

## Publication

# A comprehensive genomic history of extinct and living elephants

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Elephantids were once among the most widespread megafaunal families. However, only three species of this family exist today. To reconstruct their evolutionary history, we generated 14 genomes from living and extinct elephantids and from the American mastodon. While previous studies examined only simple bifurcating relationships, we found that gene flow between elephantid species was common in the past. Straight-tusked elephants descend from a mixture of three ancestral populations related to the ancestor of African elephants, woolly mammoths, and present-day forest elephants. We detected interbreeding between North American woolly and Columbian mammoths but found no evidence of recent gene flow between forest and savanna elephants, demonstrating that both gene flow and isolation have been central in the evolution of elephantids. Elephantids are the world's most iconic megafaunal family, yet there is no comprehensive genomic assessment of their relationships. We report a total of 14 genomes, including 2 from the American mastodon, which is an extinct elephantid relative, and 12 spanning all three extant and three extinct elephantid species including an ~120,000-y-old straight-tusked elephant. a Columbian mammoth, and woolly mammoths. Earlier genetic studies modeled elephantid evolution via simple bifurcating trees, but here we show that interspecies hybridization has been a recurrent feature of elephantid evolution. We found that the genetic makeup of the straight-tusked elephant, previously placed as a sister group to African forest elephants based on lower coverage data, in fact comprises three major components. Most of the straight-tusked elephant's ancestry derives from a lineage related to the ancestor of African elephants while its remaining ancestry consists of a large contribution from a lineage related to forest elephants and another related to mammoths. Columbian and woolly mammoths also showed evidence of interbreeding, likely following a latitudinal cline across North America. While hybridization events have shaped elephantid history in profound ways, isolation also appears to have played an important role. Our data reveal nearly complete isolation between the ancestors of the African forest and savanna elephants for ~500,000 y, providing compelling justification for the conservation of forest and savanna elephants as separate species.

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