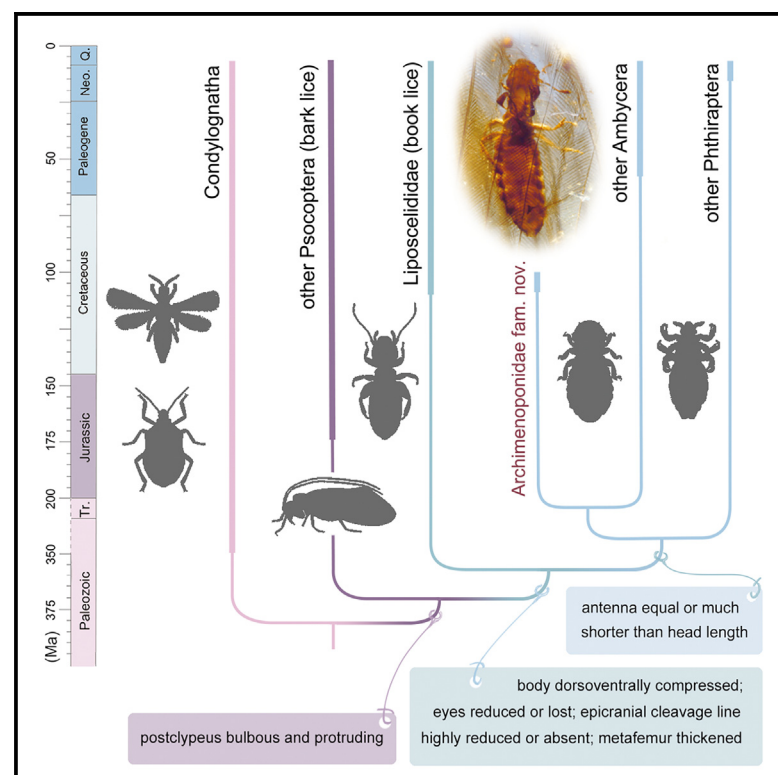


Current Biology

Stem chewing lice on Cretaceous feathers preserved in amber

Graphical abstract



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In brief

Zhang et al. report two chewing lice, preserved together with feathers in mid-Cretaceous Myanmar amber and representing the earliest true lice, and push back the origin of parasitic lice by at least 55 million years. It is of remarkable importance for understanding the origin and evolution of this significant group of parasitic insects.

Highlights

- Cretaceous true lice push back the origin of parasitic lice by 55 million years
- Evolutionary patterns from free-living booklice to parasitic lice are revealed
- Antennae and tarsi reductions have independently occurred in Amblycera and other lice

Report

Stem chewing lice on Cretaceous feathers preserved in amber

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SUMMARY

Phthirapteran lice (true lice or parasitic lice) are a major group of ectoparasitic insects living on their bird or mammal hosts during their entire life cycle.¹ Due to their highly specialized lifestyles, they are extremely poorly represented in fossil records.² Molecular clock estimations have speculated extensively about the origin time of parasitic lice,^{3,4} yet none have been confirmed unequivocally. Herein, we report a new family of stem chewing lice, based on two adult insects associated with several semiplume feathers preserved within a piece of Kachin amber from the mid-Cretaceous. They display some defining characteristics of the Amblycera, an early-diverging lineage of the crown lice group. These features include a wingless body, chewing mouthparts, narrow and small thorax, and short tarsus with elongated euplantulae. Our phylogenetic analysis places the new taxa in the Amblycera, and the discovery thus pushes back the lice fossil records by at least 55 million years. Furthermore, the new specimens show primitive characters such as compressed and club-shaped terminal segments of antennae, maxillary and labial palps, and unmodified femora of hind legs, providing key information for the evolutionary relationship between free-living booklice and parasitic lice. This suggests that some ectoparasitic characters defining the crown lice group might have evolved among amblyceran and non-amblyceran lice in parallel. These newly described fossil specimens imply at least a Cretaceous age of Phthiraptera.

RESULTS

Living lice are ectoparasitic insects with nearly 5,000 representative species.¹ As ectoparasites, they exhibit a remarkable level of host specificity unparalleled in most other parasites.⁵ Parasitic lice are vectors of major human and animal diseases and have significant medical and veterinary value.⁶ Like most ectoparasitic insects,^{7,8} true lice are sparse in fossil records. Their pre-Eocene fossil records were debatable while the Eocene fossil lice were of modern type.^{2,9–13} The earliest and only unanimously accepted fossil louse was reported from the Eocene of Germany (44 mya),² indicating the presence of a huge undocumented louse evolutionary history in fossil records.

Herein, we document a new family of Phthiraptera, Archimenoponidae fam. nov., based on two chewing lice embedded with feathers in the mid-Cretaceous Kachin amber (Figure 1A), representing for the first-time true lice are reported unequivocally in the Cretaceous. The result of phylogenetic analysis including the major groups of Psocodea with Phthiraptera and their morphological characters indicated that Archimenoponidae is

an early clade of Amblycera, which implies that true lice appeared at least in the mid-Cretaceous. This is of remarkable importance for understanding the evolution of this significant group of parasitic insects.

Systematic paleontology

Class: Insecta Linnaeus, 1758.

Order: Psocodea Hennig, 1966.

Suborder: Troctomorpha Roesler, 1940.

Infraorder: Phthiraptera Haeckel, 1896.

Parvorder: Amblycera Kellogg, 1896.

Family: Archimenoponidae fam. nov.

Type genus: *Archimenopon* gen. nov.

Diagnosis

Body wingless and dorsoventrally flattened (Figures 1 and 2A), head wider than prothorax; clypeus directed forward, mouthparts behind clypeus (Figures 2C and 3C), mandibles parallel to the ventral surface (Figures 2H and 3C); antenna 11-segmented, first flagellomere pedunculated and the remaining segments club-shaped (Figures 2H and 3C); profemur swollen, hind leg shorter than abdomen, tarsus three-segmented, first tarsomere with

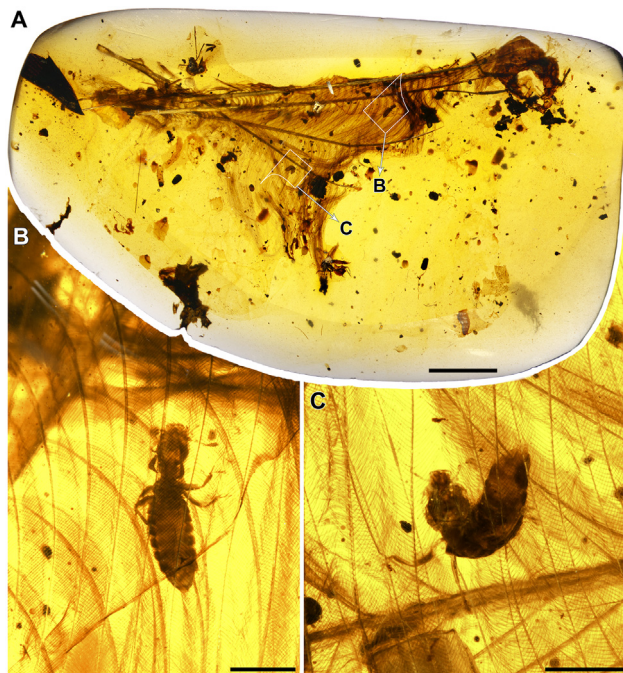


Figure 1. Photographs of the amber with *Archimenopon myanmarensis* gen. et sp. nov. from the mid-Cretaceous of Myanmar
(A) Amber with feathers and insects showing the locations of two chewing lice.
(B) Habitus of BU-MA002385-1.
(C) Habitus of BU-MA002385-2.
Scale bars: 5 mm in (A) and 0.5 mm in (B) and (C).
See also [Figures S1–S3](#).

long euplantula, second one with shorter distal euplantula, pretarsus with two claws ([Figures 2F, 2G, and 3D](#)).

Genus: *Archimenopon* gen. nov.

Type species. *Archimenopon myanmarensis* sp. nov.

Etymology

The new generic name is a combination of the Greek “archi-,” meaning ancient, and “[men]opon,” which is derived from the extant genus *Menopon*.

Diagnosis: as for family because of monotypy.

Species included. Type species.

Archimenopon myanmarensis sp. nov.

Etymology: The species name is in honor of the country Myanmar as the origin of the Kachin amber fossil.

Holotype no. BU-MA002385-1 and paratype no. BU-MA002385-2 are preserved together with feathers in a piece of amber ([Figure 1](#)).

Locality and age: Hukawng Valley, Kachin, northern Myanmar; mid-Cretaceous (98.79 ± 0.62 Ma).

Description

Adult or elder nymph, sex unknown ([Figures 1, 2, 3, and S2](#)). Body small, length 1.32 mm (holotype), wingless, dorsoventrally flattened.

Head: except for clypeus, external areas of head capsule not identified because of lack of visible sutures. Eyes not unambiguously identified, paratype head capsule sides emarginated mid-length ([Figures 3A and 3B](#)) seeming like eyes, not visible in holotype; three small parasagittal orifices only visible in

paratype, which do not look very similar to dissociated ommatidia characteristic of many living Phthiraptera. Clypeus wide even though narrower than head, directed strictly forward and mouthparts distant from clypeus fore margin and directed ventrally ([Figures 2C and 2D](#)); mandibles visible, with sharp apices overlapping each other at rest ([Figures 2H, 2I, and 3C](#)); maxillary palp 4-segmented, more than half as long as clypeus wide, palpomeres longer than wide, apical one particularly long and wide ([Figures 2C, 2D, and S2](#)); labial palp very short, two-segmented ([Figures 2I and 3C](#)); main parts of maxilla and labium difficult to be interpreted. Tentorium with bridge narrow, bearing corpotendon at mid-length and lateral widenings that might be related to anterior or posterior tentorial arms ([Figures 2A and 2B](#)). Antenna nearly 0.25 mm long, extending beyond head occipital margin, with 11 segments ([Figures 2B, 2D, 2E, 3A, and 3B](#)); scape short and cylindrical, pedicel slender than scape and twice as long as that; first flagellomere thin basally and dilated club-like distally, as long as scape and pedicel combined; other flagellomeres clearly compressed, goblet-shaped, basal thin, generally widened, first three flagellomeres equal to the following combined in length, last flagellomere small and round.

Thorax: small, shorter and narrower than head and abdomen, further details difficult to interpreted because of deformation and poor preservation. Legs moderately short, with hind (longest) femur as long as head’s width ([Figures 2A and 2B](#)); coxae narrow and short, fore coxa as long as respective tibia, touching along midline or almost so; single trochanter (mid one) visible, short and very narrow (unless a deformation of femoral base); femora moderately long, subcylindrical except profemur swollen, longer than respective tibiae; tibiae not at all incrassate, with no spurs or strong setae visible ([Figures 2F, 2G, 3A, and 3D](#)); tarsus about half as long as respective tibia, with three tarsomeres present, the first tarsal segment having a large flap-like appendage on the inner side, as long as trunk of second tarsomere (eup 1); the second tarsus bearing a small shorter finger-like process (eup 2), the third tarsomere shorter and thinner than the second one, with 2-min claws visible ([Figures 2F, 2G, 3A, 3B, and 3D](#)).

Abdomen ([Figures 3A and 3B](#)): elongated oval, with eight segments visible (apparently second through ninth ones), with ribbon-like sterna and lateroterga 2–8 apparent ventrally. Structures visible further posterior (those embraced with apical tergum, including oblique long triangular plates possibly related to genitalia) difficult to interpret. No distinct vestiture detected.

Phylogenetic positions of the new family

Phylogenetic analysis based on morphological characters is constructed to clarify the taxonomic position of the new family and to understand the relationships of clade Psocodea (barklice, booklice and true lice). The strict consensus tree indicates the new family to be embedded within Amblycera, which together with Ischnocera, Trichodectera, Rhychophthirina, and Anoplura forming a clade Phthiraptera, and Phthiraptera as a sister group of Liposcelididae ([Figures 4 and S4](#)).

Archimenoponidae fam. nov. possess bulbous and protruding postclypeus (character 10:1) and support its inclusion in Psocodea. They have shorter antenna than head (character

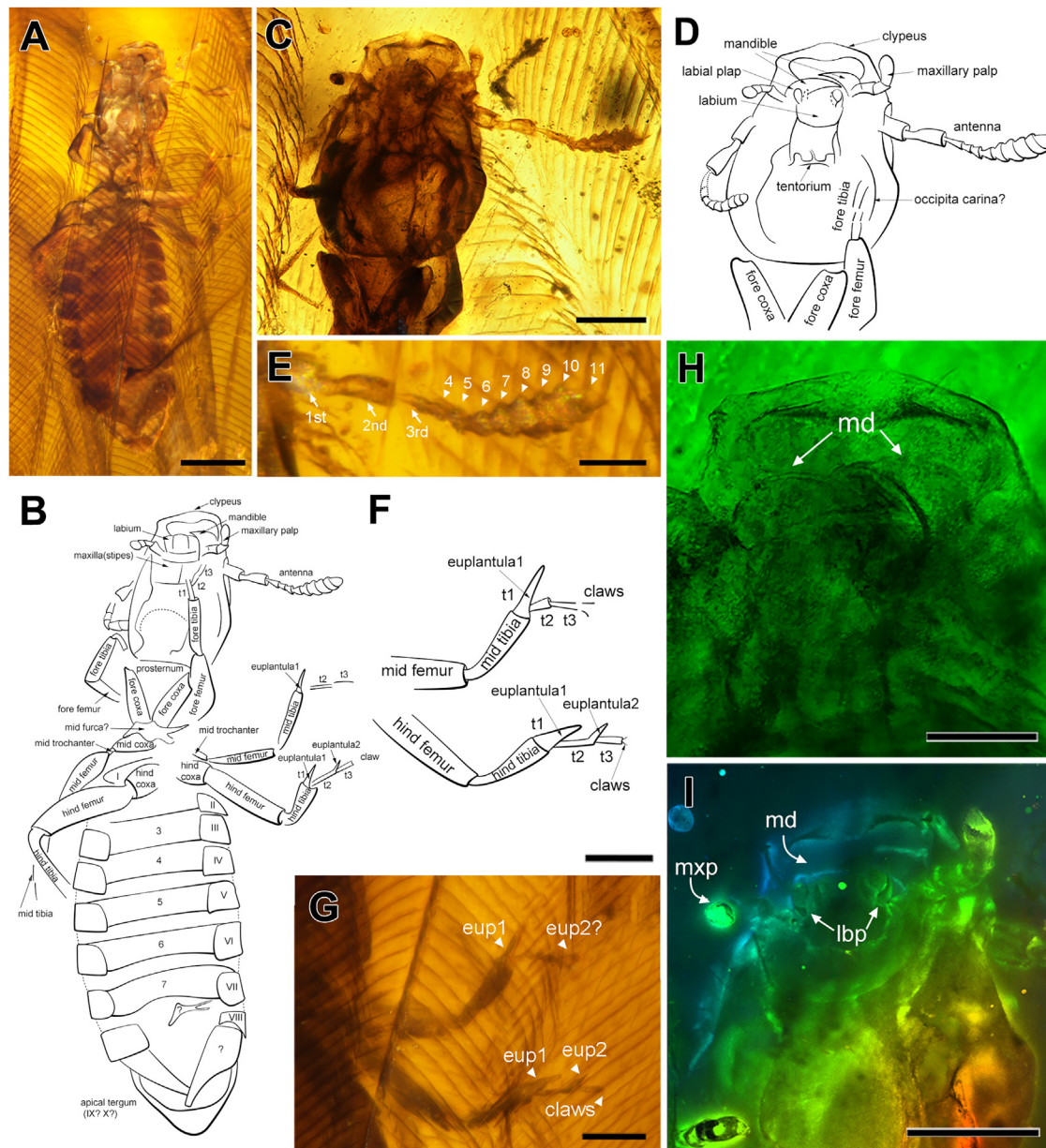


Figure 2. Holotype of *Archimenopon myanmarensis* gen. et sp. nov. no. BU-MA002385-1

(A and B) Habitus and interpretive drawing.

(C and D) Habitus and line drawing of head.

(E) Left antenna.

(F and G) Habitus and line drawing of enlargement of the legs show the details of the midleg and hindleg, especially euplantula.

(H and I) Mouthpart details under confocal laser scanning microscope (LSCM) and Leica DM5500 microscope with fluorescence filter cubes.

Scale bars: 0.2 mm in (A) and (B); 0.1 mm in (C), (D), (F), (G), and (I); and 0.05 mm in (E) and (H). Abbreviations are as follows: lbp, labial palp; md, mandible; mxp, maxillary palp; 1st, 2nd, 3rd, 4th to 11th, antennal segments; eup1, euplantula on the first tarsus; eup2, euplantula on the second tarsus; t1, first tarsomere; t2, second tarsomere; t3, third tarsomere; 1 to 7 and II to VIII, abdominal sterna and terga, respectively.

See also Figure S2.

25:0), which differentiates it from Liposcelididae and places it in Phthiraptera. Following characters further support its relationship within Amblycera: club-shaped antenna (character 26:0), compared with the filiform antenna of Liposcelididae¹⁵; pedunculated first flagellar segment (character 27:1) but compressed terminal several ones (character 28:1), and antennae

are never pedunculated in any of the other phthirapteran groups¹⁶; two euplantula (character 49:0), in other families of the Amblycera, only the euplantula of the first tarsal segment is normally present.¹⁶ Archimenoponidae fam. nov. lack antennal fossae concealed the antenna, which separates this family from other groups of Amblycera.

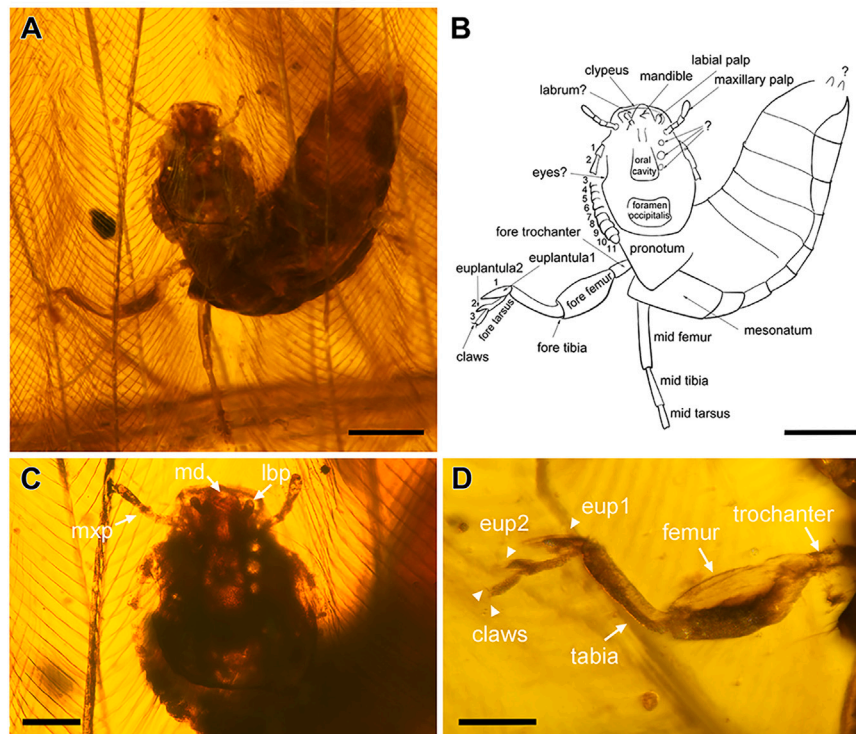


Figure 3. Paratype of *Archimenopon myanmarensis* gen. et sp. nov. no. BU-MA002385-2 (A and B) Habitus and interpretive drawing.

(C) Photograph of the head, in ventral view, showing labium, maxilla and the segments of antenna.

(D) Enlargement of forelegs, showing the swollen profemur, the first two tarsi each bearing an euplantula, and two small claws.

Scale bars: 0.2 mm in (A) and (B) and 0.1 mm in (C) and (D). Abbreviations are as follows: lbp, labial palp; md, mandible; mxp, maxillary palp; eup1, euplantula on the first tarsus; eup2, euplantula on the second tarsus.

DISCUSSION

The origin and early evolution of true lice

Fossil preservation for lice requires a special environment, making their fossils exceedingly rare. Thus, the origin and early evolution of parasitic lice are poorly understood. Some studies employed molecular clock models and molecular evolutionary analyses to attempt to infer the origin time of parasitic lice.^{3,4,14} According to the latest dating analysis, the parasitic lifestyle of Phthiraptera might have originated in 115 mya.³ Here, we have confirmed the existence of phthirapteran lice in the mid-Cretaceous. This specialized parasitism lifestyle at least originated in the mid-Cretaceous (99 mya), pushing back the known fossil records for the true lice by nearly 55 million years.

In Psocodea, the free-living Psocoptera and parasitic Phthiraptera together form a monophyletic lineage, with the monophyletic Phthiraptera derived from within the Troctomorpha as a sister group of Liposcelidae.^{3,4,6} Our results are in agreement with modern phylogenomic results. Archimenoponidae fam. nov. form one half of the basal-most split within Amblycera as defined here (Figure 4). They have some obvious “transitional” characteristics, which give an indication to understand the possible evolutionary process from free-living “barklice” and “booklice” to ectoparasitic “true lice.” As shown in Figure 4, clade A represents the divergence of the parasitic lice with the evolution of parasitic characteristics, such as the shortening of antennal length. A lineage (clade B) evolved into Amblycera, with the antennal flagellum further modified as clavate with pedunculate first segment, the terminal of antennal flagellomeres compressed, and tarsal segments acquired euplantulae. The next branch comprises the

extant Amblycera, which have developed much incrassate legs with only two-segmented tarsus and very short five-segmented antenna concealed in the antennal fossae. The other phthirapteran clade C includes all other extant lice (Anoplura, Trichodectera, Rhynchophthirina, and Ischnocera). Antennae and tarsi are also reduced in these groups. The placement of Archimenoponidae fam. nov. in the Amblycera suggests that these reductions have occurred independently in Amblycera and the clades of other phthirapteran lice.

gests that these reductions have occurred independently in Amblycera and the clades of other phthirapteran lice.

Parasitic environment and feeding habits

At least seven feathers, overlapping with each other, are embedded with these two chewing lice in the amber (Figure 1) and two related inclusions (Figure S1). Three small feathers have relatively thick shafts, each of which seems to be composed of a long calamus and a relatively short rachis. The rachis bears barbs, the details of which are not observable. Four large feathers are very similar to the semiplume feathers in living birds, each of which has a thick rachis and proportionally long barbs and barbules, but seems to bear no hooklets (Figure S3). The longest feather has a rachis approximately 23 mm long and nearly 0.4 mm in diameter at the base (Figure 1). Both lice are located between the barbs, closer to the rachis. Unfortunately, there are no details on the interactions between the lice and the feathers in the amber.

Existing Amblycera lice live on birds and mammals, and feed on skin derivatives of their hosts, such as hairs, feathers, etc. Most amblyceran lice depend on drinking blood for their egg production, meaning that they regularly drink blood throughout their lives.¹⁷ As the sister group of Phthiraptera, Liposcelidae (booklice) also live in a similar environment. Many liposcelids have been discovered in the plumage of birds and pelage of mammals even in their nests, and feed on nest debris.^{18–20} This association is thought to be a short-term commensalism which may have given rise to a permanent association in lice.²¹ The transition from saprophagous to parasitic insect does not seem to involve major dietary barriers.¹⁵ Almost all the amblyceran lice feed by shearing or scraping feathers or skin with their mandibles cutting in a horizontal plane.¹ Meanwhile, they grab feathers or hairs with

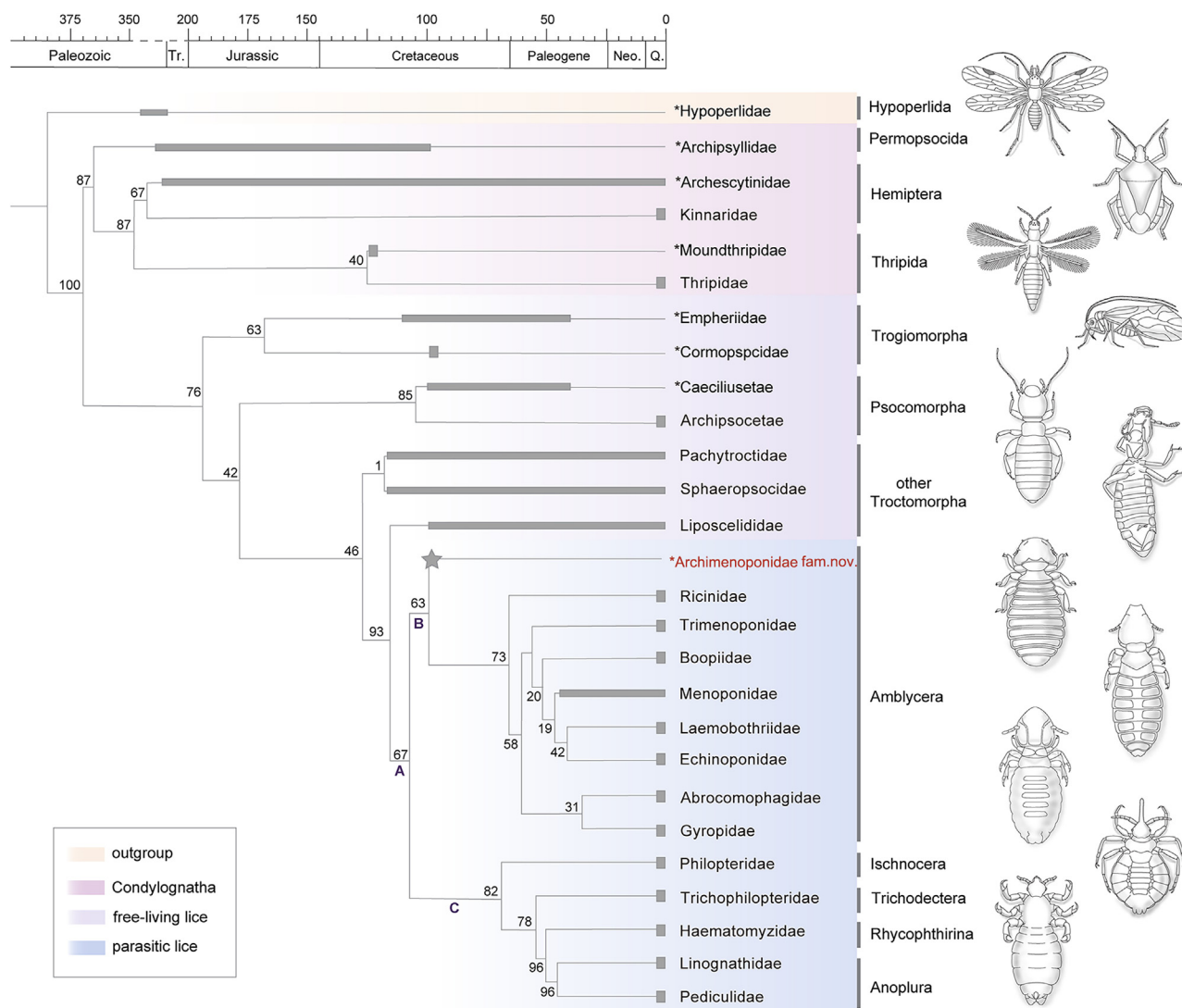


Figure 4. Results of the phylogenetic analysis

The strict consensus tree, tree length = 81 steps, consistency index (CI) = 0.73, retention index (RI) = 0.91. The timescale provides an estimate of divergences suggested by Moya et al.³ and Misof et al.¹⁴ The bold gray lines represent the fossil records. Colored parts refer to the following clades: beige, outgroup; pink, Condylgnatha (Permopsocida + Hemiptera + Thripida); purple, free-living booklice (Trogiomorpha + Psocomorpha + other Troctomorpha); blue, parasitic lice. Clade A is characterized by the antennal length equal to or much shorter than head; clade B is characterized by the club-shaped antenna, pedunculated first segment and the compressed terminal antennal flagellomeres, as well as two euplantulae; clade C is characterized by occipital apodeme extending into thorax. See also Figure S4 and Data S1 and S2.

their claws, using euplantula to assist and increase friction, preventing themselves from being shaken off by the host. The morphology of specimens of *Archimenoponidae* fam. nov. also seem to suggest that its members were more likely to have similar living and diet habits with amblycerans. And then, a transition from free-living to parasitic lice seemed to be logical.

Divergence of parasites

Parasitic insects often have a close and inseparable relationship with their hosts. A clade of Phthiraptera (Trichodectera, Rhycoptirina, Anoplura, and Ischnocera), the first three of four groups are found exclusively on mammals, and the fourth includes at least one species that occurs on a mammal (others

on birds). Amblyceran lice are known from almost all bird orders and some mammals.⁶ Many studies regarding bird and mammal lice suggested that the earliest branch within the Amblycera is Boopiidae.^{3,4} It is attractive to believe that the ancestral host of lice was a basal mammalian group like marsupials.⁶ Johnson et al. reconstructed ancestral host groups (birds versus mammals) for all parasitic lice, and all supported avian ancestral hosts.²² The occurrence of *Archimenoponidae* fam. nov. on an ancestral bird seems to imply a certain connection between them. Based on morphological evidence, the *Archimenoponidae* could have diverged from the lineage leading to the rest of the amblyceran families at an early stage. If the association between *Archimenopon* gen. nov. and birds/dinosaurs is correct, at least

for now, it implies the birds (and/or feathered dinosaurs) are the ancestral hosts of amblyceran lice, followed by subsequent transmission to mammals.

Phthiraptera (parasitic lice) and Siphonaptera (fleas) are two major lineages of extant ectoparasites. Fleas are known from at least the Middle Jurassic, after the emergence of vertebrate hosts with fur or feathers.⁷ The blood-sucking fleas diversified during the Jurassic⁸ and further specialized into modern fleas during the Mesozoic and Palaeogene. Appearance of another parasitic lineage, feather-chewing lice, appears to be delayed compared to fleas. The sister group of Phthiraptera, Liposcelididae,²³ has its oldest fossil records from the Cretaceous Kachin amber.¹⁵ Grimaldi and Engel, using the method of sister-group dating, estimated that louse minimally diverged around 100 mya or even in the earliest Cretaceous (145 mya).¹⁵ Previous related studies have reported estimations of the earliest divergence and the initial diversification within parasitic lice (~100 mya)³ or between 90 and 100 mya.⁴ The new records of Archimemonoponidae fam. nov. confirmed that parasitic and non-parasitic (liposcelidid) lineages diverged from each other before the mid-Cretaceous. In other words, the true lice diverged from the booklice (Liposcelididae) before the mid-Cretaceous (99 mya). These primitive parasitic lice might have lived on early birds or feathered dinosaurs.^{24,25} With the rapid diversification of modern bird and mammal lineages, the modern louse lineage occurred and radiated extensively, as suggested by the vast amount of extant lice.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- **KEY RESOURCES TABLE**
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 - Materials availability
 - Data and code availability
- **EXPERIMENTAL MODEL AND SUBJECT DETAILS**
- **METHOD DETAILS**
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.01.027>.

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AUTHOR CONTRIBUTIONS

T.G., H.L., and Y.W. conceived and designed the study. Y.Z., A.P.R., and T.G. performed the analyses and wrote the manuscript. Y.Z. and A.P.R. prepared the figures and line drawings. A.P.R. and C.S. revised the manuscript. Y.Z., A.P.R., F.S., H.L., and Y.W. carried out the phylogenetic analyses. W.Z. donated the amber material for studying. All authors read and approved the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Characters and states	This paper	Data S1
Phylogenetic matrix	This paper	Data S2
Software and algorithms		
WinClada/Nona (V.1.00.08)	Nixon ²⁶	Nixon ²⁶

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Taiping Gao (tpgao@cnu.edu.cn).

Materials availability

This amber is currently housed in the Three Gorges Entomological Museum, Chongqing, China.

Data and code availability

All data used for analysis in this study are included in the Main text or the [supplemental information](#) of this published article. The newly proposed names are registered under the following doi numbers in ZooBank: Archimenoponidae – [urn:lsid:zoobank.org:act:AE77FF4D-F8B0-4111-BE49-055B1B9EC208](https://doi.org/urn:lsid:zoobank.org:act:AE77FF4D-F8B0-4111-BE49-055B1B9EC208); *Archimenopon* – [urn:lsid:zoobank.org:act:806CD26F-8648-4F7A-ADF8-426CDF812461](https://doi.org/urn:lsid:zoobank.org:act:806CD26F-8648-4F7A-ADF8-426CDF812461); *Archimenopon myanmarensis* – [urn:lsid:zoobank.org:act:4C87F8BB-597B-4CEA-8247-80DBABE48E09](https://doi.org/urn:lsid:zoobank.org:act:4C87F8BB-597B-4CEA-8247-80DBABE48E09).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Two insect specimens (BU-MA002385-1; BU-MA002385-2) were preserved with seven feathers in a piece of Myanmar (Burmese) amber. The amber was collected from Kachin (Hukawng Valley) of northern Myanmar, which was dated at 98.79 ± 0.62 Mya based on U-Pb dating of zircons.²⁷ This formation contains diverse insect fossils.^{28,29} The material reported herein was collected prior to the proposed moratorium on Kachin amber acquisition, and is therefore in compliance with ethical standards. The amber specimen was acquired by Mr. Weiwei Zhang in 2016, who donated this material for studying in late 2019. This amber is currently housed in the Three Gorges Entomological Museum, Chongqing, China. The specimen is permanently deposited in well-established, in full compliance with the International Code of Zoological Nomenclature and the Statement of the International Palaeoentomological Society.³⁰

METHOD DETAILS

Photography and light microscopy

The specimens were examined and photographed under a Nikon SMZ 25 microscope with an attached Nikon DS-Ri2 digital camera system in the Fossil Insect Laboratory at CNU. The green background photographs were taken with a Leica DM5500c. The LSCM color photographs were taken using a Zeiss LSM 780 Confocal laser scanning microscope (LSCM) at CNU.

Phylogenetic analysis

Phylogenetic analysis includes a representative of Hypoperlida (Hypoperlidae) as out-groups, and Permopsocida (Archipsyllidae) and several groups of Thysanoptera (thrips) and Hemiptera (bugs) as ingroups. Twenty-one representatives' families of Psocodea are included in the analysis. Aside from the fossil groups, we specifically selected extant groups within the analysis. A total of 60 morphologic characters are listed in [Data S1](#) and the characteristic–state matrix consisting of 27 taxa and 60 characteristics is provided in [Data S2](#). Groups and character selections are referred to previous contributions.^{6,16,31–33}

Phylogenetic analysis was performed using WinClada/Nona (Version 1.00.08).²⁶ Tree search implemented a heuristic search method, and the options were set to hold 10 000 trees, 1000 replications, 100 starting tree replications, and a multiple TBR + TBR search strategy. All characteristics were considered unordered and supporting values were determined by using NONA with 1000 replications and are represented as numbers under the branch nodes.