RESEARCH ARTICLE SUMMARY

PALEONTOLOGY

Sexual selection promotes giraffoid head-neck evolution and ecological adaptation

Shi-Qi Wang*, Jie Ye, Jin Meng*, Chunxiao Li, Loïc Costeur, Bastien Mennecart, Chi Zhang, Ji Zhang, Manuela Aiglstorfer, Yang Wang, Yan Wu, Wen-Yu Wu, Tao Deng*

INTRODUCTION: Extreme evolution of animal organs, such as elongation of the giraffe's neck, has been the focus of intensive research for many decades. Here, we describe a fossil giraffoid, *Discokeryx xiezhi*, from the early Miocene (~16.9 million years ago) of northern China. This previously unknown species has a thick-boned cranium with a large disklike headgear, a series of cervical vertebrae with extremely thickened centra, and the most complicated head-neck joints in mammals known to date. The peculiar head-neck morphology was most probably adapted for a fierce intermale head-butting behavior, comparable to neck-blowing in male giraffes but indicative of an extreme adaptation in a different direction within giraffoids. This newly identified giraffoid increases our understanding the actual triggers for the giraffe's head-neck evolution.

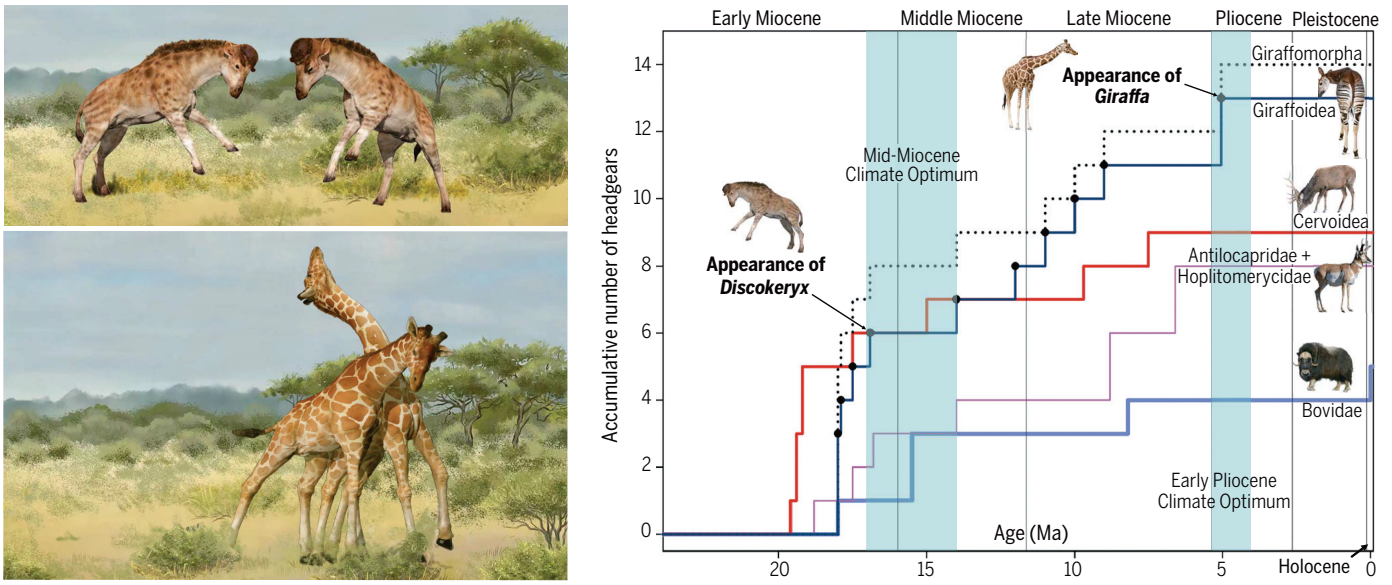
RATIONALE: The comparative anatomical studies of osteological structures, including the bony labyrinth morphology, the headgear genesis and histology, and dentitions, provide the basis for the giraffoid affinity of *D. xiezhi*, which was further supported by phylogenetic analyses and reconstructions of the fauna. Finite element analyses explain the mechanical predominance for the peculiar head-neck morphology in various head-butting modeling. Tooth enamel isotope analyses indicate the distinctiveness of the ecological niche occupied by *D. xiezhi*. Diversity of headgear within different pecoran groups reveals the different evolutionary selection pressure on these groups.

RESULTS: Finite element analysis reveals that the enlarged atlanto-occipitalis and intercervical articulations are essential for high-speed head-to-head butting. *D. xiezhi* appears to exhibit the most optimized head-butting adaptation in vertebrate evolution when compared with the models of extant head-butters. Tooth enamel isotope data show that *D. xiezhi* had the second highest average $\delta^{13}C$ value among all herbivores and a large range of $\delta^{18}O$ values, with some individuals occupying an isotopic niche differing substantially from others in the fossil community. This indicates that *D. xiezhi* was an open-land grazer with multiple sources of water intake, and their habitats likely included areas that were difficult for other contemporary herbivores to make use of.

CONCLUSION: The morphology and inferred ecology of *D. xiezhi* provide another example for understanding the neck evolution in giraffoids. Fossil giraffoids exhibit a higher degree of diversity in headgear morphology than any other pecoran group; such a diversity, associated with the complex head-neck morphology, likely indicates the intensive sexual combats between males in the evolution of giraffoids. For interspecific relationship, one possible strategy of early giraffoids is that they might have avoided competition with coeval bovids and cervids by taking advantage of other niches in the ecosystem. *Giraffa*,with its long neck, did not appear until the early Pliocene in savannah areas, when C_4 ecosystems started being vastly established. "Necking" combat was likely the primary driving force for giraffes that have evolved a long neck, and high-level browsing was likely a compatible benefit of this evolution. The ecological positioning on the marginal niches promoted the intensive sexual competition, and the fierce sexual combats fostered extreme morphologies to occupy the special niches in giraffoids. ■

The list of author affiliations is available in the full article online.
*Corresponding author. Email: wangshiqi@ivpp.ac.cn (S.-Q.W.); jmeng@amnh.org (J.M.); dengtao@ivpp.ac.cn (T.D.)
Cite this article as S.-Q. Wang *et al.*, *Science* **376**, eabl8316 (2022). DOI: 10.1126/science.abl8316

READ THE FULL ARTICLE AT
https://doi.org/10.1126/science.abl8316



Male combat in the representative giraffoids. *D. xiezhi* (head-to-head butting, top left) and the extant *Giraffa camelopardalis* (neck blowing, bottom left) show different combat styles and head-neck morphology. The right panel exhibits the accumulative number of headgears in various pecoran groups during their evolution. Note that giraffomorphs had evolved more types of headgear than other pecoran groups, which may be partly attributable to their various combat styles.

ILLUSTRATION: Y. WANG AND X. GUO