingo: the case for *Canis dingo* Meyer, 1793? *Zootaxa* **4564**: 173-197. https://doi.org/10.11646/zootaxa.4564.1.6

Sparkes, J., Körtner G., Ballard G., Fleming P.J.S. and Brown W.Y. 2014. Effects of sex and reproductive state on interactions between free-roaming domestic dogs. *PLoS ONE* **9**(12): e116053. https://doi.org/10.1371/journal.pone.0116053

Sparkes, J., Ballard, G., Fleming, P.J.S., van de Ven, R. and Körtner, G. 2016. Contact rates of wild-living and domestic dog populations in Australia: a new approach. *Oecologia* **182**: 1007-1018. https://doi.org/10.1007/s00442-016-3720-4

Spriggs, M. 1997. *The Island Melanesians*. Blackwell, Oxford.

Stephens, D., Wilton, A.N., Fleming, P.J.S. and Berry, O. 2015. Death by sex in an Australian icon: a continent-wide survey reveals extensive hybridisation between dingoes and domestic dogs. *Molecular Ecology* **24**: 5643-5656. https://doi.org/10.1111/mec.13416

Summerhayes, G.R. 2007. Island Melanesian Pasts: A View from Archaeology. Pp. 10-35, in J.S. Friedlaender (ed.) Genes, Language and Culture History in the Southwest Pacific. Oxford University Press, Oxford.

Thomson, P.C. 1992. The behavioural ecology of dingoes in north-western Australia. III. Hunting and feeding behaviour, and diet. *Wildlife Research* **19**: 531-541. https://doi.org/10.1071/WR9920531

Van Dyck, S.M. and Strahan, R. (eds.) 2008. The Mammals of Australia. Reed New Holland, Sydney.

Vernes, K., Dennis, A. and Winter, J. 2001. Mammalian diet and broad hunting strategy of the dingo (*Canis familiaris dingo*) in the wet tropical rain forests of northeastern Australia. *Biotropica* **33**: 339-345. http://dx.doi.org/10.1111/j.1744-7429.2001.tb00185.x

vonHoldt, B.M., Pollinger, J.P., Lohmueller, K.E., Han, E., Parker, H.G., Quignon, P., Degenhardt, J.D., Boyko, A.R., Earl, D.A., Auton, A., Reynolds, A., Bryc, K., Brisbin, A., Knowles, J.C., Mosher, D.S., Spady, T.C., Elkahloun, A., Geffen, E., Pilot, M., Jedrzejewski, W., Greco, C., Randi, E., Bannasch, D., Wilton, A., Shearman, J., Musiani, M., Cargill, M., Jones, P.G., Qian, Z., Huang, W., Ding, Z.-L., Zhang, Y.-p., Bustamante, C.D., Ostrander, E.A., Novembre, J. and Wayne, R.K. 2010. Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature* **464**: 898. http://dx.doi.org/10.1038/nature08837

Wang, G.-D., Zhai, W., Yang, H.-C., Fan, R.-X., Cao, X., Zhong, L., Wang, L., Liu, F., Wu, H., Cheng, L.-G., Poyarkov, A.D., Poyarkov Jr, N.A., Tang, S.-S., Zhao, W.-M., Gao, Y., Lv, X.-M., Irwin, D.M., Savolainen, P., Wu, C.-L. and Zhang, Y.-P. 2013. The genomics of selection in dogs and the parallel evolution between dogs and humans. *Nature Communications* **4**: 1860. http://dx.doi.org/10.1038/ncomms2814

Wang, G.-D., Zhai, W., Yang, H.-C., Wang, L., Zhong, L., Liu, Y.-H., Fan, R.-X., Yin, T.-T., Zhu, C.-L., Poyarkov, A.D., Irwin, D.M., Hytönen, M.K., Lohi, H., Wu, C.-L., Savolainen, P. and Zhang, Y.-P. 2016. Out of southern East Asia: the natural history of domestic dogs across the world. *Cell Research* **26**: 21-33. http://dx.doi.org/10.1038/cr.2015.147

Wilson, D.E. and Reeder, D.M. 2005. *Mammal Species of the World - A Taxonomic and Geographic Reference*. Johns Hopkins University Press, Baltimore.

Wood Jones, F.W. 1921. The status of the dingo. *Transactions of the Royal Society of South Australia* **45**, 254–263.