

The enigmatic African wolf (*Canis lupaster*): insights from morphological and molecular analyses

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Introduction

Canis lupaster, commonly known as the African wolf or African golden wolf (previously *Canis anthus*), is a medium-sized canid that exhibits wolf-like characteristics and is currently distributed across central and northern Africa (Viranta et al., 2017). Historically, due to phenotypic similarities, it was often misclassified as a subspecies of the Eurasian golden jackal (*Canis aureus*). However, recent phylogenetic studies using both mitochondrial and nuclear DNA have demonstrated that *C. lupaster* is more closely related to the gray wolf (*Canis lupus*) than to *C. aureus*, thereby validating *C. lupaster* as a distinct species (Koepfli et al., 2015; Viranta et al., 2017). The species is currently divided into three subspecies with different geographic distribution: *C. l. lupaster* in North Africa, *C. l. anthus* in Senegal, and *C. l. bea* in Kenya and Tanzania, though the genetic distinction between these subspecies remains debated (Koepfli et al., 2015). The understanding of the evolutionary history of *C. lupaster* is further complicated by its morphological and genetic similarities to other canids (especially *C. aureus*), highlighting the need for comprehensive analyses of its fossil records.

During paleontological excavations conducted by the Tanzania Human Origins Research (THOR) team at Geolocality 83 in Olduvai Gorge between 2018 and 2022, a new vertebrate assemblage was uncovered, which includes three nearly complete canid skeletons. These fossils exhibit striking morphological similarities to the extant *C. lupaster*, representing the first unequivocal fossil evidence of the African golden wolf on the continent. Radiocarbon analysis of associated ostrich eggshells dated this assemblage to approximately 38 to 33 cal ¹⁴C ka, marking it as one of the few Late Pleistocene vertebrate assemblages from Olduvai and the whole Eastern Africa.

This discovery is particularly significant, as some historical fossil reports of *C. aureus* may have been misidentified and could, in fact, represent *C. lupaster*. To address this, the project funded by the Società Paleontologica Italiana aimed at providing a detailed morphological and morphometric characterization of *C. lupaster* and comparing it with other African canids. In addition to ongoing molecular analyses, including ancient DNA studies, the project sought to

enhance our understanding of the anatomy, variation, systematics, and phylogenetic relationships of this species.

Materials and methods

The study employed a multidisciplinary approach combining paleontological fieldwork, morphological and morphometric analysis, and molecular techniques to analyse the fossils of *C. lupaster* from Olduvai Gorge.

1. **Sample collection:** fossil samples, including bones and teeth, were collected from Geolocality 83 in Olduvai Gorge during the 2018-2022 fieldwork conducted by the THOR team. These fossils, currently housed at the Leakey Camp in Olduvai Gorge, comprise three nearly complete skeletons exhibiting morphological features consistent with *C. lupaster*. Following the approval of the SPI grant, in Summer 2023 a petrosal bone was shipped to the GLOBE Institute at the University of Copenhagen for molecular analysis with all the necessary export permits from Tanzanian authorities.
2. **Morphological and morphometric analysis:** a detailed morphological analysis was conducted on the skeletons, focusing on cranial, dental, and postcranial features to differentiate *C. lupaster* from other African and Eurasian canids. Measurements were taken using digital callipers and 3D scanning technology to create detailed morphological datasets. In addition, comparative morphometric analysis was carried out using both the original data collected from the fossils and previously published datasets on extant and extinct canids.

Preliminary results and future developments

The frequent misclassification of the African golden wolf (*C. lupaster*) as the Eurasian golden jackal (*C. aureus*) has obscured the evolutionary history of the former. The discovery of exceptionally well-preserved skeletons from Olduvai provides a unique opportunity to clarify the taxonomic status of *C. lupaster* and to elucidate its relationships with other canid species. Ancient DNA (aDNA) analysis is currently underway at the GLOBE Institute. Once the presence of aDNA in the sample is confirmed, both mitochondrial and nuclear DNA sequences will be compared with existing genomic data from extant canids across Africa and Eurasia. Notably, this study will include the first-ever phylogenetic analyses of Olduvai fossil canids, aimed at determining their phylogenetic position within the Canidae in Africa.

The results of this study will be disseminated through publications in high-impact scientific journals and presentations at international conferences. This work will not only enhance the scientific community's knowledge of African golden wolves but also foster conservation efforts by highlighting the unique evolutionary lineage of this enigmatic species.

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References

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