

18 June 2004

# Science

Vol. 304 No. 5678

Pages 1701-1856 \$10



## Stardust

AT COMET WILD 2

# African Origins of the Domestic Donkey

Albano Beja-Pereira,<sup>1,2\*</sup> Phillip R. England,<sup>1</sup> Nuno Ferrand,<sup>2,3</sup>  
Steve Jordan,<sup>4</sup> Amel O. Bakhiet,<sup>5</sup> Mohammed A. Abdalla,<sup>5</sup>  
Marjan Mashkour,<sup>6</sup> Jordi Jordana,<sup>7</sup> Pierre Taberlet,<sup>1</sup>  
Gordon Luikart<sup>1</sup>

The history and origins of the donkey are particularly interesting because, together with the horse, the donkey (*Equus asinus*) has been used for the transportation of people, possessions, and produce in many cultures. This domestication marks a major cultural shift away from sedentary, agrarian life-styles toward more extensive movement and trade. Sparse archaeological evidence from Egypt suggests that donkeys, like horses, were domesticated ~5000 years ago. Exactly where this occurred is still unclear (1, 2).

We assessed domestic donkey origins by sampling donkeys from 52 countries across the Old World (table S1) and sequencing 479 base pairs (bp) of the mitochondrial DNA (mtDNA) control region (3). Phylogenetic analyses identified two highly divergent phylogenetic groups (Fig. 1) with an average corrected sequence divergence of  $15.73 \pm 0.61$  substitutions. Sequences from the same mtDNA control region from both Asian wild half-asses (*E. hemionus* and *E. kiang*) and the two extant wild African ass subspecies (*E. africanus africanus*, the Nubian wild ass, and *E. a. somaliensis*, the Somali wild ass) clearly exclude the Asiatic half-asses as progenitors of domestic donkeys (Fig. 1A). The African wild asses are therefore the likely progenitors.

A parametric bootstrap test (3) strongly rejected monophyly of domestic donkeys, supporting multiple domestications. Molecular clock analysis of complete cytochrome b sequences

(1140 bp) revealed a relatively ancient divergence (0.303 to 0.910 million years ago) between the lineages that lead to the two domestic donkey clades, vastly predating the well-established archaeological dates of the earliest known livestock domestications (~10,000 years ago). Our data suggest two separate maternal origins of the domestic donkey from two distinct wild populations.

Analysis of African wild ass samples from the two extant putative wild progenitors revealed five distinct mtDNA sequences. The average sequence divergence between the two wild subspecies ( $3.41 \pm 0.01\%$ ) is similar to that between the two domestic mtDNA lineages ( $3.29 \pm 0.01\%$ ). The two haplotypes found in the Nubian wild ass cluster within the domestic Nubian clade (Fig. 1B) (4). The Somali wild ass

sequences group closest to the domestic Somali clade but not obviously within it. The geographic distribution of the wild progenitors (3) and the finding of significantly higher ( $P < 0.01$ ) nucleotide diversity in both domestic donkey lineages in Northeast Africa (fig. S1) suggest this is the most probable location of donkey domestication. However, we cannot exclude with complete certainty a domestication of the Somali domestic group elsewhere.

If both lineages arose in Africa, it suggests that the donkey is the only ungulate domesticated solely in Africa. Moreover, this study demonstrates that the practice of animal domestication, which first emerged in the Near East, reappeared in Northeastern Africa. It provides insight into the role that this region may have played in population expansion and trade across the Old World. Domestication of the donkey may have been driven by the response of pastoralists and other societies in Northeastern Africa to the desertification of the Sahara (~5000 to 7000 years ago) (4). Finally, it provides clues for directing future archaeological studies that look for evidence of the initial domestication of donkeys.

## References and Notes

1. J. Peters, thesis, Rijksuniversiteit (1986).
2. J. Clutton-Brock, *A Natural History of Domesticated Mammals* (Cambridge Univ. Press, Cambridge, ed. 2, 1999).
3. Materials and methods are available as supporting material on Science Online.
4. F. Marshall, in *The Origins and Development of African Livestock*, R. M. Blench, K. C. MacDonald, Eds. (University College London Press, London, 2000), pp. 191–220.
5. A.B.-P. was supported by Fundação para a Ciência e Tecnologia (grant no. SFRH/BD/2746/2000) through the GABBA program from the University of Porto.

## Supporting Online Material

www.sciencemag.org/cgi/content/full/304/5678/1781/DC1

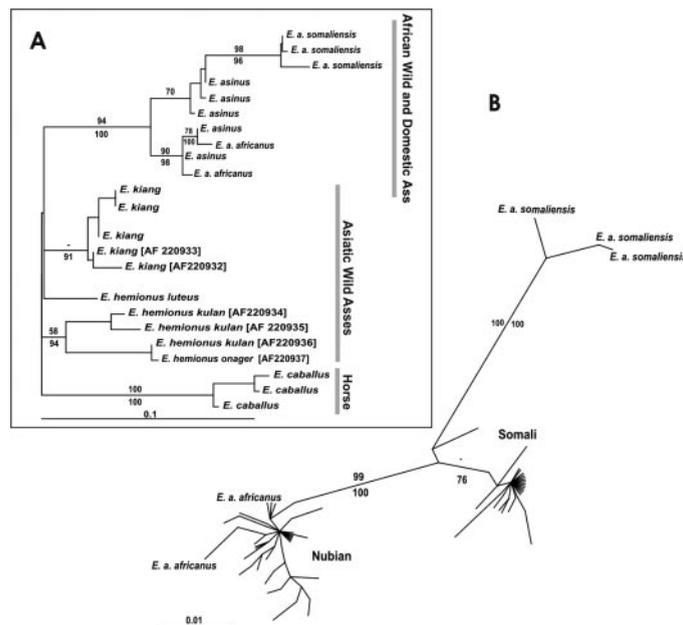
Materials and Methods

Fig. S1

Table S1

References and Notes

26 January 2004; accepted 12 April 2004



**Fig. 1.** (A) Phylogeny grouping domestic donkeys among African wild asses and excluding the Asiatic wild asses as progenitors. (B) Unrooted phylogenetic network of the domestic donkey and wild asses representing the two African subspecies (3). Numbers above and below lines are bootstrap proportions and Bayesian posterior probabilities, respectively.

<sup>1</sup>Lab. d'Ecologie Alpine, UMR CNRS-UJF 5553, 38041 Grenoble, France. <sup>2</sup>Centro de Investigação em Biodiversidade e Recursos Genéticos and SAECA, Fac. Ciências, Universidade de Porto, 44485 Vairão, Portugal. <sup>3</sup>Zoologia/Antropologia, Fac. Ciências, 4099 Porto, Portugal. <sup>4</sup>Biology Dept., Bucknell University, Lewisburg, PA, USA. <sup>5</sup>College of Veterinary Medicine, Sudan University of Science and Technology, Khartoum, Sudan. <sup>6</sup>Muséum Nat. Hist. Naturelle, CNRS-UMR 5197, F-75005 Paris, France. <sup>7</sup>Dep. de Ciencia Animal dels Aliments, Fac. Veterinària, UAB, 8193-Bellaterra, Spain.

\*To whom correspondence should be addressed. E-mail: albano.beja-pereira@ujf-grenoble.fr