

TECHNICAL RESPONSE

PALEONTOLOGY

Response to comment on “Sexual selection promotes giraffoid head-neck evolution and ecological adaptation”

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Hou *et al.* challenged the giraffoid affinity of *Discokeryx* and its ecology and behavior. In our response we reiterate that *Discokeryx* is a giraffoid that, along with *Giraffa*, shows extreme evolution of head-neck morphologies that were presumably shaped by selective pressure from sexual competition and marginal environments.

Hou *et al.* (1) challenged our view that *Discokeryx xiezhi* is a member of giraffoids and questioned its significance on giraffoid head-neck evolution and ecological adaptation (2). We disagree with their arguments for the following reasons: First, Hou *et al.* mistakenly interpreted a previous study (3) in which the horncore proper in the bovid species *Urmiatherium intermedium* is supported by the frontal only [figures 1 and 11 in (2)], as reiterated by others (4). Bovids have neither parietal supported horncores nor median positioned horncores (5). Second, a giraffe's ossicone is covered by skin but the apex becomes cornified in mature males that engage in head and neck sparring (6). In *Discokeryx*, skin must have covered the lateral surface of the headgear whereas the dorsal surface was most likely cornified, making the headgear a highly specialized ossicone. In bovids, the suprapariosteal tissues induce horncore formation and normally there is no suture separating bony elements in horncore development (7). In *Discokeryx* and *Tsaidamotherium hedinii*, the epiphyseal line is clear, showing a developmental ossification different from that of bovids.

Third, the histological slices of *Discokeryx* and *Honanotherium* show thick lamellar bones that are clearly different from those of the bovid *Turcocerus* in which secondary osteons predominate (2), reflecting obvious and convincing differences in the two types. Fourth, Hou *et al.* misunderstood our interpretation of the cornual vein in giraffes and *Discokeryx*. The cornual veins do not pass through the cranial bone in bovids, in contrast to giraffes and *Discokeryx* where they pass through the large foramen on the parietal bone before joining the superficial temporal vein (8). Fifth, the bony labyrinth as a conservative organ remains mostly unaffected under various environmental or behavioral selective pressures compared to teeth and long bones, which is important for phylogenetic reconstruction (9). Giraffoid labyrinths show a distinct morphology in that the posterior ampulla insertion of the lateral semicircular canal is very close to that of the posterior canal, which is present in all giraffoids known but absent in all bovids examined, including the earliest species *Eotragus artenensis* (Fig. 1). The giraffoid condition is also present in *Tsaidamotherium hedinii* (Fig. 1), a feature phylogenetically distancing the species from Bovoidea (9). Moreover, a lack of canines in *Discokeryx* specimens is not sufficient evidence to exclude it from giraffoids. Similarly, the canine is unknown in the unequivocal giraffid *Canthumeryx* (10), whereas *Orangemeryx* has one-lobed lower canines (11) but is still placed in Giraffoidea (1). Further, lack of keratinous integument is not a synapomorphy for giraffids, not to mention the cornified apex of the giraffe ossicone (6).

Hou *et al.* modified some characters and character codings of our dataset and, using a different method, obtained a different tree topology [figure 1 in (1)]. Without knowing what has been changed, we cannot respond to their result adequately. Nonetheless, their

phylogeny (1) is similar to ours in that *Discokeryx* is grouped with *Prolibytherium* but differs in having a more basal position for Prolibytheriidae. However, in their phylogeny (1), Cervidae as a basal group of Pecora (more basal than *Discokeryx*) is untenable, which also broadly contradicts the molecular phylogeny in which Antilocapridae are at the base of pecorans and Cervidae pairs with Bovoidea (12). What surprises us is the deep insertion of *Tsaidamotherium* within bovids [figure 1 in (1)]. As clearly illustrated [figure S5, I to J, in (2)], the horncore of *Tsaidamotherium* is on the parietal bone, as in giraffoids but not bovids. Along with the epiphyseal line and bony labyrinth feature stated above, *Tsaidamotherium* is, in our view, a giraffoid and not a bovid. Hou *et al.*'s phylogeny suggests either an awkward horn-core evolution in ruminants or problematic character codings in their analysis.

Hou *et al.*'s five reasons (1) to question our interpretation of the implications of *Discokeryx* on giraffoid evolution are largely off target. First, *Discokeryx* is a giraffoid by our phylogeny; even so, one cannot assume “an antecedent of the behavior of modern giraffids” (1). Second, we do not think Hou *et al.* intended to offer a scenario where head-butting could evolve to necking behavior; their second argument is an empty statement. Third, neck elongation induced by necking combat was postulated long ago (13) but was miscredited to us (1). Nonetheless, as an alternative to the traditional feeding hypothesis for elongation of giraffe necks, both need to be tested by new evidence. Our study better corroborates the necking combat hypothesis without ruling out the traditional one; both mechanisms may have worked for the neck elongation of giraffes. Fourth, the statement “the headgear diversity of giraffoids has been overweighted by artificially using different criteria in different pecoran groups” (1) is confusing. Strong correlation between horn and antler morphology and fighting styles in bovids and cervids has been shown (14). That giraffoid headgear morphologies are more diverse than those of other ruminants is partly attributable to the fibrocartilage ossification of ossicones that fuse to the cranium with greater flexibility of changes (15). Head-butting behavior in *Discokeryx* is supported by the most extreme head-neck structures ever known in mammals. These are by no means overweighted and artificial. Fifth, suggesting that that the mammals included in the Halamagai fossil assemblage must have dietary overlaps (1) could be misleading. The complex fluvial sediments, representing a high-energy tephonomic setting, have buried a wide diversity of mammals, of which some could have lived in nonoverlapping niches.

To summarize, we feel more strongly than before that *D. xiezhi* belongs to Giraffoidea.

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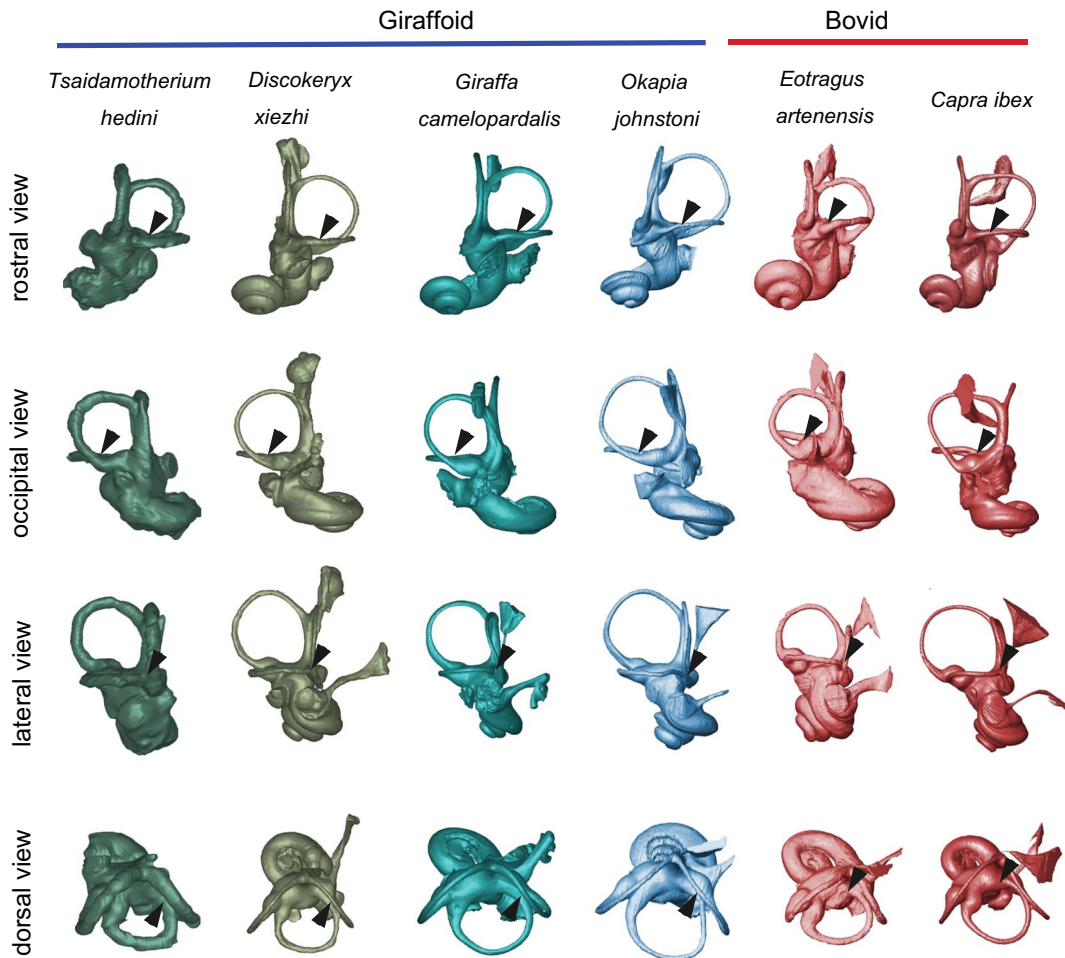


Fig. 1. Bony labyrinth of some bovids and giraffoids. The black arrowheads indicate the insertions of the lateral semicircular canal (LSC) of posterior ampulla (pa), which are different in giraffoids and bovids but are common within each group; not to scale.

Discokeryx and *Giraffa* are two examples within giraffoids that show extreme evolution of head-neck morphologies, which were most likely shaped by selective pressure from sexual competition and marginal environments.

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