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Out of Africa, but how and when? The case of hamadryas baboons (*Papio hamadryas*)

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ABSTRACT

Many species of Arabian mammals are considered to be of Afrotropical origin and for most of them the Red Sea has constituted an obstacle for dispersal since the Miocene–Pliocene transition. There are two possible routes, the 'northern' and the 'southern', for terrestrial mammals (including humans) to move between Africa and Arabia. The 'northern route', crossing the Sinai Peninsula, is confirmed for several taxa by an extensive fossil record, especially from northern Egypt and the Levant, whereas the 'southern route', across the Bab-el-Mandab Strait, which links the Red Sea with the Gulf of Aden, is more controversial, although post-Pliocene terrestrial crossings of the Red Sea might have been possible during glacial maxima when sea levels were low.

Hamadryas baboons (*Papio hamadryas*) are the only baboon taxon to disperse out of Africa and still inhabit Arabia. In this study, we investigate the origin of Arabian hamadryas baboons using mitochondrial sequence data from 294 samples collected in Arabia and Northeast Africa. Through the analysis of the geographic distribution of genetic diversity, the timing of population expansions, and divergence time estimates combined with palaeoecological data, we test: (i) if Arabian and African hamadryas baboons are genetically distinct; (ii) if Arabian baboons exhibit population substructure; and (iii) when, and via which route, baboons colonized Arabia.

Our results suggest that hamadryas baboons colonized Arabia during the Late Pleistocene (130–12 kya [thousands of years ago]) and also moved back to Africa. We reject the hypothesis that hamadryas baboons were introduced to Arabia by humans, because the initial colonization considerably predates the earliest records of human seafaring in this region. Our results strongly suggest that the 'southern route' from Africa to Arabia could have been used by hamadryas baboons during the same time period as proposed for modern humans.

Introduction

When modern humans (*Homo sapiens*) dispersed out of Africa is a central question in the study of human evolution. Recently discovered archaeological evidence in Jebel Faya, United Arab Emirates, points to the presence of modern humans in Arabia by ca. 125 thousand years ago (kya) (Armitage et al., 2011). That study stresses the Bab-el-Mandab Strait in the southern Red Sea as a possible immigration route during glacial maxima, when sea levels

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were low, as an alternative to a northern route via the Sinai Peninsula (Beyin, 2006, 2011). Humans are not the only mammal that evolved in Africa and colonized Arabia. Many species of Arabian mammals are considered to be of Afrotropical origin (Delany, 1989), with 62 species in nine orders known to occur on both sides of the Red Sea (Harrison and Bates, 1991; Yalden et al., 1996). These taxa colonized Arabia at different times. For most of them the Red Sea has constituted an obstacle for dispersal since the Miocene–Pliocene transition 5.3 million years ago (mya) (Fernandes et al., 2006; Bailey et al., 2007; Bailey, 2009). There are two routes, the 'northern' and the 'southern', that would have enabled terrestrial mammals to move between Africa and Arabia (Beyin, 2006, 2011; Bailey, 2009) (Fig. 1). The 'northern route', crossing the Sinai Peninsula, is confirmed for several taxa by an extensive fossil record, especially from northern Egypt and the Levant (Tchernov, 1992; Cavalli-Sforza et al., 1993; Lahr and Foley, 1994). Immigrations via this route presumably occurred during several 'Green Sahara Periods' when humid conditions opened dispersal corridors across the eastern Sahara for savannah species (Blome et al., 2012; Drake et al., 2013; Larrasoaña et al., 2013). The 'southern route', across the Bab-el-Mandab Strait, which links the Red Sea with the Gulf of Aden, is more controversial, although post-Pliocene (2.5 mya) terrestrial crossings of the Red Sea might have been possible during glacial maxima when sea levels were low (Bailey et al., 2007). There is, however, disagreement as to whether the palaeoceanographic and palaeoecological data are compatible with the scenario of land bridges (Rohling, 1994; deMenocal, 1995; Rohling et al., 1998, 2009; Siddall et al., 2003; Fernandes et al., 2006).

Baboons (*Papio* spp.) have been proposed as an analogous model for human evolution as they evolved during the same period and in the same habitats (Jolly, 1970, 2001; Strum and Mitchell, 1987; Rodseth et al., 1991; Elton, 2006). At present, five or six species of baboons are usually recognized, although their taxonomic status is still debated: chacma (*Papio ursinus*), Kinda (*Papio kindae*), yellow (*Papio cynocephalus*), olive (*Papio anubis*), hamadryas (*Papio hamadryas*), and Guinea baboon (*Papio papio*) (Jolly, 1993, 2013; Kingdon, 1997; Szmulewicz et al., 1999; Groves, 2001; Frost et al., 2003; Grubb et al., 2003; Zinner et al., 2009; Anandam et al., 2013; Butynski et al., 2013). The fossil record and mitochondrial sequence data both suggest that modern *Papio* originated in southern Africa ca. 2.5 mya, from where they dispersed to the north and west (Benefit, 1999; Newman et al., 2004; Zinner et al., 2011, 2013). The current distribution of *Papio* includes much of sub-Saharan Africa, excluding most of the central and West African rain forests. The hamadryas baboon is the only baboon found outside of Africa and one of the few primate species exhibiting female-biased dispersal (Hapke et al., 2001; Hammond et al., 2006; Kopp et al., 2014). At present, this species inhabits Ethiopia, Eritrea, Somalia, Djibouti and possibly Sudan, and south-western Arabia along the Red Sea from Yemen to south-western Saudi Arabia (Anandam et al., 2013; Swedell, 2013) (Fig. 1). Cranial and dental remains of *Papio* sp. from the Middle Pleistocene (800–200 kya) recovered at Asbole, Ethiopia, show strong affinities to extant *P. hamadryas* (Alemseged and Geraads, 2000), indicating a long presence of hamadryas baboons on the African side of the Red Sea.

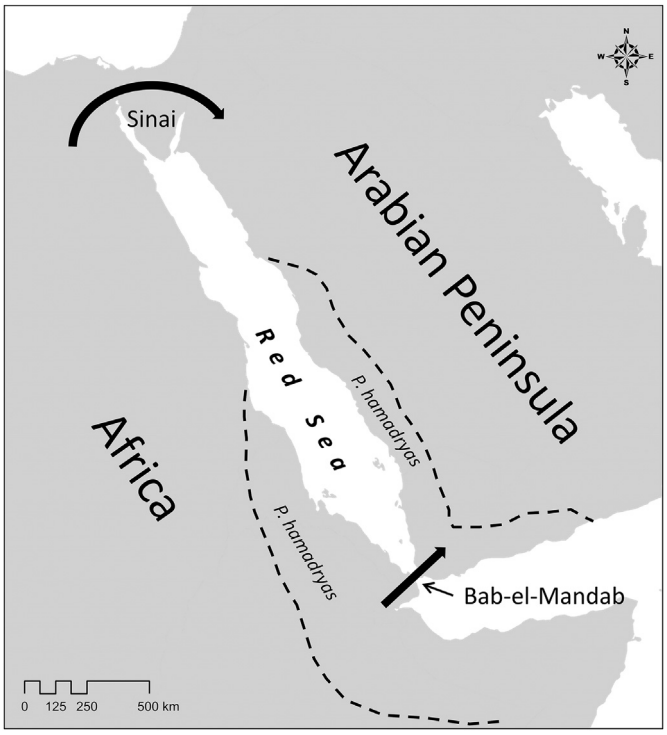

Figure 1. Geographic range and hypothetical immigration routes of hamadryas baboons from Africa into Arabia. Dashed lines indicate the approximate borders of the geographic range of hamadryas baboon in Africa and Arabia (after Yalden et al., 1977, 1996; Harrison and Bates, 1991). Thick arrows indicate the southern and northern dispersal routes.

The hamadryas baboons of Arabia were thought to be smaller than those in Africa and, as such, referred to as *Papio arabicus* (Thomas, 1900) or *P. hamadryas arabicus* (Ellermann and Morrison-Scott, 1951; Harrison, 1964; Corbet, 1978; Harrison and Bates, 1991). Kummer et al. (1981) found, however, that hamadryas baboons on both sides of the Red Sea are morphologically and behaviourally similar. Groves (2001, 2005) also found no significant differences between African and Arabian representatives of this species and, as such, considers hamadryas baboons as monotypic.

Three hypotheses have been put forth to explain the presence of hamadryas baboons in Arabia (Kummer, 1995):

(i) Hamadryas baboons in Arabia are remnants of a past continuous distribution around the Red Sea (northern route; Fig. 1). To our knowledge, however, no *Papio* fossils or subfossils have been discovered in the Levant, in northern Egypt, or in northwestern Arabia. Dispersal events could have been favoured during Green Sahara Periods, e.g., in Marine Isotopic Stage (MIS) 5 (130–71 kya; Blome et al., 2012; Drake et al., 2013; Larrasoaña et al., 2013).

(ii) Hamadryas baboons immigrated to Arabia across the southern Red Sea (southern route; Fig. 1), e.g., via a temporary land bridge, during periods of sea level lowstand of the Red Sea (MIS 12: ca. 440 kya; MIS 10: ca. 340 kya; MIS 6: ca. 130 kya; MIS 4: ca. 65 kya; MIS 2: ca. 20 kya; Rohling, 1994; Rohling et al., 1998, 2009).

(iii) Hamadryas baboons were introduced into Arabia by humans (Thomas, 1900; Kummer et al., 1981). Ancient Egyptians are known to have translocated baboons. For example, there are drawings from the Eighteenth Dynasty (1540–1304 Before the Common Era [B.C.E.]) in which boats from Punt (which is probably Eritrea) brought hamadryas baboons to Egypt (Kummer, 1995; Moritz et al., 2010). It is conceivable that these ships reached Arabia (Phillips, 1997). Moreover, there is evidence for trade between Northeast Africa and Arabia during earlier times, e.g., in the Predynastic Period (5000–3100 B.C.E.; Ward, 2006; Boivin and Fuller, 2009; Boivin et al., 2009) and the Bronze Age (c. 3500–1200 B.C.E.; Boivin and Fuller, 2009; Boivin et al., 2009), which had the potential for the translocation of baboons.