Feather Quill Knobs in the Dinosaur *Velociraptor*

Alan H. Turner,[1]* Peter J. Makovicky,[2] Mark A. Norell[1]

Some nonavian theropod dinosaurs were at least partially covered in feathers or filamentous protofeathers (*1*). However, a complete understanding of feather distribution among theropod dinosaurs is limited because feathers are typically preserved only in lagerstätten like that of Solnhofen, Germany or Liaoning, China. Such deposits possess clear taphonomic biases toward small-bodied animals, limiting our knowledge regarding feather presence in larger members of feathered clades.

We present direct evidence of feathers in *Velociraptor mongoliensis* based on the presence of quill knobs on the posterior forearm. In many living birds, raised knobs along the caudal margin of the ulna reveal where the quills of the secondary feathers are anchored to the bone by follicular ligaments. Quill knobs are variably present in extant bird species and are present in only a few basal taxa such as *Ichthyornis* (*2*), so their absence does not necessarily indicate a lack of feathers. Their presence, however, is a direct indicator of feathers of modern aspect (e.g., feathers composed of a rachis and vanes formed by barbs).

The specimen IGM (Geological Institute of Mongolia) 100/981 was collected at the Gilvent Wash locality near Ukhaa Tolgod (Campanian Djadokhta Formation). The specimen is estimated to have been 1.5 m long and to have weighed roughly 15 kg. It possesses several characteristics found in *V. mongoliensis*, a common dromaeosaurid in the Djadokhta Formation. IGM 100/981 preserves six low papillae on the middle third of the caudal margin of the ulna (Fig. 1). These are regularly spaced about 4 mm apart. Topographically, these papillae correspond to the quill knobs in living birds. Given their spacing in IGM 100/981, we estimated that there is space for eight additional secondary feathers. This suggests that 14 secondaries were present in *Velociraptor*, which compares well with the 12 or more secondaries in *Archaeopteryx* (*3*). About 18 secondaries are suggested for the dromaeosaurid *Microraptor* (*4*), whereas its close relative *Rahonavis* appears to have possessed just 10 (*5*).

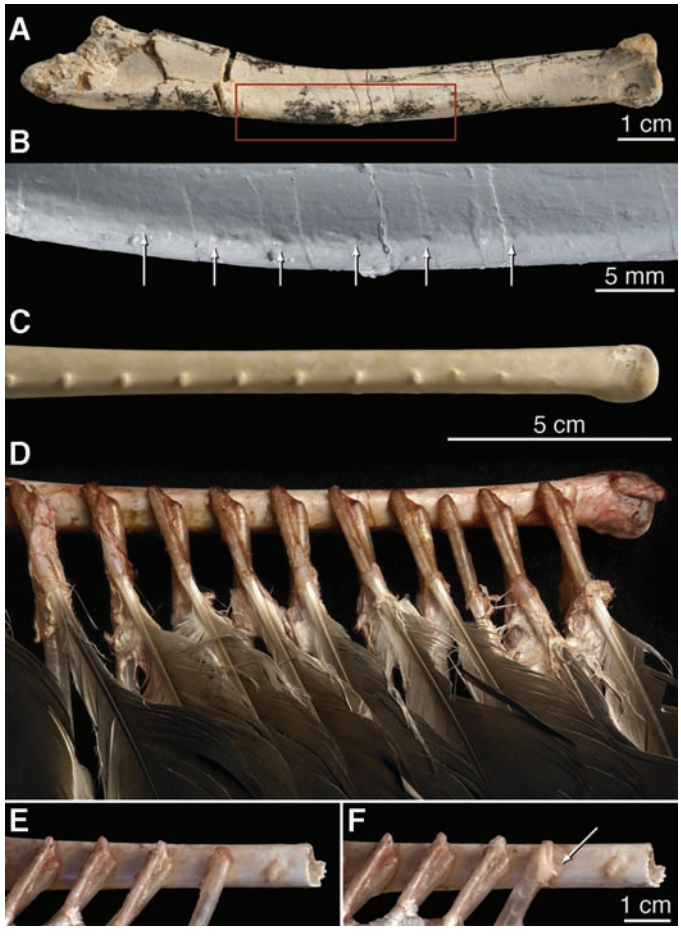

Fig. 1. (**A**) Dorsal view of right ulna of *Velociraptor* IGM 100/981. (**B**) Detail of red box in (A), with arrows showing six evenly spaced feather quill knobs. In (B), a cast of IGM 100/981 was used. (**C**) Dorsal view of right ulna of a turkey vulture (*Cathartes*). (**D**) Same view of *Cathartes* as in (C) but with soft tissue dissected to reveal placement of the secondary feathers and greater secondary coverts relative to the quill knobs. (**E**) Detail of *Cathartes*, with one quill completely removed to reveal quill knob. (**F**) Same view as in (E) but with quill reflected to the left to show placement of quill, knob, and follicular ligament. Follicular ligament indicated with arrow.

Such variation is expected because extant birds display variable counts even within species (*3*).

Known coelurosaurs with wing feathers of modern aspect are small basal members of their respective clades. Some have been considered possibly volant (*4*, *5*), and it has been suggested that the large-bodied, derived members of the feathered theropod clades may not have retained feathers or only retained feathers while juveniles (*6*). This *Velociraptor* specimen indicates this is not the case for at least one lineage of dromaeosaurids. An examination of the living families of birds shows a significant correlation between the absence of ulnar papillae and the loss and/or reduction in volancy, even though some strong flyers lack papillae (*7*). This raises the possibility that ulnar papillar reduction or absence in large-bodied derived dromaeosaurids reflects loss of aerodynamic capabilities from the clade's ancestral members. Quill knobs in *Velociraptor* could reflect retention of feathers from smaller possibly volant ancestors, but such feathers may have had other functions. Although thermoregulatory effects of secondaries on the ulna would be negligible, such feathers could have been used for display (*1*), in shielding nests for thermal control (*8*), or for creating negative lift during incline running (*9*). Whether this feature represents retention of an ancestral function or the cooption for other purposes, the presence of quilled feathers on the posterior of the arms in a medium-sized derived, clearly nonvolant dromaeosaur can now be established.

References and Notes

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Supporting Online Material

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Materials and Methods
Fig. S1
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[1]Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024–5192, USA. [2]Department of Geology, The Field Museum, 1400 South Lake Shore Drive, Chicago, IL 60605–2496, USA.

*To whom correspondence should be addressed. E-mail: turner@amnh.org

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