

# The Genomic History of Elephants Supports the Existence of a Third Modern Species and has Important Implications for Conservation

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## Abstract

*African elephants have historically been classified as a single species. New research into the genomic history of proboscideans has confirmed that the African savanna elephant (*Loxodonta africana*) and the African forest elephant (*Loxodonta cyclotis*) are in fact distinct species. The depauperate genetic variability of *L. africana* which may be due to a bottleneck in their evolutionary history increases their species vulnerability. *Loxodonta cyclotis* is currently vulnerable and its numbers are in sharp decline. Reclassifying these elephants as distinct species would prove useful to future studies and promote unique conservation approaches for each species, which are likely necessary to prevent the further decline and potential extinction of elephant populations.*

Keywords: Proboscidean, Phylogeny, Species, Genetic Bottleneck, Conservation

## 1 INTRODUCTION

The predecessors of modern elephants, such as giant mammoths and mastodons, originated in Africa and roamed throughout much of North America and Eurasia. Comprising 164 recognized species and subspecies<sup>1</sup>, these ancient proboscideans were much more diverse than the modern species they gave rise to: the African elephant (*Loxodonta africana*) and its smaller cousin the Asian elephant (*Elephas maximus*). From Carl D. Illiger's designation of elephants as Proboscidea in 1811<sup>1</sup> up until very recently, these two were thought to be the only living proboscideans. However, according to genetic evidence, African elephants actually comprise two separate species, bringing the total number of extant proboscidean species up to three<sup>2</sup>. The African savanna elephant (*Loxodonta africana*) and the African forest elephant (*Loxodonta cyclotis*) should be classified as distinct species by conservation organizations so that both unique groups may be preserved. The number of elephants in Africa was estimated to have decreased by between 104,000 and 114,000 from 2007 to 2016 due to poaching and loss of habitat<sup>3</sup>. Despite the World Wildlife Fund listing African forest elephants (designated as a subspecies of African elephants) as vulnerable and "in sharp decline", there is no official estimate of their population size. Updating the modern elephant family tree to include a third species is an important scientific advancement with implications for both elephant conservation and future study. By recognizing forest and savanna elephants as

distinct species, conservation efforts can be designed to address the specific needs of each species to ensure their ongoing preservation. Furthermore, updating the elephant family tree to reflect accurate data will be useful for researchers studying both ancient and modern proboscideans.

The earliest proboscideans first appeared on the African continent between five and ten million years ago<sup>2,1</sup>. These creatures were relatively small and had short trunks<sup>1</sup>, although they would eventually give rise to the larger and more recognizable modern elephants. The extant Asian elephant is clearly morphologically distinct from its African relatives with its shorter stature, smaller ears, elongated skull shape, and straighter, more downward-facing tusks<sup>4</sup>. There are also notable differences between the two African species, although these have previously been insufficient to officially recognize them as distinct. *Loxodonta cyclotis* is smaller, has rounded ears, straighter and thinner tusks, and different skull morphology than its savanna-dwelling cousin<sup>5</sup>. In addition, the habitat of forest elephants is much smaller than that of savanna elephants<sup>6</sup>.

Distinguishing species based solely on morphology has incorrectly dictated ideas of elephant evolutionary history. It was previously<sup>1</sup> suggested that the Asian elephant was most closely related to an extinct species called the straight-tusked elephant (*Palaeoloxodon antiquus*) based on their morphology, but recent work<sup>2</sup> has shown that this is unlikely. This more precise classification of species, based not only on morphology but also on phylogeny and biology, led to two conclusions<sup>2</sup>: first that the most recent common ancestors



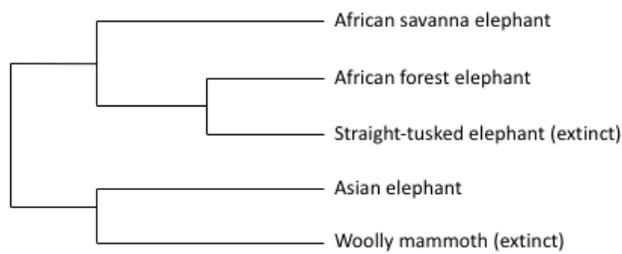


Figure 1: Revised tree of phylogenetic relationships among elephant species based on straight-tusked elephant genome analysis. Branch lengths are not proportional to time. Data from Meyer et al.<sup>7</sup>

(MRCAs) are different than previously determined, and second that there are three extant elephant species. African elephants should therefore be officially recognized as two distinct species based on their morphology, phylogeny, and biology.

## 2 THE ELEPHANT FAMILY TREE

Of the 164 recognized proboscidean species<sup>1</sup>, only two were believed to be extant. However, Shoshani<sup>1</sup> acknowledged that there may be three living species of elephants, and later studies outlined by Grubb et al.<sup>8</sup> suggested that African forest and savanna elephants should be classified separately based on morphology. This evidence was insufficient to justify the separate classification of African species. A recent phylogenetic tree (Fig. 1) based on genomic analysis of *P. antiquus*<sup>7</sup> recognized separate African species. This was confirmed<sup>2</sup> by performing genetic analysis on samples from a variety of living and extinct proboscideans.

The MRCA of the extinct straight-tusked elephant and the African forest elephant lived closer to modern times than did the MRCA of both modern African species (Fig. 1). The forest elephant is therefore more closely related to *P. antiquus* than it is to the concurrent savanna elephant. In fact, *L. africana* and *L. cyclotis* have been genetically isolated, meaning there has been no genetic exchange between their ancestors, for approximately 500,000 years<sup>2</sup>. Since the two African species diverged earlier in history than the forest elephant and the straight-tusked elephant, they have been genetically distinct species for a long period of time.

## 3 MODERN ELEPHANT GENETICS

Palkopoulou et al.<sup>2</sup> sequenced the genomes of 14 proboscideans and aligned them to a reference genome from an extant African savanna elephant. Different molecular features of the data such as divergence between nucleotides and

mitochondrial diversity were used to construct phylogenetic trees, which gave overviews of the relationships between the genomes. This and other genetic studies of modern and extinct elephants provide two points of compelling evidence for the existence of two distinct species in Africa.

First, there is no significant gene flow between modern African forest and savanna elephants<sup>2,6,9</sup>, although there was considerable interbreeding between ancient elephant species<sup>2</sup>. The two types of elephants currently living in Africa are therefore arguably more distinct than their ancient relatives, which are classified as separate species.

Second, despite having a smaller geographic range<sup>6</sup> and therefore less opportunity to accumulate genetic diversity, forest elephants are more genetically diverse than their savanna counterparts<sup>5</sup>. Genetic samples from savanna elephants were nearly identical<sup>5</sup>, indicating a genetic bottleneck event in their past. Bottlenecks decrease genetic variability in a species and can be extremely detrimental to species survival. Lack of genetic variation in other African animals such as the cheetah (*Acinonyx jubatus jubatus*) can lead to difficulty breeding in captivity, high rates of juvenile mortality, spermatozoal abnormalities, and increased vulnerability to zoonotic diseases<sup>10</sup>. These factors are important considerations for the field of conservation biology as they can complicate efforts to conserve threatened species.

## 4 CONCLUSION

Proving the existence of two African elephant species has important implications for immediate conservation efforts as well as future scientific research. The classification of forest and savanna elephants as separate species will directly impact conservation and management approaches by promoting individualized efforts to protect each species as a distinct group. Widely accepted data that accurately depicts the relationships between modern and extinct elephant species will allow for more consistent data collection in the future, furthering our biological understanding of the past and present.

The loss of a subspecies is not as devastating as the extinction of an entire species. Organizations such as IUCN and the World Wildlife Fund can focus their efforts on saving both African elephant species from extinction if they recognize them as such, rather than classifying *L. cyclotis* as a subspecies of African elephant. Unique conservation efforts directed towards each species are important<sup>2,7,6,9</sup>. Despite the vulnerability of forest elephants in particular, the official census<sup>3</sup> paints a grim picture for all remaining elephants in Africa, making them a broad priority for conservation efforts. Separate studies of forest and savanna elephants are required in order to better understand these unique animals



and shape conservation approaches tailored to each. A wider approach, based on the old single African species idea, could result in the loss of one or both African elephant species.

Using our current knowledge of each species ecology, we can begin to identify better conservation approaches. African forest elephants live in dense vegetation and are therefore difficult to identify and study without specialized techniques such as thermal imaging<sup>11</sup>. More comprehensive study of these elusive animals requires the use of techniques and technologies that are customized to their behaviour. Savanna elephants are easier to observe in their open habitat but likely require different conservation approaches due to their limited genetic variation. Careful breeding programs to prevent any further decrease in savanna elephant genetic diversity would not be applicable to the more genetically diverse forest elephant populations. Interbreeding between the two species, which may occur if they are housed together in captivity under the assumption of belonging to a single species, would destroy any genetic differences between the species. If these species are not conserved separately, we may end up losing both.

In addition to the importance this has in regard to elephant conservation, accurate genetic data is critical to general scientific inquiry and knowledge. An updated elephant family tree will help guide future molecular studies on genetics and genomic histories, as well as more traditional biological studies on the behaviour, distribution, and population changes of African forest and savanna elephants. In addition, the techniques used<sup>2</sup> to determine historical relationships between proboscidean genomes can be applied to broader studies on the genomic history of other species.

The history of elephants is more interesting and complicated than once thought. Two species of elephants reside in

Africa; *L. africana*, the savanna elephant, and *L. cyclotis*, the forest elephant. They differ in their morphology, phylogeny, and biology. The two types have been genetically distinct for half a million years and show different levels of genetic diversity. They should therefore be recognized as separate species. Additional genomic analysis of ancient specimens can help further unravel the past while the recognition of distinct African elephant species will shape current studies and conservation efforts, thereby helping save more elephant species from extinction. Genetic study is vital to the field of biology in terms of the past, present, and future.

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