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Report

Mid-Mesozoic Flea-like Ectoparasites of Feathered or Haired Vertebrates

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Summary

Parasite-host associations among insects and mammals or birds are well attended by neontological studies [1]. An Eocene bird louse compression fossil [2, 3] and several flea specimens from Eocene and Oligocene ambers [4–8], reported to date, are exceptionally similar to living louse and flea taxa. But the origin, morphology, and early evolution of parasites and their associations with hosts are poorly known [9, 10] due to sparse records of putative ectoparasites with uncertain classification in the Mesozoic, most lacking mouthpart information and other critical details of the head morphology [11–15]. Here we present two primitive flea-like species assigned to the Pseudopulicidae Gao, Shih *et* Ren familia nova (fam. nov.), *Pseudopulex jurassicus* Gao, Shih *et* Ren genus novum *et* species nova (gen. *et* sp. nov) from the Middle Jurassic [16] and *P. magnus* Gao, Shih *et* Ren sp. nov. from the Early Cretaceous in China [17]. They exhibit many features of ectoparasitic insects. Large body size and long serrated stylets for piercing tough and thick skin or hides of hosts suggest that these primitive ectoparasites might have lived on and sucked the blood of relatively large hosts, such as contemporaneous feathered dinosaurs and/or pterosaurs or medium-sized mammals (found in the Early Cretaceous, but not the Middle Jurassic).

Results

Herein, we report from the mid-Mesozoic of China two well-preserved fossil ectoparasitic insects, exhibiting many features of ectoparasitic insects, e.g., wingless body covered with stiff, posteriorly directed setae and bristles, short and beaded antennae, reduced eyes, absent ocelli, robust mouthparts with serrated stylets (laciniae), scythe-like pretarsal claws, and ctenidia on the tibiae. These specimens share with extant fleas, especially with the most basal flea lineage Tungidae [18], some striking similarities, but given a lack of some diagnostic features of Siphonaptera, their systematic positions are deemed as Order incertae sedis.

Taxonomy

Order Incertae sedis.

Family Pseudopulicidae Gao, Shih *et* Ren fam. nov.

Diagnosis. Robust and elongate piercing-sucking mouthparts with serrated stylets; antennae with more than 15 segments, flagellomeres compact; thorax relatively small, apterous; legs elongate with numerous stout setae, distinct ctenidia on the tibiae, and pretarsus with strong scythe-shaped claws; body covered with stiff, posteriorly directed setae and bristles.

Remarks. Different from extant fleas in the absence of pronotal and genal ctenidia on body (except for Tungidae), lack of the uniquely modified jumping hind legs, distinct ctenidia on the tibiae, more developed eyes, detailed structure of mouthparts with serrated stylets, antennae with more than 15 segments, not laterally compressed abdomen, and larger body size. Although *Tarwinia* [11] possesses many similar diagnostic characters, it is tentatively excluded from Pseudopulicidae fam. nov. due to lacking mouthpart information.

Pseudopulex Gao, Shih et Ren, gen. nov.

Type species. *Pseudopulex jurassicus* Gao, Shih *et* Ren sp. nov.

Etymology. The generic name is a combination of prefix pseudo-, indicating "with visual similarity to," and Latin word of Pulex, meaning "flea." Gender masculine.

Species included. The type species and *Pseudopulex magnus* Gao, Shih *et* Ren sp. nov.

Diagnosis. Same as familial diagnosis.

Pseudopulex jurassicus Gao, Shih et Ren, sp. nov., see Figures 1A–1J and Figures S1A–S1C available online

Holotype. CNU-NN2010001, a well-preserved almost complete body in ventral view (Figures 1A and 1B; Figures S1A and S1B). Deposited in the Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China.

Locality and Age. Jiulongshan Formation, the Late Middle Jurassic (Bathonian-Callovian boundary, 165 million years ago [Mya]) [16]; Daohugou Village, Ningcheng County, Inner Mongolia, China.

Etymology. The specific epithet *jurassicus* derives from Latin "*jurassicus*," referring to the age of this fossil.

Diagnosis. Different from *P. magnus* by the number of antennal segments, presence of tibiae ctenidia, and maxillary laciniae. Serrated teeth of *P. jurassicus* cover the entire surface of stylet, whereas those of *P. magnus* cover only the edges.

Description. Body length 17.00 mm excluding antennae. Head small and trapezoid shape. Eyes reduced and ocelli absent. Antennal flagellum 16 segments visible, short and stout, slightly compressed, connected to both sides of head in clear depressions (Figure 1G). Mouthparts specialized, long and strong (at least 3.44 mm), much longer than twice the length of head, labrum unclear, maxillary palps three segments visible as preserved, labial palps four segments preserved, but the exact number unknown, maxillary laciniae forming some deeply notched serrations, extending from base to tip (Figures 1A–1F). Thorax small, about one-fifth of the abdomen in length. Abdomen not laterally compressed, with eight segments based on eight spiracles (segmentation is not clear), covered with dense and long bristles directing posteriorly, possessing a pygidium with sensilia on the ninth tergite (Figure S1C). Legs unusually long, coxae slightly enlarged, tibiae bearing pseudocombs with short stout

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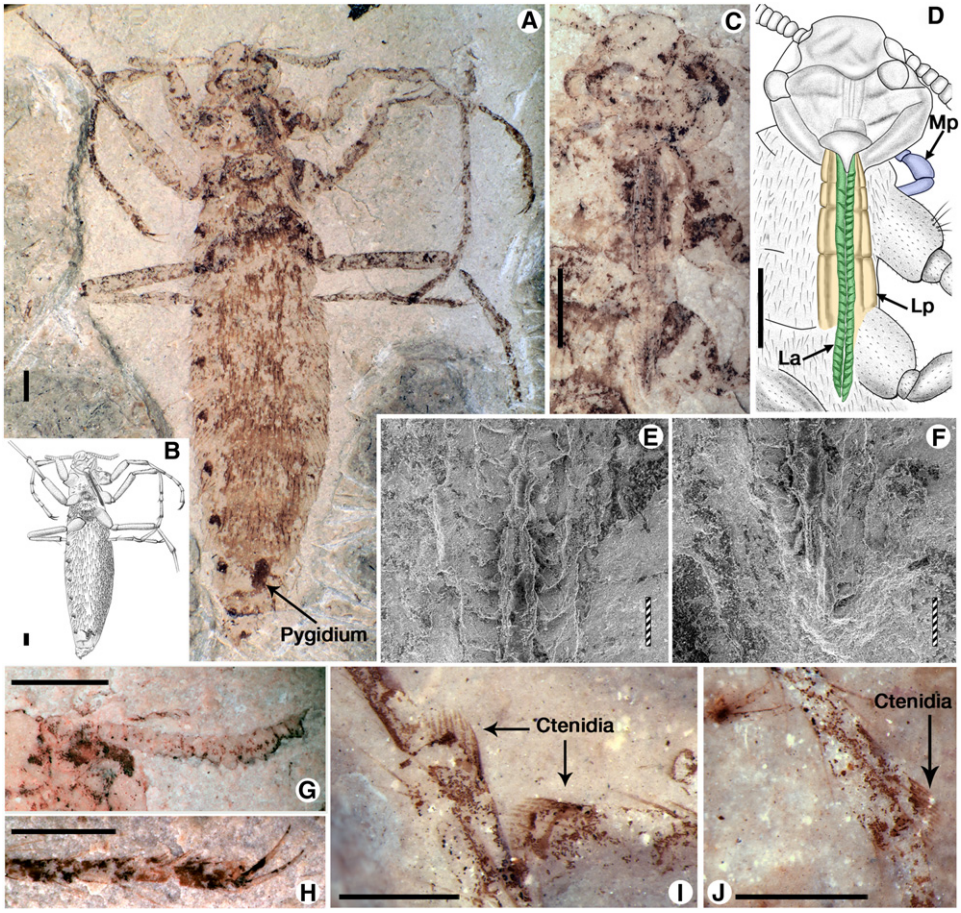

Figure 1. Holotype of *Pseudopulex jurassicus* Gao, Shih *et* Ren gen. *et* sp. nov., from the Late Middle Jurassic Jiulongshan Formation of Northeastern China, CNU-NN2010001

(A and B) Photograph and line drawing.
(C and D) Mouthpart photograph and morphological identification. Abbreviations are as follows: La, laciniae; Lp, labial palp; Mp, maxillary palp.
(E and F) SEM of mouthpart, middle, and tip parts.
(G) Right antenna.
(H) Claw of the left foreleg.
(I and J) Ctenidia of the tibiae.
Scale bars represent 1 mm (solid) and 0.1 mm (stippled) (see also Figure S1).

bristles (ctenidia, Figures 1A, 1B, 1I, and 1J), all legs possessing many spurs of different lengths, tarsus with five subsegments, and a pair of large scythe-like claws on the last tarsomeres of all legs (Figure 1H).

Pseudopulex magnus Gao, Shih et Ren, sp. nov., see Figures 2A–2F and Figures S2A and S2B

Holotype. CNU-ND2010002, a well-preserved almost complete body in ventral view (Figure 2A; Figures S2A and S2B).

Locality and Age. Yixian Formation, the Early Cretaceous (Early Aptian, 125 Mya); Duolun Village, Duolun County, Inner Mongolia, China [17].

Etymology. The specific name *magnus* is from Latin "*magnus*," referring to the large body size of this species.

Diagnosis. Different from *P. jurassicus* for the number and shape of the antennal segments, distinctly sharper maxillary laciniae, and much larger body size.

Description. Body huge, with length of nearly 22.82 mm excluding antennae; head relatively smaller, antenna with >16 segments, obviously compressed, shorter and more stout, placed in deep grooves on both sides of head; mouthparts elongate, robust, nearly 5.15 mm in length, maxillary laciniae bearing rows of teeth at the edges, each with a number of small cutting notches on the margin, other parts of laciniae covered with several parallel longitudinal ridges from base to tip (Figures 2B–2F). Abdomen massive (Figure 2A), not laterally flattened, basal segments wide but weakly and gradually narrowing toward apex; replete with dense setae and bristles; tarsus with five subsegments and a pair of large scythe-like claws on the last tarsomere; ctenidia not evident probably due to poor preservation; numerous spurs of various sizes on the inner sides of tibia and tarsus.

Discussion

Fossil insect ectoparasites with uncertain taxonomic placements from the Mesozoic are sparse, with only a few putative fossil specimens reported [9, 10]. *Saurophthirus longipes* with short and slender suctorial mouthparts from the Early Cretaceous Zaza Formation of Baissa is probably a mecopteroid ectoparasite of obscure relationships [13]. *Strashila*

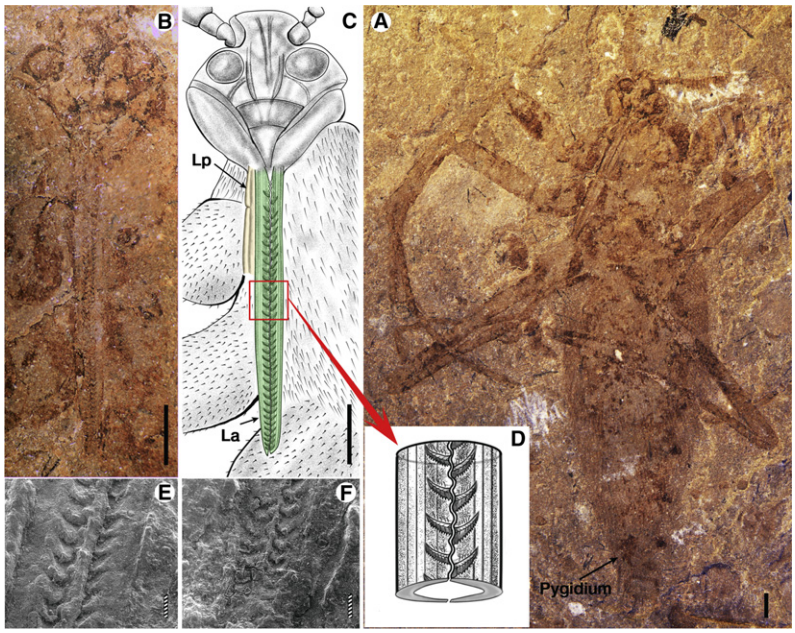

Figure 2. Holotype of *Pseudopulex magnus* Gao, Shih *et* Ren sp. nov., from the Early Cretaceous Yixian Formation of Northeastern China, CNU-ND2010002

(A) Photograph.

(B and C) Mouthpart photograph and morphological identification. Abbreviations are as follows: La, laciniae; Lp, labial palp.

(D) Enlarged drawing of laciniae.

(E and F) SEM of mouthpart, middle, and tip parts.

Scale bars represent 1 mm (solid) and 0.1 mm (stippled) (see also Figure S2).

incredibilis from the Late Jurassic of eastern Siberia [14] and *Vosila sinensis* and *Parazila saurica* from the Middle Jurassic of China [15] are probable ectoparasites of obscure taxonomic relationships and not related to fleas [9, 10]. *Tarwinia australis* from the Early Cretaceous of Australia [11], which possesses a reduced, wingless thorax, laterally flattened body, ctenidia on the tibiae, and a pygidium with sensilia to support its close relationship to fleas, but lacking mouthpart information, antennal flagellum with 15 segments, and long, slender legs with moderate-sized hind coxae have fueled debate regarding its attribution as fleas [9]. Due to insufficient fossil records, early associations among ectoparasitic insects and their hosts are still unclear.

Pseudopulex jurassicus and *P. magnus* possess many ectoparasitic characteristics such as wingless body covered with stiff, posteriorly directed setae and bristles, ocelli absent, eyes reduced, and legs with stout setae, and robust and elongate blood-feeding mouthparts modified for puncturing. The characteristics of elongate and slender legs with scythe-shaped pretarsal claws, row of ctenidia on the tibiae, and robust and elongate mouthparts differentiate these two new species from lice. Molecular studies indicate that Boreidae is the sister group to the fleas [18]. Short and beaded antennae and robust and elongate mouthparts separate these two from members of Boreidae. Compared to *Saurophthirus longipes* [18], the later lacks such strong mouthparts with rows of serration at the edges and a row of ctenidia on the tibiae. Hence, we can rule out placing these two species in the orders of Phthiraptera or Mecoptera.

As mentioned above, these two species have some flea features; the most convincing is that *Pseudopulex* possesses a pygidium with sensilia (although larger in size), which is found only in the recent fleas. Other similarities include robust and elongate piercing-sucking mouthparts, relatively small thorax without wings, strong scythe-shaped claws on pretarsus, and body covered with stiff, posteriorly directed setae and bristles. *Pseudopulex* is different from extant fleas by the following characteristics: absence of ctenidia on the body but presence of distinct ctenidia on the tibiae, lack of the uniquely modified jumping hind legs, and the laterally compressed body. Furthermore, *Pseudopulex* has more-developed eyes, longer antennae (more than 15 segments), and larger body size (17 mm for *P. jurassicus* and 22.8 mm for *P. magnus* versus about 2 mm for extant fleas) than extant fleas. It is interesting to note that Pseudopulicidae has some characters similar to Tungidae, considered to be the most basal flea lineage [18]. Both of them have robust and strong mouthparts with heavily denticulate laciniae, while lacking pronotal ctenidium and genal ctenidium on the body, which is covered with some irregular bristles [19–21]. The available information suggests that Pseudopulicidae is closely related to Siphonaptera and may represent a stem taxon of the siphonapteran lineage, but given that it lacks some diagnostic characters of Siphonaptera, it is deemed as Order incertae sedis in classification.

The piercing-sucking mouthparts are about 3.44 mm long for *P. jurassicus* and 5.15 mm for *P. magnus*, more than twice as long as the head, which are in sharp contrast to about 1.5 mm (about 0.6 times as long as the head) for *Saurophthirus longipes* and less than 1.0 mm for extant fleas [22]. The laciniae bear two rows of sharp teeth each with a backward cusp for cutting and piercing the tough skin or hides of the hosts [1]. Besides long stylet mouthparts, both specimens have body lengths of 17.0 and 22.8 mm, respectively, indicating that their hosts should have been relatively large with thick body covering (hairs, feathers, and/or tough hides). A broad diversity of feathered dinosaurs (body length from 25 to 100 cm), feathered pterosaurs (85 to 90 cm), and small mammals (8 to 20 cm) have been reported from the Middle Jurassic Jiulongshan Formation at the Daohugou site, and feathered dinosaurs (11.6 to 220 cm), feathered pterosaurs (60 to 240 cm), birds (15 to 100 cm), and small- to medium-sized mammals (5 to 68.2 cm) have been reported from the Early Cretaceous Yixian Formation, both of which are in northeastern China. Detailed information of the body sizes of the representative haired or feathered vertebrates is summarized in Tables S1 and S2 of the Supplemental Information.

Pseudopulex, with significantly large body sizes and elongate, unusual mouthparts with long serrated stylets, would not have found life on smaller mammals suitable owing to their relatively easy detection and removal and given that their proboscides would be ponderous in the relatively soft dermal tissues of early, rodent-like mammals. Morphology of *P. jurassicus* and *P. magnus* suggests that these large insects might have fed on feathered dinosaurs, pterosaurs, or medium-sized mammals (found in the Early Cretaceous, but not the Middle Jurassic), using their robust claws to grasp hairs

or feathers and piercing the thick and tough hides of these animals with their stout, elongate mouthparts. *Pseudopulex* would not have been good at jumping or running for their slender legs, so they spent much of their life on their hosts with hairs or feathers, using their ctenidia on the tibia and stiff, posteriorly directed setae and bristles on their body to avoid being thrown off. In addition, the mouthparts with their backward cusps could be used as an anchoring tool [23], further attaching them to their hosts so as to avoid becoming dislodged during terrestrial or aerial locomotion. The elongate and stout proboscides of *Pseudopulex* would have been significantly overmatched for the relatively thin and sensitive skin of small mammals and birds, further suggesting that these were adapted for animals with a much thicker hide.

It has been widely accepted that mammals were the primary hosts of primitive fleas and only later did fleas move from mammals to birds [18, 22]. *Pseudopulex* provides novel insight into the early evolution of flea-like insects. It is proposed that their ectoparasitic lifestyle might have originally arisen to victimize feathered dinosaurs or pterosaurs and then transitioned to other hosts (mammals and birds), diversifying alongside the latter by reducing body size, shortening stylet mouthparts, and minimizing serrated structure.

Experimental Procedures

Fossil file morphology was studied on digitized photographs using CorelDraw X4 and Adobe Photoshop CS5, and scanning electron micrographs (SEM) were taken under ESEM (Quanta200F, FEI) in the Beijing Museum of Natural History.

Supplemental Information

Supplemental Information includes two figures, two tables, and Supplemental Results and can be found with this article online at doi:10.1016/j.cub.2012.03.012.

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