An updated description of the Australian dingo (*Canis dingo* Meyer, 1793)

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Abstract

A sound understanding of the taxonomy of threatened species is essential for setting conservation priorities and the development of management strategies. Hybridization is a threat to species conservation because it compromises the integrity of unique evolutionary lineages and can impair the ability of conservation managers to identify threatened taxa and achieve conservation targets. Australia's largest land predator, the dingo *Canis dingo*, is a controversial taxon that is threatened by hybridization. Since their arrival <5000 yBP (years Before Present) dingoes have been subject to isolation, leading to them becoming a unique canid. However, the dingo's taxonomic status is clouded by hybridization with modern domesticated dogs and confusion about how to distinguish 'pure' dingoes from dingo-dog hybrids. Confusion exists because there is no description or series of original specimens against which the identities of putative hybrid and 'pure' dingoes can be assessed. Current methods to classify dingoes have poor discriminatory abilities because natural variation within dingoes is poorly understood, and it is unknown if hybridization may have altered the genome of post-19th century reference specimens. Here we provide a description of the dingo based on pre-20th century specimens that are unlikely to have been influenced by hybridization. The dingo differs from the domestic dog by relatively larger palatal width, relatively longer rostrum, relatively shorter skull height and relatively wider top ridge of skull. A sample of 19th century dingo skins we examined suggests that there was considerable variability in the colour of dingoes and included various combinations of yellow, white, ginger and darker variations from tan to black. Although it remains difficult to provide consistent and clear diagnostic features, our study places morphological limits on what can be considered a dingo.

Introduction

A sound understanding of the taxonomy of threatened taxa is essential for setting conservation priorities and the development of species management strategies (Mace, 2004). A poor understanding of species taxonomy can hamper biodiversity conservation efforts by preventing the identification of unique evolutionary units, particularly if the species of potential conservation concern possesses morphological traits that are similar to those of closely related species (Daugherty *et al.*, 1990). This is particularly true in canids where separate lineages easily hybridize and produce fertile offspring (Roy *et al.*, 1994). Without the taxonomic tools to identify unique evolutionary lineages, it may not be possible to make accurate population estimates of species, identify threatened taxa or develop management strategies to enhance the conservation status of threatened taxa (Bacon & Bailey, 2006).

Australia's largest land predator, the dingo (also known in Australia as wild dog), is an example of a controversial taxon that is threatened by hybridization with domestic dogs. Based on molecular (Savolainen *et al.*, 2004) and archaeological evidence (Gollan, 1984), dingoes have been present on the Australian continent for at least 3000–5000 years. Genetic evidence suggests that dingoes originated from domestic dogs from East Asia (Oskarsson *et al.*, 2011). Since its arrival in Australia and prior to the arrival of European colonists, the dingo had been subject to at least 3000 years of isolation from other canids, and presumably had been subject to genetic drift, and natural selection, leading to it become a unique canid (Corbett, 1995).

Recent research has documented the positive role that dingoes have on biodiversity conservation through their regulation of trophic cascades (Letnic, Ritchie & Dickman, 2012). In particular, dingoes appear to benefit species threatened by

Figure 1 'Dog of New South Wales' from Mazell & Phillip (1789).

invasive red foxes, owing to their suppressive effects on fox abundance. However, efforts to harness the ecological interactions of dingoes are hampered by the uncertain taxonomy of the dingo (Letnic *et al*., 2012). In particular, the dingo's taxonomic status is clouded by hybridization with feral dogs and confusion about how to distinguish 'pure' dingoes from dingo-dog hybrids (Radford *et al*., 2012).

The poor taxonomic discrimination of dingoes from their hybrids with feral dogs is of particular concern as dingoes and dingo/dog hybrids are considered major pests to agriculture because they kill livestock, and current policies in some jurisdictions of Australia aim to exterminate dingo-dog hybrids, but conserve dingoes (Letnic *et al*., 2012). Confusion exists, in part, because the scientific description of *Canis dingo* (Kerr, 1792; Meyer, 1793) is based on a rudimentary picture (Fig. 1) and brief description included in the journal of Australia's first colonial governor, Arthur Phillip (Mazell & Phillip, 1789), and there is no surviving original specimen against which the identities of putative hybrid and 'pure' dingoes can be assessed. The dingo was first named as *Canis antarticus* (Kerr, 1792) based on the picture and description given by Arthur Phillip (Mazell & Phillip, 1789). However, a subsequent description of *C. dingo* based on the same material was given by Meyer (1793). The name *C. antarticus* was suppressed in favour of *C. dingo* because the latter name was in common usage [International Commission of Zoological Nomenclature (ICZN) 1957]. Since its initial description, other names have been proposed for the dingo such as *C. familiaris australasiae* (Desmarest, 1820), *C. australiae* (Gray, 1826), *C. dingoides* (Matschie, 1915) and *C. macdonnellensis* (Matschie, 1915).

Although the dingo has been subject to various reclassifications and changes in nomenclature, debate remains over what morphological characters can be used to distinguish dingoes, feral dogs and their hybrids (Jones, 2009; Radford

et al., 2012). Visual assessment of external characters is the most common technique for classifying dingoes, feral dogs and their hybrids. This approach relies upon the use of expert knowledge to identify traits that distinguish dingoes from hybrids. However, Elledge *et al*. (2008) found some corroboration between classifications made through genetic and skull analysis methods, but none between either analytical method and visual assessment. Similarly, Newsome & Corbett (1985) could not distinguish between individuals classified using skull measurements as dingoes or dingo-dog hybrids on the basis of their coat coloration. Newsome, Corbett & Carpenter (1980) and Newsome & Corbett (1982) used measurements of skull morphology to discriminate dingo, dog and hybrid skulls, but did not know the level of hybridization within the dingo samples. Molecular studies that have attempted to discriminate between the genotypes of dingoes and their hybrids have used captive animals held by breeders of dingoes, but it was unknown to what extent that selection by breeders may have influenced the genotypes of captive dingoes, or indeed if hybrids existed in the pedigrees of the captive animals (Wilton, Steward & Zafiris, 1999). In summary, current methods to classify dingoes, feral dogs and dingo-dog hybrids based on morphology, pelage and genetics appear to have poor discriminatory abilities because natural variation within dingoes is poorly understood; further, it is unknown if hybridization may have altered the genome and phenotypes of the 20th and 21st century reference specimens.

A better description of the dingo, based on specimens that are unlikely to have been influenced by hybridization, is required to provide a benchmark against which to assess the identities of dingoes in Australia. Such a description would assist conservation and wildlife managers to classify dingoes and to understand how the morphology of contemporary wild *Canis* differs from pre-European dingoes. The purpose of this paper is to provide that description.

Materials and methods

Specimens

Because Australia was colonized by Europeans in 1788 and was only sparsely inhabited by European settlers prior to 1900 CE (Common Era) (Powell, 1991), we assumed that dingoes collected prior to this date would be less likely to have been influenced by hybridization with domestic dogs. We searched the collections of museums held in Australia, Europe and the US to locate dingo specimens that were known to or likely to pre-date 1900 CE. The sample of 69 dingo skull specimens and six skin specimens we subsequently located included specimens taken by collectors in the 19th century and specimens collected from archaeological and paleontological deposits where museum data indicated that they pre-dated 1900 (Supporting Information Table S1).We used radiocarbon (C^{14}) dating to determine if specimens from cave deposits that lacked data on their context pre-dated 1900 (Supporting Information Table S2). Radiocarbon dating for specimens from the Western Australian Museum Palaeontology collections, 76.9.385, 76.9.384, 65.12.104, B3227b, B3227a, was

Table 1 Descriptions of measurements

Description	Number
Length of auditory bulla (measured from where it abuts the paraocciptal process to the internal carotid foramen, excluding any projection on the foramen)	1
Maximum maxillary width (measured at the junction of p^4 and M^l teeth)	2
Mid-crown width of P^4 tooth (measured through the highest cusp in a lateral direction)	3a
Greatest length of P^4	3b
Greatest breadth of P^4	3c
Basal crown length of C^1 (measured along tooth row)	4
Opisthion to inion (measured from a central inion point and not including the notch in the opisthion if present)	5
Width of both nasal bones (measured at premaxilla-maxilla suture)	6
Cranial height (measured from the upper notch of the external auditory meatus to the bregma, including the sagittal crest)	7
Distance between the posterior alveolar rims of C^l–P^4	8
Height of the foramen magnum	9
Greatest breadth of the foramen magnum	10
Skull length (inion to prosthion which is the most anterior point on inter premaxillary suture)	11
Skull height (basioccipital to highest point of the sagittal crest)	12
Maximum post-orbital width (ectorbital to ectorbital)	13
Zygomatic breadth (zygion to zygion)	14
Viscerocranium length (nasion to prosthion)	15
Greatest neurocranium breadth = greatest breadth of the braincase (euryon to euryon)	16
Greatest mastoid breadth = greatest breadth of the occipital triangle (otion to otion)	17
Length of the cheektooth row (measured along the alveoli on the buccal side)	18
Condylobasal length: arboreal border of the occipital condyles to prosthion	19
Greatest length of M^l	20a
Greatest breadth of M^l	20b
Maxillar distance between P^1 and P^1 taken from the posterior alveolar rim	25
Dorsal width of incisive bone taken from mid-alveolar rims of canines	26
Greatest width of zygomatic arch taken from the base of suture between the zygomatic bone and zygomatic arch	27
Total length of palate	28
Premaxillary width between C^1 and C^1 taken from the alveolar rim across the base of the incisive bone	29
Basal length of the first incisor (measured along tooth row)	31
Premaxillary width taken between the two largest incisors taken from the alveolar rim across the base of the incisive bone	32
Length of parietal bone taken from central inion point on the sagittal crest to the bregma	34
Greatest width of auditory bulla	39
Maxillary distance between P^4 and P^4 taken from the anterior end of P^4 along the alveolar rim	41

completed at Beta Analytic Radiocarbon Dating Laboratory, Miami, Florida.

The selection of domestic dog *C. familiaris* specimens we examined included breeds of similar size to dingoes which are, or have frequently been used as stock-working dogs and hunting dogs in Australia and thus could reasonably be expected to have interbred with dingoes. These breeds included Australian cattle dogs, kelpies, collies and greyhounds, and included specimens used by Newsome *et al.* (1980).

Measurements

We took skull measurements with digital callipers (to the nearest 0.01 mm) based on measurements given in Corbett (1995), Macintosh (1975) and Von Den Driesch (1976) (Table 1, Fig. 2). Additional measurements of Indian wolves were obtained from Gollan (1982). Measurements for total dingo series are given in Table 2.

Pelage coloration was recorded both from skins collected in the 19th century which showed little discoloration from preservation or age, and from 18th century artists' representations of dingoes and early explorers and colonists' reports of dingo coloration. We based the coloration and markings criteria on Elledge *et al.* (2008).

Diagnosis of dingoes from dogs

We first used stepwise discriminant function analysis to identify suitable measurements for the separation of dingoes from dogs, producing a subset of 12 measurements for further analysis. We then used a principal component analysis of variables, standardized by size by dividing each measurement by the geometric mean of all the measurements of that specimen (Mosimann, 1970), to investigate separation between dogs and dingoes. We used canonical variates analysis to quantify the separation of dingoes from dogs. We then compared each individual dingo measurement to those of dogs
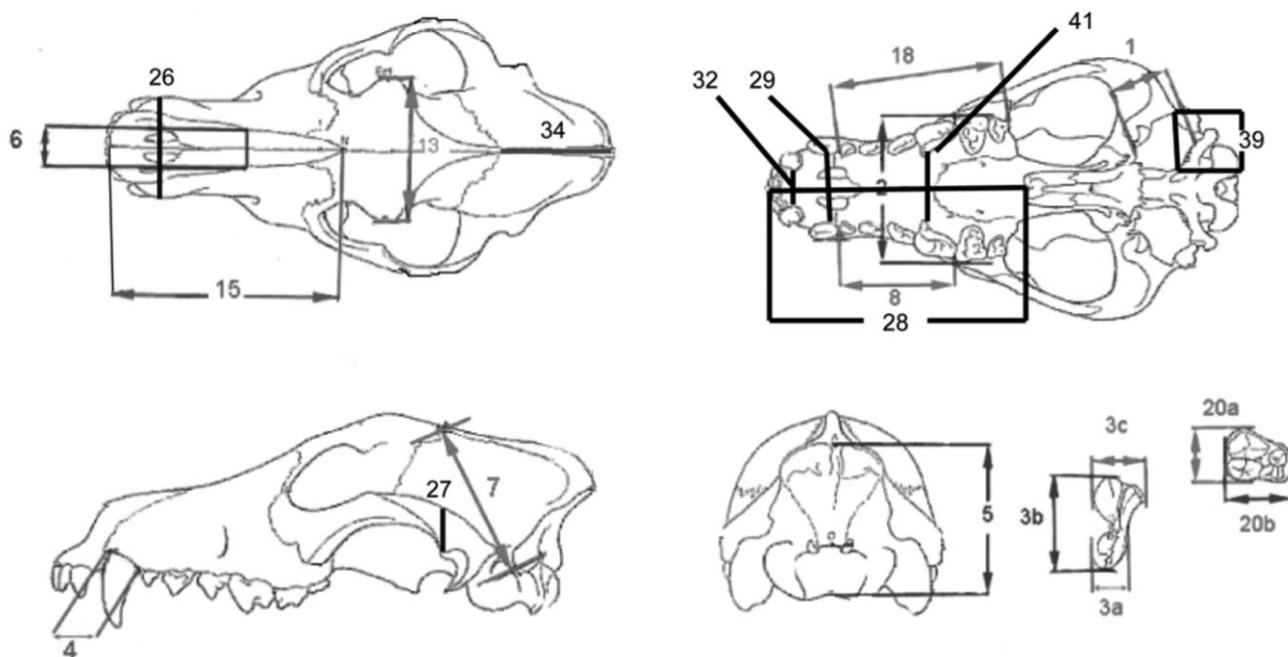
Figure 2 Skull measurements used on dingo series.

Table 2 Measurements of pre-1900 CE dingoes

Measurement	N	Minimum	Maximum	Mean	SD
2 Maximum maxillary width	69	52.10	70.80	59.03	3.69
25 Maxillary distance	47	26.08	37.77	31.70	2.67
29 Premaxillary width	45	17.22	27.23	21.42	2.01
19 Condylobasal length	63	147.25	199.80	176.89	11.06
8 Distance C^1-P^4	66	43.46	60.08	52.50	3.69
18 Length of the cheektooth row	61	54.62	72.31	64.24	3.57
4 Basal crown length of C^1	51	8.56	12.19	10.12	0.94
31 Basal length of first incisor	33	4.45	7.94	6.13	0.69
28 Palate length	48	73.97	100.00	87.62	5.28
5 Opisthion to inion	65	37.90	55.33	47.42	3.74
15 Viscerocranium length	60	72.55	104.07	90.78	6.94
13 Maximum post-orbital width	54	40.58	63.51	51.51	4.51

using analysis of covariance, with skull length as the covariate. To enable easier diagnosis, and allowing for size, we plotted each measurement against the total skull length.

Diagnosis

Differences from the wolf *Canis lupus*

The dingo differs from the wolf *C. lupus*, including the smaller Indian wolf *C. lupus pallipes*, in being smaller in size in all measurements (mean wolf condylobasal length = 207.10 ± 2.10 s.e., mean pre-1900 CE dingo condylobasal length = 176.89 ± 1.39; t_{90} = 12.10, $P < 0.001$). Dingoes also have more variable pelage coloration, such as black and tan variants,

which are not found in wolves. Corbett (1995) shows separation of wolf skulls from dingo skulls using canonical variates analysis, but does not give any scores, and included the larger northern European and American wolves rather than the Asian wolves from which dingoes were thought to be derived (Oskarsson *et al.*, 2011).

Differences from domesticated dogs *C. familiaris*

There is some separation between dingoes and domesticated dogs along PC2 in the size-adjusted principal component analysis (Fig. 3), which accounts for 63.1% of the total variance (Table 3). This is mainly composed of a contrast between
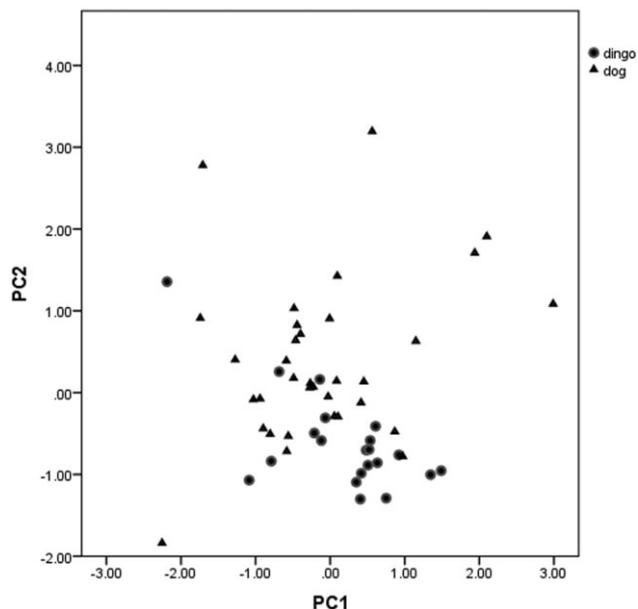
Figure 3 Plot of factor scores on first two axes of size-adjusted principal component scores on pre-1900 CE dingoes and domestic dogs.
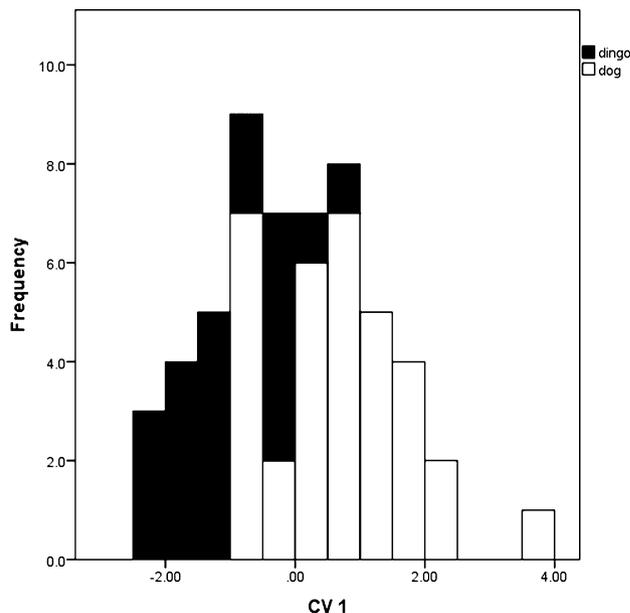

Figure 4 Canonical variate scores separating pre-1900 CE dingoes from domestic dogs.

Table 3 Principal component loadings for size-standardized measurements for dingoes and dogs

	Component		
	1	2	3
2 Maximum maxillary width	−0.841	−0.157	0.166
25 Maxillary distance	−0.784	0.214	0.441
29 Premaxillary width	−0.798	0.171	0.428
19 Condylobasal length	0.815	0.254	0.146
8 Distance C^1-P^4	0.836	−0.283	0.216
18 Length of the cheektooth row	0.783	−0.182	0.031
4 Basal crown length of C^1	−0.198	0.350	−0.681
31 Basal length of first incisor	−0.142	0.712	−0.225
28 Palate length	0.744	0.367	0.297
5 Opisthion to inion	0.372	−0.495	0.160
15 Viscerocranium length	0.594	0.563	0.043
13 Maximum post-orbital width	−0.109	−0.837	−0.278
Eigenvalue	5.053	2.303	1.182
% Variance	42.106	19.196	9.846

Table 4 Standardized canonical coefficients for measurements separating pre- 1900 CE dingoes from domestic dogs

	Function 1
2 Maximum maxillary width	0.420
25 Maxillary distance	−0.097
29 Premaxillary width	−0.018
19 Condylobasal length	−0.823
8 Distance C^1-P^4	0.214
18 Length of the cheektooth row	−0.802
4 Basal crown length of C^1	0.018
31 Basal length of first incisor	0.379
28 Palate length	−0.760
5 Opisthion to inion	−0.631
15 Viscerocranium length	2.558
13 Maximum post-orbital width	−0.085

maximum post-orbital width and opisthion to inion length with crown length of the first incisor and viscerocranium length (Table 3). Canonical variates analysis did show some separation for the non-size-adjusted measurements for domesticated dogs and dingoes (Fig. 4), with differences largely resulting from a contrast of viscerocranium length and maximum maxillary width with condylobasal length, length of cheektooth row and plate length (Table 4).

The dingo differs from the domestic dog *C. familiaris* and its hybrids by restriction of pelage colours to combinations of yellow, black and white, and in skull measurements including relatively larger palatal width (Fig. 5a,c,g,j, Table 5), relatively longer rostrum (Fig. 5e,f,i,k, Table 5), relatively shorter skull height (Fig. 5b,d, Table 5) and relatively wider top ridge of skull (Fig. 5h, Table 5).

Note that owing to the enormous variation in dog phenotypes, dog breeds used in the analysis were restricted to those of similar size and structure to dingoes.

Differences from other 'dingo forms'

Note that the following canids are considered by some authors as actual dingoes with some geographical variation (Corbett, 1985, 1995). Others recognized them as separate forms (Gollan, 1982).
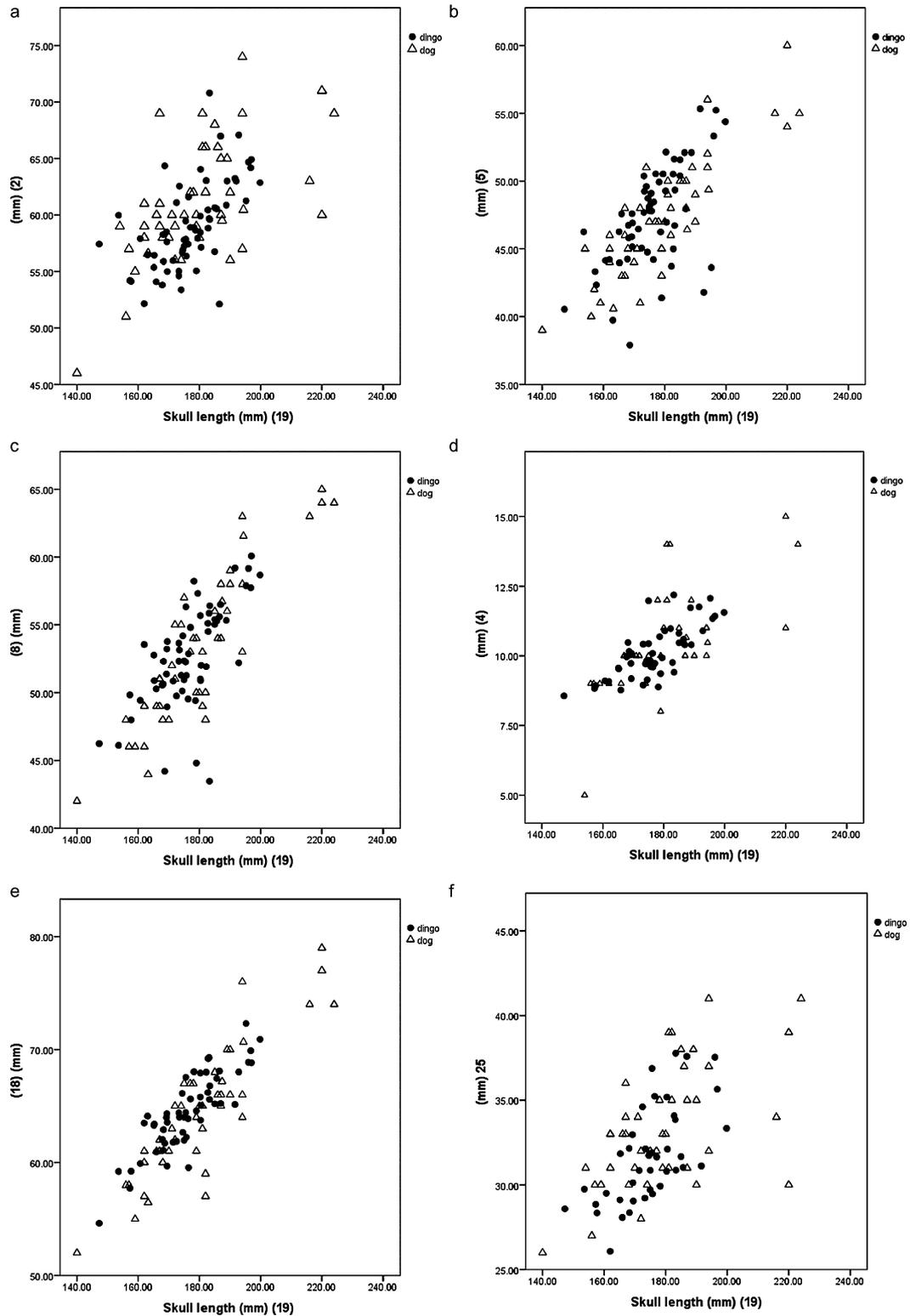
Figure 5 Bivariate plots comparing pre-1900 CE dingoes with domestic dogs with maximum skull length as *X* axis (a) maximum maxillary width, (b) height of back of skull to inion on base of skull, (c) distance between the posterior alveolar rims, (d) basal crown length C^1, (e) length of the cheektooth row, (f) maxillar distance, (g) palate length, (h) width of top ridge, (i) length of nasal area, (j) premaxillary length, (k) distance C^1–P^4, (l) crown length of first incisor.
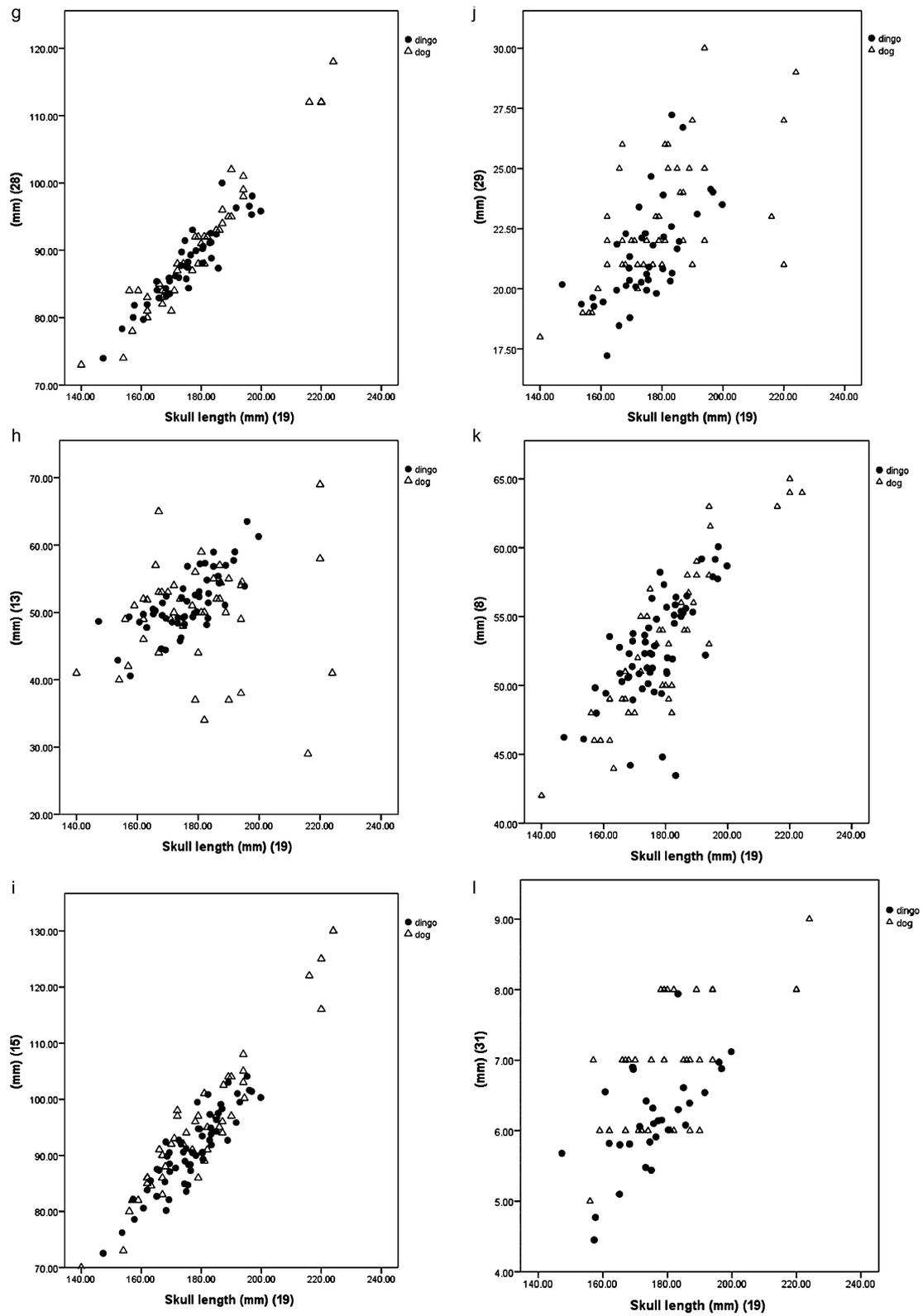
Figure 5 Continued.

Table 5 ANCOVA values comparing cranial measurements on pre-1900 CE dingoes to domestic dogs with skull length (19) as covariate

Measurement	F	d.f.	P
2 Maximum maxillary width	5.20	1,104	0.025
25 Maxillary distance	25.71	1,80	0.052
29 Premaxillary width	5.15	1,80	0.025
8 Distance C^1-P^4	0.359	1,101	0.550
18 Length of the cheektooth row	5.67	1,96	0.019
4 Basal crown length of C^1	0.05	1,82	0.824
31 Basal length of first incisor	11.34	1,64	0.001
28 Palate length	2.84	1,82	0.09
5 Opisthion to inion	1.81	1,100	0.182
15 Viscerocranium length	12.85	1,100	0.001
13 Maximum post-orbital width	2.92	1,93	0.091

1 Different from the New Guinea singing dog *Canis hallstromi* by its greater height at the withers (Koler-Matznick *et al.*, 2003). It resembles the New Guinea singing dog in most other morphological characteristics (Koler-Matznick *et al.*, 2003).

2 Different from Thai pariah dogs, as defined by Corbett (1985), by being larger in cranial (total skull length of pre-20th century dingoes 189.0 mm ± 1.8; Thai pariah dog male = 179.5 mm ± 3.1, female = 173.2 mm ± 3.6) and external measurements (Corbett, 1985).

Description

Dingoes are dog-like and possess a fairly broad head, tapered muzzle, erect ears and a bushy tail (Kerr, 1792; Fig. 6). Relative to similar-sized domestic dogs, dingoes have longer and more slender muzzles. The 19th century dingoes we examined, like wolves but unlike many dogs, do not possess dewclaws on the hind legs (Ciucci *et al.*, 2003). Dingoes can have five basic pelage colours: yellow, brown, ginger/red, black and white (Cairns, Wilton & Ballard, 2011). These colours occur in various combinations and 19th century skin specimens included animals that are entirely white (Fig. 6), entirely yellow/brown (Fig. 6), entirely black, yellow with white patches (Fig. 6), particularly at the tip of the tail and ankles (Fig. 6), and yellow with black fur along the dorsal parts of the body (sable, Fig. 6). The original specimen of *C. dingo* (Fig. 1) illustrated in Mazell & Phillip (1789) was uniformly brown on its dorsal surface, with the face, underparts and feet being white (Kerr, 1792). Other pre-1800 paintings included colours such as dark brown, reddish brown, and sandy with sabling (Supporting Information Figure S1).

The specimen of *C. macdonnellensis* (Matschie, 1915) ZMB 22418 at the Museum für Naturkunde, Berlin, and the specimen of *C. familiaris australasiae* (Desmarest, 1820) at the Muséum National d'Histoire Naturelle, Paris, were both predominantly yellow with some dark fur along the dorsum (sabling).

Historical records describing dingo colours are scant, and mostly not detailed (Elledge *et al.*, 2006). The earliest report of a dingo from 1697 is of a 'yellow-dog' near Jurien, Western Australia (Abbott, 2008). Collins (1798) reported dingoes in the Sydney region as 'two colours, the one red with some white about it, and the other quite black'. Explorer Mitchell (1839) reported a 'small black native dog' in northern central New South Wales in 1832. Historical descriptions of dingoes from Western Australia during the period 1826–1890, compiled by Abbott (2008), include red, yellow, black, black and white, white, tan and tawny animals.

Mitochondrial and Y-chromosome DNA

Mitochondrial variation at the control region is posited to be low in dingoes, with over 50% of animals sampled in previous studies having a control region haplotype, A29, with all other samples only differing by one base pair (Savolainen *et al.*, 2004; Oskarsson *et al.*, 2011). This haplotype was shared with dogs from East Asia, South-East Asian islands and Arctic America (Savolainen *et al.*, 2004). Similarly, only two Y-chromosome haplotypes (H3 and H60) were found in dingoes, the first shared with south-east Asian dogs and the second derived from Taiwanese haplotypes, shared only with the New Guinea singing dog (Ardalan *et al.*, 2012). More recently, dingoes have been found to exhibit a unique chromosome haplogroup characterized by one single-nucleotide polymorphism and 14 single tandem repeats (Sacks *et al.*, 2013).

Discussion

We have provided a morphological description of the dingo based on specimens and information that are unlikely to have been influenced by hybridization with domestic dogs. By providing a description for the dingo, our study provides a benchmark against which the identities of canids can be assessed. Using our description, it is now possible to classify canids in Australia as dingo-like based on morphological grounds.

Diagnosing the dingo

Diagnosing what constitutes a dingo remains difficult due to the overlap in morphological characters with domestic dogs, localized adaptations in dingoes and morphological variation through time (Radford *et al.*, 2012). Identification of diagnostic morphological characters is also difficult, especially when there is more variation within the domestic dogs in shape and size than in the whole Canidae (Drake & Klingenberg, 2010). Our morphological analyses showed that there is considerable overlap between domestic dogs and dingoes for most morphological characters. This was particularly the case for some Australian breeds, such as the Australian cattle dog, which are thought to have dingo ancestry (Arnstein, Cohen & Meyer, 1964). A similar degree of overlap in shape exists between North American wolves and closely related husky dogs (Clutton-Brock, Kitchener & Lynch, 1994).

Consistent with previous studies, a broad cranium, widening of the palate and shortening of the rostrum were characteristics separating domestic dogs from dingoes (Newsome *et al.*, 1980; Newsome & Corbett, 1982). Previous studies have

Figure 6 Colour variation in museum specimens of dingoes: (a) ginger collected between 1801 and 1803 (MNHN_2 M 2010.671), (b) sable collected 1820 (MNHN_2 M 2010_672), (c) black collected in the early 19th century (BMNH 50.11.30.22), (d) black collected in 1856 (C1829), (e) sable collected in 1842 (BMNH 1842.9.19.1), (f) white collected in the late 19th century (BMNH 1939.1697). Specimens (a) and (b) are from the Muséum National d'Histoire Naturelle, Paris; (c), (e) and (f) are from the Natural History Museum, London; and (d) is from the Museum Victoria.

regarded widening of the palate and shortening of the rostrum as indicators of domestication in dogs (Clutton-Brock, 2012). The 19th century skin specimens we examined possessed erect ears and a bushy tail. These characteristics were considered to be typical traits of dingoes in the original description given by Kerr (1792) and also in subsequent studies (Corbett, 1995; Elledge *et al.*, 2008). Pre-20th century dingoes lacked dew-claws on the hind legs (Clutton-Brock, Corbet & Hills, 1976; Ciucci *et al.*, 2003).

The range of coat colours that can occur in dingoes is a controversial subject, with some authors only accepting black,

and black and tan dingoes (Macintosh, 1975; Newsome & Corbett, 1985; Jones, 2009), while others only accepting yellow or light brown (ginger) and rejecting animals with dark dorsal fur (sable) (Elledge *et al.*, 2008). The small sample of 19th century dingo skins and 18th century illustrations of dingoes we examined shows that there was considerable variability in the colour of dingoes, and that their coloration was not restricted to just yellow and white animals, but also included various combinations of yellow, white, brown and black. The range and combinations of coat colours in these skins and illustrations were consistent with historical accounts

from the 19th century and observations of dingoes made by Newsome & Corbett (1985). Markings such as white spots restricted to feet, chest spot, neck flash, underbelly and tail tip, as used by the Australian National Kennel Council in the dingo breed standard (http://www.ankc.org.au/Breed_Details.aspx?bid=103), are not recorded in most early accounts, and are not present in all pre-1900 CE skins or illustrations.

The presence of individuals with sable pelage (dark dorsal coloration and lighter lateral coloration: Fig. 6b,d) in the sample of 19th century skins suggests that this coloration is not necessarily indicative of hybridization as has been suggested by previous authors (Corbett, 1995; Elledge *et al.*, 2008). The sample of skins and illustrations we examined did not include animals with brindle coloration. Brindle, dingo-like dogs appear in the historical record from the 1890s, and could plausibly be the result of hybridization, particularly as it is a colour pattern found in greyhounds, which were brought into Australia in 1788 and are not found in most older dog breeds (Cairns *et al.*, 2011). However, the small sample size of specimens we examined does not allow inferences to be made as to whether brindle individuals are dingo-dog hybrids or dingoes.

C. lupus dingo, *C. familiaris dingo* or *C. dingo*?

There has long been a confusion regarding the identities and classification of wild mammal species and their descendent domestic forms (Gentry, Clutton-Brock & Groves, 1996). Many authors classify domesticates as subspecies of the species from which they are thought to be descended (Wilson & Reeder, 2005). Following Corbett (1995), most recent authors quote the dingo as *C. lupus dingo* on the assumption that they, along with domestic dogs, were descended from a common ancestor, the grey wolf *C. lupus*. However, recent research has suggested that *C. lupus* is a species complex, which contains distinct clades and cryptic species (Aggarwal *et al.*, 2007; vonHoldt *et al.*, 2011), and that *C. familiaris* and *C. dingo* do not fall within any modern wolf clade (Freedman *et al.*, 2014). In addition, as domesticated forms do not fall into the definition of subspecies, the ICZN has recommended retaining the different specific names for wild and domesticated animals and naming wild ancestors of domesticates using the first available specific name based on a wild population (ICZN, 2003). Hence, we argue that because the ancestry of the dogs and dingoes is unknown, and because the dingo was first described as a distinctive wild form and differs from wolves, New Guinea singing dogs and domestic dogs in many behavioural, morphological and molecular characteristics (Macintosh, 1975; Corbett, 1995; Wilton *et al.*, 1999), and they are effectively reproductively isolated in undisturbed natural environments and thus like *C. hallstromi* can be considered a distinct taxon (Koler-Matznick *et al.*, 2003). Furthermore, because the dingo was first described as *C. dingo* Meyer 1793, and this decision was later upheld by ICZN (1957), we propose that *C. dingo* is the correct binomial.

Conservation and management

Our study reveals that the pelage criteria used in previous studies to diagnose dingoes (Newsome & Corbett, 1985; Elledge *et al.*, 2008) do not encompass the morphological variation present in pre-20th century specimens. Many managers currently cull animals they believe to be hybrids based on pelage coloration. In particular, animals with sable pelage are frequently culled because they do not conform with previous criteria used to define dingoes (M. Letnic, pers. obs.). Our findings suggest that such culling may be unwarranted because animals with this coloration appear in the illustrations and skin specimens from 18th and 19th centuries (Fig. 6). Indeed, there is a risk that the use of pelage to diagnose dingoes may result in humans selecting for yellow dingoes because this common colour morph of dingoes is widely perceived as being the colour of 'pure' dingoes (Elledge *et al.*, 2006). The next step for the conservation and integrity of dingoes is to define characters to separate dingoes from hybrids, allowing for natural selection and recognizing the variation naturally present in dingoes.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Pre-1800 paintings of Australian dingoes. (a) A portrait of a large 'Dog from New Holland' by George Stubbs, 1772, (b) 'Dog of New South Wales' from White, J. (1790), *Journal of a voyage to New South Wales*. London: J. Debrett. (c) 'A native dog' from Woodthorpe, V & Barrington, George, 1755-1804. History of New South Wales (1802). *A native dog*. Published by M. Jones, [London](Paternoster Row). (d) 'A wild Dog or Dingo of New South Wales' watercolour on paper, watermarked '1794 by J Whatman'. Volume 01: New South Wales drawings ('The Lambert Drawings'), Acknowledgements. Mitchell Library, State Library of New South Wales.

Table S1. List of pre-1900 CE dingo specimens used in analyses.

Table S2. Dates of previously undated dingo cave specimens.