

RESEARCH

Open Access



A cretaceous fly trap? remarkable abdominal modification in a fossil wasp

Qiong Wu¹, Lars Vilhelmsen², Xiaoqin Li¹, De Zhuo³, Dong Ren¹ and Taiping Gao^{1*}

Abstract

Background Carnivorous insects have evolved a range of prey and host capture mechanisms. However, insect predation strategies in the fossil record remain poorly understood.

Results Here, we describe †*Sirenobethylus charybdis* n. gen. & sp., based on sixteen adult female wasps in Kachin amber from the mid-Cretaceous, 99 Mya (million years ago), and place it in Chrysidoidea: †Sirenobethylidae n. fam. The fossils display unique morphological modifications on the tip of the abdomen consisting of three flaps from the modified abdominal sternum 6 and tergum and sternum 7; the lower flap formed from sternum 6 is preserved in different positions relative to the other flaps in different specimens, indicating that they form some sort of grasping apparatus. Nothing similar is known from any other insect; the rounded abdominal apparatus, combined with the setae along the edges, is reminiscent of a Venus flytrap. Phylogenetic analysis suggests that the new family is a separate lineage close to the base of Chrysidoidea.

Conclusions †*Sirenobethylus* probably was a koinobiont parasitoid wasp; the abdominal grasping apparatus may have been used to temporarily immobilize the host during oviposition. The new fossils suggest that Chrysidoidea displayed a wider range of parasitoid strategies in the mid-Cretaceous than they do today.

Keywords Sirenobethylidae, Chrysidoidea, Morphology, Grasping apparatus, Phylogeny

Background

Insects are the most diverse group of animals on the planet, with more than 1 million described species and probably several times more undescribed; recent estimates suggest approximately 5.5 million species in total [1, 2]. Their highly adaptable exoskeleton has allowed them to radiate and colonize a wide range of habitats and develop highly efficient and innovative solutions to a range of challenges posed by their surroundings [3,

4]. Among other mechanisms, carnivorous insects have evolved a range of prey capture mechanisms [5, 6]: the forelegs of praying mantises (Mantodea) and mantis flies (Neuroptera: Mantispidae) [7]; the capture basket formed by the spiny legs of adult dragonflies (Odonata); the prehensile labial ‘mask’ employed by dragonfly nymphs [8]; the modified fore legs of female dryinid wasps (Hymenoptera: Dryinidae) for immobilizing hosts temporarily [9]; the hair-trigger mandibles of trap-jaw ants (Formicidae: *Odontomachus*) [10]; the fore and midlegs of heel-walkers (Mantophasmatodea) for swooping on prey [11]; the large hind tarsal claws of hangingflies (Mecoptera: Bittacidae) for grasping prey [12].

The fossil insect fauna from the Cretaceous (Albian – Cenomanian; 99 Mya) Kachin amber provide unique insights into insect evolution [13, 14]; in addition to confirming the ancestry of features observed in modern organisms, it displays occasional examples of ancient

*Correspondence:

Taiping Gao

tpgao@cnu.edu.cn

¹ College of Life Sciences, Capital Normal University, Beijing 100048, China

² Natural History Museum of Denmark, SCIENCE, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark

³ Beijing Xiachong Amber Museum, 9 Shuanghe Middle Road, Beijing 100023, China



morphologies without obvious modern parallels. With regard to potential prey capture mechanisms, the most prominent example so far might be the remarkable mandibles of the ‘saber-tooth’ haidomyrmecine ants [7, 15]. In the present paper, we describe an even more bizarre possible host capture/immobilization mechanism in the abdomen of a chrysidoid wasp. The rounded abdominal apparatus, combined with the setae along the edges, is reminiscent of a Venus flytrap (Droseraceae: *Dionaea muscipula*), a carnivorous plant using two opposing specialized leaves to capture insect prey [16].

Results

Systematic paleontology

Order Hymenoptera Linnaeus, 1758.

Infraorder Aculeata Latreille, 1802.

Superfamily Chrysidoidea Latreille, 1802.

Family †*Sirenobethylidae* Wu, Vilhelmsen & Gao fam. nov.

ZooBank LSID: urn:lsid:zoobank.org:act:EAEC75B2-83B0-4C0E-A4F8-4F18DA024D15.

Type genus. †*Sirenobethylus* Wu, Vilhelmsen & Gao gen. nov.

Diagnosis. Head hypognathous, with medial line on vertex. Antenna with nine flagellomeres, antennal sockets simple, close to posterior margin of clypeus; clypeus projecting and acute in lateral view, slightly convex; mandibles with four apical teeth along truncate apical margin; occipital carina distinct, complete. Propleuron not exposed in dorsal view; prosternum small, diamond-shaped, exposed; notauli present. Female macropterous. Second abdominal (first metasomal) segment in dorsal view with angular anterolateral corners; tergum 7 longer than wide, distinctly narrower than other terga; sternum 6 wider than other sterna, laterally expanded distally, paddle-shaped, projecting posteriorly, posterior margin concave, with a dozen very long, slender setae; many thick spines on dorsal surface of sternum 6. Sternum 7 with median part accommodating ovipositor shaft dorsally and two lateral parts curving outwards before approaching median part distally; median and lateral parts of sternum 7 separated by weakly sclerotized areas. Sting sheaths on either side of the sting, apparently shorter than sting.

Included genus. †*Sirenobethylus* Wu, Vilhelmsen & Gao gen. nov.

Genus †*Sirenobethylus* Wu, Vilhelmsen & Gao gen. nov.

ZooBank LSID: urn:lsid:zoobank.org:act:B3548EEB-BF75-4CA3-8E63-23C1B399A47C.

Type species. †*Sirenobethylus charybdis* Wu, Vilhelmsen & Gao sp. nov.

Etymology. The new generic name is a combination of the Greek ‘*sireno-*’ meaning ‘female humanlike beings

with alluring voices in Greek mythology’, and ‘*bethylus*’, from the nominal genus of Bethyridae. ‘*Sireno-*’ is also a reference to Mammalia: Sirenia, as the ‘tail’ of the wasp in ventral view resembles that of a manatee. The gender is masculine.

†*Sirenobethylus charybdis* Wu, Vilhelmsen & Gao sp. nov. (Figs. 1–3).

ZooBank LSID: urn:lsid:zoobank.org:act:75AEB71E-2DCD-4CBA-9EB9-5DEE7CFD0465.

Etymology. The epithet refers to *Charybdis*, the sea monster in Greek mythology who alternately swallowed and disgorged copious amounts seawater three times a day.

Diagnosis. As for the genus.

Materials. Holotype. Female, CNU-HYM-MA-2015124.

Locality and horizon. The amber specimen was collected from Kachin (Hukawng Valley) of northern Myanmar, which is dated at 98.79 ± 0.62 Mya [17, 18].

Description. See Additional file 1: Figs. S1–S16, Dataset S1 [19–27], Additional file 2: Table S1.

Discussion

Phylogenetic position of †*Sirenobethylus* gen. nov.

We describe a new genus †*Sirenobethylus*, from mid-Cretaceous Kachin amber, based on sixteen specimens. The new genus is readily attributed to the Aculeata by its concealed posterior abdominal segments and ovipositor apparatus [28]. †*Sirenobethylus* has 9 flagellomeres and forewing with 8 closed cells, which is different from Vespoidea sensu lato [29] and Apoidea (antenna with 10 flagellomeres in female and forewing usually has 10 or 9 closed cells) [30, 31]. Therefore, †*Sirenobethylus* probably belongs to Chrysidoidea. We retrieve this superfamily as monophyletic (Fig. 4, Additional file 1: Dataset S2) [32], unlike some recent molecular studies [33].

All †*Sirenobethylus* specimens examined are macropterous females; given the unique diagnostic traits in, e.g., wing venation, and the somewhat isolated phylogenetic position of the new taxon (Fig. 4), it is not possible to associate these females with any males known from Kachin amber. They have the forewing venation similar to †Chrysopsenellidae, including a long pterostigma, a closed subdiscal cell, and vein 2 m-cu absent (Fig. 1A and D). Therefore, the new genus is much more similar to †Chrysopsenellidae than extant groups. However, †*Sirenobethylus* has comparatively complete hind wing venation, including two closed cells also exhibited by †Plumalexiidae and Plumariidae, but different from other groups of Chrysidoidea [34]. All these features suggest that †*Sirenobethylus* could be a stem group of Chrysidoidea, which is consistent with our phylogenetic analyses (Fig. 4, Additional file 3: Table S2). Furthermore, †*Sirenobethylus* has a unique combination of diagnostic

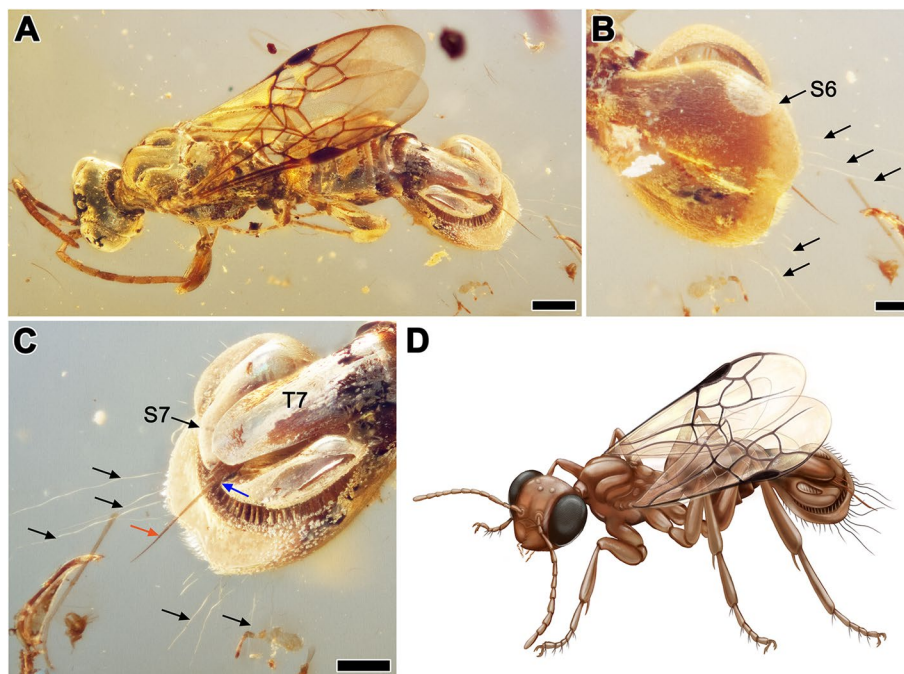


Fig. 1 †*Sirenobethylus charybdis* sp. nov., holotype (specimen CNU-HYM-MA2015124) female. **A** Dorsal view as preserved. **B** The tip of abdomen and ovipositor in ventral view, showing trigger hairs (black arrows). **C** The tip of abdomen and ovipositor in lateral view, showing trigger hairs (black arrows), ovipositor (orange arrow) and groove on the sternum 7 (blue arrow). **D** Habitus reconstruction. Scale bars: **A** 0.5 mm; **B** 0.3 mm; **C** 0.2 mm. Abbreviations: S6 sternum 6; T7 tergum 7; S7 sternum 7

characters within Chrysidoidea. For these reasons, we place †*Sirenobethylus charybdis* gen. & sp. n. in its own family, the †Sirenobethylidae.

Possibly function of the abdominal apparatus

The abdominal apparatus of †*Sirenobethylus*, including the sixth sternum and the seventh tergum and sternum, form three superimposed horizontal flaps, modified into a complex composite structure. The composite structure is round and resembles that of the Venus flytrap (Droseraceae: *Dionaea muscipula*), the carnivorous plant that captures insects between its leaves [16]. The upper flap (tergum 7) is elongate and tongue-shaped; the middle flap (sternum 7) extends laterally far beyond the dorsal flap and is extensively membranous. The lower flap (sternum 6) is expanded distally and laterally, forming a paddle-shaped structure (Fig. 1B); the thick spines on the dorsal part of the lower flap are elongate and scattered in the middle, but shorter and more densely placed along the edges (Additional file 4: Video S1). Furthermore, micro-CT (micro computed tomography) reconstruction shows two apodemes on the anterolateral corners of the lower flap, just inside the constriction where the sternum 6 meets the posterior margin of sternum 5 (Additional file 5: Video S2). The posterior margin of the lower flap has a dozen

very long, slender setae extending from it. The tip of the abdomen often has numerous setae in the extant Aculeata, but they are not as long [35, 36]. The eighth tergum of †*Sirenobethylus* is hidden beneath the upper flap and the sting and is shorter than the upper flap (Fig. 2D). The sting of †*Sirenobethylus* extends through a groove on the dorsal side of the middle flap, below the upper flap; the sting sheaths are situated on either side of the sting, and are apparently shorter than the sting (Fig. 1C). Among the existing Aculeata with stings, most have sheaths that are about as long as the sting itself [28].

The abdominal apparatus of †*Sirenobethylus* is unlike anything previously reported from any extant wasp or indeed any insect known to us [5, 37]. From the morphology and the different states of position of the lower flap preserved in different specimens, it seems evident that the apparatus had some grasping function. We consider two different possible usages for the apparatus: 1) It may have had a function during mating, restraining the male. Due to the lack of male fossil evidence, we cannot determine the role of the apparatus in the mating process. Indeed, it would be unique for insect females to restrain the males during mating, rather than the other way around. We consider this an unlikely function of the abdominal apparatus. 2) It might have served to restrain

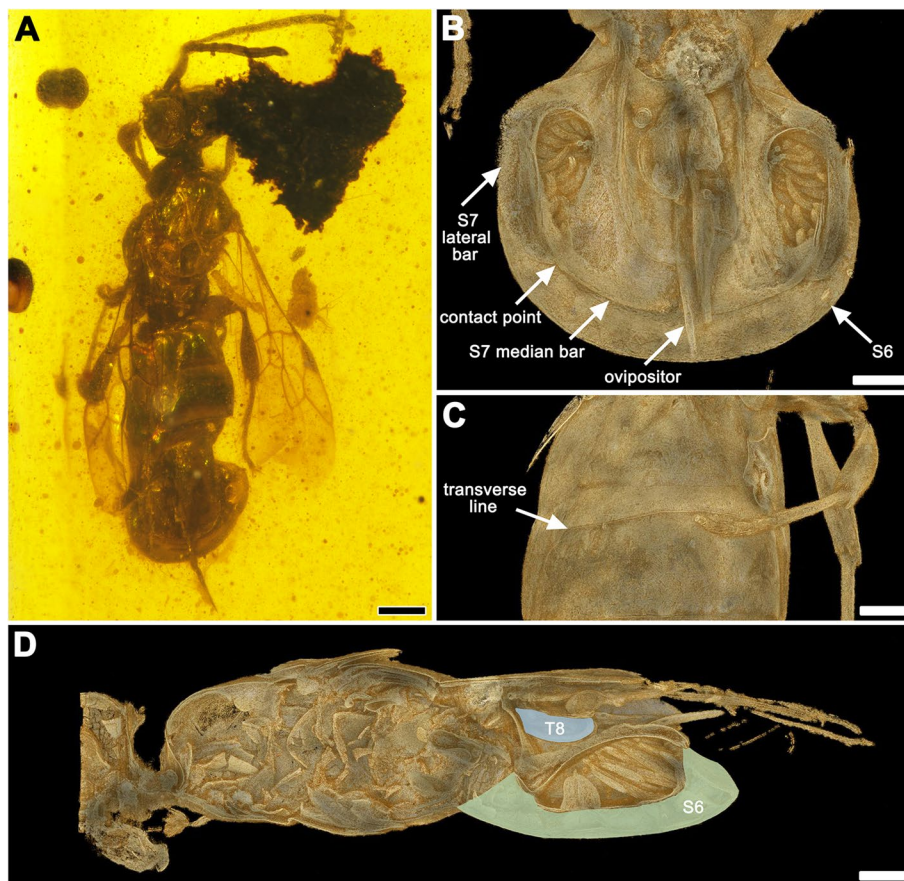


Fig. 2 Photographs and micro-CT reconstructions (volume renderings) of †*Sirenobethylus charybdis* sp. nov., paratype (specimen CNU-HYM-MA2015119) female. **A** Dorsal view as preserved. **B** Micro-CT reconstruction of the tip of abdomen in dorsal view, showing sternum 6, sternum 7 lateral bar, sternum 7 median bar and the contact point between the two, ovipositor (white arrows). **C** Micro-CT reconstruction of sternum 3 with transverse line. **D** Micro-CT reconstruction of the interior abdomen in lateral view; blue area indicates extent of tergum 8, green area indicates sternum 6. Scale bars: **A** 0.5 mm; **B–D** 0.2 mm. Abbreviations: S6 sternum 6; S7 sternum 7; T8 tergum 8

a host temporarily during oviposition. We consider this to be the most likely function of the abdominal apparatus and will elaborate on this in the following.

The fortuitous preservation of the flaps in different relative positions in various specimens of †*Sirenobethylus*, i.e., ‘open’ with the lower flap depressed relative to the middle and dorsal flaps (Figs. 3F–H, Additional file 1: Figs. S2, S10, S13) versus ‘closed’ with the ventral flap closely appressed to the middle and dorsal flaps (Figs. 1C, 2D, 3E, Additional file 1: Figs. S4, S5, S7, S9, S11, S14, S16) indicates that together they form a grasping apparatus. The very elongate hairs along the posterior margin of the ventral flap (Figs. 1D, 3C and D) might have served as ‘trigger hairs’ forewarning the parasitoid of an approaching host and perhaps indicating the host’s position based on the number of hairs that the host touches [38]. The setae on the lower flap are long and sparse in the middle, and short and dense along the edges and presumably flexible (Fig. 2D); the extensive membranous areas on the

middle flap (Fig. 2B) appear relatively soft. We speculate that the coarse setal brush inside the ventral flap and the extensive membranous areas on the middle flap might have served to cushion the host during oviposition rather than crushing it, indicating that the host may not have been permanently incapacitated during the procedure and that †*Sirenobethylus* might have been a koinobiont parasitoid rather than a predator [27]. For these reasons, we suggest that the abdominal apparatus could have served to temporarily grasp and immobilize the host during oviposition. In addition, the sting of †*Sirenobethylus* is situated in a groove on the dorsal side of the middle flap, and among the sixteen specimens, six specimens have stings preserved with grooves directed downward, which would allow the †*Sirenobethylus* to easily sting the captured host (Figs. 1C, 3E–G, Additional file 1: Figs. S5F, S8G, S10D, S11D, S12H, S16E).

Based on the reconstruction from micro-CT data (Fig. 2, Additional file 4: Video S1, Additional file 5: Video

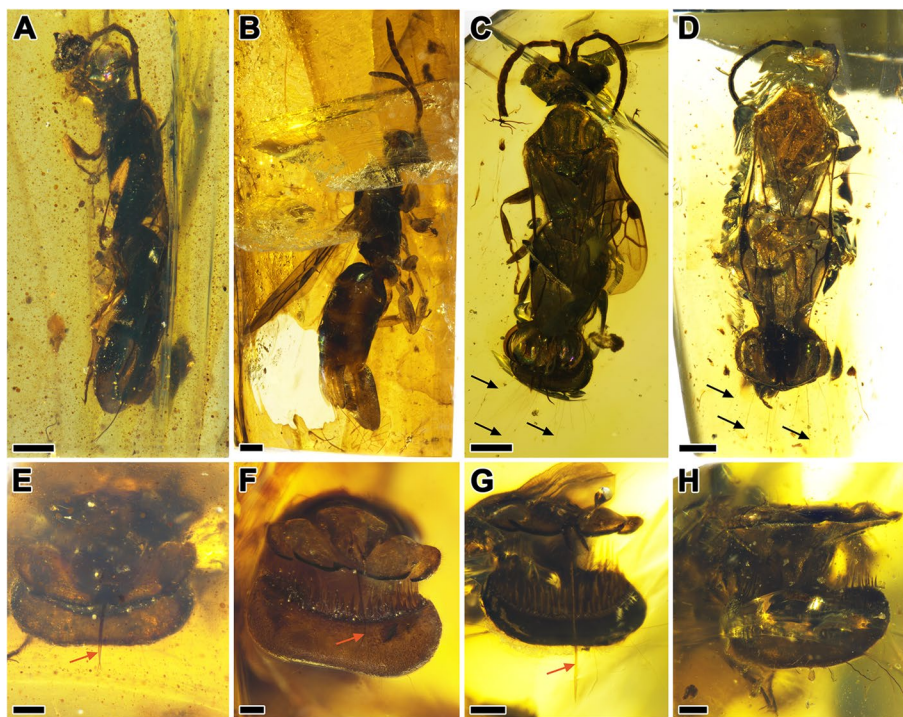


Fig. 3 Photographs of †*Sirenobethylus charybdis* sp. nov. females. (**A, B**) Lateral view of specimens CNU-HYM-MA2015132 and CNU-HYM-MA2015125. (**C, D**) Dorsal view of specimens CNU-HYM-MA2015129 and CNU-HYM-MA2015122, showing trigger hair (black arrows). (**E–H**) Abdominal terminal in posterior view of specimens CNU-HYM-MA2015132, CNU-HYM-MA2015125, CNU-HYM-MA2015129, CNU-HYM-MA2015122, showing ovipositor (orange arrows), respectively, with upper + middle and lower flap in different relative positions (e.g., E: closed; H: fully open). Scale bars: **A–D** 0.5 mm; **E–H** 0.2 mm

S2), the lower flap rotates around the point where sternum 6 is overlapped ventrally by sternum 5. Adductor muscles inserting on the lower side of the anterolateral apodemes would raise the lower flap towards the middle flap, closing the apparatus, whereas abductor muscles inserting on the upper part of the apodemes would depress the lower flap away from the middle flap. For quick operation, especially when closing the apparatus to grasp the host, the muscles would have to be of substantial size. We speculate that the abductors and adductors might have arisen from tergum 3 and sternum 3, respectively; these are the largest sclerites in the abdomen and each have a transverse line on their anterior part that might indicate the attachment sites of the muscles.

The extant Chrysidoidea sensu lato [27, 30] display a range of life histories: parasitoids of wood-living beetle larvae (Scolebythidae), parasitoids of beetle or Lepidoptera larvae (Bethylidae), parasitoids of sawfly cocoons (Chrysidae: Cleptinae), egg-parasitoids of stick insects (Chrysidae: Amiseginae and Loboscelidinae), kleptoparasitoids in nests of solitary bees or wasps (Chrysidae: Chrysinae), parasitoids of nymphs of webspinners/embioplerans (Sclerogibbidae) or parasitoids of nymphs of Auchenorrhyncha (Dryinidae, Embolemidae) [27].

Given this diversity and the lack of information from a number of chrysidoid families, including the extant Plumariidae, it is not possible to infer potential hosts for †*Sirenobethylus* by mapping lifestyles on the phylogeny, although most of the aforementioned groups have also been reported from Kachin amber [39].

The females of some Dryinidae have developed a host restraining apparatus on the forelegs [40]; they use their chelate fore tarsi to immobilize their elusive hosts (leafhoppers, treehoppers and planthoppers) during oviposition. These dryinid females are often wingless, have large eyes and elongate legs, and pursue their hosts actively prior to oviposition [9]. In contrast, †*Sirenobethylus* was probably not able to pursue hosts over longer distances given the position of the putative capture apparatus at the posterior end of the body and its overall habitus compared to dryinid females (smaller eyes, shorter legs). However, the elaborate grasping apparatus indicates that †*Sirenobethylus* was indeed targeting highly mobile prey, and the hosts might have been homopteran hoppers (like for dryinids) or small winged insects, like flies, the elongate trigger hairs perhaps eliciting a short posterior lunge if a potential target came within range. We imagine it would have waited with the apparatus open, ready to

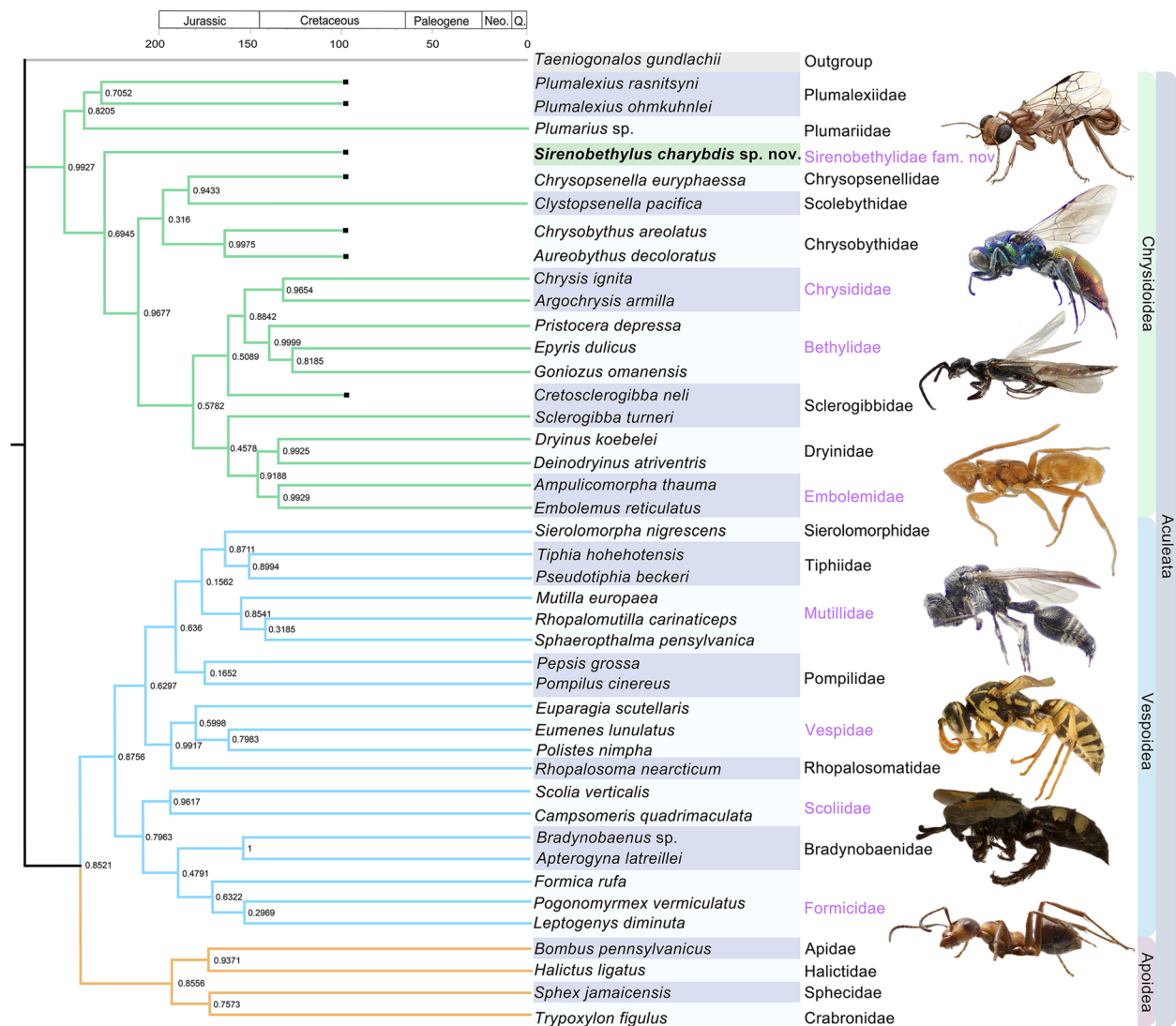


Fig. 4 Bayesian phylogenetic tree based on morphological characters. The large black dots show the age of the Kachin amber species; the branch nodes of this phylogenetic tree are not time-calibrated, the geological time scale refers only to the fossil taxa. The numbers on the branch nodes are posterior probabilities. Green branches: Chrysoidea; blue branches: Vespoidea; orange branches: Apoidea. Families with habitus images associated indicated in purple: †*Sirenobethylus charybdis* (Sirenobethylidae), *Chrysis ignita* (Chrysididae), *Pristocera depressa* (Bethylidae), *Embolemus ruddii* (Embolemidae), *Rhopalomutilla carinataiceps* (Mutillidae), *Polistes nimpha* (Vespidae), *Scolia quadripunctata* (Scoliidae), *Formica rufa* (Formicidae)

pounce as soon as a potential host activated the capture response. Our findings suggest that Chrysoidea displayed a wider range of parasitoid strategies in the mid-Cretaceous than they do today.

Conclusions

We report new mid-Cretaceous fossils of Chrysoidea, suggesting that †*Sirenobethylidae* is a separate lineage close to the base of Chrysoidea based on phylogenetic analysis. Based on our detailed analyses of the morphology of the specimens at our disposal, we infer that †*Sirenobethylus* was probably a koinobiont parasitoid wasp,

the unique grasping mechanism at the tip of the abdomen possibly being used for temporary host capture. Our new findings indicate that by the mid-Cretaceous, some early Chrysoidea had evolved unique parasitoid strategies.

Methods

Material availability

All specimens were collected from Noiye Bum hill, about 18 km southwest of Tanai Village in the Hukawng Valley, northern Myanmar (26° 21′ 33.41″ N, 96° 43′ 11.88″ E) [17, 18]. All amber specimens are stored in the Key Lab

of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University (CNUB; Dong Ren, Curator), Beijing, China. Extant specimens examined are stored in the Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark. The wing venation nomenclature is based on Rasnitsyn (1980) [41].

No datasets were generated or analysed during the current study.

Optical microscopy, photography

The specimens studied were examined and photographed using a Leica M205A stereomicroscope equipped with a Leica DFC425 camera and LAS software. The amber specimens were examined under a Leica M205C stereomicroscope. Figure 1 of the holotype specimen, Fig. 4 of habitus images of extant specimens and Additional file 1: Fig. S7C and D were taken with a BK + Imaging System from Visionary Digital equipped with a Canon EOS 7D camera. The other images of the amber specimens were taken with a Nikon SMZ 25 microscope with an attached Nikon DS-Ri2 digital camera system or a Nikon ECLIPSE Ni microscope with an attached Nikon DS-Ri2 digital camera system.

Micro-CT scanning

The paratype CNU-HYM-MA2015119 was scanned at the micro-CT laboratory of YKLP (Yunnan Key Laboratory for Paleobiology) with an X-ray microscope (3D-XRM), Zeiss Xradia 520 versa. Scanning parameters are as follows: beam strength: 60 kV/5w, filter: no, resolution: 1.94 μm , exposure time: 5 s, number of TIFF images: 1718. Volume rendering and 3D reconstruction were performed using the open-source software Drishti 2.4 [42]. The 3D-reconstruction models of the abdomen of the specimen are displayed in Fig. 2, and the original scan data has been deposited in Dryad (Wu et al., 2025; <https://doi.org/https://doi.org/10.5061/dryad.4b8gthtq9>).

Phylogenetic analysis

Our phylogenetic analyses included one species of non-aculeate wasp (Trigonidae: *Taeniogonalos gundlachii*) as outgroup/root, 19 species of Chrysidoidea (7 fossil, 12 extant), 19 species of Vespoidea (19 extant), and four species of Apoidea (4 extant) as ingroups to clarify the phylogenetic position of the new fossil taxon (see Additional file 3: Table S2). We scored 57 morphological characters (see Additional file 1: Dataset S3) [43–50].

Bayesian analyses were performed in MrBayes version 3.2.7 [51]. Only variable characters were coded, and non-applicable morphological characters were treated as missing data. Equal transition probabilities between the states and among-character rate variation were assumed,

allowing the different characters to evolve at different rates. Bayesian phylogenetic analysis used the Mk model, were conducted with four independent runs. Convergence was assessed by the average standard deviation of split frequencies (ASDSF < 0.01), and the potential scale reduction factor (PSRF < 1.005). After 20 million generations, the topology converged with an ASDSF < 0.004, and PSRF values < 1.001. 50% of the generations were then discarded as burn-in. The posterior probabilities were plotted as relative branch support in the final tree (allcompat. tre) using FigTree v.1.4.3 [52]. The halfcompat. tree can be found in the Additional file 1: Fig. S17.

Abbreviations

CT	Computed tomography
Mya	Million years ago
S2, S3, S4, S5, S6 and S7	Sternum 2, 3, 4, 5, 6 and 7
T2, T3, T4, T5, T6, T7 and T8	Tergum 2, 3, 4, 5, 6, 7 and 8
1st	First
6th	Sixth
7th	Seventh

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12915-025-02190-2>.

Additional file 1: Figures S1–S17, Dataset S1–S3. Fig. S1 Photographs of *†Sirenobethylus charybdis* sp. nov., holotype female. Fig. S2 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S3 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S4 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S5 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S6 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S7 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S8 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S9 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S10 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S11 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S12 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S13 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S14 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S15 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S16 Photographs of *†Sirenobethylus charybdis* sp. nov., paratype female. Fig. S17 Halfcompat tree based on morphological characters in Bayesian analyses. Dataset S1. Systematic paleontology. Dataset S2. Phylogenetic analysis. Dataset S3. Morphological characters list.

Additional file 2: Table S1. Body structure measurements of all specimens.

Additional file 3: Table S2. The character-state matrix.

Additional file 4: Video S1. CT scan of the lateral of the abdomen.

Additional file 5: Video S2. CT scan of the dorsal of the abdomen.

Acknowledgements

We thank the editorial board of BMC Biology, and in particular Dr. Caitlyn Cardetti. We thank three anonymous reviewers for their valuable comments on this manuscript. We appreciate Ms. Xiaoran Zuo for the habitus reconstruction pictures and thanks Dr. Zhipeng Zhao for his help in discussion and the early CT construction of the specimens.

Authors' contributions

TPG conceived and designed the experiments. QW, LV, XQL, DZ, DR, and TPG performed the analyses and experiments. QW prepared photographs and line drawings. QW, LV, and TPG wrote the manuscript. All authors read and approved the final manuscript.

Funding

This project was supported by a grant from the National Natural Science Foundation of China (Nos. 32470468, 32270467, 32020103006). The Support Project of High-level Teachers in Beijing Municipal Universities in the Period of 14th Five-year Plan (No. BPHR20220114).

Data availability

All data generated or analysed during this study are included in this article and its supplementary information files. The sixteen Kachin amber specimens (CNU-HYM-MA2015118 – CNU-HYM-MA2015133) reported in this study were purchased by Mr. Fangyuan Xia in April, 2015 and donated to the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University in May, 2016. They are deposited in the “Fossil Insect Collection” of the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China. Correspondence and requests for materials should be addressed to Dr. Dong Ren, rendong@mail.cnu.edu.cn or Dr. Taiping Gao, tpgao@cnu.edu.cn. Nomenclature acts established herein are registered in ZooBank (www.zoobank.org) following the requirements of the International Code of Zoological Nomenclature and listed under LSID: urn:lsid:zoobank.org:pub:33EF6F52-752D-4283-BF54-150854595F34. The original photo data of the CT scans were deposited on Dryad (<https://doi.org/https://doi.org/10.5061/dryad.4b8gt9>).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Received: 4 December 2024 Accepted: 8 March 2025

Published online: 27 March 2025

References

- Stork NE. How many species of insects and other terrestrial arthropods are there on Earth? *Annu Rev Entomol.* 2018;63:31–45.
- Eggleton P. The state of the world's insects. *Annu Rev Env Resour.* 2020;45:61–82.
- Tihelka E, Cai CY, Giacomelli M, Lozano-Fernandez J, Rota-Stabelli O, Huang DY, et al. The evolution of insect biodiversity. *Curr Biol.* 2021;31:1299–311.
- Wang B, Xu CP, Jarzembowski EA. Ecological radiations of insects in the Mesozoic. *Trends Ecol Evol.* 2022;37:529–40.
- Grimaldi DA, Engel MS. Evolution of the insects. New York: Cambridge University Press; 2005.
- van de Kamp T, Mikó I, Staniczek AH, Eggs B, Bajerlein D, Faragó T, et al. Evolution of flexible biting in hyperdiverse parasitoid wasps. *P Roy Soc B-Biol Sci.* 2022;289:20212086.
- Lai DH, Chen PC, Li SM, Xiang XZ, Ou HH, Kang NY, et al. The associated evolution of raptorial foreleg and mantispid diversification during 200 million years. *Natl Sci Rev.* 2023;10:nwad278.
- Corbet PS. Dragonflies: Behaviour and Ecology of Odonata. New York: Cornell University Press; 1999.
- Virla EG, Moya-Raygoza G, Guglielmino A. A review of the biology of the pincer wasps (Hymenoptera: Dryinidae). *Austral Entomol.* 2023;62:274–99.
- Gronenberg W, Tautz J, Hölldobler B. Fast trap jaws and giant neurons in the ant *Odontomachus*. *Science.* 1993;262:561–3.
- Zompro O, Adis J, Weitschat W. A review of the order Mantophasmatodea (Insecta). *Zool Anz.* 2002;241:269–79.
- Setty LR. Biology and morphology of some North American Bittacidae (Order Mecoptera). *Am Midl Nat.* 1940;23:257–353.
- Grimaldi DA, Engel MS, Nascimbene PC. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *Am Mus Novit.* 2002;3361:1–71.
- Ross AJ. Complete checklist of Burmese (Myanmar) amber taxa 2023. *Mesozoic.* 2024;1:21–57.
- Barden P, Perrichot V, Wang B. Specialized predation drives aberrant morphological integration and diversity in the earliest ants. *Curr Biol.* 2020;30:3818–24.
- Durak GM, Speck T, Poppinga S. Shapeshifting in the Venus flytrap (*Dionaea muscipula*): Morphological and biomechanical adaptations and the potential costs of a failed hunting cycle. *Front Plant Sci.* 2022;2:970320.
- Cruickshank RD, Ko K. Geology of an amber locality in the Hukawng Valley, northern Myanmar. *J Asian Earth Sci.* 2003;21:441–55.
- Shi GH, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang MC, et al. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Res.* 2012;37:155–63.
- Brothers DJ. A new Late Cretaceous family of Hymenoptera, and phylogeny of the Plumariidae and Chrysidoidea (Aculeata). *Zookeys.* 2011;130:515–42.
- Evans HE. Discovery of the female *Plumarius* (Hymenoptera, Plumariidae). *Psyche-J Entomol.* 1967;73:229–37.
- Brothers DJ. The first female Plumariidae (Hymenoptera: Chrysidea) from Southern Africa. XVII International Congress of Entomology, Hamburg, Abstracts. 1984;26.
- Engel MS, Grimaldi DA. Cretaceous Scolebythidae and phylogeny of the family (Hymenoptera: Chrysidoidea). *Am Mus Novit.* 2007;3568:1–16.
- Lepeco A, Melo GAR. Revisiting the phylogeny of the scolebythid wasps (Hymenoptera: Aculeata) through Bayesian model evaluation and parsimony, with description of a new fossil family of Chrysidoidea. *Zool J Linn Soc-Lond.* 2024;201:57–85.
- Melo GAR, Lucena DAA. †Chrysobythidae, a new family of chrysidoid wasps from Cretaceous Burmese amber (Hymenoptera, Aculeata). *Hist Biol.* 2020;32:1143–55.
- Engel MS, Grimaldi DA. The first Cretaceous sclerogibbid wasp (Hymenoptera: Sclerogibbidae). *Am Mus Novit.* 2006;3515:1–7.
- Bohart RM, Kimsey LS. A synopsis of the Chrysididae in America North of Mexico. *Mem Amer Ent Inst.* 1982;33:1–266.
- Finnamore AT, Brothers DJ. Superfamily Chrysidoidea. In: Goulet H, Huber JT, editors. Hymenoptera of the World: an identification guide to families. Ottawa: Agriculture Canada; 1993. p. 130–60.
- Kumpanenko A, Gladun D, Vilhelmsen L. Functional morphology and evolution of the sting sheaths in Aculeata (Hymenoptera). *Arthropod Syst Phylo.* 2019;77:325–38.
- Brothers DJ, Finnamore AT. Superfamily Vespoidea. In: Goulet H, Huber JT, editors. Hymenoptera of the World: an identification guide to families. Ottawa: Agriculture Canada; 1993. p. 161–278.
- Sharkey MJ. Phylogeny and classification of Hymenoptera. *Zootaxa.* 2007;1668:521–48.
- Finnamore AT, Michener CD. Superfamily Apoidea. In: Goulet H, Huber JT, editors. Hymenoptera of the World: an identification guide to families. Ottawa: Agriculture Canada; 1993. p. 279–357.
- Blaimer BB, Santos BF, Cruaud A, Gates MW, Kula RR, Mikó I, et al. Key innovations and the diversification of Hymenoptera. *Nat Commun.* 2023;14:1212.
- Zhang YM, Bossert S, Spasojevic T. Evolving perspectives in Hymenoptera systematics: bridging fossils and genomes across time. *Syst Entomol.* 2025;50:1–31.
- Rasnitsyn AP, Brothers DJ. The first plumalexiid wasp (Hymenoptera: Chrysidoidea, Plumalexiidae) from the mid-Cretaceous Burmese amber. *Cretaceous Res.* 2020;115:104568.
- Kochetkov DN, Loktionov VM. New and little known species of spider wasps (Hymenoptera: Pompilidae) from the Russian Far East. *Far East Entomol.* 2019;382:1–9.
- Tu BB, Lelej AS, Chen XX. Review of the genus *Cystomutilla* André, 1896 (Hymenoptera: Mutillidae: Sphaerophthalminae: Sphaerophthalmini), with description of the new genus *Hemutilla* gen. nov. and four new species from China. *Zootaxa.* 2014;3889:71–91.
- Grimaldi DA. The Complete Insect: Anatomy, Physiology, Evolution, and Ecology. Princeton: Princeton University Press; 2023.
- Escalante-Perez M, Scherzer S, Al-Rasheid KA, Dottinger C, Neher E, Hedrich R. Mechano-stimulation triggers turgor changes associated

- with trap closure in the Darwin plant *Dionaea muscipula*. *Mol Plant*. 2014;7:744–6.
39. Ross AJ. Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2024. *Palaeoentomology*. 2025;8:12–28.
 40. Ponomarenko NG. Family Dryinidae (Dryinids). In: Medvedev GS, editor. *Keys to the Insects of the European Part of the USSR*. Moscow: Publications House Nauka; 1978. p. 16–27.
 41. Rasnitsyn AP. Origin and Evolution of Hymenoptera. *Trudy Paleontologicheskogo Instituta*. 1980;174:1–192 ([In Russian]).
 42. Limaye A. *Drishiti*: a volume exploration and presentation tool. *Proceedings of the SPIE*. 2012;8506. <https://doi.org/10.1117/12.935640>.
 43. Brothers DJ. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *Kans Univ Sci Bull*. 1975;50:483–648.
 44. Brothers DJ, Carpenter JM. Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). *J Hymenopt Res*. 1993;2:227–304.
 45. Perrard A, Grimaldi DA, Carpenter JM. Early lineages of Vespidae (Hymenoptera) in Cretaceous amber. *Syst Entomol*. 2017;42:379–86.
 46. Wu Q, Yang HR, Shih CK, Ren D, Zhao YY, Gao TP. Vespids from the mid-Cretaceous with club-shaped antennae provide new evidence about the intrafamilial relationships of Vespidae. *Zool J Linn Soc-Lond*. 2020;193:217–29.
 47. Vilhelmsen L. Head capsule characters in the Hymenoptera and their phylogenetic implications. *ZooKeys*. 2011;130:343–61.
 48. Mason WRM. Key to superfamilies of HYMENOPTERA. In: Goulet H, Huber JT, editors. *Hymenoptera of the World: an identification guide to families*. Ottawa: Agriculture Canada; 1993. p. 65–100.
 49. Lucena DAA, Melo GAR. Chrysidid wasps (Hymenoptera: Chrysididae) from Cretaceous Burmese amber: phylogenetic affinities and classification. *Cretaceous Res*. 2018;89:279–91.
 50. Lucena DAA, Almeida EAB. Morphology and Bayesian tip-dating recover deep Cretaceous-age divergences among major chrysidid lineages (Hymenoptera: Chrysididae). *Zool J Linn Soc-Lond*. 2022;194:36–79.
 51. Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, et al. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Syst Biol*. 2012;61:539–42.
 52. Rambaut A. FigTree. Computer software and documentation distributed by the author; 2013. <http://tree.bio.ed.ac.uk/software/figtree/>. Accessed March 1, 2025.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.