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

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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-avian 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 unevicenced 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.

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