Journal of Archaeological Science: Reports xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

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

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ARTICLE INFO

Article history:
Received 26 February 2015
Received in revised form 26 February 2016
Accepted 1 March 2016
Available online xxxx

Keywords:
Dingo
Australia
Holocene
Dog domestication
Genetics

ABSTRACT

The phylogenetic origin of the dingo (*Canis dingo*) is an enigma. Introduced to Australia during the Holocene, debate continues regarding the exact timing of its introduction and whether it was by early agriculturalists, hunter-gatherers or sea-faring traders. The expanding array of genetic research on both dog domestication and dingoes adds fuel to this debate. Here we synthesise recent genetic studies of dingo origins. We then evaluate a list of potential groups who could have been responsible for their introduction, and suggest that Toalean or other hunter-gatherers from south Sulawesi were the likely suspects. We conclude with suggestions for further archaeological and genetic research that have the potential to clarify not just the origin of the dingo, but the movement of people around Oceania (here broadly defined as the entire insular region between South East Asia and Australia), and by extrapolation, aspects of Holocene cultural change.

1. Introduction

The relationship between dogs and humans is one of the most defining symbiotic relationships in the history of humanity. Dogs were the first species to be domesticated by people, with some arguing this relationship began as long as 35,000 years ago (Ovodov et al., 2011). Dogs witnessed human dispersal around the world, stood beside people for the rise of cereal domestication (even evolving genetically to digest grains) (Axelsson et al., 2013), played a role in the evolution of human hunting, and some speculate in the extinction of Neanderthals (Shipman, 2015; Taçon and Pardoe, 2002). In short, dogs have been an integral part of the development of complex social organization, and generally, where there were modern humans, there were dogs … well, mostly. The spread of dogs to Australia is an exception - archaeological evidence suggesting the dingo (*Canis dingo*, Crowther et al., 2014), did not reach the continent until the mid-late Holocene (3500–5000 kya) (Fillios et al., 2012). If dogs and humans walked together for potentially 30,000 years, why did it take so long for people to bring canines south? In Australia, dogs appear to be a relatively late arrival – post-dating human settlement by at least some 40,000 years. How did dogs get to Australia, when, why and by whom?

This paper addresses just one of these many questions, and asks who brought the first dog (dingo) to Australia? Here we review the recent genetic evidence for the dingo's origins (Table 1, Fig. 1) and propose there were at least five different groups of people who could have introduced dogs: Indian mariners, Lapita peoples, a Timor group, Taiwanese peoples and Toalean hunter gatherer peoples from south Sulawesi. Drawing on the genetic evidence for the dingo's origins, augmented by the archaeological record, we evaluate the evidence for each group, and suggest the most parsimonious answer may well be an immediate origin in Sulawesi.

Given the symbiotic nature of the canine-human relationship, understanding the origin of the dingo will enable us to better understand the movement of people around Oceania (Australia, South East Asia). Importantly, understanding potential contact with people outside of Australia will contribute to understanding the raft of significant human behavioural and cultural changes that characterize the Holocene (10,000 BP–present) in this part of the world (cf. Lourandos, 1983). Dogs are not only important as the first human domesticate, but also as the only one whose domestication predates the emergence of agriculture, making them a valuable proxy for human hunter-gatherer migrations (Larson and Bradley, 2014; Larson et al., 2012; Zeder et al., 2006).

2. Background

2.1. Holocene Australia

Unravelling the origins of the dingo has the potential to contribute valuable information about the movement of peoples around Oceania during a period of significant cultural change. Frequently encompassed by the term 'intensification' (Lourandos, 1983), Holocene changes

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http://dx.doi.org/10.1016/j.jasrep.2016.03.001
2352-409X/

include demographic shifts as reflected in a higher frequency of archaeological sites and artefact densities (e.g. Attenbrow, 1987; Hughes and Lambert, 1982; Johnson and Brook, 2011; Lourandos, 1983; Morwood, 1987; McConnell and O'Connor, 1999; Ross, 1985; Smith and Ross, 2008), changes in human technology, characterized by an increase in backed artefacts, points, tulas, adzes (Gould, 1969; Hiscock and Attenbrow, 1998), increased rock art diversity and regionalisation (e.g. see Flood, 1997; Layton, 1992; Taçon, 1993, 2011) and a shift in the exploitation of prey species to smaller body sizes (Dortch, 2004a, 2004b; Dortch and Wright, 2010; Fillios et al., 2010; Morwood, 1987). The driving forces behind these cultural and technological changes are still debated, with changing subsistence strategies aimed at risk reduction (Hiscock, 1994), climate change (Dortch, 2004a, 2004b; Dortch and Wright, 2010; Johnson and Wroe, 2003) and the interaction between human intensification and increased ENSO variability (Prowse et al., 2013) all cited as factors. The dingo may also be one of these driving factors of change, and thus potentially an important element in constructing Holocene dynamics. The arrival of a new commensal species would almost certainly have made an impact on aspects of human subsistence strategies – perhaps altering hunting practices or changing the types of species exploited (e.g. Balme and O'Connor, in this issue; Fillios et al., 2010). Either of these possibilities could have had a flow on effect that might be seen in technological changes (e.g. shift in artefact type).

Diffusionist explanations for cultural change have lost popularity since the 1960s, with Hiscock (1994, 2008) and Hiscock and Attenbrow (1998) arguing in several places for an adaptive model to explain these changes. A more recent wave of human migration (or simply contact) is rarely viewed as a serious potential factor in Holocene cultural transformations. It is commonly accepted that from arrival in Australia to first European contact, Aboriginal Australians were genetically isolated. Uncovering the spatio-temporal origins of the dingo could potentially change this assertion. While recent genetic research corroborates archaeological data suggesting that Australia has the earliest evidence for the expansion of anatomically modern humans out of Africa (65,000+ years, see Rasmussen et al., 2011; Reich et al., 2011), the genetic history of Aboriginal Australians is just beginning to be explored in better detail (Nagle et al., 2016) to address the possibility of subsequent contact with other cultural groups.

Furthermore, the exact nature of Holocene trade routes and subsequent cultural contacts, are still debated. Although Pleistocene migration and colonisation continues to be explored with increasing archaeological fieldwork by a number of collaborative teams in northern Australia and Island Southeast Asia (ISEA), less research has focused on potential Holocene contact. Sea-faring peoples presumably brought the dingo to Australia, yet little is known about them. Were these seafarers part of a wave of human migrations that contributed to the current Aboriginal gene pool (as controversially proposed by Pugach et al., 2013; see below) or were they early transient merchants who traded the dingo as a commodity for other goods? Did the dingo arrive by accident, the result of mid-Holocene shipwrecks off Australia's northern shores? It has been proposed by Alan Wilton that Australian dingoes could conceivably have descended from a single pregnant dog (in Dayton, 2003). Resolving the origin of the dingo could potentially alter our current understanding of some of these significant Holocene changes, while at the same time adding valuable information to the opacity encasing the movement of people around Oceania during the Pleistocene and Holocene (c.f. O'Connell and Allen, 2004; Rasmussen et al., 2011).

2.2. Archaeological evidence for dingoes

To date, the most comprehensive study on the dingo has been based on observable morphological and metrical characteristics (Gollan, 1980). The origin of the dingo is still an enigma, partly because of the limited efficacy of purely morphological approaches in resolving

Table 1
Summary of recent genetic research with implications for dingo origins.

Study	Method	Samples	Probable origin	Probable route	Arrival in Australia
Savolainen et al. (2004)	mtDNA; identified mtDNA type A29	211 dingoes, 676 dogs, 38 Eurasian wolves, 19 pre-European archaeological Polynesian dog samples	East Asia	South China to Taiwan, the Philippines, ISEA and into Australia	c. 5000–6000 BP
Oskarsson et al. (2011)	mtDNA: mapping of haplotypes A29, Arc1, Arc2	674 dogs, 232 dingoes, 3 NGSD	South China; NGSD and dingoes share a common ancestor	South China to MSEA to Indonesia to Australia	4600–18,300 BP
Ardalan et al. (2012)	Y-chromosome (SNPs): haplotypes H3, H60	2 dingoes (47 characterized), 1 NGSD	SE Asia to New Guinea	New Guinea	–
Sacks et al. (2013)	Y-chromosome (SNPs)	338 dingoes, NG singing dogs, SE Asian dogs, modern European breeds	SE Asia and Taiwan	Taiwan	4000–5000 BP
Freedman et al. (2014)	Whole genome sequencing (SNPs)	1 dingo, 1 basenji, 1 golden jackal, 3 wolves	China	–	–
Greig et al. (2015)	Complete mitochondrial genomes (mitogenomes) sequenced	14 colonisation era dogs from Wairu Bar, NZ	China	Southern China to MSEA, Borneo, Sulawesi to northern Australia	–
Shannon et al. (2015)	Mitochondrial and Y chromosome diversity	4676 purebred dogs (161 breeds), 549 village dogs from 38 countries (no dingoes sampled)	Central Asia (Nepal/Mongolia)	–	–