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TECHNICAL RESPONSE

DINOSAUR EVOLUTION

Response to Comment on “A Jurassic ornithischian dinosaur from Siberia with both feathers and scales”

Pascal Godefroit,^{1*} Sofia M. Sinitza,² Danielle Dhouailly,³ Yuri L. Bolotsky,⁴ Alexander V. Sizov,⁵ Maria E. McNamara,^{6,7} Michael J. Benton,⁷ Paul Spagna¹

Lingham-Soliar questions our interpretation of integumentary structures in the Middle-Late Jurassic ornithischian dinosaur *Kulindadromeus* as feather-like appendages and alternatively proposes that the compound structures observed around the humerus and femur of *Kulindadromeus* are support fibers associated with badly degraded scales. We consider this hypothesis highly unlikely because of the taphonomy and morphology of the preserved structures.

Although Lingham-Soliar considers that we disregarded the taphonomic tribulations of >150-million-year-old fossils (1), he fails to explain the marked regionalization across the dinosaur's body of taphonomic processes implied by his own hypothesis. Indeed, more than 500 isolated bones and partial skeletons have been collected at Kulinda so far (2), revealing that the different integumentary structures are systematically associated with specific anatomical regions: small nonoverlapping scales in the distal hindlimb (distal tibia and pes) and the manus, larger imbricated scales in the tail, monofilaments in the head and the thorax, groups of 6 to 7 filaments that diverge from a basal plate in the proximal parts of the limbs (humerus and femur), and clusters of ribbon-shaped elements around the proximal tibia.

Lingham-Soliar does not query our interpretation of the scales around the distal hindlimb and tail [figure 2, A to C, in (2)]. These are preserved as continuous dark carbonaceous outlines with a high degree of relief, and yet with no preserved internal or surface structures or textures. In other body regions [figure 2, E to I, and figure 3 in (2)], however, integumentary features are preserved as a series of discrete, near-two-dimensional outlines and include numerous filaments. If, according to Lingham-Soliar's hypothesis (1), those filaments represent collagen fibers or fiber bun-

dles, it is surprising that they are not preserved in the numerous (more than 20) partial or whole tails of *Kulindadromeus*, given that the tail should have contained particularly high amounts of collagen for structural support. Moreover, Lingham-Soliar (1) fails to explain how scales should be selectively degraded and/or dislocated around the humerus and femur but never around the distal tibia and tail. Indeed, the scales adjacent to the humerus and femur are organized into a regular hexagonal pattern and are thus unlikely to be severely degraded, in contrast to Lingham-Soliar (1). To our knowledge, there is no taphonomic or biological mechanism that could explain different modes of preservation of integumentary features in the tail and in the distal parts of the limbs, versus those in proximal regions. Thus, the different morphological and taphonomic characteristics of the structures preserved in the tail and distal parts of the limbs, and those preserved in the rest of the body, support our interpretation that the two sets of features represent fundamentally different structures—the fossilized remains of scales and feathers, respectively.

Further, the morphology and arrangement of the fossil structures are not consistent with those of degraded collagen. In Lingham-Soliar's previous studies of purported integumentary collagen in fossils [e.g., (3–7)], the collagen is preserved as very densely packed, abutting fibers. In contrast, the simple monofilament structures in *Kulindadromeus* are widely spaced, filling only a 30 to 40% fraction of visible area [(2), e.g., figure 2I]. Is Lingham-Soliar arguing for selective preservation of only some collagen fiber bundles? Additionally, the monofilaments in *Kulindadromeus* show constant width along their length and are straight to slightly curved. We have not observed these features in our ongoing experiments simulating the degradation of avian collagen. Instead, our experiments reveal that the collagen fiber bundles of the dermal stratum compactum progressively dissociate and ultimately degrade into a dense tangled mass of highly anastomosing fibrils (Fig. 1). Our decay experiments using feathers, however, reveal that these are much more robust and retain gross morphological characteristics for a longer period during decay. This is consistent with other studies demonstrating that collagen has a lower preservation potential than keratin (8–10). The state of preservation of the monofilaments thus supports our interpretation that they represent keratinous structures rather than collagen fibers or fiber bundles.

Lingham-Soliar (1) also states that “varied filament angles” are evident in the *Kulindadromeus* fibers and uses this as evidence that they are collagen fiber bundles. He is correct in that the monofilaments above the head [figure 2, E and F, in (2)] in INREC (Institute of Natural Resources, Ecology, and Cryology, Chita, Russia) K4/22 do show marked variation in orientation. However, in this case, Lingham-Soliar does not invoke taphonomic processes (effects of transport and decay) to explain the observed random orientation of particularly thin filaments. Ninety percent of the thicker filaments around the ribcage [figure 2, G and I, in (2)] are consistently angled within a 10° to 15° interval in INREC K4/33. The orientation and organization of the filaments associated with the “basal plates” around the humerus and femur are also regular [figure 3, A to E, in (2)].

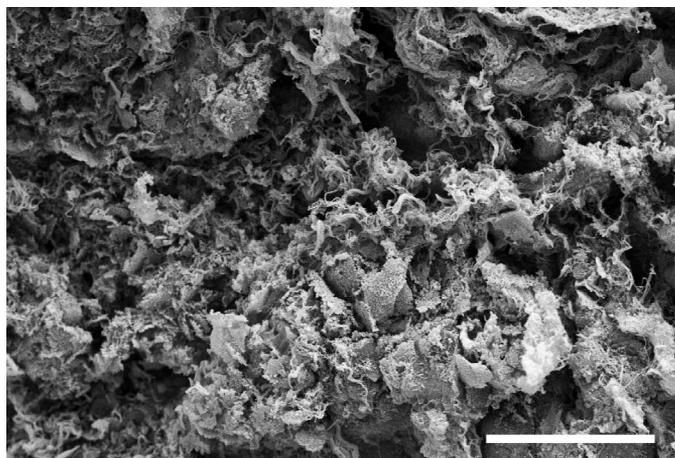


Fig. 1. Scanning electron micrograph of dermal collagen from the extant zebra finch, *Poephila guttata*, degraded for 6 months in artificial freshwater in the laboratory. [Image courtesy of MEM/Patrick Orr (University College Dublin)]

¹Directorate, Earth and History of Life, Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B-1000 Brussels, Belgium. ²Institute of Natural Resources, Ecology, and Cryology, 26 Butin Street, 672 014 Chita, Russia. ³UJF-CNRS FRE 3405, AGIM, Université Joseph Fourier, Site Santé, 38 706 La Tronche, France. ⁴Institute of Geology and Nature Management, FEB RAS, 1 Relochny Street 675 000, Blagoveschensk, Russia. ⁵Institute of the Earth Crust, SB RAS, 128 Lermontov Street, 664 033 Irkutsk, Russia. ⁶School of Biological, Earth, and Environmental Science, University College Cork, Cork, Ireland. ⁷School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK.

*Corresponding author. E-mail: pascal.godefroit@naturalsciences.be

This highlights an important contradiction in Lingham-Soliar's hypothesis between the purported severe degradation and dislocation of the scaly structures around the humerus and femur and the observed constant orientation and organization of the so-called underlying collagen support fibers.

Lingham-Soliar compares the size of the filaments in *Kulindadromeus* with that of bundles of collagen fibers in marine tetrapods. The validity of a direct comparison between integumentary collagen in marine tetrapods and a terrestrial dinosaur is uncertain given the marked differences in mechanical stresses acting upon the skin in these different animals. Indeed, Lingham-Soliar and his colleagues showed that the organization of collagen fibers into thick bundles is linked to high tensile stiffness and efficiency of the locomotory organs in high-speed marine tetrapods (4, 7). In the basal theropod *Sinosauropteryx*, collagen forms parallel strands of thin (< 0.05 mm) fibers (5), contrasting with the discrete and much thicker (up to 0.4 mm) monofilaments in *Kulindadromeus*.

Lingham-Soliar (1) states that ribbon-like structures occur as structural collagen in blood vessels, the linea alba (which separates the central band of abdominal muscles), and the rectus sheath. The arrangement, size, and morphology of the ribbon-like structures are strongly dissimilar to those of a network of circulatory vessels, which typically shows frequent branching and a reduction in

diameter distally. Additionally, thick bands of connective tissue in the linea alba and rectus sheath occur in the human body where large muscles connect either to each other or to bone. It is highly unlikely that *Kulindadromeus* possessed similar particularly large muscles in the region of the tibia, and thus it is unlikely that the ribbon-like structures represent structural collagen. Lingham-Soliar also claims that the ribbon-like structures could also plausibly represent plant or inorganic material. Energy-dispersive x-ray spectroscopy reveals a primarily carbonaceous composition for those structures. Various paleobotanists (E. Bugdaeva, Sun Ge, J. Dejax, and C. Prestianni) failed to recognize plant material in these fossil structures. Again, it would be extremely difficult to explain why plant material is consistently located adjacent to the distal tibia in *Kulindadromeus* and arranged in such regular arrays.

In conclusion, we affirm our interpretation of the simple and branched integumental appendages in *Kulindadromeus* as feather-like structures. This interpretation is the most parsimonious, given the increasing fossil evidence of widespread feather-like structures among dinosaurs [e.g., (11–14)] and their likely presence in other archosauriforms (15, 16). Lingham-Soliar's model (1) requires three unlikely taphonomic scenarios: (i) collagen in *Kulindadromeus* was preserved bet-

ter than keratin during decay; (ii) decay processes were highly selective, preferentially removing parts of scales only in specific body regions; and (iii) decay of collagen in *Kulindadromeus* resulted in lower abundance and spacing of fibrils than exists, to our knowledge, in any extant organism.

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