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Response to Lingham-Soliar: Dinosaur protofeathers: pushing back the origin of feathers into the Middle Triassic?

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In a recent article, Lingham-Soliar (in press) comments on the identification of integumental structures in dinosaurs, concluding that "the scientific methodology is questioned by its failure to make phenomena perceivable by objective means, by questionable rationalizations in critical issues, and by lack of consideration of exceptions to the postulated thesis". A major part of his article focuses on the identification of bristle-like integumental structures on the tail of a psittacosaur fossil from the early Cretaceous of China (Mayr et al. 2002). Lingham-Soliar (in press) harshly criticized this latter study as unsound, but since its results were incorrectly reflected and some of the claims are incorrect, I feel urged to respond to his notes.

A theropod ancestry of birds has been proposed long before any integumental structures were known, and is supported by numerous derived skeletal similarities (see, e.g., Prum 2002 for a review). Interpretation of the filamentous structures in theropod dinosaurs from the early Cretaceous Jehol Formation as feather homologues is certainly more plausible than Lingham-Soliar's hypothesis that they represent ossified tendons "after decay and displacement", which is at odds with the fact that ossified tendons are usually tightly attached to the vertebral column, which in the skeletons in question is hardly dissociated.

Psittacosaurs are not closely related to birds, and I agree with Lingham-Soliar that an a priori homologization of the bristle-like tail appendages with avian feathers is not warranted.

Contrary to the impression caused by Lingham-Soliar's (in press) incomplete citation, however, the psittacosaur bristles have not been interpreted as "protofeathers" by Mayr et al. (2002). The full paragraph, of which Lingham-Soliar cited only the first sentence, reads "[i]f the "bristles" of *Psittacosaurus* can be shown to be homologous to the filamentous structures of theropod dinosaurs, similar structures may have already been present in a more comprehensive clade including ornithischian dinosaurs. At present, however, this conclusion would be premature and more detailed investigations on the microstructure and biogeochemistry [...] of the integumentary structures of *Psittacosaurus* and theropod dinosaurs need to be carried out. Without further evidence, there remains the possibility that the "bristles" of *Psittacosaurus* are greatly modified scales" (Mayr et al. 2002: 364).

Lingham-Soliar (in press) further questioned interpretation of a dark stripe along these bristles a hollow lumen, whose presence would conflict with an interpretation of these structures as collagen fibers or ossified tendons. I will not discuss whether a lumen represents a "nothingness" (Lingham-Soliar in press) or may eventually be filled with organic matter. However, this stripe, which occurs in the center of numerous bristles, certainly is not an artifact of "some form of diagenesis" (see the detailed description in Mayr 2002). Lingham-Soliar (in press) noted that "what seriously undermines this thesis for a hollow lumen is the presence of a degraded bristle in one area". However, interpretation of the allegedly "degraded" psittacosaur bristle (Lingham-Soliar in press: fig. 3) is simply incorrect. Examination of the original fossil would have immediately shown that the bristles are not preserved on the same level as the surrounding matrix, but are elevated relative to it (probably because a sand blasting tool was used for preparation, which more easily removed the soft matrix than the harder fossil remains). The shape of the bristles thus does not necessarily reflect their original shape at the time the fossil was embedded in the sediment, and the frayed margins of some bristles are an artifact of the preparation of the fossil that was done before its acquisition by Forschungsinstitut Senckenberg. In the case of the bristle Lingham-Soliar

depicted in the out-of-focus inset of his Figure 3, the outer tube is not "degraded", but was destroyed during preparation.

If Lingham-Soliar had examined the actual specimen, he would have also recognized that the allegedly darker color of the two bristles in the upper right corner of his Figure 3 is a photographic artifact of vignetting, i.e., reduced brightness in the image periphery. Certainly we do not "see the 'black' color extending the entire diameter of the 'bristle'", and in the original image (Mayr et al. 2002: fig. 3c) the narrow black stripe is clearly visible in at least the lower of these bristles.

Lingham-Soliar (in press) left it to the reader, to decide whether the study of Mayr et al. (2002) represents good science. However, interpretation of subtle features from digital images alone hardly is a step in the right direction, and I also question whether the "Adobe Photoshop Eyedropper tool" constitutes the "up-to-date technology" the author asks for the interpretation of fossils.

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