

PALEONTOLOGY

Mouthpart homologies and life habits of Mesozoic long-proboscid scorpionflies

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Mesozoic long-proboscid scorpionflies (Mesopsychoida) provide important clues to ancient plant-pollinator interactions. Among them, the family Aneuretopsychidae is especially important because its mouthparts are vital to deciphering the early evolution of Mesopsychoida and putatively the origin of fleas (Siphonaptera). However, the identification of mouthpart homologs among Aneuretopsychidae remains controversial because of the lack of three-dimensional anatomical data. Here, we report the first Aneuretopsychidae from Late Cretaceous Burmese amber, which have short maxillary palpi and elongate mouthpart elements consisting of one pair of galeae and one hypopharynx. Their mouthparts are identical to those of Pseudopolycentropodidae (= Dualulidae, new synonym) but are not homologous to those of Siphonaptera. Our phylogenetic analysis provides robust evidence for the debated monophyly of Mesopsychoida. Our results suggest that the long-proboscid condition has most likely evolved once in Mesopsychoida, independently from fleas, and further reveal the variety and complexity of mid-Cretaceous pollinating insects.

INTRODUCTION

Mesopsychoid scorpionflies (Mecoptera) are peculiar, conspicuous Mesozoic insects with distinctively elongate proboscides and were presumably a critical group of pollinators, providing insights into the nature of plant-pollinator interactions before the rise of angiosperms (1–4). The superfamily Mesopsychoida has encompassed five families—Nedubroviidae, Mesopsychidae, Aneuretopsychidae, Pseudopolycentropodidae, and Dualulidae (3, 5), although the last is herein recognized as a synonym of pseudopolycentropodids. The long-proboscid condition was thought to independently have originated multiple times among mesopsychoids (5, 6), largely based on inconclusive evidence suggesting nonhomologous elements comprising the siphonate mouthparts in different families. The clade is of further interest in that some mesopsychoids have been implicated as extinct sister groups to the fleas (Siphonaptera), suggesting a substantial transition from plant feeding to blood feeding among these ancient mecopterans (7–9).

Among Mesopsychoida, Aneuretopsychidae was the first known group of mecopteran insects with a long siphonate proboscis, associated with feeding on pollination drops from contemporaneous gymnosperm reproductive structures (2). This family, in particular, is key to understanding both the early evolution of highly modified mouthparts in Mesopsychoida and putatively the origin of fleas. It has recently been argued to be an extinct sister group of fleas,

purportedly between the Boreidae and Pansiphonaptera (Siphonaptera and their extinct stem groups among the protosiphonapteran grade), and supported by their elongate mouthpart structures (7–9). Nonetheless, the aneuretopsychid proboscis was interpreted to be of labial origin and be composed of a labial tube that ends with an absorptive pseudolabellum (3, 5, 6, 10), in contrast to the maxillary origin of the proboscis of Siphonaptera and some other Mesopsychoida (7, 11, 12), this at least implying potentially independent origins of these structures. The conflict remains unresolved owing to the lack of fossils with sufficient three-dimensional preservation to reveal comparative anatomical data from the mouthpart components. The two-dimensional preservation of mouthparts in most compression fossils commonly hinders a detailed investigation [e.g., Kalligrammatidae; (13)]. Until now, all previously known aneuretopsychids were from two-dimensionally preserved fossils from Central Asia and northeastern China, with no species having been described from amber (14). Here, we report a new genus including two new species of Aneuretopsychidae from Late Cretaceous Burmese amber [99 million years (Ma)], which reveal anatomically noteworthy new details of the elongate mouthpart elements.

RESULTS

Systematic paleontology

Aneuretopsychidae Rasnitsyn and Kozlov, 1990.

Burmopsyche gen. nov.

LSID (Life Science Identifier). urn:lsid:zoobank.org:act:15E5EB7B-004B-4AA7-A807-F2EE5C095EF0.

Etymology. The generic name is derived from Burma, the original English name of Myanmar, and “-psyche,” a typical suffix of generic names in Aneuretopsychidae. Gender: feminine.

Type species. *Burmopsyche bella* sp. nov.

Other species included. *Burmopsyche xiai* sp. nov.

Diagnosis. Head triangular in dorsal view, with ocelli raised on ocellar dome, with lateral and medial ocelli at edges of dome. Maxillary palps three-segmented. Antennae moniliform, slender, shorter than

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proboscis. Wings membranous, without spots or patterns of infuscation aside from pigmented pterostigma between termination of Sc and R_1 . Forewing ovate to subtriangular, relatively broad at base, with more or less distinct tornus and narrow but extended clavus; Sc reaching middle of wing length or beyond, with strong humeral vein and short distal branch to costal margin; R_1 long and simple, braced to Rs by three crossveins; Rs separating from R_1 proximally, in basal one-fifth of wing; Rs four-branched with two forks, of which Rs_{1+2} fork distinctly shorter than that of Rs_{3+4} ; stem of M elongate and straight, forking nearly at wing midlength, distal to Rs fork; M three-branched; connection between M and CuA obtuse Y-shaped, with prominent, strong upper arm (“ M_5 ”) and lower arm (base of CuA) much shorter, crossvein-like; CuA long, reaching at least three-fourths of wing length or more, straight in basal half, then broken line-shaped, with three crossveins to M; CuP long, braced to CuA by two strong crossveins, which form a characteristic hexagonal cell; three anal veins long and subparallel to CuP and to each other; A_1 and A_2 connected by strong, oblique crossvein forming “pseudo-loop” (apomorphy of family); A_3 with long oblique crossvein to wing margin. Hind wing subtriangular, with wide folding vannus and well-developed jugum; hind wing R_1 bearing a distinctive row of setal hooks along its medial third (potentially to link with posterior portion of forewing during flight); venation of remigium more or less similar to forewing. Legs slender, with setation of femora and especially tibiae arranged in transverse linear series, those of tibiae and tarsi longer and stiffer on inner surfaces; distitarsi slightly expanded with ventral surfaces flattened to faintly concave and covered in microtrichia; pretarsal claws large, broadly arched, and widely separated by broad and blunt unguitactor. Female cercus dimerous (two cercomeres).

Remarks. The new genus undoubtedly belongs to Aneuretopsychidae based on the opisthognathous siphonate mouthparts, the presence of pseudo-loop in the anal area of the forewing, and the well-developed jugum of the hind wing. It differs from other genera of Aneuretopsychidae by the relatively small body size [except for *Aneuretopsyche minima*; Rasnitsyn and Kozlov, 1990 (2)], three-segmented maxillary palps, and three-branched M in both fore- and hind wings.

In addition to the two species described here, there are two additional undetermined specimens embedded in the same piece of amber, at least one of which may represent a third species of the genus (see note S1 and fig. S1).

Burmopsyche bella sp. nov. (Figs. 1, A to J, and 2, A, C, D, and fig. S2)

LSID. urn:lsid:zoobank.org:act:204B591A-2B9F-40F8-88C0-67D8C5FB5BFC.

Etymology. The specific epithet is from the Latin “*bellus*,” meaning “beautiful.”

Materials. NIGP166158, two adults preserved in an amber piece: holotype, NIGP166158a, a well-preserved incomplete specimen of unknown sex (distal part of abdomen is missing, legs partly preserved); paratype, NIGP166158b, a nearly complete female (forewings apices missing) embedded in the same piece of amber. Paratype, NIGP166159, a nearly complete female of somewhat smaller size, with right wings partially destroyed.

Locality and horizon. Noiye Bum Village, Tanaing Town, northern Myanmar; lowermost Cenomanian, Upper Cretaceous.

Diagnosis. Body length 7 to 8 mm. Forewing length 8 to 10 mm; fork of Rs_{1+2} slightly shorter than stem; fork of Rs_{3+4} about 1.3× as long as its stem, longer than fork of Rs_{1+2} ; M_1 simple, M_{2+3} with distinct fork; CuA long, in basal half straight, in distal half broken line-like, hexagonal cell as long as distal portion of CuA.

Description. Head spheroidal in lateral view, length 1.02 mm, width 0.77 mm, approximately half of greatest width of thorax, with prolonged siphonate mouthparts. Three prominent ocelli present on vertex (not visible in holotype, but well preserved in paratype NIGP166159); compound eyes large and rounded, occupying most of the head. Antennae connected to head in frontal region below ocelli; scapus poorly visible, elongate; pedicellus relatively large, apically dilated; flagellum moniliform, with approximately 49 to 50 flagellomeres (42 in paratype NIGP166159), up to three times wider than long; each flagellomere slightly flattened, with three setal whorls (proximal, medial, and distal), with medial whorl composed of the most prominent setae and positioned slightly closed to proximal whorl. Entire length of antenna (in holotype) 4.10 mm. Proboscis thin, flexible, consisting of three lobes, apparently lacking any terminal absorptive structures such as pseudolabellae. Hypopharynx greatly slender, about 3.80 mm long, needle-like at tip; galeal sheaths of proboscis as long as hypopharynx. Other head and mouthpart structures, including clypeus, labrum, and maxillary palpi not visible as preserved.

Thorax length 3.12 mm, width 1.79 mm, pronotum very small, mesonotum and metanotum subequal in size. Legs entirely covered with annulate setae (shown in paratype NIGP166158b); coxae and femora not shortened; tibiae slightly longer than femora; tarsi five-segmented, basitarsus longest, nearly as long as remaining tarsomeres combined; pretarsi with two curved claws and unpaired arolium. Abdomen (based mainly on the paratype NIGP166158b) stout, slightly shorter than wings, preabdominal segments obscured, postabdominal (VI to XI) segments tapering apically. Cerci dimerous, distal cercomer filamentary (in paratype NIGP166158b, dorsally curved as preserved; in NIGP166159, straight), with dense, non-isometric setae.

Forewing oblong-subtriangular, with distinct tornal angle at about 0.7× wing length with blunt apex. Forewing length about 10.5 mm, maximum width 4.15 mm, length/width ratio 2.5:1. Sc long, straight, reaching beyond middle of wing, with strong humeral vein at base and short distal branch to costal margin, in apical portion connected to R_1 by short crossvein $sc-r_1$. R_1 long, simple, in distal third gently curved toward wing apex. Pterostigma well developed, extensive, at base extending toward Rs_{1+2} along r_1-rs_{1+2} crossvein, in distal part bounded by R_1 . Rs separating from R_1 in basal one-fifth of wing, four-branched, forking somewhat before middle of wing; fork of Rs_{1+2} slightly shorter than stem; fork of Rs_{3+4} about 1.3× as long as its stem, longer than fork of Rs_{1+2} ; stem of Rs_{3+4} with distinct curve at first crossvein to M. Base of medial vein braced to base of R_1 by short crossvein $r-m$. M forking at center of wing distal to Rs fork, having three branches meeting wing margin, M_1 simple, M_{2+3} with distinct fork. CuA long, ending nearly at three-fourths of wing length just beyond tornus, in basal half straight, in distal half broken line-like, braced to CuP by two long crossveins, of which distal one is strongly oblique; hexagonal cell as long as distal portion of CuA. CuP long, ending somewhat before or beyond level of Sc apex, apical portion of CuP after distal $cua-cup$ crossvein sharply curved toward wing margin. Three anal veins long and subparallel to CuP and to each other, A_2 reaching middle of wing length, at level of M fork; A_1 and A_2 connected by strongly oblique crossvein, which is relatively short and located slightly distal to cubito-medial Y-vein; A_2 markedly curved at this point. Space posterior to third anal vein wide, crossed by oblique crossvein from A_3 to wing margin. Crossveins numerous, concentrated mainly in distal half of wing, arranged in three more or less distinct rows; crossveins mostly forwardly inclined or upright.

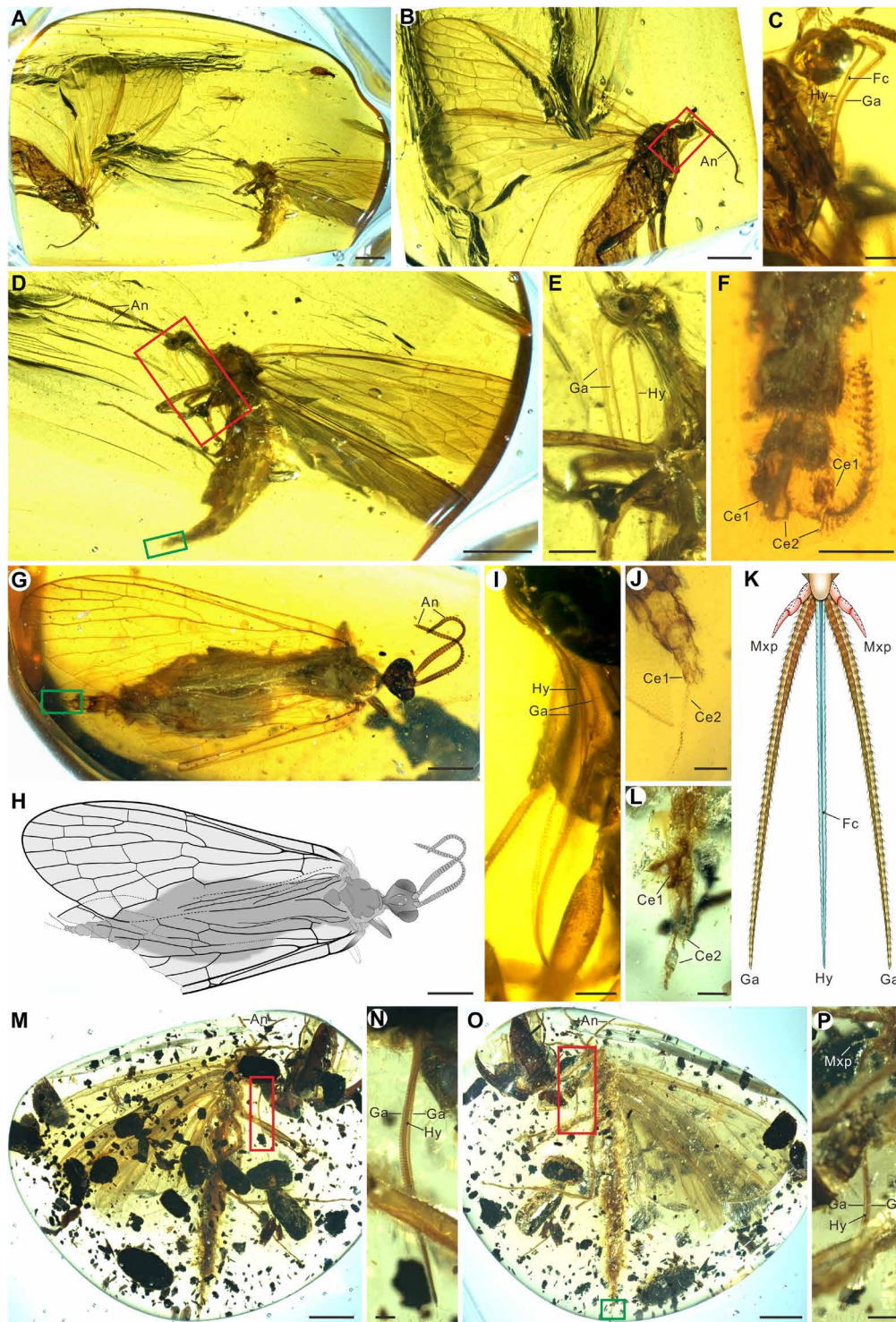


Fig. 1. Aneuretopsycheidae from Late Cretaceous Burmese amber. (A) *Burmopsyche bella* gen. et sp. nov.; holotype, NIGP166158a (left); paratype, NIGP166158b (right). (B and C) *Burmopsyche bella* gen. et sp. nov.; holotype, NIGP166158a. (B) Habitus in lateral view. (C) Head and proboscis, enlarged from the red template in (B). (D to F) *Burmopsyche bella* gen. et sp. nov.; paratype, NIGP166158b. (D) Habitus in lateral view. (E) Head and proboscis, enlarged from the red template in (D). (F) Genitalia, enlarged from the green template in (D). (G to J) *Burmopsyche bella* gen. et sp. nov.; paratype, NIGP166159. (G) Habitus in dorsal view. (H) Line drawing of (G). (I) Proboscis. (J) Genitalia, enlarged from the green template in (G). (K) Reconstruction of mouthparts of Aneuretopsycheidae (note the opisthognathous orientation of mouthparts). (L to P) *Burmopsyche xiai* sp. nov.; holotype, NIGP171685. (L) Genitalia, enlarged from the green template in (O). (M) Habitus in right lateral view. (N) Proboscis, enlarged from the red template in (M). (O) Habitus in left lateral view. (P) Proboscis, enlarged from the red template in (O). An, antenna; Ce1, cercus segment 1; Ce2, cercus segment 2; Fc, food channel; Ga, galea; Hy, hypopharynx; Mxp, maxillary palp. Scale bars, 2 mm (A, B, D, M, and O), 1 mm (G and H), 0.5 mm (C, E, and P), and 0.2 mm (F, I, J, L, and N). Photo credit: B.W., Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

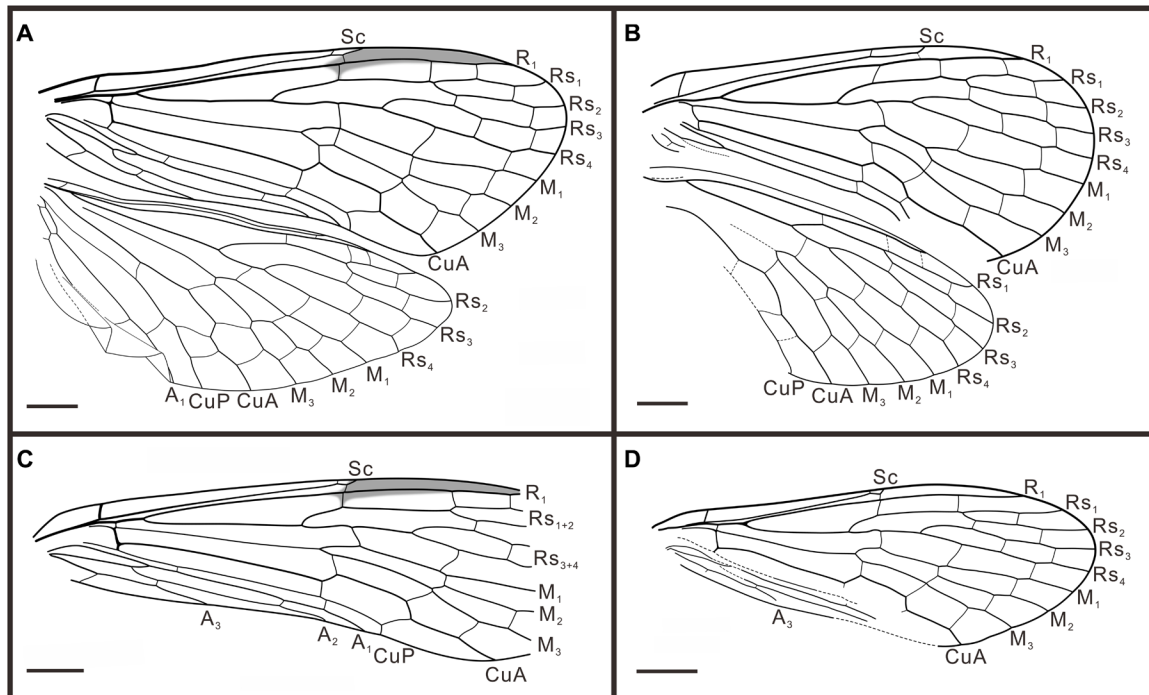


Fig. 2. Wing venation of Aneuretopsychidae from Late Cretaceous Burmese amber. (A) *Burmopsyche bella* gen. et sp. nov.; holotype, NIGP166158a. (B) *Burmopsyche xiai* sp. nov.; holotype, NIGP171685. (C) *Burmopsyche bella* gen. et sp. nov.; paratype, NIGP166158b; forewing. (D) *Burmopsyche bella* gen. et sp. nov.; paratype, NIGP166159; forewing. Scale bars, 1 mm.

Hind wing delicate, somewhat smaller than forewing, subtriangular in shape, with distinct apical angle and smooth tornus. Hind wing length about 8.45 mm, width of remigium about 3.6 mm. Bases of all main veins close to wing base. Costal space narrow, Sc long and simple, with short apical crossvein to R_1 . Pterostigma not developed. Vein R_1 with distinctive row of long, anteriorly directed hooked setae. Branching pattern of Rs and M and arrangement of crossveins similar to forewing. Spaces between cubital and anal veins expanded, crossed by long crossveins: three in intercubital space, one in space CuP- A_1 , and one in space A_1 - A_2 (in addition to two short basal crossveins a_1 - a_2). Veins CuP and A_1 fused for short distance before separating close to wing base. Vannus folded twice, vannal (claval) fold apparently located behind A_1 ; vein A_3 and jugal (anal) fold not discernible, as well as jugal veins, if present.

Burmopsyche xiai sp. nov. (Figs. 1, L to P, and 2B)

LSID. urn:lsid:zoobank.org:act: C925539E-A099-47F8-A9AA-4537153887DC.

Etymology. The specific name honors Mr. Fangyuan Xia, director of the Lingpoge Amber Museum in Shanghai.

Holotype. NIGP171685, a nearly complete female with distal parts of antennae missing.

Locality and horizon. Noiye Bum Village, Tanaing Town, northern Myanmar; lowermost Cenomanian, Upper Cretaceous.

Diagnosis. Body length about 12 mm. Forewing length about 9 mm; fork of Rs_{1+2} about as long as its stem; fork of Rs_{3+4} about 2.5× as long as stem; M_{1+2} with deep fork, M_3 simple and more or less smooth at crossvein junctions; CuA long, ending nearly at 0.8× of wing length just beyond tornus, hexagonal cell relatively short, half as long as distal portion of CuA.

Description. Body length 12.1 mm, thorax length 3.0 mm, abdomen length 7.2 mm. Head length 1.9 mm, seriously distorted; with pro-

longed siphonate mouthparts. Most of the head and body structures obscured. Preserved part of antenna, 1.63 mm. Maxillary palpi short, about 0.53 mm long, three-segmented. Proboscis about 3.08 mm long.

Thorax length 3.07 mm, width 0.62 mm. Legs with short, dense setae (visible only in hind tibiae and tarsi), hind legs distinctly longer than fore and mid legs. Length: profemur 1.31 mm, protibia 1.92 mm, protarsus 1.48 mm; mesofemur 1.54 mm, mesotibia 1.97 mm, mesotarsus 1.64 mm; metafemur 2.28 mm, metatibia 2.08 mm, metatarsus 1.81 mm; tarsus pentamerous, basitarsus longest, but shorter than other four tarsomeres combined; pretarsus obscured. Abdomen slender, tapering apically, length 7.16 mm, with two cercomeres.

Forewing ovate, with rounded apex, claval area and posterior (inner) margin not visible (overlapped by hind wing), tornal angle unclear. Forewing length 8.95 mm, maximum width 4.3 mm, length/width ratio 2:1. Sc long, straight, reaching beyond middle of wing, with strong humeral vein at base possibly having a short vein to costal margin at about middle of wing length; Sc near apex connected to R_1 by short crossvein sc- r_1 . R_1 long, simple, gently curved toward apex of wing. Pterostigma not preserved. Rs separating from R_1 in basal one-fifth of wing length, forking somewhat before middle of wing; fork of Rs_{1+2} , about as long as its stem; fork of Rs_{3+4} , about 2.5× as long as stem, longer than fork of Rs_{1+2} ; stem of Rs_{3+4} with distinct curve at first crossvein to M. Medial vein fork near center of wing somewhat distal to Rs fork, having three branches meeting wing margin, M_{1+2} with deep fork, M_3 simple and more or less smooth at crossvein junctions. Base of CuA slightly inclined backward, forming an obtuse Y-vein with long M-arm (“ M_5 ”). CuA long, ending nearly at 0.8× of wing length just beyond tornus, in basal half straight, in distal half broken line-shaped, braced to CuP by two relatively short crossveins; hexagonal cell relatively short, half as long as distal portion

of CuA. CuP long, ending at least at the level of Sc apex or beyond; apical part of CuP not visible but must be quite long and without sharp curve to wing margin. A₁ long and subparallel to CuP, its distal portion not visible; other anal veins visible only at their bases. A₁ and A₂ connected by long, strongly oblique crossvein possibly located somewhat before cubito-medial Y-vein; portion of A₂ distal to this crossvein not visible. Space posterior to A₃ narrow, crossed by short oblique crossvein from A₃ to wing margin. Crossveins numerous, concentrated mainly in distal half of wing, indistinctly arranged in three rows, mostly upright or inclined backward.

Hind wing subtriangular in shape, with obtuse apex and smooth tornus; length about 7.6 mm, width of remigium 3.35 mm. Both hind wings slightly bent at costal margin toward wing plane, such that Sc not visible. Pterostigma not developed. Branching pattern of remigium more or less similar to forewing, except for more expanded intercubital space crossed by three long crossveins instead of two as in forewing. Vannus folded, details of venation not discernible.

Phylogenetic analysis

Our parsimony-based phylogenetic results (figs. S3 and S4) are largely similar to those of Lin *et al.* (5) with respect to the basal part of the topology, from the outgroup *Permithone* to *Permotipula*. This is expected, because few alterations were required to the original matrix for these taxa. The distal nodes, however, reflect our corrections in the identity of mouthpart homologies and associated character coding. The most important outcome of these differences is the monophyly of Mesopsychoidae, mainly supported by the presence of siphonate mouthparts including the hypopharynx with a food channel and elongate galeae with sclerotized bands, in contrast to a prior paraphyletic arrangement (5). In this scheme, Mesopsychoidae forms the sister group to the clade encompassing Siphonaptera and Diptera that was also previously obtained with this dataset. These same clades are further retrieved with high support values in our Bayesian treatment (fig. S5), although, in this case, *Permotipula* and the clade *Choristotanyderus* + *Liassophila* are tentatively resolved as stem taxa of the Siphonaptera + Diptera clade. Boreidae (Boreomecoptera) were not included in either Lin *et al.* (5) or the present analysis and would presumably fall with the Siphonaptera + Diptera clade, although this requires future testing.

Both parsimony and Bayesian results retrieve a clade regrouping Pseudopolycentropodidae and *Dualula*. We synonymize Dualulidae under the former family, given that the reduced hind wings of *Dualula* represent a case of convergence (Fig. 3).

DISCUSSION

The Aneuretropsychidae, a very small fossil family with only seven described species so far, was long considered to originate and disappear during the mid-Mesozoic (Middle Jurassic to Early Cretaceous). Recently, wings assigned to basal Aneuretropsychidae were recorded in the Upper Permian of Russia (14), in the same beds where the earliest Mesopsychidae and Nedubroviidae were found (15, 16), suggesting that the first radiation of Mesopsychoidae probably took place before the Mesozoic (Fig. 3). The prior latest representatives of Aneuretropsychidae were from the Lower Cretaceous Yixian Formation (early Aptian, 125 Ma) of China (3) and Zaza Formation (Aptian) of Transbaikalia (2). Earlier studies suggested that Aneuretropsychidae became extinct during the Aptian-Albian gap (125 to 100 Ma), that is, by the end of the Early Cretaceous (3). Our amber fossils demon-

strate that this group persisted until as recently as the earliest Late Cretaceous, and albeit only slightly beyond the end of the gap, they nonetheless represent the latest occurrence of Aneuretropsychidae.

Our amber fossils reveal that the aneuretropsychid proboscis is not labial but maxillary in origin, consisting of one pair of galeae and one unpaired central hypopharynx, which is identical to that of Pseudopolycentropodidae *sensu lato* (5, 12, 17). The hypopharynx slightly tapers apically with the lateral sides curving upward and with a dorsally open food channel on the upper surface, which presumably passes directly into the large suction pump of the pharynx (Fig. 1, C and E). It lacks microtrichia but has a series of fine, transverse grooves and serrations on the ventral surface (Fig. 1, I and K, and fig. S2). The galea is flattened with a deep, narrow longitudinal furrow on the mesal surface, while the outer surface of the galea is furnished with dense microtrichia and sclerotized bands (Fig. 1, C, E, and I, and fig. S2). The sclerotized bands may allow the proboscis to curve significantly but not coil as in Lepidoptera (moths and butterflies). During feeding, the galeae come together temporarily and enclose the hypopharynx, thus forming a functional proboscis (Fig. 1, N and P, and fig. S2).

Our phylogenetic results strongly support the monophyly of Mesopsychoidae and demonstrate that an elongate proboscis is one of its key synapomorphies (Fig. 3), challenging the view that the long-proboscid condition independently has originated two or three times in this clade (5, 6). Aneuretropsychidae and Pseudopolycentropodidae (including Dualulidae as a synonym) share the same arrangement and composition of mouthpart elements comprising their elongate proboscis. The other two families of Mesopsychoidae—Mesopsychidae and Nedubroviidae—likely have the same composition to the mouthparts, although this remains unclear because these structures are not well preserved in compression fossils, from which these families are exclusively known. More finely and completely preserved fossils, especially amber specimens of these two families, are required to further clarify the conditions of these groups. Furthermore, our topologies demonstrate that the strong reduction of hind wings in the former Dualulidae is nothing more than another example of autapomorphic wing reduction, common across many groups of insects, including several examples in Cretaceous amber, such as mesochrysoptine and dipteromantispine lacewings (18, 19).

The proboscis of Mesopsychoidae differs structurally from the highly modified piercing mouthparts of Siphonaptera, the latter of which consist of a pair of elongate laciniae enclosing the labrum laterally and the food canal posteriorly (11, 20). Siphonapteran mouthparts are distinguished by laciniae bearing rows of backward-projecting teeth (to cut the skin) enclosed by labial palpi for protecting the labrum and laciniae; both are specialization for consuming blood (21). Our phylogenies reveal that neither Aneuretropsychidae nor Mesopsychoidae are the sister group to Siphonaptera, thus rejecting the previous hypothesis of an Aneuretropsychidae + Siphonaptera clade and removing the aneuretropsychids from implications surrounding the origin of fleas.

These long-proboscid scorpionflies most likely fed on liquid pollination drops of gymnospermous reproductive structures and perhaps engaged in pollination mutualisms with gymnosperms. Nonetheless, such floral visitation may not have been obligate, much like modern mosquitoes where females feed on blood and males feed on nectar (17). The flattened distitarsi and widely separated claws suggest grasping structures, and it is possible that *Burmopsyche* fed opportunistically on the hemolymph of other insects, at least in females, as similarly demonstrated for *Parapolycentropus* (17). Thus,

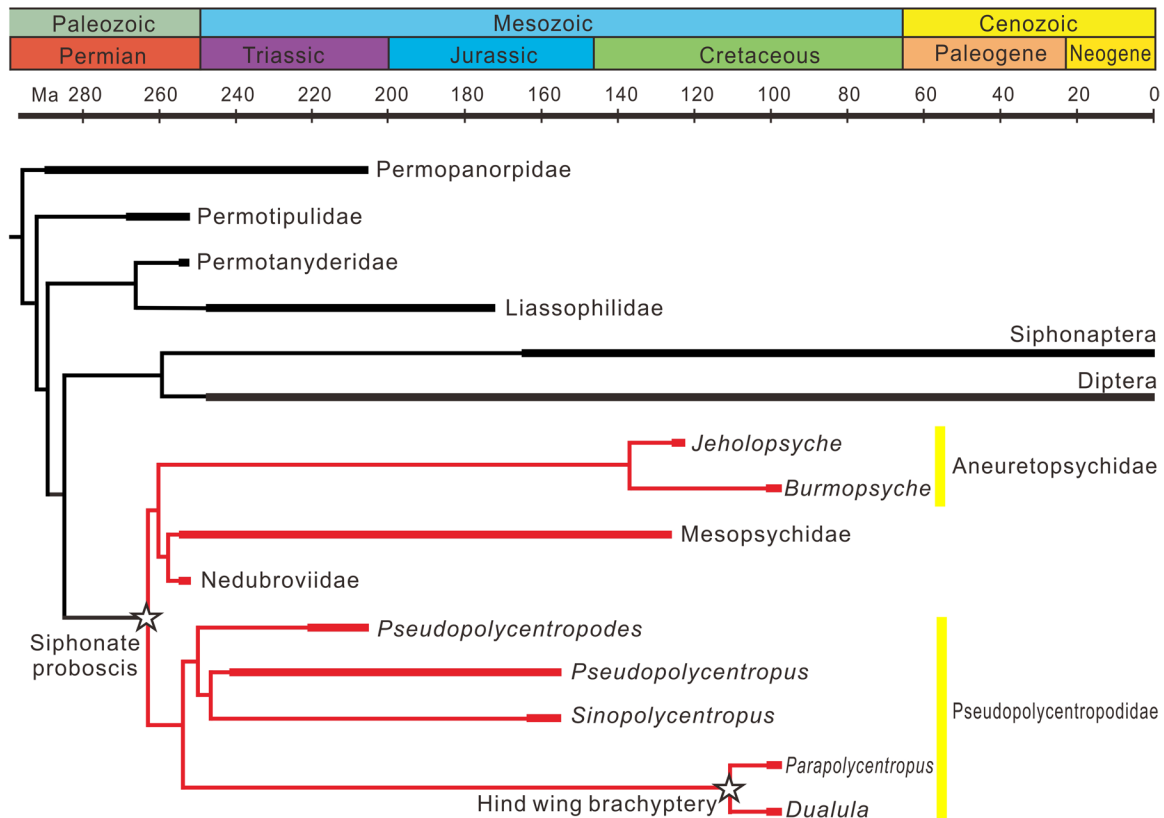


Fig. 3. Evolutionary history of Mesopsychoidae and related groups based on the parsimony analyses. Thick lines indicate the known extent of the fossil record. Branches representing Mesopsychoidae are shown in red (see the Supplementary Materials for details of the phylogenetic analyses).

the ecological associations of mesopsychoids may be more complex and varied than simply obligate pollinators. Instead, these siphonate scorpionflies likely jointly fed on other insects while simultaneously visiting gymnosperms for pollination drops. Kalligrammatid lacewings had convergently evolved similar mouthparts, of which the ligulae are enclosed by a pair of half-tubular galeae with cuticular bands (13), suggesting that both groups might share a similar feeding mechanism and that kalligrammatids might have a similarly more complex feeding ecology, including facultative predation, and thereby more similar to other predatory Neuroptera. In the Burmese amber forest, at least five families of long-proboscid insects (Mecoptera: Aneuretopsychidae and Pseudopolycentropodidae *sensu lato*; Neuroptera: Kalligrammatidae and Sisyridae; Diptera: Zhangsolvidae) have been discovered, further revealing the variety and complexity of mid-Cretaceous pollinating insects (13, 22, 23).

MATERIALS AND METHODS

Materials and depository

The amber insects were obtained from an amber mine located near Noije Bum Village, Tanaing Town. The U-Pb dating of zircons from the volcanoclastic matrix of the amber gave a maximum age of 98.8 ± 0.6 Ma (24, 25). The three specimens (NIGP166158, NIGP166159, and NIGP171685) are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; one specimen (BA18002) is deposited in the Lingpoge Amber Museum in Shanghai.

Optical microscopy

Specimens were photographed using a Zeiss Stereo Discovery V16 microscope system at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. All images were taken by using digitally stacked photomicrographic composites of approximately 40 individual focal planes using the image editing software Helicon Focus 6 (www.heliconsoft.com), as described by Schmidt *et al.* (26).

Morphological terminology

Morphological terminology generally follows Grimaldi and Johnston (17) for the wing venation and body. Abbreviations of wing venation are as follows: Sc, subcostal; R₁, first branch of the radius; Rs, radial sector; M₁, first branch of the media; M₂, second branch of the media; M₃, third branch of the media; CuA, anterior cubitus; CuP, posterior cubitus; A₁, first branch of the anal vein; A₂, second branch of the anal vein, A₃, third branch of the anal vein.

Phylogenetic analysis

The dataset is composed of 38 taxa and 54 discrete characters (data files S1 and S2), modified from Lin *et al.* (5). All 54 characters were subsequently unordered and unweighted, with *Permithone* used as outgroup. Bayesian phylogenetic analyses were performed using MrBayes v.3.2.6 × 64 (27) and parsimony analyses with TNT v.1.5 (28). Equal weight traditional heuristic tree branch swapping (tree bisection reconnection) and an equal weight new technology search implementing ratchet were used as methods of parsimony analysis with TNT (29). The heuristic tree bisection reconnection search was

performed using 1000 replicates and 10 trees saved per replicate, while the new technology analysis with ratchet followed default settings provided by TNT. Bayesian tree searches followed an Mkv+ Γ model (30) with four chains sampled during four runs for 1,000,000 Markov chain Monte Carlo generations, a tree sampled every 1000 generations, and burn-in of 20%.

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. The ZooBank LSIDs can be resolved, and the associated information can be viewed through any standard web browser by appending the LSID to the prefix “<http://zoobank.org/>”. The LSID for this publication is [urn:lsid:zoobank.org:pub:9942FBBB-9810-4D1E-A7BC-85C411F1880A](http://zoobank.org/pub:9942FBBB-9810-4D1E-A7BC-85C411F1880A).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/10/eaay1259/DC1>

Supplementary Materials and Methods

Fig. S1. *Burmopsyche* sp., BA18002 from Late Cretaceous Burmese amber.

Fig. S2. Proboscis of Aneuretopsychidae from Late Cretaceous Burmese amber.

Fig. S3. Majority rule consensus heuristic cladogram of mecopteran relationships (with cut at 50%) based on 38 fossil and extant taxa and 54 discrete characters.

Fig. S4. Majority rule consensus ratchet-based cladogram of mecopteran relationships (with cut at 50%) based on 38 fossil and extant taxa and 54 discrete characters.

Fig. S5. Maximum clade credibility tree of mecopteran relationships based on 38 fossil and extant taxa and 54 discrete characters, using a Bayesian Mkv+ Γ model.

Data file S1. List of characters for phylogenetic analysis.

Data file S2. Data matrix for phylogenetic analysis.

[View/request a protocol for this paper from Bio-protocol.](#)

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Mouthpart homologies and life habits of Mesozoic long-proboscid scorpionflies

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