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REVIEWS AND DISCUSSIONS

Reply to: "Insects with 100 Million-Year-Old Dinosaur Feathers are not Ectoparasites" and "Crawlers of the Scale Insect *Mesophthirus* (Homoptera Xylococcidae) on Feathers in Burmese Amber—Wind Transport or Phoresy on Dinosaurs?"

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Abstract—We described ten nymph specimens of an insect, *Mesophthirus engeli* (incertae sedis), from the mid-Cretaceous Myanmar (Burmese) amber, preserved together with partially damaged dinosaur feathers. Based on the ectoparasitic morphological characters of these tiny insect nymphs, we concluded that *Mesophthirus engeli* was the earliest known feather-feeding insect and that integument-feeding behaviors of insects appeared during or before the mid-Cretaceous along with the radiations of feathered dinosaurs including birds. Grimaldi and Vea raised some concerns about these feather-feeding insects and supposed that the nymphs of *Mesophthirus engeli* were crawlers of scale insects, i.e. nymphal stages of Coccoidea, coincidentally co-occurring with damaged feathers. Shcherbakov (2022, this issue) accepted and developed the argumentation of Grimaldi and Vea (2021). We would like to address their concerns here.

Keywords: *Mesophthirus*, Myanmar amber, mid-Cretaceous, feather-feeding, ectoparasitic insect, fossil

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INTRODUCTION

Our study (Gao et al., 2019) of *Mesophthirus engeli,* a new taxon from mid-Cretaceous Burmese (Myanmar) amber is based on only two nymphal stages, so we were very cautious about the taxonomic position of these supposedly feather-eating insects and did not assign them to any one of the known orders of insects. *Mesophthirus* Gao , Shih, Rasnitsyn & Ren, 2019 are certainly not true Mallophaga, and there is no reason to expect them to have the typical characters of the latter. In particular, the size of eggs and early nymphs mentioned by Shcherbakov (2022, this issue), could have remained small or even decreased, and strong adaptations for reliable fixation onto the feathers and hair of the host had not yet developed. There is even less reason to believe that they were as host-specific as a modern feather-feeding insect. Nymphs of *M. engeli* Gao, Shih, Rasnitsyn & Ren, 2019 (Fig. 1) indeed show a number of morphological characters similar to those of the nymphs of both Coccoidea and Phthiraptera (Price and Graham, 1997), such as small eyes, short antennae with a small number of short segments, tarsi with one claw and a small number of segments, a wingless and dorsoventrally flattened body, short legs, etc., as described in our work and listed by Grimaldi and Vea (2021).

In fact, these characters are common in various ectoparasitic insects (Price et al., 2003). However, *M. engeli* is easily distinguished from the nymphs of mealybugs by its body shape being round-quadrangular, and not almost regular oval (cf. Grimaldi and Vea, 2021, text-figs. 1a, 1b); clear boundaries between the

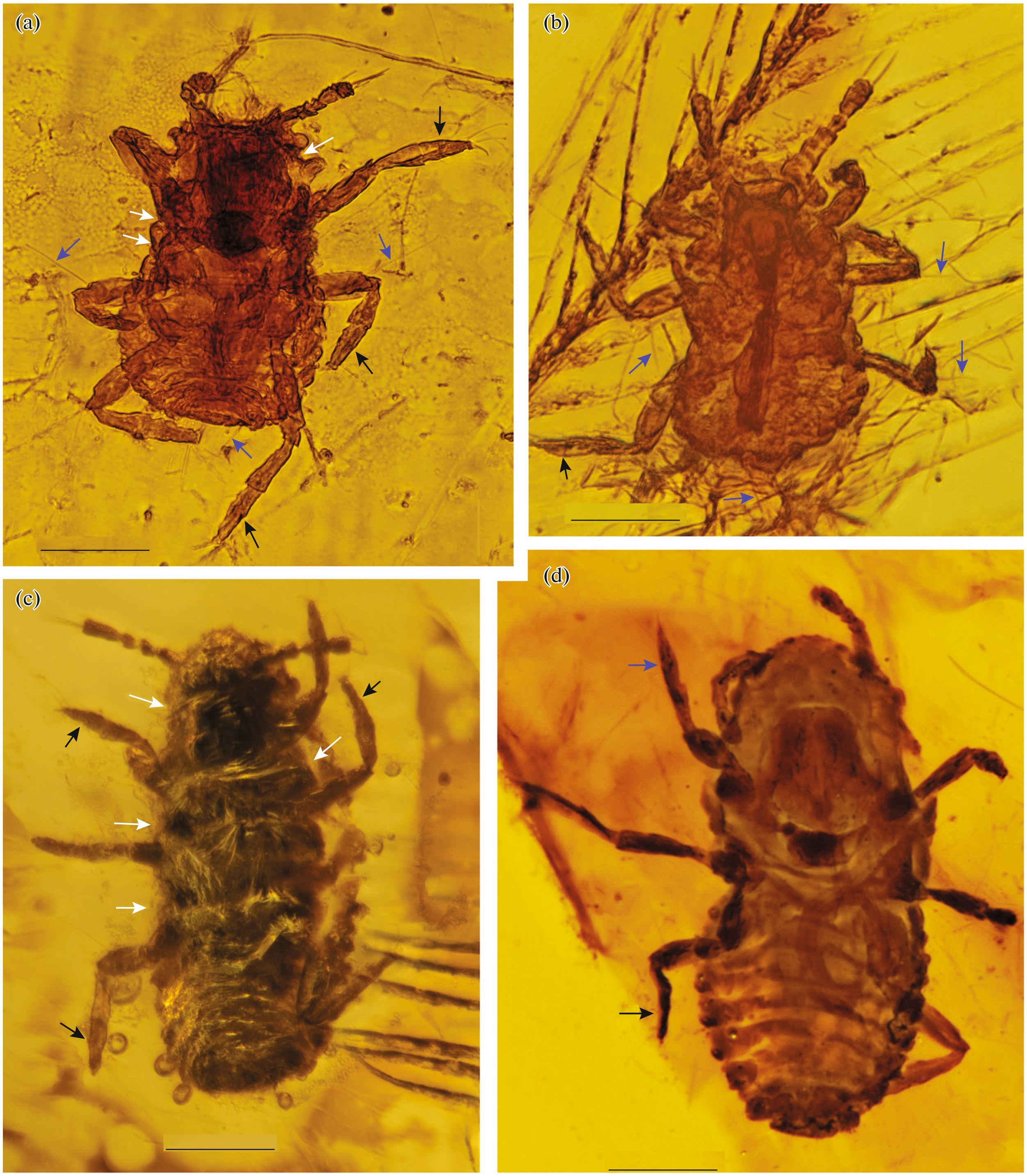

Fig. 1. *Mesophthirus engeli* Gao, Shih, Rasnitsyn et Ren, 2019 from Mid-Cretaceous Burmese amber: (a) paratype CNU-MA2016005, (b) paratype CNU-MA2016001, (c) paratype CNU-MA2016010, (d) holotype CNU-MA2016009; (a, b) younger nymphs, (c, d) nymphs of the next instar; all the same scale. White arrows indicate the boundary of the head, thoracic and abdominal segments; black arrows indicate the boundaries of tarsal segments; blue arrows indicate long hairs; scale bar 50 μm.

head, prothorax, mesothorax, and metathorax, thorax, and the first segment of the abdomen (white arrows in Fig. 1), in contrast to the oval body of scale insects, almost always without constrictions (see Grimaldi and Vea, 2021, text-figs. 1a and 1b).

The only exceptions are the most basal scale insects (some Orthezioidea), but they are also characterized by the same oval body with a relatively narrow head and a tapering apex of the abdomen. The tarsus has two long segments (Fig. 1, black arrows), with claw-

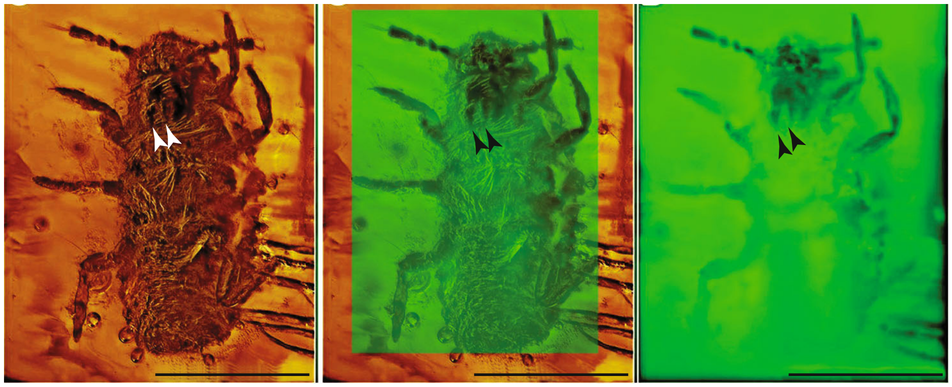

Fig. 2. *Mesophthirus engeli* Gao, Shih, Rasnitsyn et Ren, 2019 from Mid-Cretaceous Burmese amber, paratype CNU-MA2016010; on the left in incident light, on the right in transmitted light, in the middle—a combination of incident and transmitted light; the arrows show the shading originally taken for the jaws; scale bar 0.1 mm.

like pretarsus (Fig. 1a, fore tarsus): tarsi of larvae and female scale insects are single-segmented, rarely two-segmented, with very short basal segment. In addition to well-marked setae, three on the apex of the antenna and two on the pretarsus, one very long, thin setae on each femur (first discovered by Shcherbakov; corresponding fossa on femur often more visible than seta itself) and much shorter setae on apex of abdomen (Fig. 1, blue arrows). On the contrary, most scale insects are characterized by a pair of long setae at the top of the abdomen.

Two successive developmental stages of *M. engeli* (Figs. 1a, 1b and 1c, 1d, respectively) differ very clearly in size as well (body length 141–143 and 167–229 μm, respectively; Gao et al., 2019, pl. 1), and based on the body shape (according to Shcherbakov, the head of the earliest instar nymphs is turned up and the apex of the abdomen is retracted), the contour is concave or straight in front and behind, while in the later instar nymphs the anterior and posterior ends of the body are more straightened and the contour is rounded. In scale insects, the first two nymphal stages differ much more strongly, and the rare sexual dimorphism of scale insect crawlers does not reveal an analogy with the two forms of *Mesophthirus* nymphs, since the dimorphism of crawlers is associated with settlement adaptations (Cook et al., 2000), which is not the case for *Mesophthirus* nymphs. Some remarks of our opponents are fair and very important. We described the gnawing mouthparts of *Mesophthirus* (Gao et al., 2019, p. 2, figs. 2b, 3e). In fact, we mistook an incidental darkening, possibly of a secondary nature, of the ventral shield of *Mesophthirus* (Fig. 2, arrows) for mandibles and palps: an easy error of excessive enthusiasm and insufficient caution in conclusions. On the other hand, Grimaldi and Vea, followed by Shcherbakov, find in the *Mesophthirus* a piercing-sucking apparatus typical of mealybugs and, in particular, stylets housed in a loop-like manner in a special structure called the crumena. In our opinion, they are making the same mistake. The object that Grimaldi and Vea identify in *Mesophthirus* as crumena with stylets, firstly, varies its shape from individual to individual (Figs. 1a, 1b, 1d), which is much more consistent with an intestine than a crumena, and secondly, its content is sinuous, not sclerotized [weakly darkened, except for the case when two branches of the loop overlap each other (Figs. 1a, 1b, 1d)].

Stylets are composed of thin, flexible, but very dense filaments, which should be very distinct and only smoothly curved in the light, and not sinuous (cf. Grimaldi and Vea, 2021, text-fig. 1a), and such a structure is completely absent in *Mesophthirus*. Obviously, the structure in *Mesophthirus* is simply an intestine, traced approximately from the level of the posterior dorsal border of the head, if not even more rostral, making a wide loop in the abdomen (in its anterior half at the second nymphal stage) and extending to the anus (cf. Figs. 1a, 1b, 1d, traced by the white line in Fig. 3). What Shcherbakov designates as the final loop of folded stylets (long arrow in his text-fig. 2a) corresponds to the intersegmental border, exactly the same as in front of, behind and to the left of the designated area. Unfortunately, no actual mouthparts can be found in *Mesophthirus*.

Our erroneous identification of the mandibles prevented us from correctly attributing the sclerite that escaped attention (Gao et al., 2019, text-figs. 2a, 2c) and determine its boundaries. This is probably a clypeus, less likely is its homology with the prosternum of wingless Psocoptera of the family Liposcelididae, considered as the closest to the ancestors of biting and sucking lice (see, for example, Nel et al., 2005, text-fig. 5; Polilov, 2016, text-figs. 3.1, c, 3.4, c, 3.16, b). The clypeus is weakly expressed in younger nymphs (Figs. 1a, 1b), but clear and dense in older ones (Figs. 1c, 1d). In younger nymphs, the tentorium shows through the clypeus, confirming that this is the clypeus. The distal margin of the clypeus runs close to the anterior margin of a clearly demarcated (in older

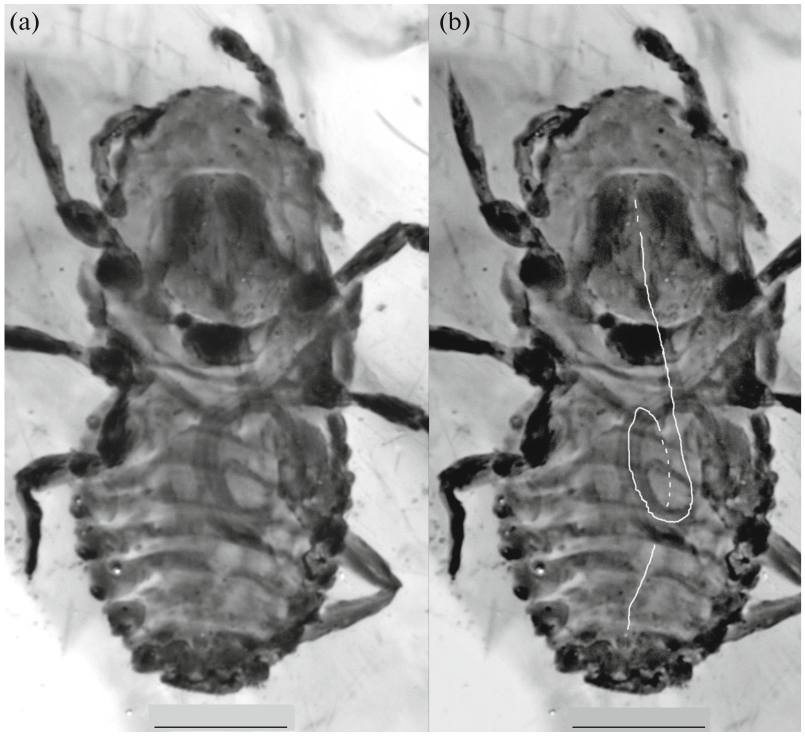

Fig. 3. *Mesophthirus engeli* Gao, Shih, Rasnitsyn et Ren, 2019 from Mid-Cretaceous Burmese amber, holotype CNU-MA2016009 (green channel), gut (traced white, on the right); scale bar 50 μm.

nymphs) transverse plate with lateral cords along the posterior margin of the clypeus towards the fore coxae.

This is either a large labrum, like in Psocoptera (in Rhynchota, the labrum is always small, narrow; Singh, 1971), or a prosternum. True, in incident light (Fig. 1c) it does not stand out at all, so it cannot be ruled out that this is an internal structure. In any case, a transverse plate with a wide straight distal edge cannot be a vestige of a jointed proboscis, especially since the "stylets", as our opponents understand them, pass along the side of this plate, and not along the center of its front edge, i.e., not through the tip of a 'proboscis'.

There is an extensive literature on different types of feathers of birds and feathered dinosaurs in Burmese amber (Xing et al., 2016a, 2016b, 2017, 2019). Based on the alternating position of barbs on the shaft of the feather and barbules on the shaft and barbs, we consider the feathers with *Mesophthirus engeli* to be from non-Pennaraptoran coelurosaurs, known from Burmese amber.

The collection of our laboratory (Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China) contains many feathers in Burmese amber. In the course of this study, in search of feather-eating arthropods, we examined more than two thousand samples of amber with feathers. As indicated in our article (Gao et al., 2019), only two feathers were found in two pieces of amber (AMBER No. 01 and AMBER No. 02) with insects attached to feathers, and all these 10 insects, of similar structure, were assigned to *M. engeli.* All other feathers studied over the past three years were almost completely free from damage. Only the feather in AMBER No. 01 with nine nymphs of *M. engeli* was damaged (holes). Such damage could be caused by some arthropods. Indeed, *M. engeli* No. CNU-MA2016006 (Gao et al., 2019, text-fig. 1g) and CNU-MA2016007 (ibid., fig. 1d) are preserved with legs and/or antennae fixed on barbules; fragments of a feather were also found under no. CNU-MA2016001, around head no. CNU-MA2016004 (ibid., Fig. 1c, red arrows) and CNU-MA2016005 and near no. CNU-MA2016008 (e.g., Gao et al., 2019, text-figs. 1b, 1e, 1f, 1i). The microscopic and more or less regular size of the holes in the feather, affecting only the barbules, i.e., the most delicate elements of the feather, indicate very small size and selective behavior of the cause of these holes, and excludes random occurrence or feeding by ordinary keratophages, as Shcherbakov (2022, this issue) suggests. This makes it most plausible that *Mesophthirus* was responsible for this damage. All these data confirm that the insects described by us are preserved in situ, and their accidental presence on a feather seems completely unbelievable. Moreover, nothing of the kind has yet been identified from Burmese amber, despite the fact that over the past two decades, hundreds of experienced specialists and amateurs have looked through millions of pieces of amber and found there myriads of tiny insects (including many scale insects), spiders, mites, plants, etc. Under these circumstances, the chance of finding TWO pieces of amber with TEN specimens of *Mesophthirus* on two feathers, one of them with numerous obvious traces of characteristic damage, entirely randomly, is beyond any conceivable probability.

Based on these considerations and on the observed and documented morphological features of the nymphs we have described, we believe that *Mesophthirus engeli* is not a vagrant mealybug and is not closely related to Hemiptera. Until new material is obtained, primarily of the adult insect, which would make it possible to clarify its position in the system, *M. engeli* should be considered as an insect of unclear position (Order incertae sedis), feeding on feathers and, possibly, close to the roots of the parasitic branch of Psocoptera (Psocodea: Parasita), including biting and sucking lice.

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CONFLICT OF INTERESTS

The authors declare that they have no conflicts of interest.

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