illustrates how substantial changes in feather morphology can be between molts and therefore rather argues against the hypothesis instead of supporting it: "The remiges and rectrices in [the young] and [older juvenile] are apparently not natal down, but they are significantly different from each other, suggesting that significant morphological changes took place in feather development even after the hatchling stage" [4]. Pigeons, as an additional extant example, are unique in that they develop their first generation of pennaceous feathers as a direct continuation of their neoptiles, creating a unique feather morphology in juveniles not exhibited by the adults or any other living bird [5,6]. The actual age, and therefore also the developmental status, of DIP-V-15103 is unknown, as it is a highly incomplete and furthermore solitary fossil. There is no frame of reference that would allow us to age this specimen reliably, even though its hypothesized general juvenile nature appears plausible, based on its size. The question remains, however, what kind of developmental stage we find preserved here and what type of plumage it bears. Until any younger or older conspecifics have been discovered it remains unknown what their plumage actually looked like and whether it corresponded to or differed from the one exhibited by DIP-V-15103.

Second, closed vanes only apply to (most) volant species. There are numerous flightless extant birds that exhibit a broken-up vane of their pennaceous feathers as adults [7]. Considerations about sternal evolution at the stem of Aves, for instance, indicate that flightlessness may very well have occurred in several maniraptoran lineages [8]. The only information available for the species represented by DIP-V-15103 is a less than four centimeter-long fragment of the tail. Based on this information alone it cannot be reliably hypothesized whether the species was volant or not as the entire locomotor apparatus is not preserved in the fossil and tail feathers in isolation are critical to infer the flight capabilities of an animal.

Third, the morphology of the juvenile plumage of extant birds is incredibly diverse [9,10], and the fossil record of feather types among non-avian dinosaurs is equally impressive [4]. The absence of evidence for another case matching the situation in DIP-V-15103 therefore cannot be considered the evidence for the absence of such.

In conclusion, I do not challenge the overall potential importance of DIP-V-15103 and that this specimen complements our knowledge about the early and frequently underestimated diversity of feather morphology among dinosaurs. However, given the evolutionary implications for our understanding of feather formation as hypothesized by Xing and colleagues [1] by calling it "primitive plumage" and by suggesting a "barbule-first evolutionary pattern", I argue for a bit more caution at the present time. The actual phylogenetic placement of DIP-V-15103 appears to be not sufficiently resolved, and the proposed developmental trajectories appear to be based on insufficiently objective evidence.

## REFERENCES

1. Xing, L., McKellar, R.C., Xu, X., Li, G., Bai, M., Persons IV, W.S., Miyashita, T., Benton, M.J., Zhang, J., Wolfe, A.P., *et al.* (2016). A feathered dinosaur tail with primitive plumage trapped in Mid-Cretaceous amber. Curr. Biol. *26*, 3352–3360.
2. Koschowitz, M.-C., Lambertz, M., Fischer, C., and Sander, P.M. (2014). On the origin of feathers—Response. Science *346*, 1466–1467.
3. Persons, W.S., and Currie, P.J. (2015). Bristles before down: a new perspective on the functional origin of feathers. Evolution *69*, 857–862.
4. Xu, X., Zheng, X., and You, H. (2015). Exceptional dinosaur fossils show ontogenetic development of early feathers. Nature *464*, 1338–1341.
5. Burmeister, H. (1840). System der Pterylographie von Christian Ludwig Nitzsch (Halle: Eduard Anton).
6. Boas, J.E.V. (1931). Federn. In Handbuch der vergleichenden Anatomie der Wirbeltiere, 1. Band, L. Bolk, E. Göppert, E. Kallius, and W. Lubosch, eds. (Berlin-Wien: Urban & Schwarzenberg), pp. 565–584.
7. Prum, R.O. (1999). Development and evolutionary origin of feathers. J. Exp. Zool. (Mol. Dev. Evol.) *285*, 291–306.
8. Lambertz, M. and Perry, S.F. (2015). Remarks on the evolution of the avian sternum, dinosaur gastralia, and their functional significance for the respiratory apparatus. Zool. Anz. *255*, 80–84.
9. Schaub, S. (1912). Die Nestdunen der Vögel und ihre Bedeutung für die Phylogenie der Feder. Verhandl. Naturforsch. Ges. Basel *23*, 131–182.
10. Foth, C. (2011). The morphology of neoptile feathers: ancestral state reconstruction and its phylogenetic implications. J. Morphol. *272*, 387–403.

Institut für Zoologie, Rheinische Friedrich-Wilhelms-Universität Bonn, 53115 Bonn, Germany. Sektion Herpetologie, Zoologisches Forschungsmuseum Alexander Koenig, 53113 Bonn, Germany.
E-mail: lambertz@uni-bonn.de

## Correspondence

# Response to: Phylogenetic placement, developmental trajectories and evolutionary implications of a feathered dinosaur tail in Mid-Cretaceous amber

Lida Xing[1,2,13,*], Ryan C. McKellar[3,4,13,*], Xing Xu[5,13], Gang Li[6,13], Ming Bai[7,13], W. Scott Persons IV[8], Tetsuto Miyashita[8], Michael J. Benton[9], Jianping Zhang[2], Alexander P. Wolfe[8], Qiru Yi[6], Kuowei Tseng[10,11], Hao Ran[12], and Philip J. Currie[8]

In his correspondence, Markus Lambertz [1] raises some concerns about the phylogenetic placement and feather development of DIP-V-15103, the amber-entombed tail section that we recently reported [2] as fragmentary remains of a non-pygostylian coelurosaur (likely within the basal part of Coelurosauria). We here would like to respond to these concerns.

To be clear, our assessment of DIP-V-15103 as a non-avialan theropod is not based solely on osteological evidence, but rather on a combination of osteological *and* integumentary evidence; nor is the presence of pronounced ventral grooves the only discernible osteological character. The basic forms of the vertebrae, as revealed by CT scanning, make a substantial contribution to the phylogenetic placement. As described in our original publication: "The vertebrae are elongate, with anteroposterior lengths double the maximum diameter of the tail" and "the vertebrae lack prominent neural arches, transverse processes, or haemal arches." Such a morphology is inconsistent with caudal vertebrae from the anterior segment of all avian and non-avian

theropod tails, where the centra are subequal in height, length and width and where the neural spines and transverse processes are prominent. Thus, we concluded that "the preserved segment is only a small mid to distal portion" of the tail. The evolution of tails within the avialans (the clade that contains long-tailed birds and their modern relatives) is characterised by reduction in the total numbers of caudal vertebrae, which results in short caudal series comprised only of subequal centra with prominent projections. Unlike DIP-V-15103, pygostylian (short) bird tails possess only caudal vertebrae with subequal centra and terminal pygostyles. The presence of pronounced ventral grooves on the centra of DIP-V-15103 is another, more specific trait that supports this diagnosis.

Still, based on osteology alone, the possibility that DIP-V-15103 is a non-pygostylian avialan (*i.e.,* a long-tailed bird, such as *Archaeopteryx* and *Jeholornis*) remains. Both *Archaeopteryx* and *Jeholornis* possess suitably long posterior series of elongate and projection-less centra to have contributed the segment preserved in DIP-V-15103. However, *Archaeopteryx* and *Jeholornis* are also known to possess terminal fronds of complex feathers, while DIP-V-15103 possesses an entirely different feather form and different plumage arrangement. On this basis, we also disagree with the assessment that it "cannot be reliably hypothesized whether the species was volant" [1]. The feather fronds of long-tailed birds and those of some small troodontids and dromaeosaurids (dinosaurs closely related to avialans) have generally been interpreted as structures utilized in flight or in gliding, and we would argue that the absence of such a structure in DIP-V-15103 indicates it was less well-adapted for flight than a true avialan or such eumaniraptorans.

It is possible that DIP-V-15103 represents a non-pygostylian avialan that, because it was a juvenile, possessed (for whatever ontogenetic reasons) a hitherto unknown type of plumage arranged in multiple lateral tracks, which would later be replaced by a frond of more complex pennaceous feathers. However, we regard invoking such drastic and unevidenced developmental changes to explain the observed features of DIP-V-15103 to be a far less parsimonious explanation. As was originally stated, there is some room for uncertainty whether the specimen bears feathers that are characteristic of the adult plumage. The basal pennaraptoran *Similicaudipteryx* is thought to perhaps have two adult-like plumages (closed-vane, pennaceous feathers with variations in the rachis) [3,4], and basal members of Pygostylia are known to have juveniles with precocial plumage, which are both sources of uncertainty. There is a great deal of variation known within extinct coelurosaur plumage. However, there is also no evidence among any of the extant or extinct coelurosaurs suggesting that, once pennaceous barbules yielding an open-vaned feather (with loose barbs) have been produced, subsequent feather generations might form a closed-vane (aerodynamically functional) flight feather from the same follicle.

Regardless of whether DIP-V-15103 hatched with precocial plumage, or has already undergone a moult to produce adult-like feathers, the evidence that is currently available does not suggest that the individual would have undergone a major structural reorganization to include barbules with hooklets later in life. Moreover, even if such an ontogenetic sequence of events did occur and DIP-V-15103 does represent an early avialan, it is not "absolutely critical" to our arguments regarding feather evolution that the plumage of DIP-V-15103 corresponds to the final pennaceous feathers of an adult. After all, ontogeny does often (although not always) recapitulate phylogeny, and neoteny is a well-documented and common evolutionary phenomenon. Ultimately, we will not be able to address all the developmental questions that DIP-V-15103 raises until a larger sample set becomes available. Until we are better able to pair fossils of juveniles with adults and have a more extensive understanding of plumage in both life stages, modern birds and their development will strongly shape our expectations for the data missing from the fossil record. Hopefully the amber fossil record holds additional discoveries that will help to shed some more light on evolutionary-developmental pathways, as well as some of the more peculiar developments found among stem group lineages. DIP-V-15103 provides us with a first glimpse of exceptionally preserved plumage set in a firm phylogenetic context, but the full extent of its implications remains to be determined.

## AUTHOR CONTRIBUTIONS

W.P., R.M., L.X.: writing; all authors: editing, systematic, or ontogenetic input.

## REFERENCES

1. Lambertz, M. (2017). Phylogenetic placement, developmental trajectories, and evolutionary implications of a feathered dinosaur tail in Mid-Cretaceous amber. Curr. Biol. *27*, XXX-XXX.
2. Xing, L., McKellar, R.C., Xu, X., Li, G., Bai, M., Persons IV, W.S., Miyashita, T., Benton, M.J., Zhang, J., Wolfe, A.P., *et al.* (2016). A feathered dinosaur tail with primitive plumage trapped in Mid-Cretaceous amber. Curr. Biol. *26*, 3352–3360.
3. Xu, X., Zheng, X., and You, H. (2010). Exceptional dinosaur fossils show ontogenetic development of early feathers. Nature *464*, 1338–1341.
4. Prum, R.O. (2010). Moulting tail feathers in a juvenile oviraptorisaur. Nature *468* (E1), http://dx.doi.org/10.1038/nature09480.

[1]State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing 100083, China. [2]School of the Earth Sciences and Resources, China University of Geosciences, Beijing, 100083, China. [3]Royal Saskatchewan Museum, Regina, Saskatchewan, S4P 4W7, Canada. [4]Biology Department, University of Regina, Regina, Saskatchewan, S4S 0A2, Canada. [5]Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China. [6]Institute of High Energy Physics, Chinese Academy of Science, Beijing 100049, China. [7]Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, China. [8]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada. [9]School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK. [10]Department of Exercise and Health Science, University of Taipei, Taipei 11153, China. [11]Department of Geology, Chinese Culture University, Taipei 11114, China. [12]Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection, Ministry of Education, Guilin 541004, China.
[13]Co-first authors.
*E-mail: xinglida@gmail.com; ryan.mckellar@gov.sk.ca