

# Response to Comment on “A Diverse Assemblage of Late Cretaceous Dinosaur and Bird Feathers from Canadian Amber”

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Dove and Straker question our interpretations of plumage from Late Cretaceous Canadian amber. Although we are able to refute concerns regarding both specimen taphonomy and misidentification as botanical fossils, unequivocal assignment to either birds or dinosaurs remains impossible, as we stated originally. However, reported observations and their further refinement herein are insufficient to falsify the hypothesized dinosaurian origin for protofeathers.

Dove and Straker (*1*) raise concerns over whether our recent Report (*2, 3*) of plumage from Late Cretaceous Canadian amber contains sufficient evidence to support conclusions of both avian and dinosaurian origins for inclusions. Specifically, they question two specimens (UALVP 52821 and UALVP 52822) interpreted as representatives of stages I and II in Prum’s (*4*) evolutionary-developmental model, as well as a specimen (TMP 96.9.334) interpreted as representative of stage IV with specializations for water uptake. Although some uncertainty is inherent to all interpretations of fragmentary fossils, Dove and Straker’s (*1*) technical concerns can be addressed readily with the specimens.

Concerning TMP 96.9.334, there is a fundamental error in their interpretation (*1*) of our paper, because we did not suggest that this specimen represents dinosaur plumage. Instead, we proposed that this specimen likely belongs to stage IV (*3*), representing Cretaceous bird plumage with structural features linked to its possible use in water uptake (*2, 3*). Points raised (*1*) regarding fine anatomical detail are the same features that suggested to us that placement within stage IV was more appropriate than stage V. Other criticisms (*1*) represent different interpretations of our discussion and figures of specimen taphonomy (*3*).

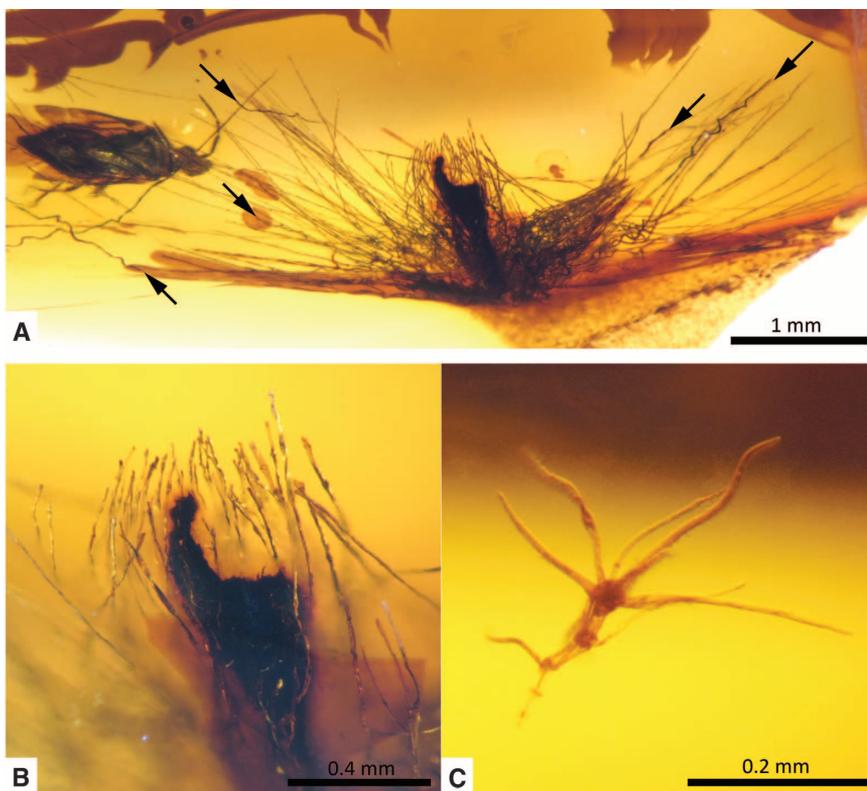
Dove and Straker (*1*) are correct in asserting that there is no clear indication of unsegmented basal cells within TMP 96.9.334 barbules and that it is unusual to observe coiling within the segmented portion of the barbule (pennulum), because these features are unknown in modern bird feathers. As Dove has illustrated and discussed [figure 138 in (*5*)], some modern (stage V) bird plumage retains traces of segmentation or

“multiple cells” within the curled basal portion of the barbule. The lack of a defined basal plate does not exclude TMP 96.9.334 from being a feather fragment, whereas the suggestion that these filaments are more comparable to *Populus* seed trichomes (*1*) is incorrect. Although coiled, trichomes are not segmented (noded) (*6, 7*) and would not be expected to consistently straighten apically. Furthermore, Salicaceae, the family that

contains *Populus*, is unknown before the latest Paleocene (*8*).

Taphonomic effects that led Dove and Straker (*1*) to critique TMP 96.9.334 were described in our original work [(*3*), p. S9], but benefit from additional clarification. The TMP 96.9.334 barbules all coil in a counter-clockwise direction. The five or so barbules (Fig. 1A) that coil clockwise have been sheared from the main mass, likely as a result of resin flow (*3*). These dislocated barbules do not indicate “coiling at mid and distal positions” (*1*), and their nodal expansions clearly indicate that they are pointing in the wrong direction. The central structure in TMP 96.9.334 is almost certainly a rachis (Fig. 1B): It is solid, not a clump of filaments, and has the appropriate size and cross-sectional shape (*9*).

Concerning UALVP 52821, Dove and Straker (*1*) chose to emphasize filament size over morphology, critiquing the match between dimensions in *Sinosauropteryx* protofeathers and the filaments in Canadian amber. Overlooking the fact that UALVP 52821 appears to contain just the distal tips of filaments (*3*), filament diameters are not “an order of magnitude smaller” (*1*) than those reported for *Sinosauropteryx*. In fact, the work (*10*) cited by Dove and Straker (*1*) contains no diameter measurements, because the



**Fig. 1.** Photomicrographs of TMP 96.9.334 and comparison image of a trichome preserved in Canadian amber. (A) Overview of TMP 96.9.334, with dislocated barbules indicated by arrows at barbule bases. (B) Cross section of rachis where it is truncated at the surface of the amber piece, with rachis surrounded by truncated barbule apices. (C) Stellate trichome (University of Alberta specimen).

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authors had difficulty isolating single filaments. Later work provided generalized estimates that included smaller filaments “considerably narrower

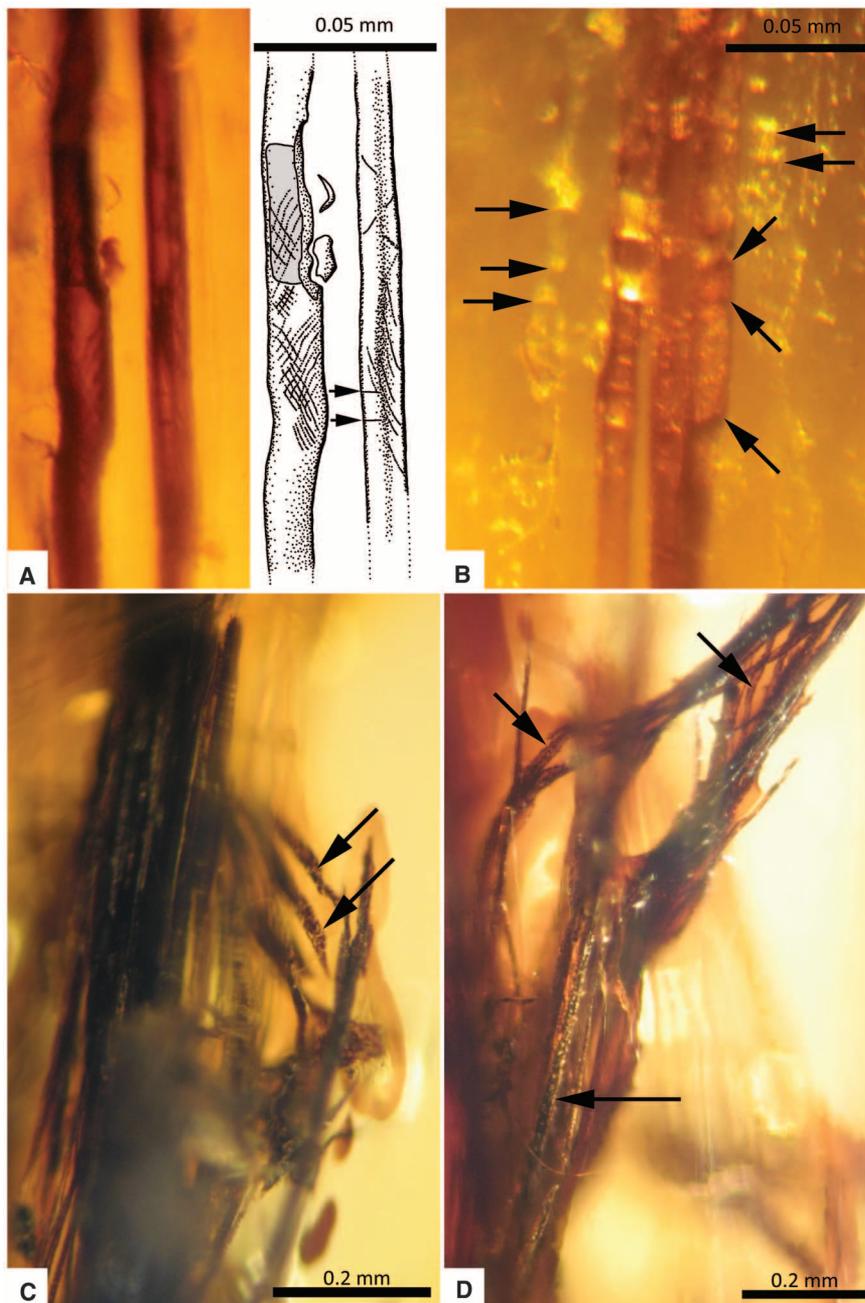
than 0.1 mm” (11) and cautioned that measurements may be overestimates due to filament overlap (11) and taphonomy (11, 12). If the structures

measured by Lingham-Soliar *et al.* (12) were indeed collagen fibers (internal structures), their measurements have no bearing on our study of integumentary structures. Subsequent work (13) indicated that many of the filaments surrounding *Sinosauropteryx* and *Sinornithosaurus* were pigmented and thus cannot be dismissed as collagen fibers. This also bears on the comparison between UALVP 52821 and 52822 with *Populus* trichomes [figure 1 in (1)]. Trichomes lack pigmentation (Fig. 1C) and are often branched or multicellular (6, 7). And again, Salicaceae are unknown from the Cretaceous (8).

Dove and Straker (1) appear to advocate mammalian hair as a better match to UALVP 52821 than *Sinosauropteryx* protofeathers. Although they critique our use of diameter and hollowness as criteria for excluding mammalian hair, they overlook our most important criterion, cuticular scales. UALVP 52821 lacks cuticular scales, which was discussed at length (3). The internal divisions envisaged by Dove and Straker [figure 1, A to C, in (1)] are taphonomic artifacts (Fig. 2).

Dove and Straker (1) misinterpreted the results of our spinning disk confocal microscopy (SDCM) and laser scanning confocal microscopy (LSCM) analyses (3), which were reported as inconclusive for identifying keratin, because amber autofluorescence overwhelms any autofluorescence signal of keratin in inclusions (3). There is no possibility of distinguishing between  $\alpha$  and  $\beta$ -keratin within this amber, and we did not claim to have identified keratin based on these analyses (3). Our interpretation of structure within UALVP 52821 in no way hinges upon LSCM data; the hollow, cylindrical structure of the filaments is plainly visible using light microscopy [figures S3B, S4A, and S11B in (3)]. We analyzed unequivocal feather fragments (TMP 96.9.997) for comparison to UALVP 52821 because the unpigmented zone of these specimens provided the best chance of detecting keratin (3). Keratin was not identifiable using emission profiles in TMP 96.9.997, which rendered the analysis of additional specimens futile. The same problem occurred with UALVP 52821.

We understand the recommendation for further analyses and destructive sampling (1). However, UALVP 52821 and UALVP 52822 are currently the only representatives of putative protofeathers in amber. The 11 plumage fragments (2, 3) stem from a survey of more than 4000 inclusion-bearing pieces of amber. At a minimum, ~100,000 amber pieces were collected (14, 15) over a span of decades to obtain these samples. Destructive analysis of such rare specimens is not justified when it is unlikely to produce irrefutable results (3). The specimens were not found with dinosaur skeletal remains, so their biological affinity will remain open to debate. At present, the evidence supports a dinosaurian source for the filaments. Dove and Straker (1) have suggested neither a new analytical technique nor a more parsimonious interpretation for the specimens involved.



**Fig. 2.** Additional taphonomic details within photomicrographs of UALVP 52821 and 52822. (A) Diagrammatic explanation of taphonomic and structural features in UALVP 52821, bright-field image [figure S4C in (3)]. Stippling indicates topography, as well as the apparent cross-hatched surface or wrinkles within the outer wall of each filament. In the left filament, the gray area denotes an internal bubble in the vicinity of a large hole in the filament. In the right filament, horizontal arrows indicate cracks in the outer wall that do not extend all the way across the filament, and the filament appears to have collapsed along its midline, likely as a result of bending or torsion. (B) Taphonomic features in UALVP 52821 [figure S4D in (3)]. This is a dark-field image, highlighting surface details. Fractures within the amber appear as bright spots and are present in positions removed from the filaments (horizontal arrows); dark regions correspond to holes within the filaments (inclined arrows). (C and D) “Internal divisions” noted by Dove and Straker in UALVP 52822 (1) represent variations in pigmentation or cracks in the outer wall of the filament (inclined arrows) and do not appear to correspond to segmentation or internal divisions. (D) Bright spots in a linear arrangement (on the filament indicated with a horizontal arrow) appear to correspond to cross-hatching observed in UALVP 52821.

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