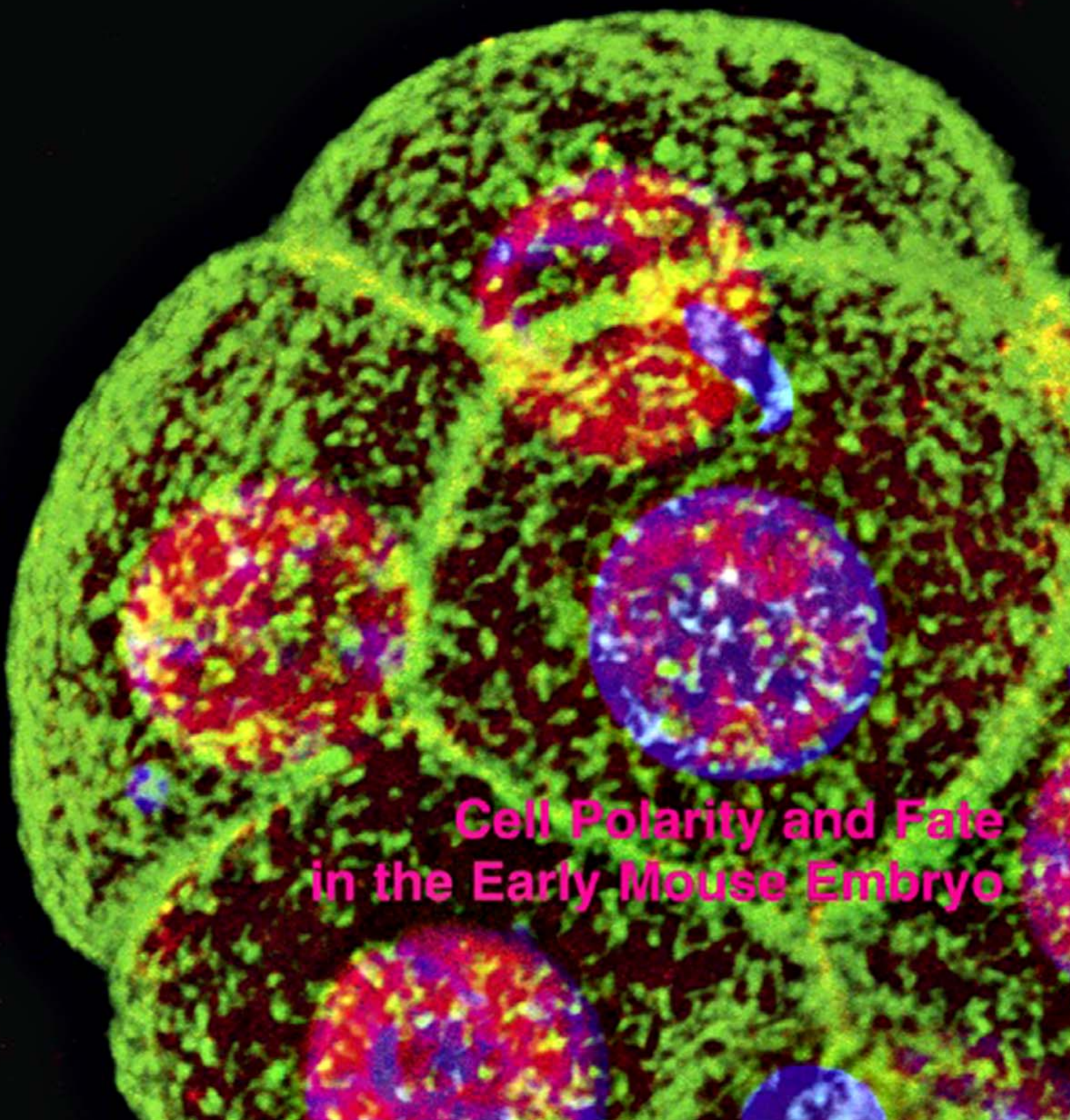
Current Biology

Volume 23
Number 13

July 8, 2013

www.cellpress.com



Cell Polarity and Fate in the Early Mouse Embryo

Current Biology 23, 1261–1266, July 8, 2013 ©2013 Elsevier Ltd All rights reserved http://dx.doi.org/10.1016/j.cub.2013.05.040

Report

New Transitional Fleas from China Highlighting Diversity of Early Cretaceous Ectoparasitic Insects

Taiping Gao,[1] Chungkun Shih,[1] Alexandr P. Rasnitsyn,[2,3] Xing Xu,[4] Shuo Wang,[4,5] and Dong Ren[1,*]
[1]College of Life Sciences, Capital Normal University, Beijing 100048, China
[2]Paleontological Institute, Russian Academy of Sciences, Moscow 117997, Russia
[3]Department of Palaeontology, Natural History Museum, London SW7 5BD, UK
[4]Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
[5]Graduate University of Chinese Academy of Sciences, Beijing 100049, China

Summary

Fleas are a group of highly specialized blood-feeding ectoparasites whose early evolutionary history is poorly known [1, 2]. Although several recent discoveries have shed new light on the origin of the group [3, 4], a considerable gap exists between stem fleas and crown fleas. Here we report a new transitional flea, *Saurophthirus exquisitus* sp. nov., assigned to a new family Saurophthiridae fam. nov., from the Lower Cretaceous Yixian Formation of northeastern China. Saurophthirids are more similar to crown fleas than other stem fleas in having a relatively small body size, relatively short and slender piercing-sucking stylet mouthparts, comparably short and compact antennae, rows of short and stiff bristles on the thorax, and highly elongated legs. The new finding greatly improves our understanding of the morphological transition to the highly specialized body plan of extant fleas. However, saurophthirids also display several features unknown in other fleas, and some of these features are suggestive of a possible ectoparasitic relationship to contemporaneous pterosaurs, though other possibilities exist. The new fossils, in conjunction with previous discoveries, highlight a broad diversity of ectoparasitic insects in the mid-Mesozoic.

Results

Fleas are a group of highly specialized blood-feeding ectoparasitic insects characterized by small size, laterally compressed body, highly modified mouthparts specializing in blood feeding, and long and robust legs specialized in jumping. The early evolutionary history of fleas is poorly known due to a sparse fossil record. Six definite flea fossils have been described from Eocene and Miocene ambers: *Palaeopsylla klebsiana* Dampf, 1911; *Palaeopsylla dissimilis* Peus, 1968; *Peusianapsylla baltica* Beaucournu et Wunderlich, 2001; and *Peusianapsylla groehni* Beaucournu, 2003 from Baltic amber [5–9]; and *Pulex larimerius* Lewis et Grimaldi, 1997 and *Eospilopsyllus kobberti* Beaucournu et Perrichot, 2012 from the Dominican Republic [10, 11], all of which are very similar to extant fleas.

Riek in 1970 [12] reported *Tarwinia australis* from the Early Cretaceous of Koonwarra, Victoria, Australia and considered it to be a flea-related insect, but the lack of preserved mouthparts, its antennal flagellum with 15 segments, and its long, slender legs with moderate-sized hind coxae have fueled debate regarding its classification as a flea [12, 13]. In 1976, Ponomarenko described *Saurophthirus longipes* as a pre-flea and presented its long legs, haired body, and other important ectoparasitic characters [14]. Recently, two flea-like fossils, *Pseudopulex jurassicus* and *P. magnus* assigned to Pseudopulicidae, were reported from the Middle Jurassic and Early Cretaceous deposits of northeastern China; they had very long and strong blood-sucking mouthparts with robust serrated laciniae [3, 15]. Huang et al. reported three taxa, *Pseudopulex wangi*, *Hadropsylla sinica*, and *Tyrannopsylla beipiaoensis*, from the same stratum of China and classified them to Pseudopulicidae in Siphonaptera [4, 16]. These flea-like fossils display some features seen in crown fleas but are still considerably different from extant fleas in many salient features, including their large body size, markedly projecting male genitalic structures, ctenidia on the legs, etc., which hinders our understanding of the evolution of the highly specialized body plan of extant fleas.

Herein we describe three fossils from the Late Cretaceous Yixian Formation of Liaoning Province, China, assigned to *Saurophthirus* (Insecta: Siphonaptera) (we place *Saurophthirus* into Siphonaptera; for details see the Supplemental Results available online), which has been established based on a well-preserved fossil, but one lacking some detailed structures of the mouthparts, from the Early Cretaceous of Baissa in Siberia [14]. The new findings demonstrate that *Saurophthirus* is more similar to crown fleas than other Mesozoic fleas or flea-like insects and provide significant new information on the transition to crown fleas. Based on well-preserved male and female specimens, we are able to document a striking dimorphic difference of the species.

Taxonomy

Insecta Linnaeus, 1758.

Order Siphonaptera Latreille, 1825.

Family Saurophthiridae Gao, Shih, Rasnitsyn, et Ren, fam. nov.

Type genus *Saurophthirus* Ponomarenko, 1976.

(For diagnosis and other details, see Supplemental Results.)

Saurophthirus exquisitus Gao, Shih, Rasnitsyn, et Ren, sp. nov. (Figures 1 and 3).

Diagnosis. Head length and width subequal; eyes small; antenna at least 12-segmented, fusiform in female and subclavate with palmate penultimate segment in male; hind basitarsus longer than the following tarsal segments combined; abdomen distinctly darkened apically. In contrast, *S. longipes* has female head clearly longer than wide, hind basitarsus much shorter, and abdomen not darkened apically.

Type Material. Holotype female, No. CNU-LL2010016P/C; paratype female, No. CNU-LB2010017; paratype male, No. CNU-LB2010018.

Locality and Age. The holotype was collected from the Early Cretaceous Yixian Formation, Dawangzhangzi Village,

*Correspondence: rendong@mail.cnu.edu.cn

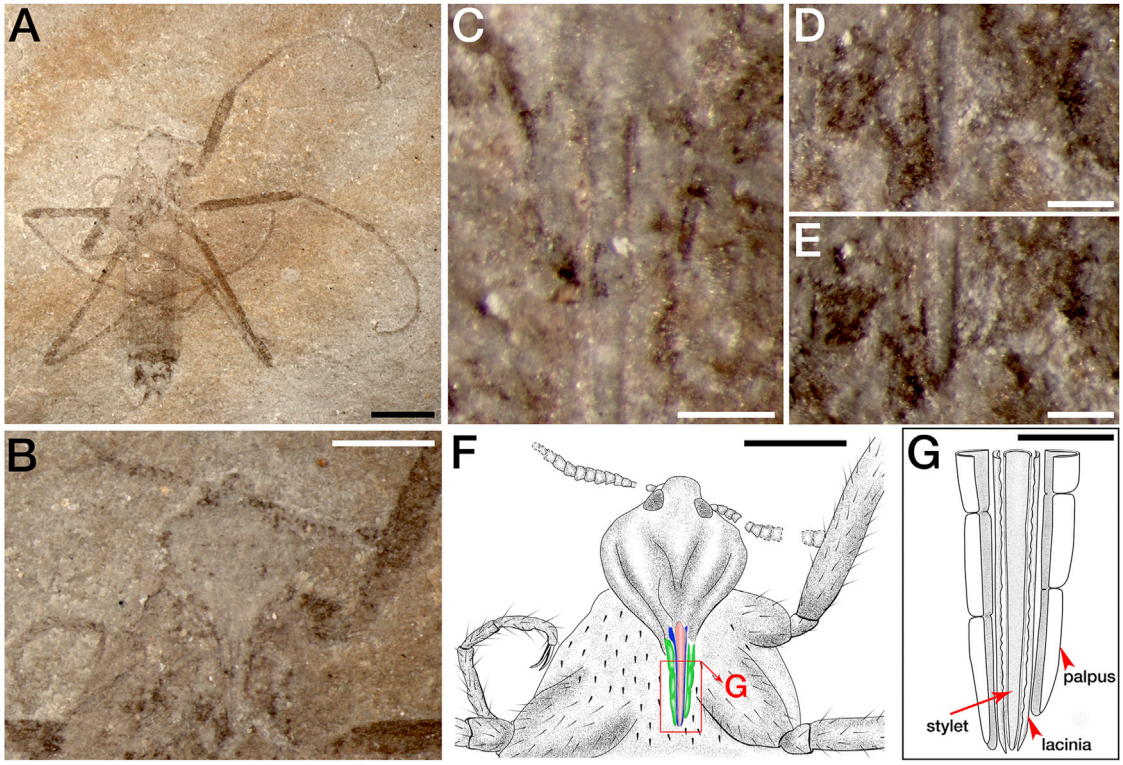


Figure 1. Holotype of *Saurophthirus exquisitus* sp. nov. Part, No. CNU-LL2010016P, from the Early Cretaceous Yixian Formation of Northeastern China
(A) Habitus.
(B) Head.
(C) Basal part of the mouthparts.
(D and E) Terminal of the mouthpart under different direct oblique light.
(F) Line drawing of (B).
(G) Line drawing of the terminal of the mouthparts, part of (F).
Scale bars represent 2 mm in (A); 1 mm in (B) and (F); 0.2 mm in (C)–(E) and (G).

Lingyuan City, Liaoning Province, China. The paratypes were collected from the Early Cretaceous Yixian Formation, Huangbanjigou Village, Beipiao City, Liaoning Province, China.

Etymology. The specific name is from the Latin "exquisitus," meaning "perfect and beautiful."

Description. Holotype female (Figures 1, 2, and S1). Body 8.46 mm long excluding antennae, somewhat dorsoventrally compressed (Figures 1A, 2A, and 2B). Head nearly round, 1.35 mm wide and 1.42 mm high. Compound eyes poorly developed, very small, ovoid, located near the antennary foveae (Figure S1A); ocelli absent. Antennae with 12 segments visible; several segments in the middle much thicker (nearly 2-fold) than the basal ones, but shorter. Piercing-sucking beak (1.22 mm) slightly shorter than the head in height (Figures 1B–1G and 2C); labial palps with three segments visible (Figure S1), reaching beak apex, rather loose (forming neither tight stylet sheaths nor syphonate tube); no mandible traceable; maxillary laciniae thin with small notches at the edge; epipharyngeal stylet wide and sword-like (Figures 1C, 1D, 1E, and 1G). Thorax about as wide as head, with morphology unclear; thoracic and one to four abdominal terga with transverse stripes of stiff bristles (Figures 1F and 2C). Legs covered with long and stiff setae (Figures 2D and 2E); all legs longer than the body. Coxae short, nearly round, all in sublateral position; hind coxae slightly longer than the fore and mid ones. Fore femur slightly longer than fore tibia; basitarsus as long as the following three tarsal segments combined; fourth tarsal segment shortest; fifth tarsal segment nearly equal to the second tarsus; fourth tarsal segment of the mid legs very short (just half of the pretarsus). Claws narrow and gently curved, with a small basal lobe (Figure 2E). Abdomen covered with long and soft setae; exact number of segments unknown; cerci small with long tufts of hairs about 1.80 mm long (Figure 2F).

Paratype Female. Figures 3A–3D, S2A, and S2B. Body 9.74 mm long, excluding antennae (Figure 3A). Head 1.72 mm wide, 1.70 mm high (Figures 3A, 3B, S2A, and S2B); eyes small; piercing-sucking mouthparts short (1.10 mm long), with palpus at least three segments; many hairs present around the segmented boundary (Figures 3B, S2A, and S2B). Antenna compact, short (1.10 mm long), 16-segmented, fixed in the antennal fovea, with every segment bowl-shaped and width nearly twice the height (Figure 3C). Abdominal segments unclear, covered with soft and long hairs (Figure 3D).

Paratype Male. Figures 3E–3K, S2C, and S2D. Body 6.9 mm long, including male genitalia but excluding antennae (Figure 3E). Head with two dark sclerites of obscure homology; eyes not unequivocally visible (Figure 3G); mouthparts about 0.41 mm long, details unclear. Antenna 16-segmented, 1.22 mm long; basal segments thin; apical segments cup-shaped and over twice as thick as the basal segments; the top one or two segments palmate (with narrow lobes extending apically; Figure 3F). Thorax much wider than head (Figures 3G and 3J). Pronotum roundly cruciform, nearly equal to head

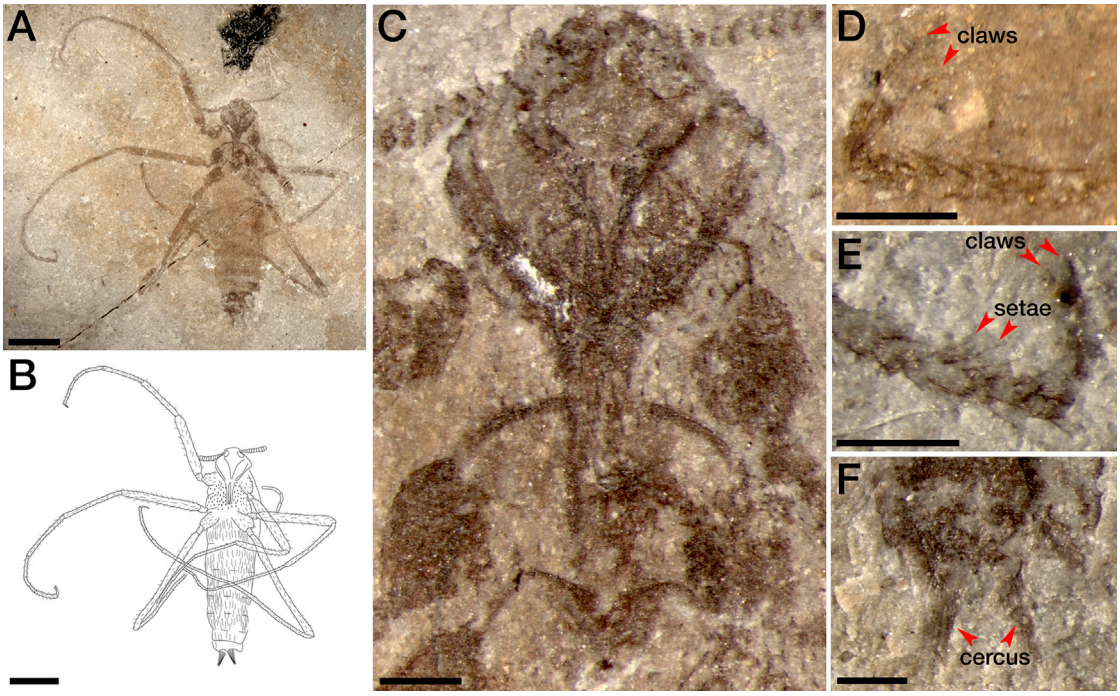


Figure 2. Holotype of *Saurophthirus exquisitus* sp. nov. Counterpart, No. CNU-LL2010016C, from the Early Cretaceous Yixian Formation of Northeastern China

(A and B) Photograph (A) and line drawing (B) of habitus.
(C) Mouthparts.
(D and E) Claws of the left hind leg (D) and right middle leg (E).
(F) Terminal of the abdomen showing the cerci.
Scale bars represent 2 mm in (A) and (B); 0.4 mm in (C)–(F). See also Figure S1.

in width and height, covered by rows of short and thick bristles (Figures 3G and 3J); transverse stripes of such bristles occur through the fourth abdominal tergum (Figures 3G, S2C, and S2D). Abdomen about as wide as thorax, with eight segments external; the tergal plates not reaching lateral on many abdominal segments, and at least some of these segments possessing distinct boundaries; the fourth segment widest, about 1.90 mm; the ninth segment internalized and of sophisticate form, possibly bearing internalized cerci. Male genitalia (Figure 3K) long, extending far beyond the body, with elongate gonocoxa and gonostylus; gonostylus and external part of gonocoxa (internal gonocoxa indiscernible) of subequal length, each much longer than any abdominal segment; visible (external) part of penis wide, lanceolate, extending beyond apex of gonostylus (Figures 3K and S2D). Legs covered by numerous hard setae (Figures 3H and 3I); all legs longer than body. Coxae small, nearly round, just slightly swollen, hind pair approaching midline. Claws long, sharp, narrow, and gently curved (Figures 3H and 3I). Fore femur slightly longer than fore tibia, the latter slightly longer than fore basitarsus; basitarsus nearly equal to the following three tarsal segments combined; fore pretarsus slightly longer than mid and hind pretarsus.

The new species displays a pronounced sexual dimorphism. The female body is long and narrow, with antenna compact and fusiform, legs particularly long and thin, all coxae sublateral, abdomen weakly sclerotized and supposedly far distensible, with indistinct segmental boundaries, and ending in two hair tufts issued by short cerci. In contrast, the male body is shorter and wider, more sclerotized with abdominal segmentation easily visible, antenna longer and subclavate with the penultimate one or two segments palmate, hind coxae approaching each other, and abdomen with no cerci in apical position.

Discussion

Ponomarenko reported the first *Saurophthirus* insect, *S. longipes*, but did not describe the mouthparts due to a lack of detailed preservation [14]. New morphological data and information from our study clearly indicate that saurophthirids share some putative synapomorphies with extant fleas that are indicative of a hematophagous ectoparasitic style. These features include a wingless and small thorax, compacted and short antenna, reduced eyes, haired body, etc. Particularly important is the supposedly unique flea synapomorphy of having piercing-sucking mouthparts formed by an epipharyngeal stylet and a pair of maxillary stylets while the mandibles are reduced. These features are also seen in other flea-like insects or stem fleas. However, compared with *Pseudopulex*, *Saurophthirus* is more similar to crown fleas in having a relatively short and slender piercing-sucking stylet mouthpart and much-swollen hind coxae. Several transitional features are also noteworthy. First, saurophthirids have medium body size (ranging from 6.9 mm for male and from 8.5 to 12.0 mm for females), between that of large *Pseudopulex* (ranging from 8.0 mm for male and from 14.8 to 22.8 mm for females) and small modern fleas (less than 5 mm). Second, extant fleas possess rows of posteriorly directed ctenidia on the body; saurophthirids lack ctenidia on the tibiae or body,

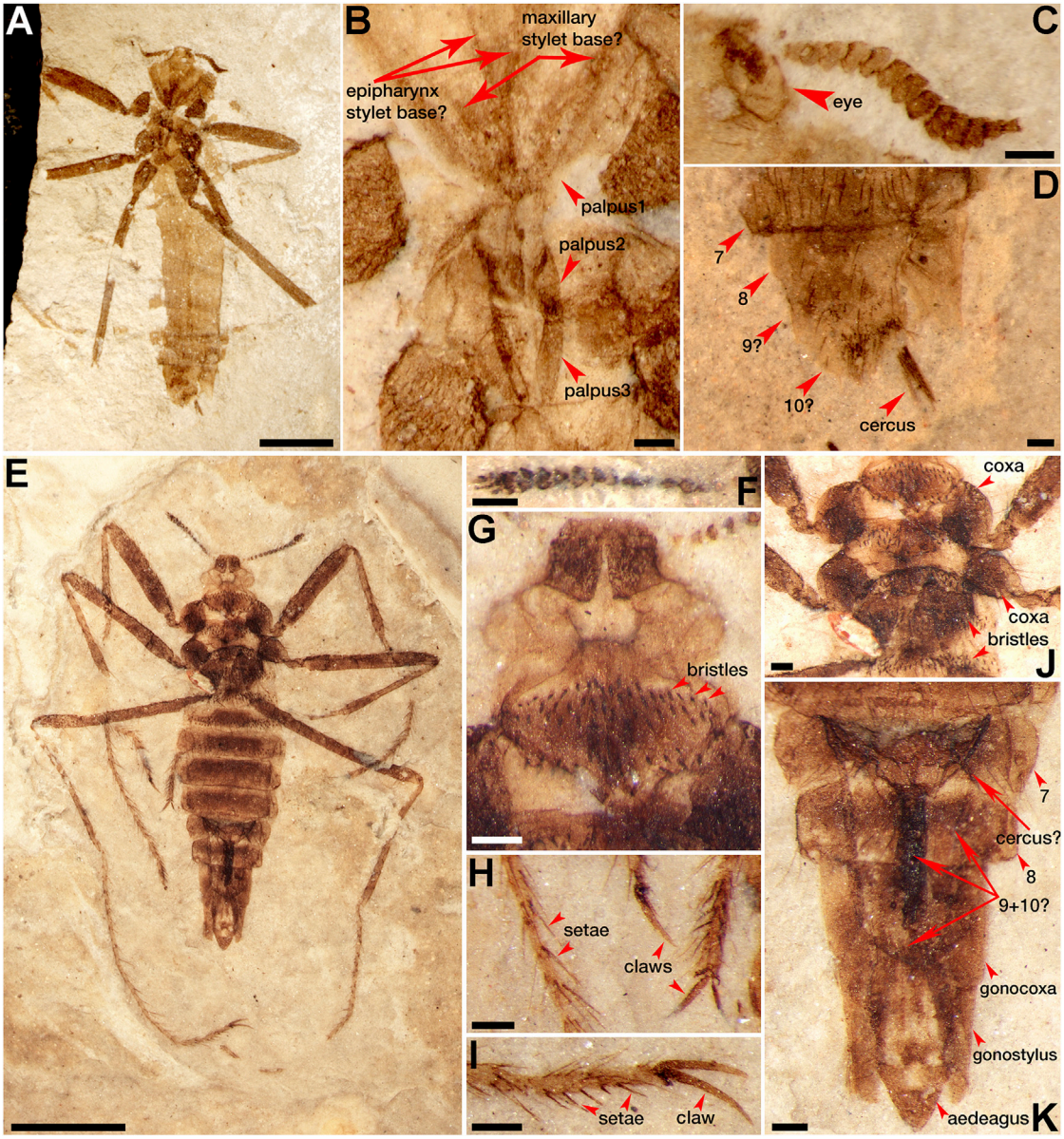


Figure 3. Paratype of *Saurophthirus exquisitus* sp. nov. from the Early Cretaceous Yixian Formation of Northeastern China

(A–D) Female, No. CNU-LB2010017.
(E–K) Male, No. CNU-LB2010018.
(A) Habitus of female.
(B) Mouthparts under alcohol.
(C) Left eye and antenna under alcohol.
(D) Terminal of the abdomen under alcohol.
(E) Habitus of male.
(F) Right antenna.
(G) Head and pronotum.
(H and I) Claws on the right legs.
(J) Thorax.
(K) Terminal of the abdomen, showing the male genitalia.
Scale bars represent 2 mm in (A) and (E); 0.2 mm in all other panels. See also Figure S2.

but they have rows of short, stiff bristles on the body (Figures 1F, 2B, 2C, 3B, 3G, 3J, S2C, and S2D), which probably represent the early evolutionary stage of body ctenidia in crown fleas. These bristles cover the thorax and the abdominal segments 1–4 (Figures 1F, 2C, 3G, S2C, and S2D), and the remaining segments are covered with long and soft hairs, a distribution pattern similar to ctenidia in crown fleas. Finally, from the description of Huang et al., *Pseudopulex wangi* and *Tyrannopsylla beipiaoensis* have large and wide male genitalia of different structure, not at all invaginated, with gonocoxa short and thick, gonostylus much narrower and attached at an angle, and penis short [4, 16]. This is also a plesiomorphic

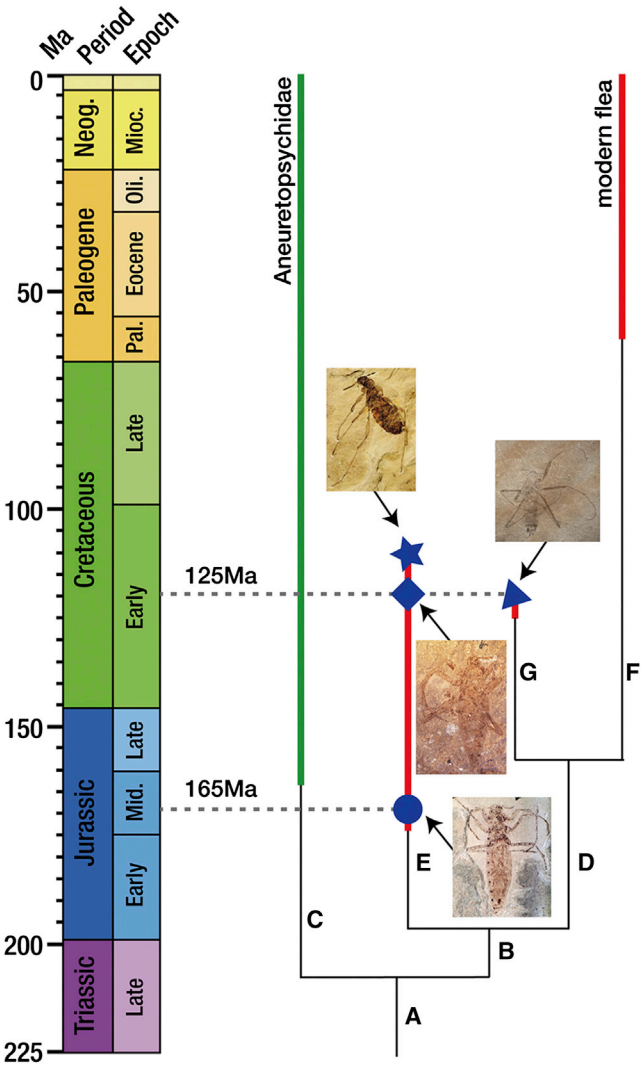


Figure 4. Phylogeny of *Saurophthirus* and Related Clades

Clade A is supported by a long proboscis with siphonate or stylet mouthparts. Clade B (flea-like insects) is supported by a wingless and small thorax, especially reduced eyes, compact antennae, posteriorly directed setae, and long legs with claws. Clade C (Aneuretopsychidae) is supported by mouthparts forming an annulated siphonate organ, with labial palps lost or nearly lost. Clade E (Pseudopulicidae) is supported by tibial ctenidia, laciniae with very sharp serrated teeth, and totally external male genitalia. Clade D is supported by the absence of ctenidia on the tibia, relatively short piercing-sucking mouthparts with notched laciniae, highly elongated legs, much-swollen hind coxae, and partially internal male genitalia. Clade F (modern fleas) is supported by saltatorial hind legs, ctenidia on the body, laterally flattened body, and completely hidden male genitalia. Clade G (Saurophthiridae) is supported by extremely long legs and body covered by bristles with regional distribution. Representative species: circle, *Pseudopulex jurassicus*; diamond, *Pseudopulex magnus*; star, *Tarwinia australis*; triangle, *Saurophthirus exquisitus* sp. nov. See also Figure S3.

state in contrast to the long, narrow, partially invaginated genitalia with long but thick penis in *Saurophthirus*, whereas the genitalia are highly reduced in extant fleas. Based on these features, we think the genitalia of *Saurophthirus* might be in a transition from totally exposed to entirely invisible.

These findings greatly improve our understanding of flea evolution (Figure 4; see also Figure S3). Aneuretopsychidae has been suggested as a sister group of Siphonaptera by the presence of a long proboscis with siphonate versus stylet mouthparts with serrate laciniae (Figure 4, clade A) [4], which is totally different from what is known in Diptera [17]. After the evolution of the nonmandibulate piercing-sucking mouthparts, other characteristics of fleas have appeared, including a wingless body, compact antennae, and reduced eyes, which are seen in stem fleas such as *Saurophthirus*, *Pseudopulex*, and *Tarwinia* (Figure 4, clade B). However, the latter two taxa uniquely share the presence of the ctenidia on the tibiae, suggesting that they represent an extinct lineage in early flea evolution (Figure 4, clade E) [13]. Compared with *Pseudopulex*, *Saurophthirus* has smaller body size, relatively short piercing-sucking mouthparts with notched laciniae, highly elongated legs, much-swollen hind coxae, and partially extended male genitalia; these features indicate that *Saurophthirus* is more closely related to modern fleas than to *Pseudopulex* and *Tarwinia* (Figure 4, clade G). This suggests that *Saurophthirus* further evolved into the modern fleas during the Cretaceous and Paleogene periods. Following these changes, characteristics of crown fleas such as laterally compressed body and robust legs specialized for jumping have evolved (Figure 4, clade F).

Our findings shed new light on the diversity of ectoparasitism and host relation for Early Cretaceous insects. The legs of *Saurophthirus* are very long and slender; every leg is longer than the body, in contrast to the aforementioned flea-like insects and true fleas. The coxae of the newly described species are swollen and nearly round, and the fore femora are thicker than the mid femora, which in turn are thicker than the hind femora. *Pseudopulex* insects have very long and strong piercing-sucking mouthparts with two rows of sharp serrated teeth on their laciniae. The length of the mouthparts is at least 3.44 mm for *P. jurassicus* and 5.15 mm for *P. magnus*, both occupying over 1/5 of the body length [3], but for *P. wangi* (holotype, female), the length of the mouthparts is about 2.5 mm, which is about 1/6 of the body length [4, 16]. Such strong structures are considered to have been used for sucking blood from feathered dinosaurs and/or pterosaurs, because these vertebrates had thick and less-sensitive body coverings [18, 19]. *S. exquisitus* sp. nov. possesses a blood-sucking mouthpart (Figures 1 and 3) that includes a wide epipharyngeal stylet and a pair of relatively reduced laciniae, protected by at least three segmented palpi. The laciniae are not as robust as those of *Pseudopulex* but are similar to those of extant fleas, lacking the sharp saw-like teeth, except that the edges have some weak notches. The piercing-sucking stylet mouthparts of *S. exquisitus* sp. nov. are about 1.22 mm long in the holotype and about 1.10 mm long in the paratype, occupying only 1/7 to 1/9 of the whole body length. Compared with *Pseudopulex*, saurophthirids have much shorter and weaker piercing-sucking mouthparts (Figure 4, clade G). Since saurophthirids have very long and thin legs with sharp claws, they represent adaptation similar to that of various extant parasites dwelling on bat wing membranes [14]. No Mesozoic bats have been discovered thus far, so pterosaurs might be the most possible candidate hosts. It should be noted that all the described *Saurophthirus* species were collected from the Early Cretaceous. Many pterosaurs began to diversify in the Early Cretaceous, e.g., *Haopterus gracilis* [20], *Feilongus youngi* [21], *Boreopterus cuiae* [22], *Gegepterus changi* [23], etc., and these pterosaurs had body sizes suitable for such relatively large ectoparasites to live on. However, we are not able to rule out the possibility that *Saurophthirus* might have preyed on other coexisting vertebrate hosts such as feathered

dinosaurs, birds, or mammals. The reported Early Cretaceous ectoparasites now include *Saurophthirus*, *Pseudopulex* and its close relatives, *Tarwinia*, and maybe strashilids and vosilids [24, 25] (but see [26] for a different opinion). These insects display considerable morphological differences, which suggest different ectoparasitic habits and hosts. Together, they highlight the diversity of ectoparasitism in the Early Cretaceous.

Experimental Procedures

These type fossils are deposited in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China. The specimens were examined under a Leica MZ16.5 dissecting microscope. Line drawings were prepared with CorelDraw X6 (version 16.0.0.707) and Adobe Photoshop CS 6.0 (version 13.0.1).

Supplemental Information

Supplemental Information includes Supplemental Results and three figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.05.040.

Acknowledgments

We are grateful to Y.Y. Yao and Y.J. Wang for suggestions and to Q. Yang and C.F. Shi for discussions and specimen preparation. D.R. was supported by the National Basic Research Program of China (973 Program; grant 2012CB821906), the National Natural Science Foundation of China (grants 31230065, 31272352, and 41272006), Project of Great Wall Scholar and KEY project of Beijing Municipal Commission of Education Project (grant KZ201310028033), and China Geological Survey (grant 1212011120115); X.X. was supported by the National Natural Science Foundation of China (grant 41120124002); and A.P.R. was supported by the Russian Academy of Sciences Presidium program "Biosphere Origin and Evolution of Geo-Biological Systems."

Received: April 17, 2013
Revised: May 8, 2013
Accepted: May 22, 2013
Published: June 27, 2013

References

1. Rasnitsyn, A.P., and Quicke, D.L.J. (2002). History of Insects (Dordrecht: Kluwer).
2. Grimaldi, D.A., and Engel, M.S. (2005). Evolution of the Insects (New York: Cambridge University Press).
3. Gao, T.P., Shih, C.K., Xu, X., Wang, S., and Ren, D. (2012). Mid-Mesozoic flea-like ectoparasites of feathered or haired vertebrates. Curr. Biol. *22*, 732–735.
4. Huang, D., Engel, M.S., Cai, C., Wu, H., and Nel, A. (2012). Diverse transitional giant fleas from the Mesozoic era of China. Nature *483*, 201–204.
5. Dampf, A. (1911). *Palaeopsylla klebsiana* n. sp., eine fossiler Floh aus dem baltischen Bernstein. Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg *51*, 248–259.
6. Peus, F. (1968). Über die beiden Bernstein-Flöhe (Insecta, Siphonaptera). Dtsch. Entomol. Z. *42*, 62–72.
7. Poinar, G.O. (1995). Fleas (Insecta, Siphonaptera) in Dominican Amber. Med. Sci. Res. *23*, 789.
8. Beaucournu, J.C., and Wunderlich, J. (2001). A third species of Palaeopsylla Wagner, 1903, from Baltic amber (Siphonaptera: Ctenophthalmidae). Dtsch. Entomol. Z. *111*, 296–298.
9. Beaucournu, J.C. (2003). *Palaeopsylla groehni* n. sp., quatrième espèce de puce connue de l'ambre de la Baltique (Siphonaptera, Ctenophthalmidae). Bull. Soc. Entomol. Fr. *108*, 217–220.
10. Lewis, R.E., and Grimaldi, D. (1997). A pulicid flea in Miocene amber from the Dominican Republic (Insecta: Siphonaptera: Pulicidae). Am. Mus. Novit. *3205*, 1–9.
11. Perrichot, V., Beaucournu, J.C., and Velten, J. (2012). First extinct genus of a flea (Siphonaptera: Pulicidae) in Miocene amber from the Dominican Republic. Zootaxa *3438*, 54–61.
12. Riek, E.F. (1970). Lower Cretaceous fleas. Nature *227*, 746–747.
13. Jell, P.A., and Duncan, P.M. (1986). Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra fossil bed (Korumburra Group), South Gippsland, Victoria. Mem. Assoc. Australas. Palaeontol. *3*, 111–205.
14. Ponomarenko, A.G. (1976). A new insect from the Cretaceous of Transbaikalia USSR: a possible parasite of Pterosaurians. Paleontol. Zh. *3*, 102–106.
15. Poinar, G.O., Jr. (2012). Palaeontology: the 165-million-year itch. Curr. Biol. *22*, R278–R280.
16. Huang, D., Engel, M., Cai, C., and Nel, A. (2013). Mesozoic giant fleas from northeastern China (Siphonaptera): Taxonomy and implications for palaeodiversity. Chin. Sci. Bull. *58*, 1682–1690.
17. Lukashevich, E., and Mostovski, M. (2003). Hematophagous insects in the fossil record. Paleontol. J. *37*, 153–161.
18. Xu, X., Zheng, X., and You, H. (2009). A new feather type in a nonavian theropod and the early evolution of feathers. Proc. Natl. Acad. Sci. USA *106*, 832–834.
19. Xu, X., Zheng, X., and You, H. (2010). Exceptional dinosaur fossils show ontogenetic development of early feathers. Nature *464*, 1338–1341.
20. Wang, X., and Lü, J. (2001). Discovery of a pterodactylid pterosaur from the Yixian Formation of western Liaoning, China. Chin. Sci. Bull. *46*, A3–A8.
21. Wang, X., Kellner, A.W.A., Zhou, Z., and Campos, Dde.A. (2005). Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. Nature *437*, 875–879.
22. Lü, J., and Ji, Q. (2005). A new Ornithocheirid from the Early Cretaceous of Liaoning Province, China. Acta Geol. Sin.-Engl. *79*, 157–163.
23. Wang, X., Kellner, A.W.A., Zhou, Z., and de Almeida Campos, D. (2007). A new pterosaur (Ctenochasmatidae, Archaeopterodactyloidea) from the Lower Cretaceous Yixian Formation of China. Cretaceous Res. *28*, 245–260.
24. Rasnitsyn, A.P. (1992). *Strashila incredibilis*, a new enigmatic mecopteroid insect with possible siphonapteran affinities from the Upper Jurassic of Siberia. Psyche (Stuttg.) *99*, 323–333.
25. Vršanský, P., Ren, D., and Shih, C. (2010). Nakridletia ord. n.—enigmatic insect parasites support sociality and endothermy of pterosaurs. AMBA Projekty *8*, 1–16.
26. Huang, D., Nel, A., Cai, C., Lin, Q., and Engel, M.S. (2013). Amphibious flies and paedomorphism in the Jurassic period. Nature *495*, 94–97.

Current Biology, Volume *23*

Supplemental Information

New Transitional Fleas from China Highlighting Diversity of Early Cretaceous Ectoparasitic Insects

Taiping Gao, Chungkun Shih, Alexandr P. Rasnitsyn, Xing Xu, Shuo Wang, and Dong Ren

Author Contributions

T.G., C.S. and A.P.R. collected, illustrated, and analyzed the data. D.R. designed the research plan and participated in morphological research. X.X. and S.W. offered vertebrate host information. T.G., C.S., A.P.R. X.X., and D.R. prepared the manuscript.

Supplemental Inventory

Supplemental Results: Systematic Paleontology

Figure S1, related to Figures 1 and 2

Figure S2, related to Figure 3

Figure S3, related to Figure 4

Supplemental References

Supplemental Results

Systematic Paleontology

Insecta Linnaeus, 1758

Order Siphonaptera Latreille, 1825

Family Saurophthiridae Gao, Shih, Rasnitsyn *et* Ren, fam. nov.

Type Genus. *Saurophthirus* Ponomarenko, 1976

Diagnosis: Medium-sized apterous insects with female body length about 8 to 12 mm and male about 7 mm, legs long and slender, longer than the body length. Head nearly round, diamond-shaped in female (of complicate but insufficiently known form in male), with compact antenna fixed in a deep socket, eyes small, ocelli absent, short piercing-sucking stylet mouthparts including a pair of thin laciniae and a wider impair stylet, and with no traces of mandibles. Thorax covered with rows of short and stout bristles, coxae round and swollen, fore femora thicker than middle femora, the latter thicker than the hind femora, femur longer than tibia, the latter slightly longer than basitarsus, pretarsus with a pair of long, narrow claws. In the male, abdomen with clear segmental boundary, but the abdomen with integuments not sclerotized, probably distensible for the female. Male genitalia long and narrow, invaginated along with the 9th segment up to base of the 7th segment of the abdomen in repose, and the aedeagus extending beyond the abdomen apex, female possessing a pair of cerci.

Genera Include: Only the type genus *Saurophthirus* with two species, *S. longipes* Ponomarenko, 1976 and *S. exquisitus* sp. nov.

Comments: Gao et al. erected Pseudopulicidae Gao, Shih *et* Ren, 2012 as order incertae sedis, based on only two well-preserved ectoparasitic insects. Huang et al. in 2013 described other three similar groups of insects, *Pseudopulex wangi*, *Hadropsylla sinica* and *Tyrannopsylla beipiaoensis,* and classified them to Pseudopulicidae in Siphonaptera [1, 2]. They also erected Tarwiniidae Huang, Engel, Cai *et* Nel, 2013 based on *Tarwinia* Jell and Duncan, 1986 from the Early Cretaceous of Australia [2]. Pseudopulicidae, Tarwiniidae and Saurophthiridae share many features with the extant fleas, like haired body, wingless and small thorax, hypognathous and blood-sucking mouthparts with long laciniae, very small eyes, short compacted antennae, legs with sharp claws, etc., so we propose to assign all of them to Siphonaptera. Saurophthiridae differs from Pseudopulicidae and Tarwiniidae by much longer legs with narrow femora and without protibial ctenidia, from Pseudopulicidae also by the following characters: smaller body size, relatively shorter piercing-sucking mouthparts without serrated laciniae, female abdomen cylindrical rather than fusiform, and male genitalia narrow and deeply invaginated into abdomen.

Saurophthirus exquisitus Gao, Shih, Rasnitsyn *et* Ren, sp. nov. (Figs. 1-3, S1, S2)

Type Material: Holotype female. CNU-LL2010016P/C, a well-preserved almost complete female body with part and counterpart. Paratype female. No. CNU-LB2010017, an incomplete female body in ventral view with legs unclear, but head structures visible. Paratype male. CNU-LB2010018, a well-preserved male specimen in ventral view, only mouthparts and part of the legs unclear.

Measurements for Holotype female: The measurements (mm) of the coxa, trochanter, femur, tibia, five segments of the tarsus, and claw in the fore legs are about: 0.58, 0.27, 2.64, 2.14, 1.65, 0.88, 0.48, 0.34, 0.70, n/a; in the mid legs: 1.02, 0.33, 3.44, 2.58, 2.14, 0.84, 0.50, 0.32, 0.66, 0.40; in the hind legs: 1.10, 0.30, 4.64, 3.51, 3.00, 0.97, 0.56, 0.35, 0.72, 0.49.

Measurements for Paratype male: The measurements (mm) of the coxa, trochanter, femur, tibia, five segments of the tarsus and claw in the forelegs are about: 0.51, 0.31, 1.80, 1.70, 1.25, 0.52, 0.34, 0.24, 0.56, 0.33, in the mid legs, 0.54, 0.28, 2.42, 1.86, 1.60, 0.77, 0.50, 0.34, 0.50, 0.32, in the hind legs, 0.62, 0.30, 3.27, 2.44, 1.96, 1.07, 0.65, 0.36, 0.55, 0.43.

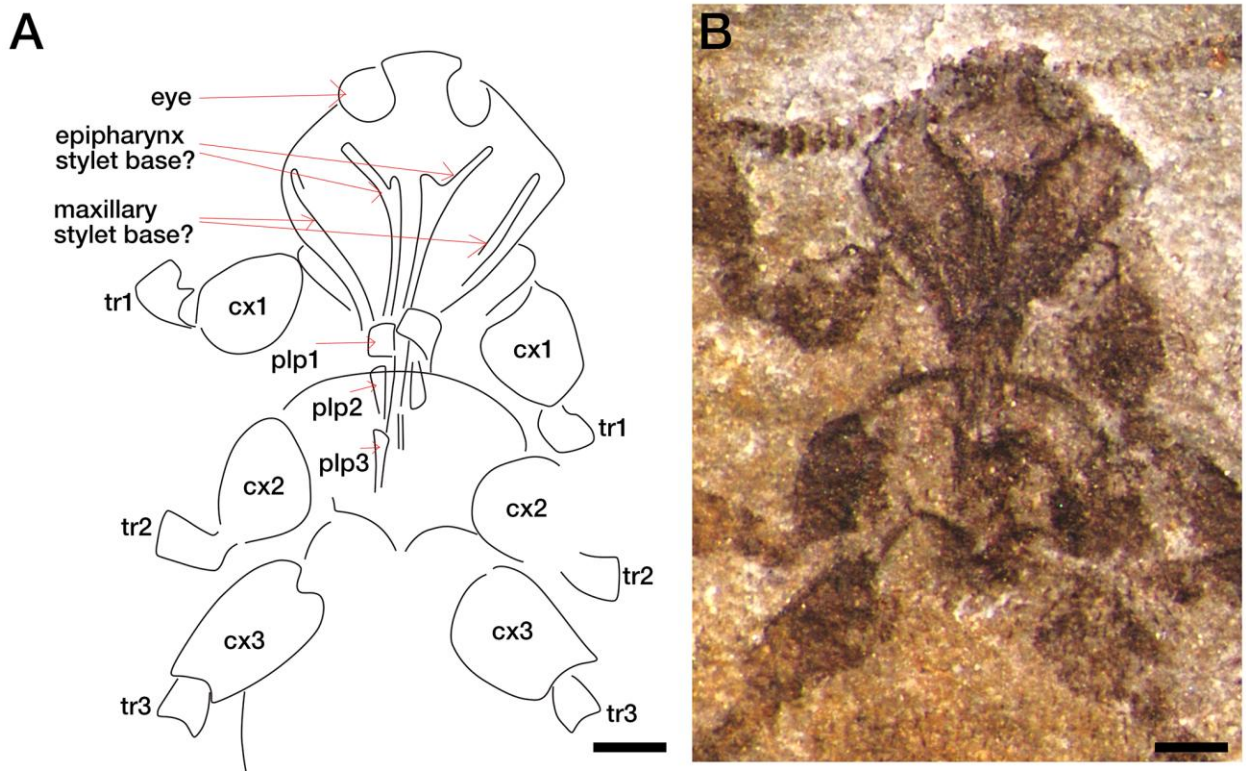


Figure S1. The Head and Thorax of Holotype of *Saurophthirus exquisitus* sp. nov. Counterpart, No. CNU-LL2010016C, from the Early Cretaceous Yixian Formation of Northeastern China, Related to Figures 1 and 2

(A and B) Line drawing and photograph, respectively.

Scale bars, 0.4 mm. Abbreviations: plp, palpus; cx, coxa; tr, trochanter.

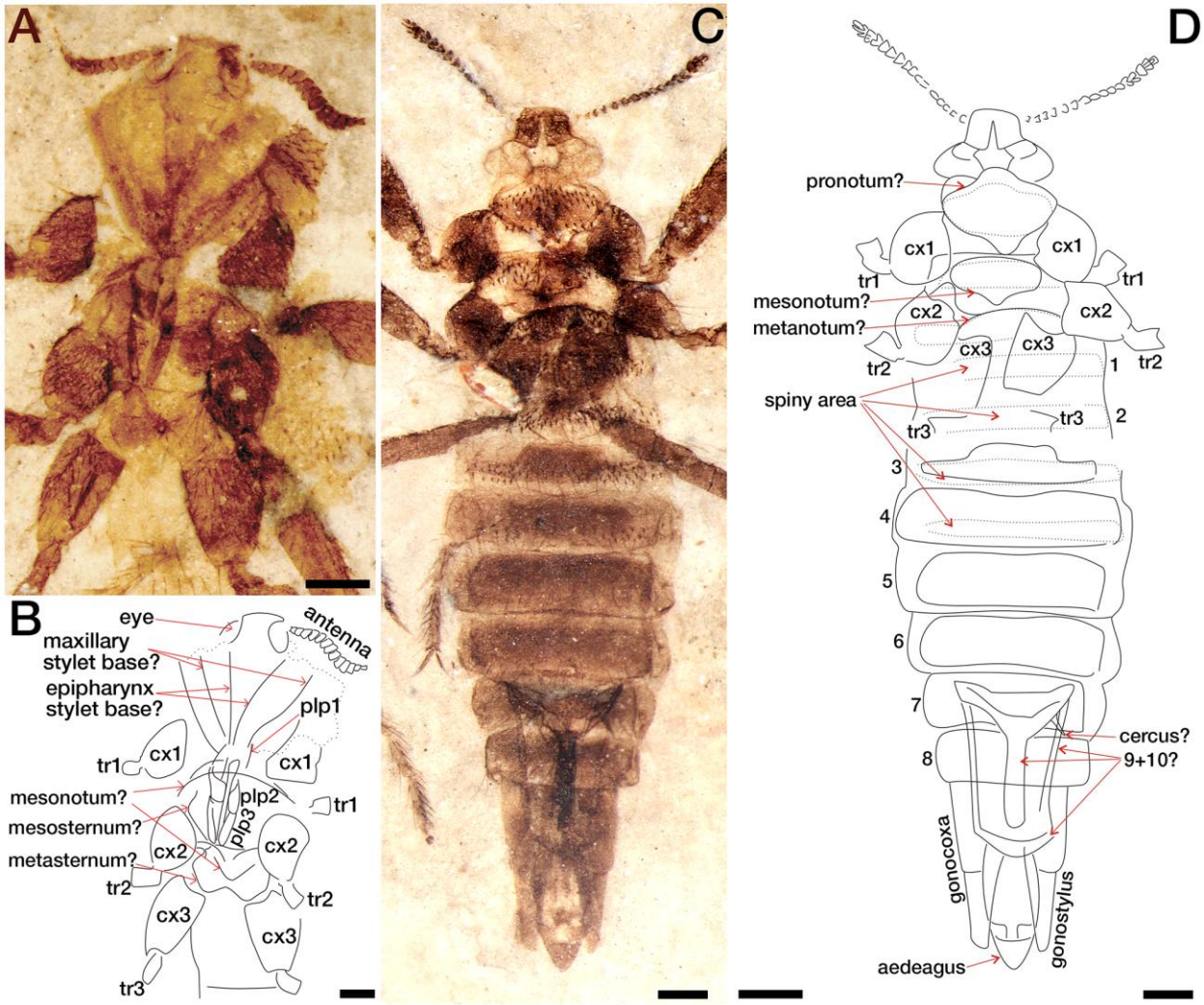


Figure S2. Line Drawings Showing Detail Structures of Paratypes of *Saurophthirus exquisitus* sp. nov., from the Early Cretaceous Yixian Formation of Northeastern China, Related to Figure 3

(A and B) Female, No. CNU-LB2010017, photograph and line drawing.

(C and D) Male, No. CNU-LB2010018, photograph and line drawing.

Scale bars, 0.4 mm. Abbreviations same as Figure S1.

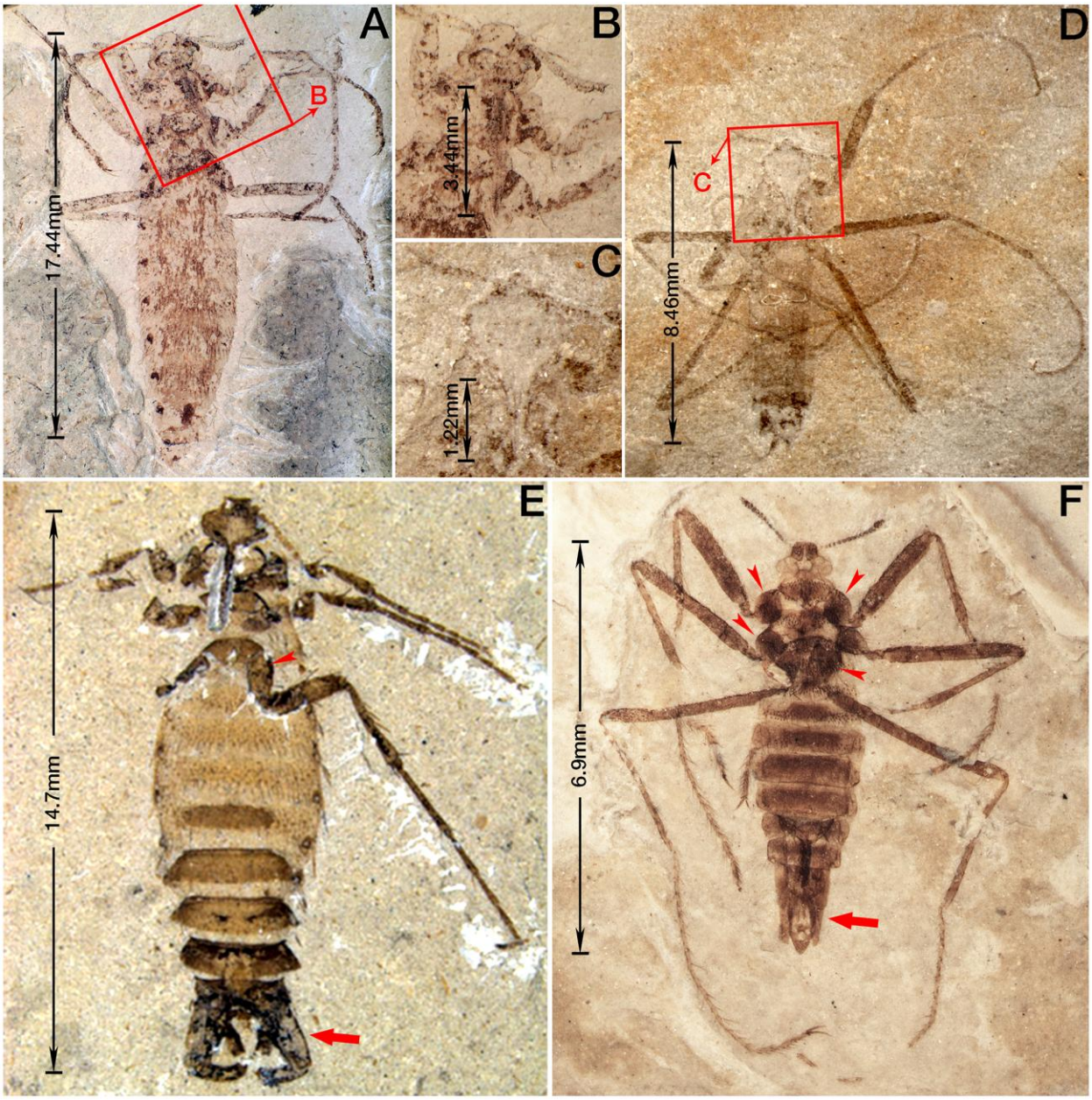


Figure S3. Comparison between Saurophthiridae and Pseudopulicidae in Detail, Related to Figure 4

(A)–(D) show the length of body and mouthpart; (E) and (F) show coxae and male genitalia.

(A and B) Photograph of the *Pseudopulex jurassicus* Gao, Shih *et* Ren, 2012, from the Late Middle Jurassic of Jiulongshan Formation, A, body; B. head

(C and D) Photograph of the holotype of *Saurophthirus exquisitus* sp. nov. (part), from the Early Cretaceous of Yixian Formation. D, body; C. head

(E) Photograph of *Tyrannopsylla beipiaoensis* Huang, Engel, Cai *et* Nel, 2013 (male), from the Early Cretaceous of Yixian Formation. (Revised from Huang et al. [1, 2].)

(F) Photograph of paratype male of *Saurophthirus exquisitus* sp. nov., from the Early Cretaceous of Yixian Formation.

Supplemental References

1. Huang, D., Engel, M.S., Cai, C., Wu, H., and Nel, A. (2012). Diverse transitional giant fleas from the Mesozoic era of China. Nature *483*, 201-204.
2. Huang, D., Engel, M., Cai, C., and Nel, A. (2013). Mesozoic giant fleas from northeastern China (Siphonaptera): Taxonomy and implications for palaeodiversity. Chinese Sci. Bull. *58(14)*, 1682-1690.