

SPECIAL ISSUE ARTICLE

What the dingo says about dog domestication

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Abstract

Worldwide, dogs (*Canis familiaris*) are certainly the most common domesticate (900 million according to the World Atlas) and are sometimes used as a proxy for human presence. Dogs were the first and therefore arguably most important species ever to be domesticated. It is widely accepted that the domestic dog is a descendent of Pleistocene gray wolves (*Canis lupus*), possibly of a population now extinct. How can an extant canid, the dingo (*Canis dingo* or *Canis familiaris*), whose status as a species and as a domesticate is controversial, improve our understanding of the ancient process of domesticating the dog? Here I review anatomical, behavioral, biogeographic, and molecular evidence on the appropriate status of dingoes in a historical context. Dingoes are now the major apex predator in Australia aside from humans. Different sources of evidence have suggested different times of arrival in Greater Australia for humans and canids and different degrees of intimacy or domestication between humans and canids. Just as domestic dogs are often accorded near-human status, dingoes have special relationships with human families, but reproductively and behaviorally they remain independent. In sum, traits of the dingo reflect its lupine ancestry, a certain degree of accommodation to human company, and unique adaptations to the demands of its habitat. Emphasizing that domestication is a long-term process, not an event, helps clarify the ambiguous status of dingoes.

KEYWORDS

Australia, canid, domestication, wolf

1 | INTRODUCTION

The knowledge of dingoes in the Western world dates to the first sighting of Australian Aborigines with canids in 1623 by Jan Carstenszoon (Sigmon & Zuiderbaan, 1976) and later by William Dampier (1699). Their observations were well before colonization and led to a widespread but erroneous assumption that dingoes had arrived in Australia with Aborigines. One commonly-used name,

Canis dingo, was proposed by Friedrich Meyer in 1793 and ratified by the International Commission of Zoological Nomenclature in 1957. However, Meyer's paper was based on the first painting of a dingo (Figure 1) and a brief description by Governor Arthur Phillip, rather than first-hand observations of the animal. No type specimen was named. Without a formal proposal, the name *Canis lupus familiaris* or *Canis familiaris dingo* came into usage. Crowther, Fillios, Colman, and Letnic (2014) and

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FIGURE 1 Portrait of a large Dog—by George Stubbs, 1772. Copyright National Maritime Museum, Greenwich, UK. Used on a Creative Commons Open Access license. This is the earliest known formal portrait of a dingo, based on information from Captain Cook's first voyage to Australia. Although the overall doglike appearance of a dingo is shown, details such as dingoes' extreme slenderness and large head are not emphasized

Smith et al. (2019) recently proposed a formal description of *Canis dingo*, the work by Crowther's team being based on pre-1900 specimens unlikely to be dingo-dog hybrids. Their aim was to clarify the formal definition of dingoes as they were when they entered Greater Australia so that current controversies over their status as a domesticated or a wild species of canid could be resolved. Despite many decades of observations of the dingo, there is still no agreement on exactly what a dingo is, partly because of imprecision in the early descriptions, which did not conform to current International Code of Zoological Nomenclature standards.

Dingoes vary in coloring, have pricked ears, a long, narrow torso and a relatively large head (Figure 2). Dingoes closely resemble free-breeding and village dogs, including some Asian village dogs and Indian Pariah dogs, which Corbett (1995) referred to as Asian dingoes. Village dogs, dingoes, and pariah dogs are highly variable in phenotype (Corbett, 1999; Crapon de Craupona & Savolainen, 2012; Corrieri et al., 2018; Elledge et al., 2008). Some scholars feel that the dingo, the iconic Australian "wild dog," is in fact the descendent of semi-domesticated village dogs that went feral after arriving in Australia, making them a subspecies of semi-domesticated dogs (see Clutton-Brock, 1999, 1995, 1977; Puja, Irion, Schaffer, & Pedersen, 2005). This poses a nomenclatural problem: if the dingo is neither a feralized domesticated nor wild, then what is the appropriate taxon?

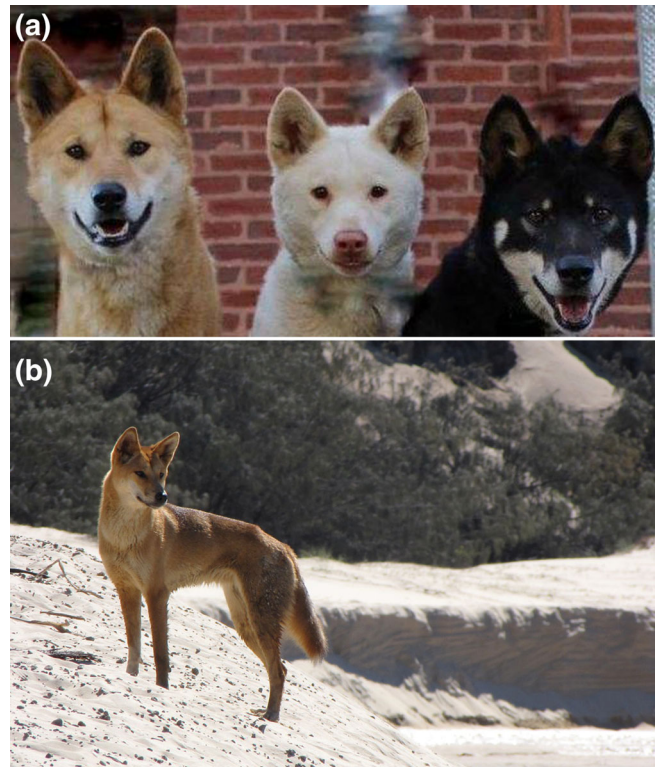


FIGURE 2 (a) Purebred dingoes, like these from the Dingo Discovery Centre, vary in coat color. This phenotypic variability hinders accurate identification of dingoes in field studies. Photo courtesy of Lyn Watson, The Australian Dingo Foundation. (b) A wild dingo, showing the large head, lean torso, and powerful shoulders. Created by Alberto 1 × 3. Used under an Open Access license Creative Commons BY-NC-SA 2.0

If the dingo is a distinctly Australian canid that evolved special adaptations due to founder effect, genetic drift, and the harsh and unpredictable climate, but not human selection during its roughly 4,000 years of isolation on Greater Australia, it should probably be given its own species designation (Crowther et al., 2014; Smith et al., 2019).

2 | BEHAVIORAL AND BIOGEOGRAPHIC EVIDENCE OF THE HUMAN-DINGO RELATIONSHIP

One of the most important signatures of domestication is an intimate involvement with humans. It is crucial to know when and how humans and dingoes arrived in Australia in order to assess their taxonomic status. Ancestral dingoes came to figure prominently in the tales, songs, dances, art, and Dreaming narratives of Indigenous Australians (Berndt & Berndt, 1999; Rose, 1992; Smith & Litchfield, 2009a; Smith & Litchfield, 2009b).

Thus some suggest that dingoes fulfill one important criterion of domestication: a special and intimate association with humans (Clutton-Brock, 1999, 1977). Zeder (2012) regards behavior toward humans and their environment as the primary target for selection during the process of domestication. However, dingoes are not managed or bred by Indigenous Australians, so humans are not exerting selective pressure upon dingoes. Wynne (2019) argues that an innate capacity for bonding closely with other species is characteristic of dogs. Reports of dingo behavior discussed below suggest that they do not possess this innate capacity for close bonding or do not exhibit it as fully as most dogs.

The oldest evidence of modern humans in Greater Australia is about 65,000 years ago, according to evidence from Madjedbebe, a site in northwest Australia (Clarkson et al., 2017; Clarkson et al., 2015). The distance to Australia from various points in Island Southeast Asia (ISEA) varied historically as sea levels rose and fell but always involved several open sea voyages of up to 100 km. This point raises the question of why modern humans got to Australia when they did and why neither they nor archaic humans in ISEA got there earlier.

At some times and places, the sea voyages would have been shorter and therefore easier. “Easier” is a relative judgment, because the journey was not simple: no other medium- to large-bodied terrestrial mammal other than humans and dingoes ever completed these voyages (without human assistance) in numbers sufficient to establish a viable population in the new area (van den Bergh, de Vos, & Sondar, 2001). There were at least eight ocean journeys per crossing, which required humans to have boats and maritime skills (e.g., Balme, 2013; Davidson & Noble, 1992; Noble & Davidson, 1991; Davidson, 2010). If, for example, people came from Timor to northwestern Australia, the open water voyage may have been up to 90–100 km (Balme et al., 2009; Kealy, Louys, & O’Connor, 2018). This distance over water was apparently a major barrier to entry into Australia by archaic humans. Between 70,000 and 65,000 years ago, sea levels were lower so water crossings were easier.

Kealy et al. (2018) incorporated island uplift, rising and falling sea levels, voyage distance, inter-island visibility, and drift models in evaluating various proposed migration routes during the time span of human arrival in Greater Australia (Sahul). The team found strong support for a northern route into Sahul, with a landing location on present-day Misool Island on the Bird’s Head Peninsula of New Guinea between 65,000 and 70,000 years ago. This accords reasonably well with the location of Madjedbebe, in the western plateau of Arnhem Land. Other early sites are scattered around mainland Australia. There is no obvious chronological trajectory of the location of early archaeological sites.

This earliest human occupation of Australia at about 65,000 years ago cannot have involved dingoes, because there was nothing resembling a dingo or domesticated dog anywhere at that time. What is more, the group of humans who became the First Australians split off from the population of other anatomically modern humans (AMHs) well before the latter reached central Europe or Asia, two often-proposed regions for the initial domestication of dogs (Freedman & Wayne, 2017; Germonpré et al., 2009; Germonpré, Lázniczková-Galetová, & Sablin, 2011; Pang et al., 2009; Savolainen et al., 2005; Shannon et al., 2016; Thalmann et al., 2013; vonHoldt et al., 2010). The archaeological “footprint” of the First Australians is therefore a key clue to their adaptations to their new continent, although it is important to consider taphonomic factors that may have influenced fossil preservation (Langley et al., 2011). The rapid spread of humans across the Australian continent, and into various habitats, suggest the First Australians lived in small, mobile groups that adapted to different habitats through the acquisition of detailed knowledge of the landscape and resources therein. For example, a survey of archaeological sites relative to the location of permanent water sources by Bird et al. (2016) revealed that all known sites older than 30,000 years old were within 20 km of permanent water sources, meaning people could reach a water source with 1 day’s walk.

As with the first humans of Australia, dingoes most likely arrived via Asia and were transported by boat from ISEA (Fillios & Taçon, 2016; Paddle, 2000) to somewhere along the north or northwest coast of Australia or the Bird’s Head Peninsula of New Guinea. This scenario is supported by the genetic and phenotypic resemblances between dingoes and New Guinea Singing Dogs (*Canis hallstromi* or NGSDs; Cairns & Wilton, 2016; Koler-Matznick, Brisbin Jr., Feinstein, & Bulmer, 2003; Surbakti et al., 2020).

It is possible canids entered Greater Australia through New Guinea and spread southward without human assistance until the Torres Strait became submerged about 11,000 years ago (Sacks et al., 2013). The recent discovery of a wild highland canid in New Guinea (McIntyre, Wolf, Sacks, Koibur, & Brisbin Jr., 2019) believed to be closely related to and genetically and phenotypically resembling dingoes and NGSDs (Figure 3(a,c)), also supports a scenario of dingo landfall through New Guinea or northern Australia. The problem with this hypothesis is that there is a very sparse record of any kind of canid in ISEA during the last 10,000 years (Higham et al., 1980). However the absence of common indicators of Neolithic culture in precolonial Australia—such as pigs, pottery, and chickens—suggests that canids arrived in Australia prior to the Neolithic expansion.

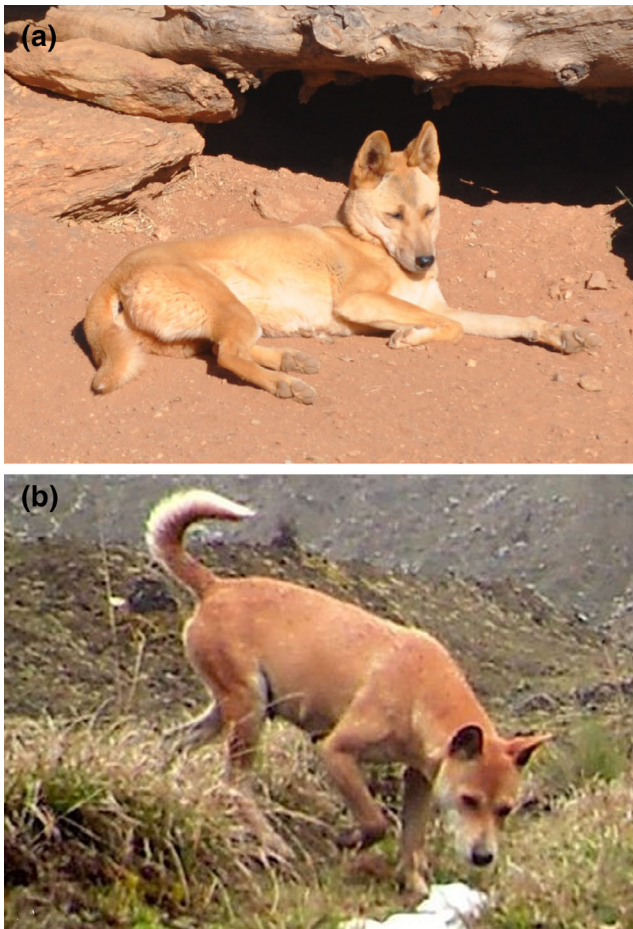


FIGURE 3 (a) The dingo (Photo courtesy of Greg Retallack) has a strong phenotypic resemblance to the newly discovered canid from highland New Guinea. (b) (Photo courtesy of the New Guinea Highland Wild Dog Foundation.) Not only the general appearance of these highland dogs, but preliminary genetic work indicates that these dogs are distinct from village dogs in the region and share a mitochondrial DNA haplotype (A29) with many dingoes

The oldest dated canid in the region but outside of Greater Australia is a dingo burial from Matja Kuru 2 cave on Timor Leste, dated to 2867 ± 26 BP (2921–3075 cal. BP; Gonzalez, Clark, O'Connor, & Matisoo-Smith, 2013, p. 14). That specimen does not represent an ancestral dingo since it is younger than the oldest dingo specimens in Australia, which are from Madura Cave on the Nullarbor Plains (Milheim & Thompson, 2010). Direct dating of two dingoes' bones yielded a date of 3450 ± 95 BP (3,905–3,446 cal. BP at 94.8%: Balme, O'Connor, & Fallon, 2018). Madura Cave is a long way from any projected landfall in the north, suggesting that once dingoes arrived on Greater Australia, they spread into and across numerous habitats, as humans had done. How long prior to 3,450 years ago was dingo landfall? Estimates of the speed of continental spread vary from a few decades (Balme et al., 2018) to 100 years (Saunders et al., 1995), or 500 years (Gollan, 1984). The dingo apparently

already had or quickly developed effective adaptations to the Australian environments. Its spread may have been facilitated by association with humans; many of the earliest sites in Australia where dingoes have been found are archaeological sites, which hints at a familiarity with humans prior to reaching Australia. Balme et al. (2018), p. 3 maintain that

the presence of dingoes on watercraft indicates that they were tamed animals when they arrived in Australia, it is likely that Aboriginal people took them up very rapidly and that this association facilitated their movement across the continent. Some idea of the potential rapidity of the commensal relationship and how this may have assisted dingo spread may be gauged by the uptake of the dog by Indigenous Tasmanians when it was introduced... at the time of European contact...

Of course, being tamed is not the same as being domesticated. Further, being transported by boat does not necessitate domestication, only a certain tolerance for human presence or confinement. Numerous undomesticated animals such as moose (Byrne, n.d.), elk and other deer, wallabies, various cuscus, pademelons, and other marsupials to Pacific islands (Heinsohn, 2003), giraffe (Ringmar, 2006), elephant (Lach, 1967), rhinoceros (Clarke, 1986), and many other animals (see e.g., Meijaard, 2003) have all been transported to new geographic locations by boat, though not necessarily as small a boat as the First Australians might have used.

Dingoes never reached Tasmania, which was isolated from mainland Australia by the flooding of the Bass Strait about 11,000 years ago, suggesting that dingoes must have arrived in Australia after that landbridge flooded. Indications and speculations about dingo origins prior to 1979 are reviewed by Barker and MacIntosh (1979); their primary conclusion is that dingoes are not indigenous to Australia but their origin is unclear. This view is widely accepted. However, given the fact that both NGSDs and the newly discovered population of canids in highland New Guinea closely resemble dingoes (Figure 4), there may have been a spread of canids between New Guinea and mainland Australia unassisted by humans prior to the flooding of the Torres Strait at $\sim 8,000$ years ago (Cairns et al., 2017; Cairns & Wilton, 2016).

3 | DINGO ORIGINS

3.1 | Modern and ancient dogs

The differences between the distribution of modern and ancient domesticated dogs imply to Frantz et al. (2016)



FIGURE 4 Dingoes have unusual flexibility of their shoulders (a) and wrists (b). Photos courtesy of Lyn Watson, Australian Dingo Foundation

that early European dogs were largely replaced by domesticated dogs originating in Western Eurasia. Archaeological and fossil remains indicate that the earliest domesticated dogs in Western Eurasia were substantially earlier (living between 15,000 and 30,000 years ago) than the earliest dogs in East Asia (which lived ~12,500 years ago). However, Pang and colleagues (Pang et al., 2009) studied the complete mtDNA genome of 169 dogs and the control region of mtDNA of an additional 1,543 dogs and obtained different results. They found dogs universally shared 10 clades, not four as originally reported (Vilà et al., 1997), but the full range of mitochondrial haplotype diversity was found only in dogs from Asia south of the Yangtze River. They hypothesized that this greater diversity was evidence of greater antiquity of dogs in Asia south of the Yangtze. However, a later study of 48,000 SNPS did not find any regular correlation between genomic diversity and geographic location (vonHoldt et al., 2010).

Pang et al. also speculated that dogs had been domesticated twice, first in an old split between Western Eurasian and East Asian canids. They concluded that the origin of modern dogs occurred in East Asia more recently than 16,300 years ago and spread westward from there, despite a lack of fossil remains; no fossil canids have been found in Central Eurasia older than 8,000 years ago (Frantz et al., 2016). They suggested that, as these southeast Asian dogs moved westward, they replaced pre-existing, indigenous Eurasian or Western Asian dogs.

Importantly, Larson et al. (2012) observed that the most ancient dog fossils are all found in Europe and Central Asia where they overlap geographically with modern breeds with relatively recent origins. In contrast, ancient or basal breeds are often found in regions where fossil evidence of ancient dogs is lacking. This may speak to cultural or taphonomic factors hindering discovery or

preservation of skeletal remains. Alternatively, the scarcity of fossils of early domesticates may reflect the role of geographic isolation in early parts of the domestication process.

3.2 | Molecular evidence

Genetically, dingoes cluster with the same clade (“clade A”) as about 71% of dog breeds and wolves do. It is to be expected that a very early or very primitive canid that is not fully domesticated will share wolf-like traits (Larson et al., 2014). Work by Savolainen et al. (2005) indicated that a sample of 211 dingoes had very few maternal haplotypes (mtDNA lineages), based on the 582 base pair regions of the mtDNA, commonly A29 and A79. These two haplotypes differ by only one substitution in the control region, suggesting that there was very little variability in the founder population and possibly only a single founding event. The A29 haplotype is also found in NGSDs, Southeast Asian and American dogs. Haplotypes that differ by only one or two substitutions from A29 are found only among Asian dogs.

In contrast, Cairns and Wilton (2016) compared complete mtDNA genomes in a sample of 25 dingoes and reported 20 different maternal haplotypes. This suggests a considerably larger founding population and quite possibly more than one founding event, unlike previous studies. It also suggests that control regions in dingoes are not phylogenetically informative (Cairns et al., 2017).

Paternal haplotypes on the Y chromosome in dingoes are few, being H3 and H60. H3 has also been found in East Asian and northern European dogs (Ding et al., 2011), while H60 is a haplotype shared with NGSDs and differs by one substitution from a haplotype found only in East Asian dogs. These findings support the idea that dingoes are feralized descendants of southeast Asia dogs.

In addition to speculations that dingoes are feralized dogs, some workers suggest that dingoes were derived specifically from Asian village dogs (Puja et al., 1977; Sacks et al., 2013; Savolainen et al., 2005; Shannon et al., 2015). However, vonHoldt et al. (2010) observed that much of the variability seen in Asia dogs is derived from Middle Eastern sources, though they do not explicitly claim that dogs were first domesticated in the Middle East.

3.3 | Sister lineages and fossils

Cairns and Wilton (2016, p. 553; see also Sacks et al., 2013) documented greater genetic variability than originally assessed in terms of the presence of additional

mtDNA and Y chromosome lineages that cluster biogeographically. Dingoes also show some unusual haplotypes (compared to domestic dogs) on either their mtDNA or Y chromosomes. Analysis of 28 mtDNA dingo genomes that were sequenced in this study, plus NGSDs, Chinese, Bali, and Kalimantan specimens, cluster dingoes and NGSDs as a monophyletic group, with a clear separation from the Chinese and island dogs. The dingoes are sorted into two lineages, one located in the southeast (SE) of Australia and the other in the northwest (NW), with the NGSD closest to but distinct from the SE dingo group. In sum, the paper suggests at least two separate events involving dingo arrival on mainland Australia. The authors remark:

Conservative molecular dating based upon mitochondrial DNA suggest that the [dog and dingo] lineages split approximately 8,300 years before present, likely outside Australia but within Oceania. The close relationship between dingoes and New Guinea Singing Dogs suggests that plausibly dingoes spread into [mainland] Australia via the land bridge between Papua New Guinea and Australia although seafaring introductions cannot be rejected.

However, the more important issue is how dingoes or their ancestors got to Greater Australia initially, a circumstance in which seafaring seems essential, rather than the movement of dingoes from New Guinea to the Australian mainland.

Cairns and Wilton suggest that dingoes, dogs, and NGSDs diverged outside of mainland Australia prior to the Neolithic expansion in Oceania. Their estimates suggest an mtDNA divergence time between the SE lineage (plus NGSDs) and the NW lineage of dingoes of at least 25,400 (5,473–93,806, 95% HPD) years BP. A fossil-calibrated divergence estimate of the NW dingo lineage is at least 12,300 years BP (12,330–47,634, 95% HPD) and the SE lineage is at least 9,700 years BP (9,765–46,889, 95% HPD). Each of these estimates of divergence time include time spans that are earlier than the age of well-accepted domesticated dog fossils anywhere. In contradiction, the physical remains of dingoes suggest their appearance on the continent no earlier than about 4,000 years ago, long after human arrival and long after the remains of widely-accepted domesticated dogs were being deliberately buried in Eurasia. Other molecularly-based estimates of the divergence of dingoes from other dogs are 4.5–11,000 years ago (Savolainen et al., 2005) or 4,600–18,300 years BP (Oskarsson et al., 2012). These estimates do not coincide well with the archaeological or fossil record of dingo.

Accepting molecular estimates and rejecting radiometric measures of time since burial requires prioritizing molecular divergences based on estimated mutation rates, which are not always clocklike in different molecules or under different conditions. Human selection might accelerate the survival and spread of particular mutations or genes. Inevitably, molecular divergence estimates vary widely depending on the mutation rate that is used. If these molecular estimates include the actual arrival dates of dingoes in Greater Australia, then Cairns and Wilton (2016) suggest the lack of dingo fossils for so many millennia after dingo landfall is due possibly to taphonomic factors and poor preservation. This suggestion does not account for finding fossil remains of animals of similar size and habits, like thylacines, preserved prior to the earliest dingo fossils in Australia. If dingoes were domesticated prior to landfall and lived with people in Australia during this period of invisibility, their long absence from archaeological sites is puzzling unless they did not have an intimate association with people. The same can be said if dingoes were domesticated animals living not in mainland Australia but Oceania, where there are few fossils and none older than the oldest ones in Australia. If the molecular estimates are taken as accurate, dingo landfall may have occurred before the flooding of the Bass Straits. This poses another serious problem because neither SE or NW dingoes reached Tasmania.

Studies of Y chromosome variability by Sacks et al. (2013) and Ardalan et al. (2012) offer support for the two immigration event theory; both teams detected an East to West biased distribution of paternal lineages H3 and H60. The possibility that the separation of SE and NW dingo populations is an effect of the dingo fence and the harassment of dingoes in SE Australia is discounted on the grounds that the dingo fence was finished too recently (in 1885) to have had such a broad effect (Cairns et al., 2017). Caution in concluding how long selective breeding might take to produce new traits is warranted by evidence from the fox farm experiment which, after only 40 years of intensive selective breeding, produced “domesticated” foxes with novel phenotypic and behavioral traits (Dugatkin, 2018; Dugatkin & Trut, 2017; Trut, 1999). Arguments that the experiment did not prove the existence of a domestication syndrome (Lord et al., 2020) do not negate the significant morphological and behavioral changes produced in a short period of intensive selection by humans.

3.4 | Genes for digestion and the mystery of the first dingoes

Zhang et al. (2018) attempted to identify genomic regions under selection during domestication and feralization,

using dingoes as a model species. Given that the derivation of dingoes from already domesticated Asian dogs, which were subsequently feralized, is a highly controversial topic, this explicit assumption undercuts the value of the work. The genomic and behavioral resemblances between dingoes and wolves could as plausibly be attributed to retention of wolflike traits rather than reversal from doglike circumstances.

Zhang's team sequenced the nuclear genomes of 10 dingoes and 2 NGSDs, searching for evidence of modifications from the wolf condition as reported in other studies involving 21 wolves, as well as modifications from the dog condition, as represented by 78 dog genomes in the literature. Differences from wolves were taken as domestication changes and differences from the dog condition were taken as feralization changes.

Principal components analysis of the entire sample produced clear separation into three groups: wolves, dogs and dingoes/NGSDs. Dingoes and NGSDs cluster tightly, well separated from the other groups, demonstrating the genetic distinctiveness of this group.

A specific dietary adaptation distinguishing dingoes from most dogs is a lower number of copies of *AMY2B*, an important gene for starch digestion. Wolves, jackals, coyotes, dingoes, and a few ancient types of dogs native to areas where agriculture was uncommon until recently, also carry only 2 copies of *AMY2B* (Axelsson et al., 2014; Thalmann et al., 2013). Two copies is generally taken to be the primitive or ancestral condition for wild-living, free-breeding canids (Arendt et al., 2014; Arendt, Cairns, Ballard, Savoleinen, & Axelsson, 2016; Axelsson et al., 2014; Cairns et al., 2017; Ollivier et al., 2018; Perry et al., 2007).

In domestic dogs, including village dogs, the number of copies of *AMY2B* ranges from 2 to 34. High copy numbers appear to be an adaptation for efficient digestion of human-derived starchy foods. This difference implies that dogs were domesticated after the onset of agriculture and that dingo ancestors diverged from other canids before that time. Ollivier et al. (2016) estimated the number of *AMY2B* genes in a sample of 13 prehistoric dogs in southwestern Europe ranging in age from 15,000 to 4,000 cal. years BP and found the onset of extra copies of this gene began by 7,000 cal. years BP at the latest. Thus the duplication of the genes roughly coincided with the onset of agriculture, which would increase the amount of starch-rich food available to dogs. Not all dogs from this date onward showed extra copies of the genes and none of the modern wolves, dingoes, or Siberian huskies in their sample had extra copies.

The candidate genes identified by Zhang et al. as subject to positive selection during feralization included five that are associated with digestion and metabolism. Zhang

et al. suggest that dingoes obtained their own food during feralization rather than eating a high proportion of vegetable food and starches if their food were scavenged from or provisioned by humans. Alternatively, if dingo ancestors were not fully domesticated upon arrival in Australia, they may never have acquired the doglike condition facilitating starch digestion.

4 | DISTINCTIVE ATTRIBUTES OF DINGOES

Although a European upon first seeing a dingo may intuitively identify it as a dog, there are a few marked differences among wolves, dogs, and dingoes. In terms of ancient remains, wolves are rarely deliberately buried, but dogs are commonly buried in various cultures and periods worldwide. According to Morey (2006:158-9), the burial of canids is one of the strongest archaeological criteria that signifies their domestication:

People have been burying or otherwise ritually disposing of dead dogs for a long time. They sometimes treat other animals in such a fashion, but not nearly as often as dogs. This presentation documents the consistent and worldwide distribution of this practice over about the past 12,000–14,000 years. Such practices directly reflect the domestic relationship between people and dogs, and speak rather directly to the timing of canid domestication... Nothing signifies the social importance that people have attached to dogs more conspicuously than their deliberate interment upon death.

Eurasian dogs occur in graves with or without humans, with grave goods, and in large canine cemeteries starting about 14,000 years ago (e.g., Clutton-Brock, 1995; Davis & Valla, 1978; Losey et al., 2011, 2013, 2018; Morey, 2006; Perri, 2017; Stager, 1991). Prehistoric dog burials or cemeteries are widespread, being found in Israel, Siberia, Russia, North America, Germany, Egypt, Japan, Peru, Spain, Jordan, China, Sudan, Ukraine, and Tunisia. Thus, Morey (2006), Clutton-Brock (1995), Wynne (2020), and others maintain that their relationship with humans is actually a distinctive or even defining attribute of dogs.

Dogs were clearly domesticated in many parts of the world well before canids arrived in Greater Australia. However, dingo burials are also documented from Australia; in fact, the earliest known dingo specimen is from a burial in Madura Cave, although it is not an elaborate one. Burial per se of the oldest known dingo in

Greater Australia could be taken as strong evidence that dingoes were domesticated before reaching Greater Australia.

Some of the dingo burials closely parallel mortuary treatment of Aboriginal humans (Gunn, Whear, & Douglas, 2010; Gunn, Whear, & Douglas, 2012). Clearly, dingoes developed special and intimate relationships with humans in many regions, which is well documented in the ethnographic literature. But, did this relationship include domestication? Particularly in Western Australia or the central arid regions, dingoes appears to have been treated “almost as members of the family rather than as personal property” (e.g., Berndt & Berndt, 1989, p. 148, 345; Cahir & Clark, 2015; Jones, 1970; Meehan, Jones, & Vincent, 1999; Meggitt, 2013; Smith & Litchfield, 2009a; Smith & Litchfield, 2009b). Dingoes figure prominently in many traditional Aboriginal rock paintings, stories, and songs; *Dingo Makes Us Human* is the title of a well-regarded ethnography (Rose, 1992). Those who propose a species level distinction for dingoes (e.g., Crowther et al., 2014; Smith et al., 2019) have argued that the dingo is a separate species, never domesticated, and represents a very primitive canid. This group points to a number of distinctive dingo traits.

Dingoes often have an intimate relationship with humans, more often probably than wolves, foxes, dholes, and other wild canids. In traditional Aboriginal societies, dingo pups are stolen from dens soon after birth and raised as highly valued family members, being fed, cossetted, cuddled, and sometimes carried for kilometers by women if the terrain is difficult. However, upon reaching sexual maturity, dingoes may leave their owners, who do not influence dingo breeding. Thus the dingo population living with people needs continuous refreshing and taming. Aborigines do not exercise intentional selection as is needed for full domestication (Clutton-Brock, 1981; Morey & Jeger, 2015; Smith, 2015b; Smith & Litchfield, 2009a; Smith & Litchfield, 2009b). However, it is not clear whether all or most dingoes have close relationships with humans, since they are perfectly capable of surviving with little or no human contact, nor is it clear whether the relationship between dingoes and humans has changed over time.

Another distinctive trait is different vocalizations: dingoes are noted for howling or chorusing, not barking (Barker & MacIntosh, 1979; Koler-Matznick et al., 2005). This is a trait also seen in wolves and primitive dog breeds including basenjis and NGSDs.

Dingoes also differ from most dogs in their reproductive and developmental schedule. Female dingoes breed once annually and only one female in a pack will breed at a time, instead of twice a year as in domestic dogs (Ballard & Wilson, 2019; Catling et al., 1992; Johnston

et al., 2001; Lord et al., 2011; Smith & Vague, 2016). This may be an adaptation to an irregular food supply or a retention from wolves. Similarly, dingo pups develop more rapidly than the pups of domestic dogs and more like wolves (Anonymous, n.d.; Barker and MacIntosh, 1979). This may be a retention from wolves, which show similarly accelerated development (Ballard & Wilson, 2019; Geiger et al., 2017; Lord, 2013).

Dingoes also differ from dogs in their sensory acuity. Traits attributed to dingoes are an unusually good sense of smell (Marrant, 2015), including an ability to smell underground water, as well as excellent hearing and large auditory bullae (Corbett, 1994). These traits clearly enhance survival in the bush.

So, too, do the extraordinarily flexible joints of dingoes. Dingoes have unusual skills in climbing trees, cliffs, rocks, and fences, preferring high vantage points (Smith, 2015b). Unlike dogs, dingoes' wrist structure permits rotation, so they are capable of using doorknobs, latches, and other devices intended to confine them and are prone to escaping. On a standardized test used to screen dogs for behavioral problems, known as the C-BARQ questionnaire, domestic dogs earned a mean score of 55.15 on escaping, whereas dingoes earned a mean score of 85.87 (Smith, 2015a; Smith 2010). Dingo shoulder joints are also unusually flexible (Figure 4). This may be a physical adaptation to climbing in difficult terrain. Wolves have not been reported to have similar abilities.

Extreme flexibility and climbing skills also occur in the Norwegian Lundehund, a rare and inbred dog that was developed on an isolated Norwegian island, where they were used for hunting puffins and puffin eggs on the cliffs (Melis et al., 2013). Lundehunds are also noted for polydactyly on all four limbs, accessory foot pads, and low genetic diversity (Pfahler & Distl, 2014). Given the geographic separation of Lundehunds and dingoes, these features are probably convergent responses to a need for climbing skills and hunting in rocky environments.

Dingoes are notable for extreme anxiety related to confinement and separation from their humans, a surprising trait in an animal that is not dependent upon humans. Dingoes exhibit a deep-seated resistance to confinement and separation from humans to whom they have bonded. There are reports of dingoes chewing through wooden doors or diving thru windows when their human companions are absent (Smith, 2010; Smith, 2015a,b,c). Even when raised in captivity, dingoes have a higher prey drive than most domestic dogs and may be dangerous to small children or other pets (MacIntosh, 1975; Oakman, 2001; Smith, 2015a,c).

One reason possibly underlying the behavioral distinctiveness of dingoes from dogs in the traits mentioned above is the former's limited genetic diversity. Genetic

studies of dingo mtDNA, Y chromosomes, and microsatellites all indicate a very limited diversity among dingoes today and in their founding population (e.g., Ardalan et al., 2012; Cairns & Wilton, 2016; Cairns et al., 2017; Oskarsson et al., 2012; Savolainen et al., 2002; Savolainen et al., 2005; Thalmann et al., 2011; Wilton, 2001; Wilton et al., 1999).

Thus, one key issue in attempts to assess dingoes is their ancestral or current independence from humans. A suggested ancestor for dingoes are Southern Asian village or free-breeding dogs: free-ranging animals that are dependent upon human-derived foods, through provisioning or scavenging. Some closely resemble dingoes in build and coloration (Figure 4). Village dogs are genetically diverse human commensals which often show an admixture of breeds with landraces adapted to local conditions. A large survey of worldwide canine genetic diversity (Shannon et al., 2015) confirmed the high genomic diversity of village dogs from East Asia, India and Southern Asia, due to admixture with European breed dogs, particularly in urban areas. Modern dogs from the Neotropics and South Pacific in this study were almost exclusively descended from European breeds even though there were dog populations in these areas prior to the arrival of European colonials and their dogs.

Unlike village dogs, dingoes have lived for millennia without human-derived food and can be entirely independent of humans under many conditions. Dependency on humans is a criterion of domestication not met by dingoes. Breeding choices among dingoes and village dogs are not directed by humans, which makes the classic mode of commensal domestication through artificial selection for traits desirable to humans impossible.

Other measures of the relationship between humans and dingoes comes from experimental settings. Dingoes clearly initiate eye contact with humans more often than wolves and about as often as dogs, but dingoes maintain that contact for a much shorter duration than dogs (Johnson, Turrin, Watson, Arre, & Santos, 2017). Similarly, when faced with an insoluble task, wolves and dingoes look to humans for solutions far less often and less quickly than dogs do. Dingoes appear to be intermediate in this behavior between wolves and dogs (Miklósi et al., 2003; Smith & Litchfield, 2009a; Smith & Litchfield, 2009b).

5 | CONCLUSIONS

Do dingoes exhibit enough behavioral, physiological, genetic, and social distinctions to sufficient to warrant a species designation? The answer is partly dependent upon the definition of species in use (see review in

Jackson et al., 2019; Ballard & Wilson, 2019; Smith et al., 2019). The classic Biological Species Concept (BSC Mayr 1967) divides two populations into separate species if they are unwilling or unable to interbreed and produce fertile or viable offspring. Reproductive isolation is key. This definition is unworkable for canids which are notorious for interbreeding, making biogeography the primary influence on reproductive isolation not genetics. Biogeographically, by virtue of long isolation on Greater Australia, dingoes would clearly be a separate species. Zhang et al. (2018) conclude from comparisons of dog, dingo, and wolf nuclear genomes that dingoes and NGSDs are clearly isolated from the other groups genomically as well. The ability to interbreed with domestic dogs or semi-domesticated dogs probably has little overall impact on dingoes or dogs at the species level, since wolves and coyotes also interbreed with dogs without much introgression. Mayden (1997) chose to emphasize the existence of different lineages that evolved separately through time, which could be applied to dingoes. This is also a biogeographic issue, often called the Phylogenetic Species Concept or PSC. Still other definitions (Groves, 2005; 2001) emphasize how species are to be recognized cladistically and the particular problem of whether a domesticate and the ancestral population from which it arose are to be given the same or different species names.

Dingoes clearly fulfill the important criterion of intimate involvement with humans, but they do not fulfill domestication criteria based on dependency upon humans or being subjected to artificial selection (breeding control) by humans. The question remains: when dingoes arrived in Sahul, were they domesticated or only semi-domesticated canids? Are they domesticated animals gone feral or wild animals not yet domesticated? There is no clear indication when the unusual traits of dingoes arose, due to the paucity of fossil or subfossil remains.

Interestingly, indigenous Australians recognized the difference between dingoes and feral domestic dogs. The Yarralin tribe from the Northern Territory of Australia distinguish between “camp dogs” (which includes dogs and dingoes) and “bush dogs” (wild-living dingoes and dogs):

Camp dogs are dependents. They are like children in that adults give them skin identities, personal names, food and shelter....In contrast dingo [bush dog] represents the other end of the dependent-wild continuum. He hunts his own food, makes his own camp, finds his own shelter, and follows his own law. (Rose, 2000, p. 176)

Any particular dingo may fall into either category and may, during a lifetime, switch from one to the other.

Bush dogs and camp dogs may be not only a single species, they may even be a single individual. Charles Darwin, visiting Australia on the HMS Beagle in 1836, came to a similar conclusion, describing dingoes as both wild and domesticated (Darwin, 1839, vol. I, p. 39).

As Zeder (2012) maintains, “Domestication [is] a process”. Larson and Fuller (2014, p. 640) echo this assessment: “Domestication can be generally considered a selection process for adaptation to human agro-ecological niches and, at some point in the process, human preferences.” In the case of dingoes, it is a process that has not finished.

The nuanced appraisal of dingo behavior and function offered by the Yarralin people provides a useful glimpse of an intermediate stage of domestication of the dingo. The dingo is an animal of considerable intelligence and adaptability to survive and thrive in highly varied and difficult circumstances, one of which is anthropogenic. The dingo is clearly not fully domesticated now nor is it necessarily a free-living, completely wild species. The dingo is a unique animal with capabilities that reflect both its lupine ancestry, a certain degree of accommodation to human company, and unique adaptations to the demands of its habitat. Since domestication is a continuum, involving mutual advantages to both humans and target species, then it is valuable to be able to observe and study an animal that is on that continuum but not either at the “wild” end or the “domestic” end. A dingo is a dingo, not a wolf or a dog.

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