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New insects feeding on dinosaur feathers in mid-Cretaceous amber

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Due to a lack of Mesozoic fossil records, the origins and early evolution of feather-feeding behaviors by insects are obscure. Here, we report ten nymph specimens of a new lineage of insect, *Mesophthirus engeli* gen et. sp. nov. within Mesophthiridae fam. nov. from the mid-Cretaceous (ca. 100 Mya) Myanmar (Burmese) amber. This new insect clade shows a series of ectoparasitic morphological characters such as tiny wingless body, head with strong chewing mouthparts, robust and short antennae having long setae, legs with only one single tarsal claw associated with two additional long setae, etc. Most significantly, these insects are preserved with partially damaged dinosaur feathers, the damage of which was probably made by these insects' integument-feeding behaviors. This finding demonstrates that feather-feeding behaviors of insects originated at least in mid-Cretaceous, accompanying the radiation of feathered dinosaurs including early birds.

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Many extant insects have ectoparasitic lifestyles, and spend lots of time or entire life (obligate) on the skin, hairs, or feathers of warm-blooded vertebrates, sucking blood or feeding on skin debris, hairs, or feathers of their hosts[1]. Ectoparasitic insects cause discomforts or sickness of hosts, reduce production of livestock, and damage avian feathers, etc[2,3]. More seriously, ectoparasites transmit diseases as vectors[4], having resulted in catastrophic illnesses and deaths in human history[3,5]. Two major groups of extant ectoparasites, Phthiraptera (true lice), and Siphonaptera (fleas), have attracted much attention from scientific community mainly due to their medical and agricultural significance. One lineage of the former group feed on feathers and soft skin of birds[6,7]. While blood-feeding insects have been described from the Jurassic and Cretaceous[8–10], integument-feeding insects have never been reported from the Mesozoic to our knowledge. The earliest known fossil louse, *Megamenopon rasnitsyni*, is from the Eocene of Germany (44 Mya)[11,12], and it is already fully modern in form and assigned within Amblycera. The evolution of feather- and other integument-feeding insects in the Mesozoic thus remains obscure[11,13], even though many feathered dinosaurs including early birds have been described from the Jurassic and Cretaceous[14].

Here, we report ten nymph specimens of an ectoparasitic insect clade, *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen et. sp. nov. assigned to Mesophthiridae Gao, Shih, Rasnitsyn & Ren, fam. nov. of order Incertae sedis. These nymph insects crawled and fed on two feathers preserved in two pieces of amber, AMBER No. 01 and AMBER No. 02, from the mid-Cretaceous of Myanmar. AMBER No. 01 includes nine specimens and AMBER No. 02 has only one specimen. The strata producing the Myanmar (Burmese) amber was radiometrically dated at 98.79 ± 0.62 Ma[15]. The date corresponds to the early Cenomanian, that is, the earliest Late Cretaceous. However, displaying clear traces of redeposition, the Myanmar amber is considered to be older than enclosing rocks[16]. Therefore, we refer the amber age informally as mid-Cretaceous.

Results

Systematic paleontology.

Insecta Linnaeus, 1758
Order Incertae sedis
Family Mesophthiridae Gao, Shih, Rasnitsyn & Ren, fam. nov.

Type genus. *Mesophthirus* Gao, Shih, Rasnitsyn & Ren, gen. nov. (Figs. 1–3)

Diagnosis. Based only on nymphs of elder developmental stages, while the adults unknown. Small insects, body wingless and dorsoventrally flattened, head fully hypognathous, slightly narrower than thorax; eyes reduced; huge mandible with at least four teeth; maxillary palp four-segmented; antenna with five antennomeres, last antennomere slightly enlarged, with two long setae and one short seta extending from apex, last antennomere longer than sub two antennomeres combined; thorax equal to abdomen in length, with pronotum distinctly longer than, and about as wide as mesonotum; tarsus with three tarsomeres, as long as tibia, basitarsus as thick as tibia, last (3rd) tarsomere very small, possessing a claw, and a pair of long and stiff setae.

Genera included. Only the type genus, *Mesophthirus* Gao, Shih, Rasnitsyn & Ren, gen. nov., described here.

Remarks. Comparing with Phthiraptera, Mesophthiridae shows several plesiomorphies: toothed chewing mouthpart, robust thorax with pronotum not reduced in length and width, leg with tarsus 3-segmented and spiracles present on meso- and metathorax as well as on the first two abdominal segments. However, several putative morphological synapomorphies are shared by these Cretaceous specimens: antenna with two apical long stiff setae and one short seta, leg with a single claw accompanied with two long clavate pretarsal setae. Based on these characters, it is difficult to place Mesophthiridae to any known order within Insecta, therefore we identify the taxon as an order incertae sedis here, pending more new material to be found in the future to further confirm its phylogenetic position. For more details concerning possible taxonomic position of the new family, see "Discussion" section.

Mesophthirus engeli Gao Shih, Rasnitsyn & Ren, sp. nov. (Figs. 1–3, Supplementary Figs. 1 and 2)

Type species. *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, sp. nov.

Etymology. The generic name is derived from the Greek prefix "meso-" and Greek "phtheir" (latinized as phthirus) meaning lice. Gender masculine. The specific name "engeli" is dedicated to Dr Michael S. Engel, for his outstanding contribution to entomological research.

Species included. Only the type species *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, sp. nov.

Diagnosis. As for family because of monotypy.

Materials. All specimens are nymphs of two different developmental stages (see "Discussion" section below). The holotype, CNU-MA2016009 (Fig. 1j and Fig. 2a–c), together with remaining six paratypes, CNU-MA2016001–CNU-MA2016003 (Fig. 1a–c), CNU-MA2016006—CNU-MA2016008 (Fig. 1g–i) and CNU-MA2016010 (Fig. 3b–e) are in an elder stage, and paratypes CNU-MA2016001 (Fig. 1a), CNU-MA2016004 (Fig. 1e) and CNU-MA2016005 (Fig. 1f) are in an earlier stage. The locations of CNU-MA2016001—CNU-MA2016009 with feather are displayed in Fig. 1, and more details about the morphology of this group are shown in Fig. 2. All these specimens are deposited in the Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China.

Locality and horizon. The amber specimen was collected from Kachin Province (Hukawng Valley) of northern Myanmar, mid-Cretaceous; see "Methods" section for more information about provenance of the specimens.

Description. Holotype, CNU-MA2016009 (Figs. 1a, j, and 2a–c). Small nymph, just 229 μm long excluding antenna (Table 1), but the largest one among these ten specimens. Head slightly thinner than the thorax in width, the length about 1/3 of the body length. Compound eyes reduced to single ommatidium, near globular shape, evidently protruding from both sides of head. Ocelli absent. Antenna short (46 μm) and robust, slightly shorter than the width or length of head, with five antennomeres. Antennal scape slightly enlarged, shorter than pedicel, the first flagellomere shortest and thinnest, and the last or 5th one longest. Two long stiff setae, longer than the last flagellomere, together with a short seta, fixed on the apex of the antenna (Fig. 2a, b). No annulations or other setulae visible. Chewing mouthpart area very clear, mandibles slightly extended vertically, enlarged and having four sharp teeth (Fig. 2b, c). The left and right mandibles apparently can cross with each other. Maxillary palpus with four segments and tapered from base to top (Fig. 2c). Thorax equal to abdomen in width, but shorter than the latter. Pronotum clear, about as wide as, and distinctly longer than either mesonotum or metanotum. Legs short, about 92, 115, and 134 μm, referring to fore leg, middle leg, and hind leg, respectively. Fore legs with coxae enlarged and nearly bulb shaped. Trochanter visible. Femora oval-shaped, much thicker and slightly longer than tibiae. Three

Fig. 1 AMBER No. 01 with the specimens of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. from the mid-Cretaceous of Myanmar. **a** Photo of the whole feather and the locations of the insects, corresponding to the Supplementary Fig. 1. **b**–**i** Paratypic specimens CNU-MA2016001 to CNU-MA2016008. **j** Holotypic specimen CNU-MA2016009. **k** Parts of the feather show complete areas at basal part and adjacent largely damaged area between barbs. Representative, star in white referring to relatively complete barbules, star in blank referring to large areas of damages. Scale bars, 1 mm (**a**), 100 μm (**b**–**j**), and 0.5 mm (**k**).

tarsomeres present, basitarsus longest, the 3rd or last tarsomere very small (Fig. 2a, b). The femora of middle legs absolutely longer than those of fore legs or hind legs. Abdomen at least eight segmented, and the first segment narrow, connecting with metathorax and forming a clear constriction between thorax and abdomen. The 4th segment widest and gradually tapered to the terminal. Spiracles presented on both sides of each abdominal segment. Adults unknown.

Descriptions of the paratypes. Additional nine specimens of paratypes are shown in (Figs. 1–3, Supplementary Figs. 1 and 2), and more detailed descriptions are given in Supplementary Note 1. In CNU-MA2016001 (about 141 μm in body length excluding antenna, Figs. 1b and 2g), CNU-MA2016004 (about 143 μm, Fig. 1e and Supplementary Fig. 2a) and CNU-MA2016005 (about 143 μm, Figs. 1f and 2d), the last antennomeres have irregular crinkling on the surface. The apical parts of their heads between two antennae, are horizontal rather than convex and arch-shaped of that of the holotype or other paratypes. In addition, these three specimens possess much fatter and softer abdomens, and are faintly delimited about the boundaries of each segments. In CNU-MA2016002 (Figs. 1c and 2h), CNU-MA2016005 (Figs. 1f and 2d), and CNU-MA2016010 (Fig. 3), only one pretarsal claw is found on the apex of every tibia (Figs. 2d, h and 3c). Two very long stiff setae protrude outside from the base of the pretarsus, and the length of these setae approximately equal to whole tarsi (Fig. 3c). The boundaries among pronotum, mesonotum, and metanotum are distinct in CNU-MA2016010 (Fig. 3c–e). In CNU-MA2016003 (Figs. 1d, 2e, f), we can clearly see the dorsoventrally compressed body shape and spiracles are present on the meso- and metathorax, and consequently on the sides of abdominal segments (Fig. 2e). The tergum is strongly sclerotized, which could be observed in CNU-MA2016003 (Fig. 2e, f) and CNU-MA2016010 (Fig. 3c–e).

Discussion

All these ten nymphs look very similar in morphology but have minor distinctions, and they may be easily divided to two different groups. The first group includes CNU-MA2016001 (Figs. 1b and 2g), CNU-MA2016004 (Fig. 1e and Supplementary Fig. 2a), and CNU-MA2016005 (Figs. 1f and 2d), and the remaining ones, including the holotype, can be arranged as the second group. The members of the first group have relatively smaller body size (under 145 μm, Table 1), much wider abdomens than their thoraxes, horizontal terminals of abdomens and apex of heads and compressed 5th antennomere. In contrast, the specimens within the second group possess bodies over 157 μm in length, heads with arched top and clavate and smooth 5th antennomere. In addition, the abdomens of these insects within the second group gradually tapered toward to terminal, and the

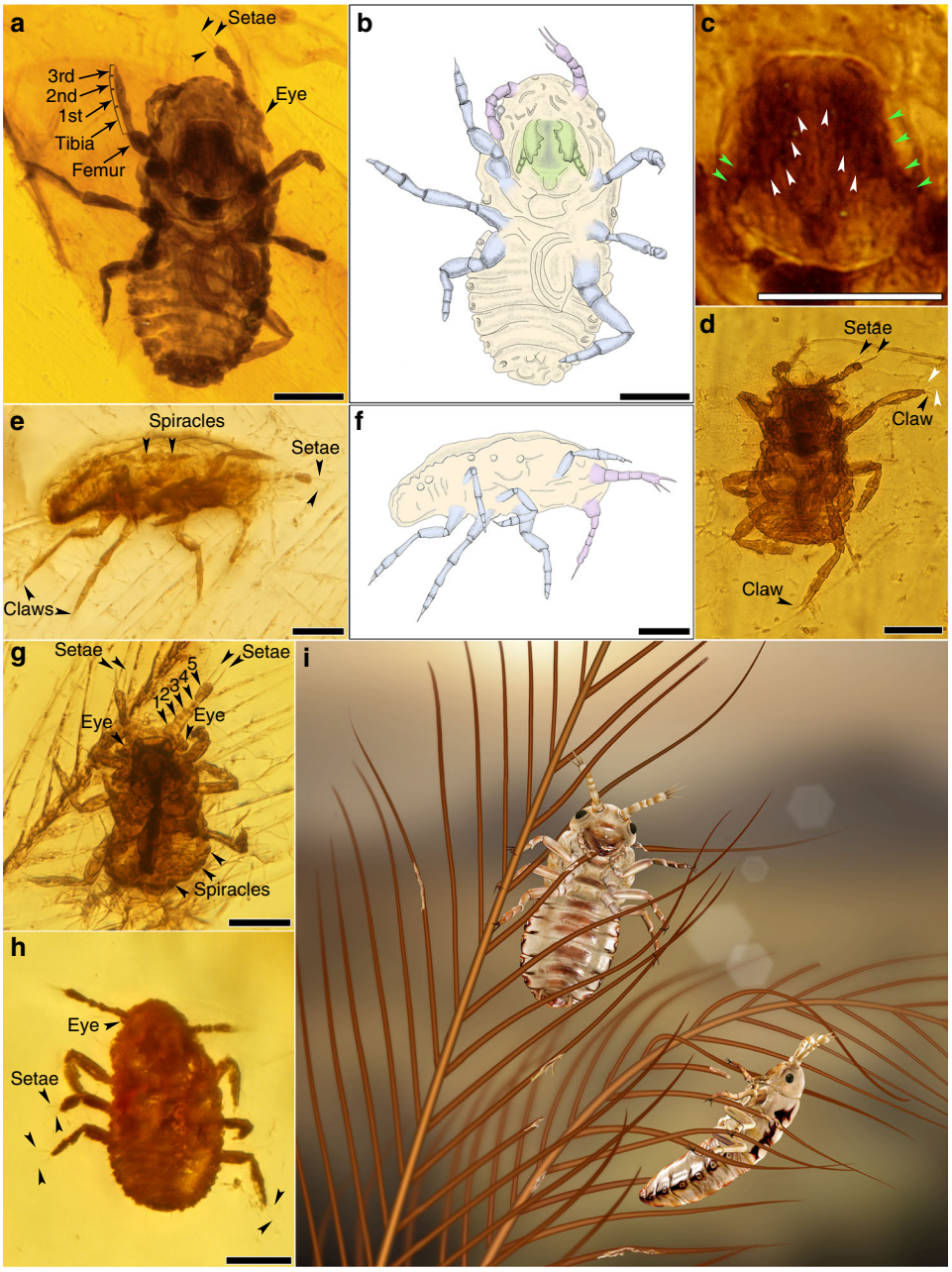

Fig. 2 Holotype and paratypes of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. within the AMBER No. 01 from mid-Cretaceous. **a**, **b** Holotype and line drawing of *M. engeli* sp. nov., CNU-MA2016009. **c** Enlargement of mouthpart of a shows details of mandible and maxillary palpi, arrows in white show teeth and arrows in green show the segments of palpi. **d** Paratype of *M. engeli* sp. nov., CNU-MA2016005, shows setae on the apex of antenna and single pretarsal claw. **e**, **f** Paratype and line drawing of *M. engeli* sp. nov., CNU-MA2016003, show spiracles on meso- and metanotum. **g** Paratype of *M. engeli* sp. nov., CNU-MA2016001, shows details of antennae, eyes, and spiracles on the side of abdominal segments, indicating the size scale of *M. engeli* sp. nov. with a feather barbule. **h** Paratype of *M. engeli* sp. nov., CNU-MA2016002, shows the two long stiff setae on the outsides of pretarsus. **i** Artist's reconstruction of *M. engeli* sp. nov. of elder development stage feeding on the feather. It was reconstructed mainly based on the morphological characters of the holotype CNU-MA2016009, with supplemental consideration of CNU-MA2016001 and CNU-MA2016003. Colors of the insects are conjectural and referring to the general color of living feather-feeding lice. Scale bars, 50 μm.

boundaries between each abdominal segment are much clearer than those of the first group. We identify these two groups as two different but adjoining developmental stages of *Mesophthirus engeli*, and their abdomens and antennae might grow to extend with age, same as the body size. We estimate that the adults of *M. engeli* should be significantly larger than these nymphs, about 0.4–0.5 mm in body lengths.

Mesophthirus shares many features of ectoparasitic function, i.e., wingless and dorsoventrally compressed body, reduced eyes, short antennae, robust and short legs unsuitable for quick movement or jump, pretarsus very small with one single claw, etc., which suggest that *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. had an ectoparasitic lifestyle. As aforementioned, these ten specimens are preserved in close association with two feathers in two pieces of amber, respectively. The two feathers are probably contour feathers, but they differ in some features. The feather embedded in AMBER No. 01 (Fig. 1a and Supplementary Fig. 1a) is 13.6 mm long as preserved and is

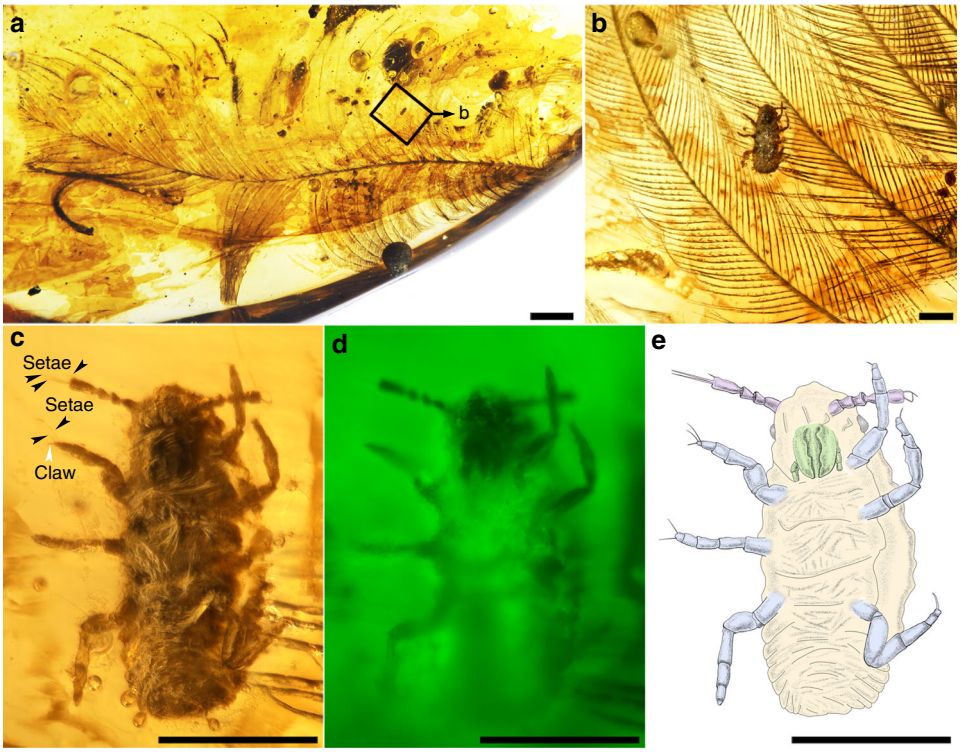

Fig. 3 AMBER No. 02 with the paratype of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. from the mid-Cretaceous of Myanmar. **a** Photo of the whole feather and the location of the insect. **b** Enlargement of the insect crawling on the feather. **c** Paratype of *M. engeli* sp. nov., CNU-MA2016010. **d** CNU-MA2016010 under green epifluorescence. **e** Line drawing of **c**. Scale bars, 1 mm (**a**), 0.1 mm (**b**–**e**).

Table 1 Dimensions of all ten specimens from mid-Cretaceous (μm).

No.	Body excluding antennae	Antenna excluding setae	Fore legs	Mid legs	Hind legs
CNU-AM2017001	141	56	>42	>81	>95
CNU-AM2017002	167	51	>76	-	>71
CNU-AM2017003	203	56	90	107	>106
CNU-AM2017004	143	51	>69	>57	>119
CNU-AM2017005	143	44	>88	>89	>119
CNU-AM2017006	198	50	>90	>88	>111
CNU-AM2017007	183	>37	>73	-	>86
CNU-AM2017008	>156	59	>100	-	>108
CNU-AM2017009	229	46	92	115	134
CNU-AM2017010	216	44	>70	100	>80

missing the proximal half. The feather has a proportionally slender rachis and two vanes of similar size. The barbs are positioned alternately along the rachis, and barbules are present along both barb ramus and rachis (rachidial barbules). These features are also seen in the feather of probably a non-pennaraptoran coelusaurian dinosaur preserved in a Myanmar amber[17]. There are nine insects of *M. engeli* found in AMBER No. 01 (Fig. 1a and Supplementary Fig. 1a). Five of them (Fig. 1c, e, f, i and j) are preserved near the feather and the other four insects are preserved with the feather (Supplementary Fig. 1). CNU-MA2016001 and CNU-MA2016003 are preserved on the vane of the feather, with feather debris around CNU-MA2016001 (Fig. 2e and g). CNU-MA2016006 (Fig. 1g and Supplementary Fig. 2b) is preserved with its legs hooking two adjoining feather barbs with the assistance of antenna (Supplementary Fig. 2b). In addition, feather debris are found around CNU-MA2016004 (Supplementary Fig. 2a) and CNU-MA2016008 (Supplementary Fig. 2d). CNU-MA2016007 is preserved with its legs tightly hugged a feather barb (Fig. 1h and Supplementary Fig. 2c). The feather of AMBER No. 02 (Fig. 3a) is nearly complete, missing the basal portion and the tip, with the preserved rachis length of 12.7 mm. It is clearly pennaceous as indicated by a robust rachis and closed vanes characterized by the pennaceous arrangement of the barbules, but it is not a flight feather based on the following features: the spacing of the neighboring barb rami is relatively wide and the distal portion of the vanes is open. This feather is probably derived from a pennaraptoran dinosaur[18]. CNU-MA2016010 is positioned in the proximal portion of the vane (Fig. 3a, b), more specifically, on the interlocking barbules between two rami.

The feather within AMBER No. 01 has multiple regions showing damages (Fig. 1a, k), though no damage has been observed in the other feather in AMBER No. 02 (Fig. 3a). Numerous neighboring barbules are missing their distal portion of variable length, resulting in many holes in both the leading and trailing vanes of the feather (Fig. 1k), which is in a stark contrast to the basal part close to rachis when the barbules are preserved intact, suggesting that this damage was caused by insect chewing instead of a damage due to use. Associated with the large toothed

mandible of *Mesophthirus* (Figs. 2a–c and 3c–e), these damaged areas might be interpreted as caused by integument-feeding behaviors by these insects. The association of the specimens of *Mesophthirus* with feathers within two different pieces of amber and the clear consumption–damage strongly suggest that *Mesophthirus* is ectoparasitic, living, and feeding on feathers (Fig. 2i). The damaged areas of the feather in the AMBER No. 01 are very similar to the consumed areas or holes of bird feathers caused by living lice[19,20]. These two feathers are significantly different from each other in general morphology, suggesting that they might belong to different dinosaur groups. If this is true, *Mesophthirus* was probably not host-specific as extant lice or fleas. However, these two feathers are possible to be derived from the same dinosaur species given that feathers are highly variable in morphology across the avian body. Nevertheless, the new findings indicate that the feather-feeding behavior of insects appeared at least as early as the mid-Cretaceous (Fig. 2i).

Since the new taxon of *Mesophthirus* is established based on only nymphs, it is difficult to place *Mesophthirus* within an accurate modern insect order, even though two developmental instars were described here. *Mesophthirus* shares several putative synapomorphies (or possibly, homoplasies) with Liposcelidae + Phthiraptera for their apterous and dorsoventral flattening body, reduced eyes, short antenna under ten antennomeres[21,22]. However, different from living lice (Phthiraptera)[6,7], *Mesophthirus* specimens have a few putative plesiomorphies, such as four-segmented maxillary palpus, spiracles on meso- and metathorax and on the first two abdominal segments, and relatively long and wide pronotum. *Mesophthirus* is also noteworthy for the two stiff and long setae on pretarsi and three clavate setae on the apex of antenna, but no other setae are found on all these ten specimens. Such specialized setae distinctly helped *Mesophthirus* to hold on to the feathers of their hosts avoiding being shaken off (Figs. 1a, g, 2g and Supplementary Fig. 2b), which are attributed to adaptations to ectoparasitic habit. Therefore, it is prudent to only provisionally assign these specimens from the mid-Cretaceous to *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen et. sp. nov. within Mesophthiridae Gao, Shih, Rasnitsyn & Ren, fam. nov. of order Incertae sedis, while more material, especially the adults to be found in the future, will further help to define the exact phylogenetic position.

In summary, the new findings provide the earliest known evidence about the origin of ectoparasitic insects feeding on feathers, which strongly support that the integument-feeding behaviors of insects appeared during or before the mid-Cretaceous along with the radiations of feathered dinosaurs including birds.

Methods

Localities and repositories. This fossil study included two pieces of amber with ten specimens of insects. Both pieces of amber were collected from the Hukawng Valley of Kachin State, in northern Myanmar, a village named Noije Bum (N26° 150′, E96°340′) about 18 km southwest of the town of Tanai[23,24]. The amber is dated as earliest Upper Cretaceous, about 98.79 ± 0.62 Ma[15,24]. The study of Burmese amber has a long history going back over 100 years, and over 1000 species of insects had been named by the end of 2018[25], including beetles[26], ants[27], termites[28], lacewings[29], etc. The amber specimens were acquired by Mr Fangyuan Xia in 2015, who donated these two pieces of amber for studying in 2016. All type specimens are permanently deposited at the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator) under the collection number CNU-MA2016001—CNU-MA2016010.

Amber preparation. The amber piece of AMBER No. 01 is nearly ovoid, about 2.6-cm long and 1.9-cm wide, but very thin (about 5 mm in maximum). The nine insects it contains are preserved in various position and distributed in different places and layers within this piece of amber, and dissection or polish may easily destroy this amber and insects. Only the left side of this amber was trimmed by razor blade, then polished with emery papers and diatomite mud. For observing the specimen of CNU-MA20160010, AMBER No. 02 was trimmed to a subtriangular chip, and the edges are about 0.9 mm in maximum.

Specimen imaging. We have tried to use Confocal Laser Scanning Microscopy and MicroXCT even SRμCT to observe more morphological characters, but with no success. It might be caused by the fact that these insects are too small and nearly semitransparent. Photographs were taken by using a Nikon SMZ 25 microscope with a Nikon DS-Ri 2 digital camera system, and the enlarged images of details of the specimens were taken using a Nikon ECLIPSE Ni microscope with a Nikon DS-Ri 2 digital camera system. Photographs with green background were taken using green epifluorescence as the light source attached to Leica DM5500B with an ANDOR Zyla digital camera system (Fig. 3d). Line drawings were prepared by using Adobe Illustrator CC and Adobe Photoshop CC graphics software.

Nomenclatural acts. This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through and standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSIDs for this publication are urn:lsid:zoobank.org:pub: F962A768-8075-4319-BBFC-BE438209533D (for publication); urn:lsid:zoobank.org:act:3040E401-99AD-4257-8784-58A46448884F (for Mesophthiridae fam. nov.); urn:lsid:zoobank.org:act:AE0355E2-5A56-48DB-8A1A-74F4FAC2ED8D (for *Mesophthirus* gen. nov.); urn:lsid:zoobank.org:act:0439DE1E-84BE-48D6-AEAB-147C2B13631D (*Mesophthirus engeli* sp. nov.).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data needed to evaluate the conclusions are present in the paper and/or the Supplementary Information files. All data related to this paper are available from the corresponding authors upon reasonable request.

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Author contributions

D.R. and T.P.G designed the research. T.P.G., X.C.Y, C.K.S., A.P.R., X.X. and D.R. performed morphological, comparative studies, and line drawings. T.P.G, S.C. and C.W. took the photographs and prepared the life reconstruction artwork. T.P.G., X.C.Y., C.K.S., A.P.R., X.X. and D.R. drafted the paper.

Competing interests

The authors declare no competing interests.

Additional information

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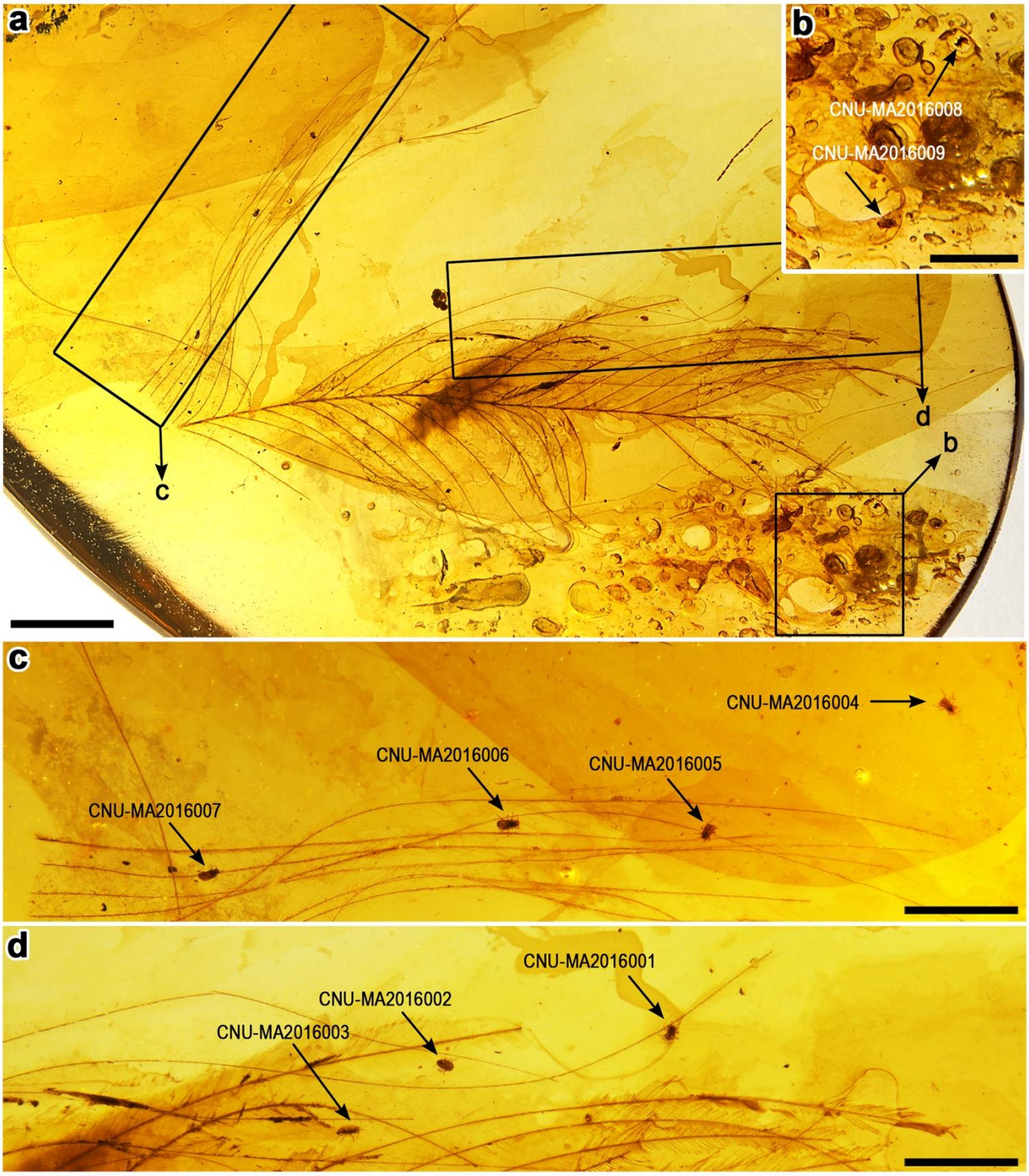
Supplementary Information

New insects feeding on dinosaur feathers in mid-Cretaceous amber

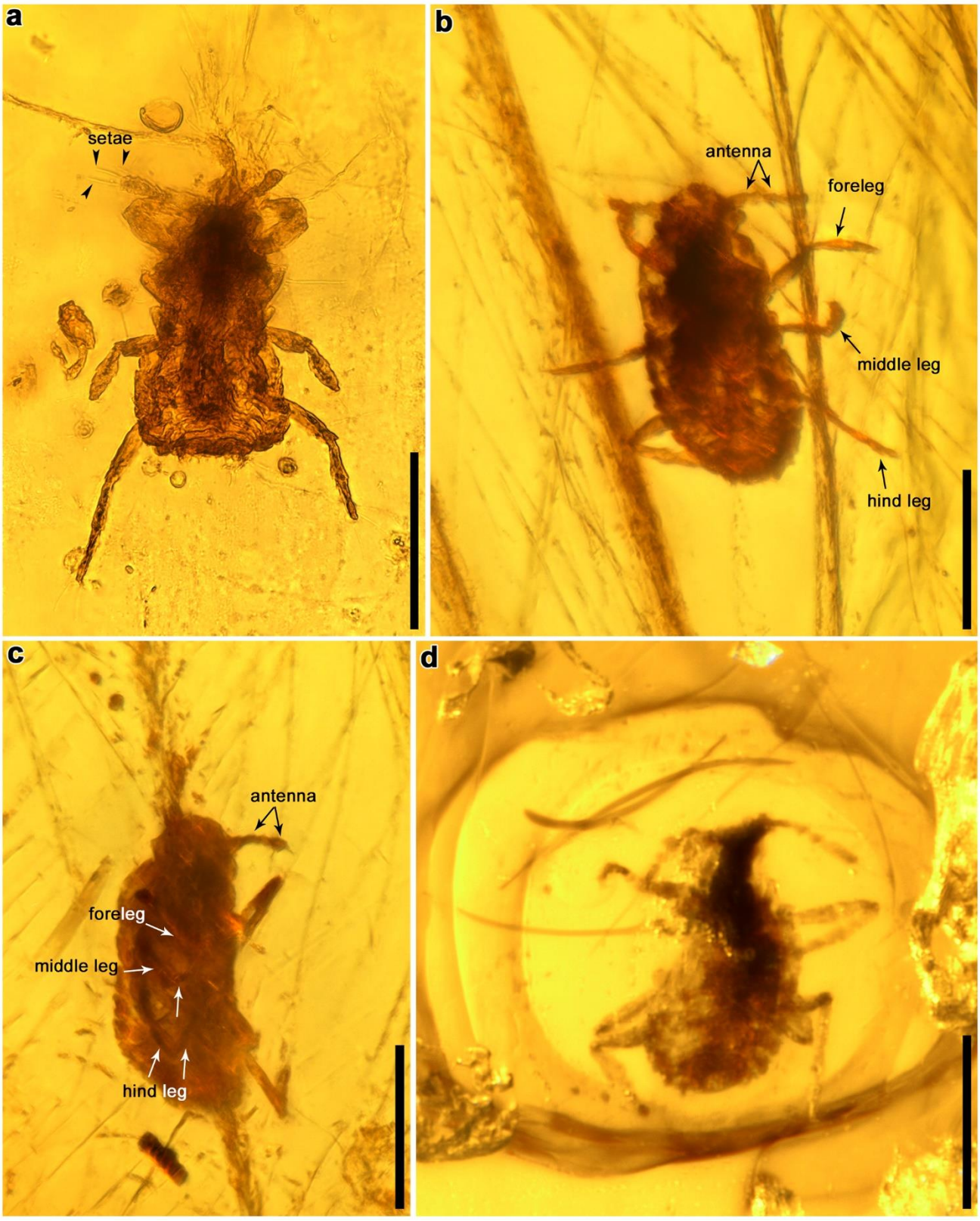
Gao et al.

This PDF file includes:

- Supplementary Fig. 1. Details of the feather within AMBER No. 01 showing locations of the specimens CNU-MA2016001 to CNU-MA2016009.
- Supplementary Fig. 2. Enlarged photos of paratypes of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. embedded in AMBER No. 01.
- Supplementary Note 1: Descriptions of the paratypes of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov.



Supplementary Figure 1 | Details of the feather showing locations of the specimens CNU-MA2016001 to CNU-MA2016009. (**a**) Photo of the AMBER No. 01 with feather. (**b**) Locations of specimens of CNU-MA2016008 and CNU-MA2016009. (**c**) Locations of specimens of CNU-MA2016004 to CNU-MA2016007. (**d**) Locations of specimens of CNU-MA2016001 to CNU-2016003. Scale bars, 2.0 mm (**a**) and 1.0 mm, (**b**–**d**).



Supplementary Figure 2 | Enlarged photos of paratypes of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. embedded in AMBER No. 01. (**a**) Specimen CNU-MA2016004 referring to Fig. 1e. (**b**) Specimen CNU-MA2016006 referring to Fig. 1g. (**c**). Specimen CNU-MA2016007 referring to Fig. 1h. (**d**). Specimen CNU-MA2016008 referring to Fig. 1i. Scale bars, 100 μm (**a**–**d**).

Supplementary Note 1:Descriptions of the paratypes of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov.

Paratype, CNU-MA2016001, the earlier developmental stage of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. (Figs 1b and 2g, Supplementary Fig. 1d).

Very tiny insect, crawling on the surface of feather, closer to the barb of feather. Details of the characters are indistinct since the specimen overlapped with the barbules and other feather fragments. Body only 141 μm in length excluding antenna. Head slightly thinner than thorax, and the division between head and thorax unclear. Eyes ovoid, nearly protruding out of the sides of the head symmetrically. Antennae robust and longer than the width of head (56 μm), thinner than the adjacent feather barbs but thicker than the barbules. Scape broader than pedicel, and the latter thicker than the 3rd antennomere. The 4th antennomere is the thinnest one, about 1/3 as long as the 5th or last antennomere, which is nearly claviform with clear constrictions. Only two long and sharp setae visible and fixed on the apex of the antenna, and can easily hold the feather barbule observed from the left antenna (Fig. 2g). Thorax longer than abdomen, but thinner than the latter. Prothorax, meso- and metathorax fused and the divisions difficult to be identified. The bases of legs distantly spaced. Profemur slightly shorter than mesofemur, and the latter shorter than metafemur, but nearly similar in thicknesses. The combination of mesotibia + mesotarsus nearly equal to that of metatibia + metatarsus in length. Abdomen soft and bilaterally extended, the boundaries between each segment ambiguously, and spiracles present on both sides of the abdomen, especially clear on the right side. The body has a rough surface without other setae. Irregular feather fragments scattered around this specimen.

Paratype, CNU-MA2016002, the elder developmental stage of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. (Figs 1c and 2h, Supplementary Fig. 1d)

Body about 167 μm in length, preserved away from the feather (Supplementary Fig. 1d). Head thinner than thorax, and the top of the head outward, forming an arched-shape. Antenna relatively thin, only 4 antennomeres visible in dorsal view. Pedicel cylindrical, and the 1st and 2nd flagellomeres nearly caliciform. The apical antennomere longest. Two stiff setae, slightly shorter than the last antennomere, extended from the apex. Thorax connected with head and abdomen tightly, but the boundaries unclear. The profemur nearly equal to mesofemur or metafemur in length. In hind legs, femur longer than tibia, and the latter equal to tarsus in length. Three tarsomeres present, protarsus very small but having two very long stiff setae protruding out of outside surface. These two setae apart from each other for a long distance. Abdomen with 6 segments visible, tapering from the basal segments to terminal.

Paratype, CNU-MA2016003, the elder developmental stage of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. (Figs 1d, 2e and 2f, Supplementary Fig. 1d)

This specimen is the only one observed in the right lateral view. Body about 203 μm high, dorsoventrally compressed. The back of the whole body clearly sclerotized, including tergum and part of the head. Head fully hypognathous, having dimly edge toward to thorax. Antenna with the 4th antennomere thinnest but equal to front antennomeres in length. The 5th or last flagellomere possessing three apical stiff setae, and two of them much longer, equal to the last flagellomere in length. Scape thicker then pedicel, and as thick as the last antennomere. The divisions of pronotum, meso- and metanotum obscured in the lateral view. Profemur thicker than protibia, and equal to the tarsus in length. The protarsus slightly longer than tibia, three tarsomeres tapered. Mesocoxae elongated, and the apical part clearly thinner than the basal part. Instead, the mesofemora and mesotibiae calycinal. Metacoxae and metatibiae slightly longer than those of middle legs. Two plate-like spiracles present on the side of mesothorax and metathorax. Abdomen short, 8 segments visible, and the terminal bending inward. Spiracles distributed on the side of each abdominal segment.

Paratype, CNU-MA2016004, the earlier developmental stage of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. (Fig. 1e, Supplementary Figs. 1c and 2a)

The specimen was preserved with a similar gesture as CNU-MA2016001, and two fore legs crossed in the front of head. Many feather fragments were found around its head. Body about 143 μm in length. Head with the antenna compact. Five antennomeres visible; the 4th one shortest, and the last one longest with many clear constrictions. Three stiff setae fixed on the top of the last flagellomere, two long and one short. Thorax clearly thinner than abdomen. Profemur thicker than mesofemur, than metafemur. Mesotibia cup-shaped, thicker but much shorter than that of hind legs. A pair of long and stiff setae present on the outside of the pretarsi of every middle and hind leg. Abdomen soft and lateral extending, but the boundaries of segments unclear.

Paratype, CNU-MA2016005, the earlier developmental stage of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. (Figs. 1f and 2d, Supplementary Fig. 1c)

Body about 143 μm in length, as high as the specimen CNU-MA2016004. Head with the eyes nearly spherical, clearly protruding out of the sides of head. The top part of the head between two antennae horizontal. Antenna with 5 antennomeres visible and compact, scape very thick, the 4th antennomere smallest and shortest, cup-shaped. The

5th or last flagellomere having many constrictions, and deformed. Thorax wider than head but clearly thinner than abdomen. In the ventral view, the divisions of prothorax, meso- and metathorax unclear, and fused together, but can be identified from the lateral sides. Bases of the left and right legs distantly spaced. Forelegs almost equal to middle legs, but slightly shorter than the hind legs. Protibia as long as combination of three tarsomeres together. The basitarsus close to cylindrical, shorter than the 2nd tarsomere, and the pretarsus very small, with only a sharp claw, which is slightly longer than the basitarsus. Two long and stiff setae protruding outside of basal part of the pretarsus, and both of them twice as long as the pretarsal claw. Abdomen bilaterally extending, the boundaries of the abdominal segments unclear. The terminal of the abdomen bending inward.

Paratype, CNU-MA2016006, the elder developmental stage of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. (Fig. 1g, Supplementary Figs. 1c and 2b)

A specimen crawling on feather and clearly holding two adjoining barbs via legs with assistance of antennae. Body about 198 μm high, with the head distinctly thinner than thorax or abdomen. The compound eyes right under antennae. Antenna as long as the width of head, and the part of head between two antennae prominent as an arch. Antenna with the 3rd and 4th antennomeres cup-shaped, equal in length. The thorax fused with the abdomen so that the division unclear. Abdominal segments cannot be distinguished, but tapered toward to the terminal.

Paratype, CNU-MA2016007, the elder developmental stage of *Mesophthirus engeli* Gao, Rasnitsyn & Ren, gen. et sp. nov. (Fig. 1h, Supplementary Figs. 1c and 2c)

The specimen distinctly wrapping a feather barb, left foreleg, left middle leg and left hind legs bending and holding the barb respectively; right foreleg and middle leg holding the same barb too. Body about 183 μm in length. The top part of head between antennae arched. The details of the thorax, legs and abdomen unclear. The terminal of abdomen slightly bending inward, and tightly attaching the barb.

Paratype, CNU-MA2016008, the elder developmental stage of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. (Fig. 1i, Supplementary Figs. 1b and 2d)

A specimen far away from the feather, but close to the specimen CNU-MA2016009, and several feather fragments distributing around. Body at least 156 μm in length. Head with the antenna longer than the width of head. Head thinner than thorax, and the latter thinner than abdomen. Profemur slightly shorter than the combined lengths of tibia and tarsus. Metafemur longer than metatibia. Metatibia cup-shaped, equal to the tarsus.

Paratype, CNU-MA2016010, the elder developmental stage of *Mesophthirus engeli* Gao, Shih, Rasnitsyn & Ren, gen. et sp. nov. (Fig. 3)

This specimen was found in the other piece of amber, AMBER No. 02, and provided more evidence and further confirmed the feather-feeding behaviors of *Mesophthirus engeli* gen. et sp. nov. CNU-MA2016010 is the second largest specimen among these new findings, the body about 216 μm in length, just smaller than the holotype CNU-MA2016009. Head fully hypognathous, slightly thinner than thorax, with the eyes protruding from both sides of head. Antenna shorter than the width or length of head, with 4 antennomeres visible, scape and pedicel relatively thick, the 2nd–4th antennomeres pedunculate, having relatively long stipe; the last antennomere club-shaped with smooth surface, and the terminal two setae very stiff, as long as the last antennomere (Fig. 3c). The top part of the head between the antennae arched, with the surface rough. Chewing mandible with the teeth structures unclear, maxillary palpus at least two segments visible. Thorax very large, equal to abdomen in length, clearly divided as prothorax, mesothorax and metathorax, no fusion, and the surface rough and scraggly, pronotum longest, reaching eyes (Fig. 3a and 3b). Legs robust. Profemur nearly equal to protibia or protarsus, but thicker than the latter. Tarsus including three tarsomeres, the basitarsus and the 2nd tarsomere thick and long, 3rd one very small, possessing one claw and two long clavate setae. The stiff and long setae as long as the tarsus and extending from the outside of protarsus, close to the basal part. The metafemur longer that mesofemur or profemur. The space between left legs and right legs very broad (Fig. 3d). Abdominal segments totally compacted, especially in the ventral view, difficult to identify the boundaries, but over 7 segments, the 1st segment widest, and gradually tapering off toward the terminal, the abdomen slightly bending to the ventral side.