

# The Multiple African Origins of Domestic Donkeys

**Diane Gifford-Gonzalez**

Anthropology Department University of California - Santa Cruz, USA

**Albano Beja-Pereira**

Research Center in Biodiversity and Genetic Resources, Vairão

Photo: Fiona Marshall

Universidade do Porto, Portugal

Molecular genetics has resolved a long archaeological and zoological debate over the origins of the domestic donkey (*Equus asinus*) from wild ancestors.

Because the ancestral species of the donkey, *Equus africanus*, is found in sub-specific forms across arid zones of Africa and into the Arabian Peninsula, and because some early domestic forms were recovered from Dynastic Egypt, it was open to debate whether the species was domesticated in Africa or in the Near East.

Phylogenetic analysis of wild and domestic mtDNA lineages of the species and its close relatives from 52 countries has identified two highly divergent phylogenetic groups, the Nubian wild ass (*Equus africanus africanus*) and the Somali wild ass (*E. a. somaliensis*), or dibokali, as representing ancestral lineages of the domestic ass, excluding Asiatic wild asses as progenitors.

Moreover, recent morphometric analyses of donkey specimens from Predynastic and Early Dynastic Egypt, plus those of later periods, has contributed to our grasp of the process of domestication of the donkey.

This presentation briefly summarizes the genetic data and notes the zooarchaeological contributions to our knowledge of the domestication and dispersion of this useful and ubiquitous equid.

# Donkeys Today



Swahili Coast



Missouri, USA

- Globally distributed in arid and semiarid regions
- Essential to rural agrarian economies
- Pastoralist women rely on donkeys to transport water, wood, children, young livestock, move home
  - key to family health and wealth



Cerezales, León, Spain  
Photo: F. González



Maasai, Kenya  
Photo: Lior Weissbrod



Photo: Nicolaisen & Nicolaisen



France



Cairo, Egypt



Cairo, Egypt



Tuareg donkeys with family gear, Niger



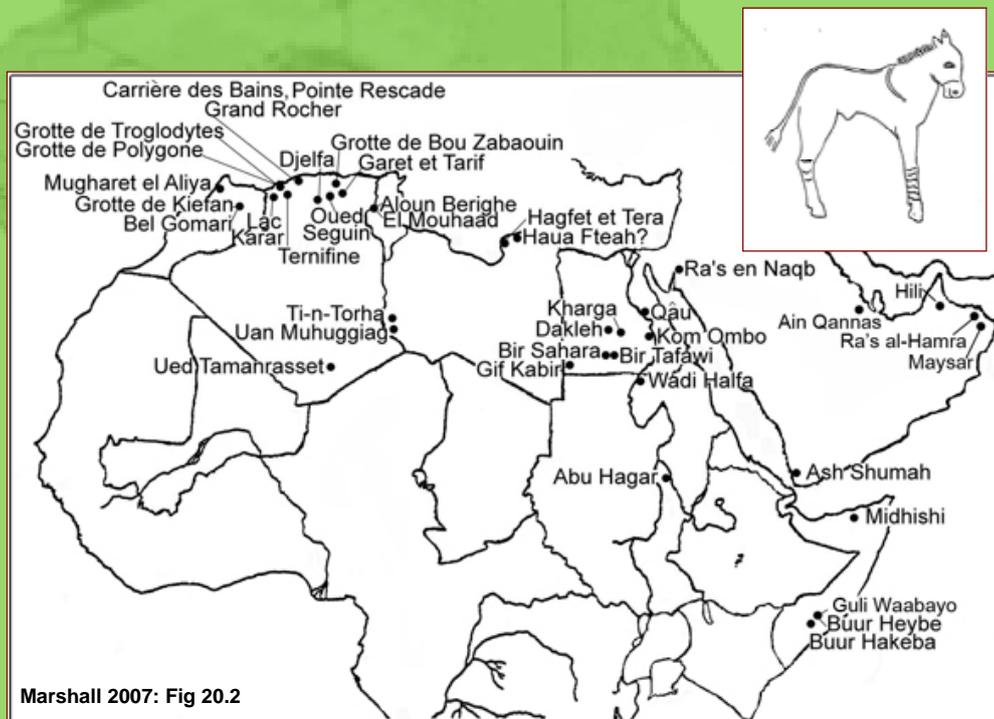
Manzanillo, Mexico

Today, domestic donkeys inhabit semiarid to arid regions of Eurasia, Africa, the Americas, and Australia. They are an integral part of small-scale farming and pastoralism, providing burden-bearing and riding stock, as well as sometimes traction. Many regional breeds exist, of different sizes and coats, and adapted to different types of environments and workloads.

Among African pastoralists, the donkey is often plays a depreciated but essential role in transporting water, wood, household furnishings, and the houses themselves, as well as children and young livestock. In other words, their work is women's work, and in documented sources, it has been as invisible yet fundamental to daily survival as that of women.

Hardy, trainable to voice or gesture command, and organized into self-defending herds, donkeys take require less herding than domestic ruminants. When they are needed, they can be loaded or ridden, and the balance of the time, they can be turned out to forage on their own, except in the most dangerous country.

## Archaeological Sites with *Equus africanus*



Data from Brandt 1986, Cattani & Bökönyi 2002, Churcher & Richardson 1978, Clark 1954, Gautier 1984, Uerpmann 1991

The African wild ass, *Equus africanus*, is found in zooarchaeological samples from Pleistocene and Holocene archaeological sites from the Atlas Mountains to Somalia. Remains of the species have also been recovered in the Arabian Peninsula, as far north as the eastern edge of the Sinai.

As surveyed by Marshall, Holocene Saharan rock art contains rare portrayals of this arid-land adapted species.

We also want to note that this presentation would not be possible without the advice and permission of Professor Fiona Marshall to use some of her own graphical materials and data. I am sorry that she is not here to join us today, as her zooarchaeological work, and that of her colleague, the late Dr. Stine Rossel, has been instrumental in developing recent insights into the domestication of the donkey.

# Predynastic Egyptian Donkey Remains

SITE	CHRONOLOGY	REFERENCES
Maadi	Predynastic, 1 <sup>st</sup> half 4 <sup>th</sup> millennium BCE	Boessneck 1989:90-92; Bökönyi 1985:495-498
El Omari	Predynastic, c 4600-4400 cal BCE	Boessneck & von den Driesch 1998:99-101
Hierakonpolis	Predynastic, Naqada I-II c 3600 BCE	McArdle 1982:12, 1992:56; van Neer et al 2004

## Early Dynastic Donkey Burials c. 3000 BCE: Tarkhan (Kafr Turki)



Flinders Petrie, W. M. 1914 Tarkhan II. School of Archaeology in Egypt, University College, London

**Predynastic Egyptian and Early Dynastic funerary sites** have yielded donkey burials, in which entire individual skeletons were interred.

This type of burial is typical of that of cattle and other domestic animals sacrificed in funerary rituals, and the inference has been that the donkeys were also domesticated.

These skeletal samples have also provided valuable source of morphometrical data for collaborative research by researchers from Harvard University and Washington University at St. Louis. Results of this research will be noted later in this presentation.

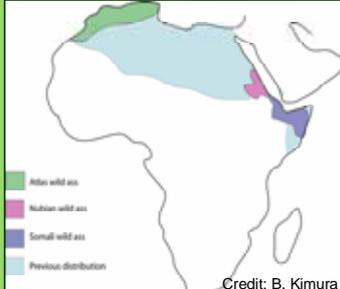
## **‘Libyan Palette’, Early Dynastic c 3000 BCE**



Flinders Petrie, W. M. F. and H. Flinders Petrie 1953  
Ceremonial Slate Palettes. *British School of Archaeology in Egypt Bulletin* 66(A):1-23.

Donkeys with their distinctive shoulder crosses are also depicted in early Dynastic Egyptian art, associated with other domestic livestock, which further supports the inference that these are truly domesticated animals.

# African Wild Asses, Past & Present



## Atlas Wild Ass *Equus africanus atlanticus*

- shoulder cross
- striped legs
- extinct 1st millennium CE



## Nubian Wild Ass *Equus a. africanus*

- smaller than Somali variety
- reddish buff
- shoulder cross
- complete dorsal stripes
- no leg stripes



## Somali Wild Ass *E. a. somaliensis*

- largest African wild ass
- red-sandy-gray
- sometimes lacking shoulder cross?
- well-marked leg stripes

After Groves 1974, 1986, 2002

Several questions arise:

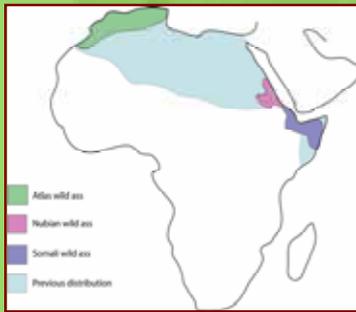
First, since *Equus africanus* subspecies were so widely distributed across the northern part of the African continent, which was the ancestral stock of the domestic donkey?

This naturally relates to the **location** of the domestication process - for example, given the evidence mentioned above, was the donkey domesticated in ancient Egypt of Nubian stock?

Given the presence of presumptively domestic donkeys are found in Predynastic Egypt, at least by 5200 years ago, what can be said about the **timing of the domestication event**?

Finally, given its proximity to the Levant and the presence of African wild ass remains in the Arabian deserts, **might the domestic donkey derive from the Near East**? Moreover, was the **Asian half-ass, or onager** (*Equus hemionus*) or other such species involved in the lineage of the domestic donkey?

# The mtDNA of Donkey Origins



- Which population(s) gave rise to the domestic donkey?
- Are varieties of the Asian wild half-ass (onager, hemione, kiang) involved?
- What is the estimated timing of event?



52 countries, sequencing 479 base pairs mtDNA



## African Origins of the Domestic Donkey

Albano Beja-Pereira, Phillip R. England, Nuno Ferrand, Steve Jordan, Amel O. Bakhiet, Mohammed A. Abdalla<sup>5</sup> Marjan Mashkour, Jordi Jordana, Pierre Taberlet, and Gordon Luikart 2004 *Science* 304:1781

This is where the contribution of genetics has been crucial. Dr. Albano Beja-Pereira and colleagues 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.

Phylogenetic analyses identified two highly divergent phylogenetic groups (with an average corrected sequence divergence of  $15.73 \pm 0.61$  substitutions). Sequences from the same mtDNA control region from Asian wild half-asses 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 note of interest is that conservation ecologist Patricia Moehlan, who has been working with the Somali subspecies, has introduced the term Somali name *dibokali* to denote this species.

# Domestic Donkey from Two African Stocks

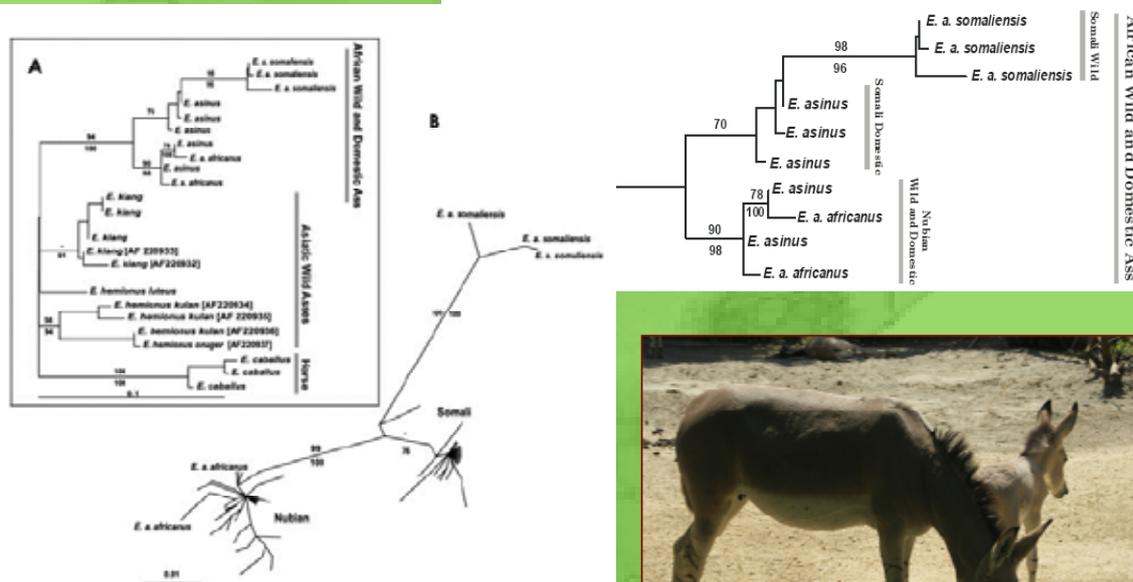


Fig. 1. (A) Phylogeny grouping domestic donkeys among African wild asses and excluding the Asiatic wild asses as progenitors. (B) Unrooted phylogenetic network of the domestic donkey and wild asses representing the two African subspecies (3). Numbers above and below lines are bootstrap proportions and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

A parametric bootstrap test **strongly rejected monophyly of domestic donkeys, supporting multiple domestications**. Molecular clock analysis of complete cytochrome b sequences (1140 bp) revealed a relatively ancient divergence (0.303-0.910 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. The Somali dibokali sequences group closest to the domestic Somali clade but not obviously within it.

The geographic distribution of the wild progenitors, and the finding of significantly higher ( $P < 0.01$ ) nucleotide diversity in both domestic donkey lineages in Northeast Africa, **suggest this is the most probable locale of donkey domestication**. However, the data cannot exclude with complete certainty a domestication of the Somali domestic group elsewhere on the other side of the Red Sea.

## Marshall & Rossel's Morphometric Study of *E. africanus*, *E. africanus* var. *asinus*

- Bern
- Basel
- Munich
- Halle
- Berlin
- London
- Chicago
- Geneva
- Nairobi
- Cairo



Stine Rossel, Fiona Marshall, Joris Peters, Tom Pilgram, Matthew D. Adams, and David O'Connor  
2008 Domestication of the donkey: Timing, processes, and indicators. *PNAS* 105(10):3715-3720.

If both lineages arose in Africa, it suggests that the donkey is the only ungulate domesticated solely in Africa.

To further assess the timing and process of domestication of these lineages, Fiona Marshall of Washington University at St. Louis and her colleague, the late Dr. Stine Rossel, then of the Peabody Museum, Harvard University, undertook a comprehensive osteological study of 53 modern domestic donkey and African wild ass skeletons, in various museum collections in Europe and Africa including those from the from 10 ~5,000-year-old donkey skeletons recently discovered entombed in an early pharaonic mortuary complex from the First Dynasty at Abydos, Middle Egypt. In addition to comparative metrical data, evidence of pathologies was also recorded.

Aspects of this research continue, with Dr. Birgitte Kimura working on DNA from archaeological specimens in the laboratory of Professor Constance Mulligan at the University of Florida, in coordination with ongoing work by Beja-Pereira, and a paper on these

Professor Marshall is continues this zooarchaeological work after Dr. Rossel's untimely death in 2007, and is engaging in ethnoarchaeological research on the role of donkeys in relation to women's work and household economy among East African pastoralists .

## Rossel's Analysis of 10 Early Dynastic Donkeys, Abydos



Photo credit: *Institute of Fine Arts/NYU*

CAIRO (youregypt.com <March 2004>

A US mission revealed 6 tombs of courtiers and servants of King Aha, who is probably the first or second king of the 1st dynasty of the Pharaonic era, at the early dynastic necropolis of Abydos, some 490 kms south of Cairo.

According to culture minister Farouk Hosni, "no important monument has been found for this king since famous archeologist Flinders Petrie discovered his tomb in 1900."

Next to Aha's complex, another enclosure of an unknown first dynasty king was discovered. Strikingly, three attached subsidiary graves contained bodies of the ten donkeys were surfaced in the enclosure. "They are intended to meet the king's transportation needs in the afterlife," said Zahi Hawas, Egyptian head of the antiquities department.

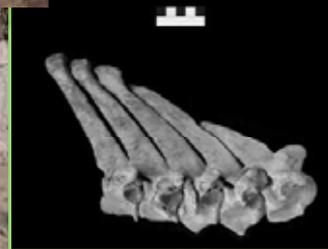
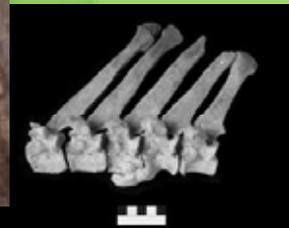
Marshall's morphometric analysis focused on metacarpals, often used to distinguish modern wild from domestic varieties of ass. She also collected data on osteopathologies in the Abydos population.

The morphometric analyses showed that the Abydos metacarpals were similar in overall proportions to those of wild ass, but individual animals' measurements varied.

Specifically, metacarpal midshaft breadths resembled those of the wild ass, but by contrast, midshaft depths and distal breadths were intermediate between those of the wild ass and the domestic donkey.

## Domestication of the donkey: timing, processes, indicators Rossel et al. *PNAS* 2008

- Donkeys important beast of burden in Egypt c 3000 BCE
- *No signs of morphological change, or even modal size changes in Early Dynastic skeletons*
  - evidence of weight-bearing stress
  - riding
  - load-bearing
- Infer long domestication process, with late physical changes.



Despite such intermediate aspects of postcranial anatomy, all of the Abydos skeletons exhibited osteopathologies consistent with load bearing, indicating these animals were used as beasts of burden prior to their deaths. The animals displayed various developmental stages of spondyloarthropathies, associated with microfractures in the vertebral bodies due to overloading and strain.

Strain-induced spondylosis is accompanied by partial to almost complete degeneration of intervertebral discs, observed on the articular facets of the entire vertebral column in all Abydos individuals. Other pathologies included compression and inclination of neural spines in thoracic vertebrae, which, depending upon location, is associated with riding or weight-bearing. The appendicular joints of all animals showed heavy wear, implying serious damaging of the articular cartilage, with lipping and even eburnation. By contrast, the researchers observed no pathologies on skeletons of modern free-living wild equids.

The Abydos osteometrics show that, despite their use as beasts of burden, donkeys were still undergoing phenotypic change during the early Dynastic period. Rossel et al. argue that this is consistent with recent studies of other domestic animals which suggest domestication is a slower and less linear process than previously thought.

# Sahara Pastoralism 6000-4000 BCE: The Context for Donkey Domestication?

## 8000 bp domestic cattle in NE Africa

- probably from N African *Bos africanus*

## By 7000 bp Asian sheep, goats in NE Africa

## African pastoralists were relatively mobile and egalitarian

- no permanent villages
- no domestic morphology grains until c. 1st millennium BCE
- wild grains and animals widely used



Marshall, Fiona and Elisabeth Hildebrand 2002 Cattle before crops: the beginnings of food production in Africa." *Journal of World Prehistory* 16(2): 99-143.

Neumann, Katharina 2005 The romance of farming: plant cultivation and domestication in Africa. In *African Archaeology: A Critical Introduction*, edited by A. B. Stahl, pp. 249-275. Blackwell, London.

In her 2007 summary on donkey domestication, Marshall builds on her own and others' earlier work on the evidence for the emergence of food production in Saharan Africa and adjacent regions. She argues that, in contrast with the rapidly sedentarizing peoples of Southwest Asia among whom plant domestication emerged, Africans of the early Holocene Sahara were increasingly mobile. As rainfall abated from its late Pleistocene-early Holocene high levels, reliance on local wild grain yields became impossible, leading to an increase in mobility, relative to the earlier, more sedentary Terminal Pleistocene adaptations.

Within this adaptation, wild grain gathering and hunting still had a place, but so also did domestic cattle (about which Dan Bradley has told us) and by 7000 bp domestic sheep and goats from Southwest Asia. Such transhumant lives apparently were so successful that they withstood the challenges of repeated drying cycles, up to about 4500 years ago, when the core of the Sahara was abandoned by such people. Neumann has argued that the late appearance of domestication is the result of such long success of a mobile herding and hunting/gathering strategy.

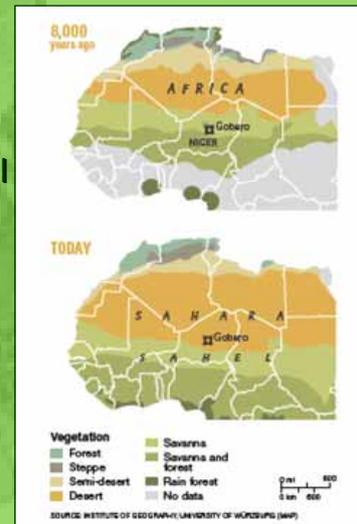
# Donkey Domestication in Context

Domestication of the Donkey: Timing, Processes, Indicators  
Rossel et al. *PNAS* 2008

## After 7000-6500 bp Nubian stock donkey domesticated

- likely by pastoralists
- during period of Saharan desiccation
- facilitated rapid response to unpredictable rainfall
- long distance mobility, exchange

## Donkey domesticated from Somalian stock sometime thereafter



Credit: National Geographic 2008

Both Marshall and Beja-Pereira et al. have argued that domestication of the donkey may have been driven by the aridification of the Sahara ~5000 to 7000 years ago. They see this process as a response of pastoralists and other societies in Northeastern Africa the need to cover more distance in search of foods for humans and livestock alike

In fact, the domestication of the donkey may have strongly contributed to that long-term resilience of Saharan pastoralism, as well as to the rise of early social complexity. By permitting the transport of loads of water, foodstuffs, and commodities, of homes, people, and vulnerable young livestock across challenging dry areas, these hardy animals “bridged” the increasingly broad spaces between productive lands. If not the legendary - and later - camelid “ship of the desert,” they were at least “skiffs of the desert,” used by Dynastic Egyptians for provisioning desert outposts and by others in coping with the logistics of arid landscapes.

The substantially later first occurrences of *Equus asinus* in Southwest Asian sites - such as at Tal-e Malyan c 2800 calBCE - further suggest a diffusion of this useful domesticate from Africa.

Aranguren-Mendez, J., A. Beja-Pereira, R. Avellanet, K. Dazama and J. Jordana 2004 Mitochondrial DNA variation and genetic relationships in Spanish donkey breeds (*Equus asinus*). *Journal of Animals Breeding and Genetics* 121:319-330.

**Thanks to Fiona Marshall, Birgitte Kimura,  
for images and data**



Doubtless new developments in the mtDNA analyses of various regional breeds of donkeys will reveal more about their travels and uses in association with humans. For example, a recent study by Aranguren-Mendez, Beja-Pereira, and others shows that Spanish breeds of donkey show particular affinities to Moroccan donkeys, as might be expected, given the history of the Iberian peninsula, and that these show both source matrilineages in their mtDNA, but that Zimbabwean donkeys' mtDNA derives solely from the Somalian wild ass.

Thus, after fundamentally establishing the source ancestry, DNA analysis can reflect patterns of livestock introductions, "founder's effect" and other historical developments that archaeologists may then attempt to explain with their broader historical and contextual data.

In closing, we wish to thank again our colleagues Fiona Marshall and Birgitte Kimura for their generosity in helping us produce this presentation.