

TECHNICAL COMMENT

PALEONTOLOGY

Comment on “Sexual selection promotes giraffoid head-neck evolution and ecological adaptation”

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Wang *et al.* (Research Articles, 3 June 2022, eabl8316) reported an early Miocene giraffoid that exhibited fierce head-butting behavior and concluded that sexual selection promoted head-neck evolution in giraffoids. However, we argue that this ruminant is not a giraffoid and thus that the hypothesis that sexual selection promoted giraffoid head-neck evolution is not sufficiently supported.

The newly described mammal *Discokeryx xiezhi*, from the early Miocene of northern China, has disk-shaped headgear and complicated head-neck joints, supposedly used in fierce head-butting behavior (1). This was seen as an unusual precursor of the “necking” combat of modern giraffes, and the switch in combat mode was suggested as a key reason why giraffes evolved their long necks. Further, it is suggested (1) that these early giraffoids avoided competition with coexisting bovids and cervids by taking marginal niches, which promoted intensive sexual competition.

Wang *et al.* (1) highlight six key cranial characteristics supporting the giraffoid affinity of *Discokeryx*, all of which we regard as problematic. First, neither the parietal participation in headgear support nor the median position of frontal or parietal headgear are diagnostic features of Giraffoidea, as these features are also present in bovids (2). Second, dermal origin of headgear does not support giraffoid affinity as bovid horncores also have a dermal origin (3, 4); moreover, it is impossible to recognize dermal bone based on the developed bone of *Discokeryx* because the microscopic structure of the developed bone is not diagnostic of its embryonic origin (5). Third, it is not clear that giraffid bone histology shows lamellar structure or large-scale osteons (6); figures in Wang *et al.* (1) show only thick lamellar bone (with several layers of lamellae) surrounding vascular canals in the thin sections of the headgear of *Discokeryx*, *Honanotherium*, and the bovid *Turcocerus* sp., which is a common

character in a typical developed secondary osteon. Therefore, osteons cannot demonstrate “horn” differentiation between giraffoids and bovids. Fourth, in giraffids there is only one foramen on the parietal bone beneath the

ossicone, indicating the existence of the coronal vein that joins the superficial temporal, as in other horned ruminants (7), which is mistaken for the foramen far behind an ossicone (1). Finally, similar semicircular canals in *Discokeryx*, extant giraffes, and the bovid *Tsaiamotherium* suggest that this feature most likely does not have phylogenetic significance (1). In addition, the bilobed lower canine, which is considered one of the most diagnostic features of Giraffidae (8), has not yet been found in *Discokeryx* or other Pecora. The headgear of *Discokeryx* was described as covered with keratinous integument—which is not found in giraffids.

Wang *et al.*'s phylogenetic analysis (1) reached the result that *Discokeryx* was a sister group of the bovid *Tsaiamotherium*. We checked their data matrix and found that some important characters and taxa were omitted, in addition to some problematic scoring. The upper dentition and some skull characters of

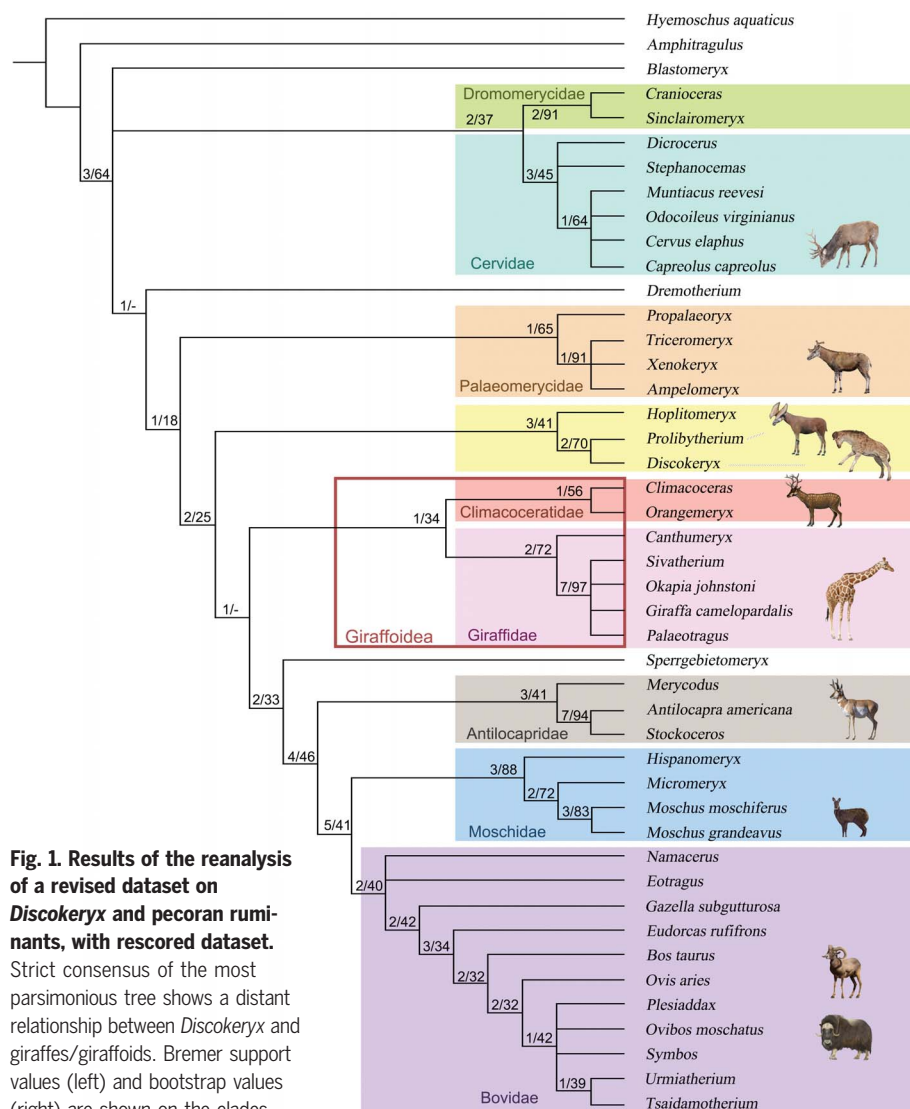


Fig. 1. Results of the reanalysis of a revised dataset on *Discokeryx* and pecoran ruminants, with rescored dataset.

Strict consensus of the most parsimonious tree shows a distant relationship between *Discokeryx* and giraffes/giraffoids. Bremer support values (left) and bootstrap values (right) are shown on the clades.

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Tsaidamotherium are coded with a question mark even though the data are available (9), whereas the astragalus was coded in all fossil taxa, a character that had not been reported in some extinct Pecora including *Discokeryx*. We evaluated the phylogenetic data without adding taxa or characters, clarified some ambiguous statements of the headgear characters, rescored the inaccurate coding, and produced a strict consensus parsimony tree based on morphological data (Fig. 1). Our reanalysis shows that *Discokeryx* is not in the clade of giraffoids but rather is a more primitive ruminant with a stem phylogenetic position, whereas *Tsaidamotherium* is certainly in the clade of bovids. Our results indicate that character coding is very important in phylogenetic analyses and should be considered carefully.

Aside from the systematic position of *Discokeryx*, we have concerns about the argument concerning head-neck evolution in giraffes. Wang *et al.* (1) claimed “intensive sexual combats” in the evolution of giraffoids based on more diverse headgear and head-neck morphologies than

in other ruminant groups. Further, they argued (1) that “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”. We query these claims for four reasons. First, as we argue, *Discokeryx* is not a giraffoid. Second, there is no evidence that ‘necking’ caused neck elongation (10). Third, the headgear diversity of giraffoids has been overweighted by artificially using different criteria in different pecoran groups, thus it cannot be used to infer “intensive sexual combats” in giraffoids. Fourth, the reference to *Discokeryx* living in marginal niches in which sexual selection was intense is belied by the fact that it is part of a fossil fauna including many other mammals, and that there were dietary overlaps between *Discokeryx* and other mammals. Similarly, giraffoids were also claimed as having lived in marginal niches (1), which were in fact shown to be a dominant part of late Miocene faunas (11) and spanned the entire dietary spectrum of browsing, mixed feeding, and grazing (12).

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