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Short communication

A new wasp genus of Cirrosphecidae (Hymenoptera: Apoidea) from mid-Cretaceous amber of northern Myanmar

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ABSTRACT

A new apoid genus with one new species *Heterosphex wuni* Li, Rosa, Melo and Shih gen. et sp. nov. is described in Cirrosphecidae based on a male wasp from mid-Cretaceous Myanmar (Burmese) amber. The new taxon is placed in Cirrosphecidae due to its swollen, ring-like metanotum with anterior margin surrounding the scutellum; omaular sulcus and omaular carina absent; propodeum short, with rounded edges and distinctly slanted; metapostnotum extending as a narrow triangle onto posterior surface of propodeum; notaulus not indicated; claws with subapical teeth; and mid tibia with one spur. A key for genera and species of Cirrosphecidae is provided. Up to date, all taxa in Cirrosphecidae are known only from mid-Cretaceous Myanmar amber.

1. Introduction

Cirrosphecidae, a family of apoid wasps known only from mid-Cretaceous Myanmar (Burmese) amber, had its status raised to family by Rosa and Melo (2021). Originally, this taxon was described by Antropov (2000) as a subfamily of Sphecidae, based on only one Myanmar amber species *Cirrosphex admirabilis* Antropov, 2000. Now, it includes two subfamilies: Cirrosphecinae Antropov, 2000, with two genera *Cirrosphex* Antropov, 2000 and *Haptodioctes* Rosa and Melo, 2021; and Glenocephalinae Rosa and Melo, 2021 with one genus *Glenocephalus* Rosa and Melo, 2021 (Antropov, 2000; Rosa and Melo, 2021).

Members of Cirrosphecidae look like ordinary crabronid wasps, but as shown by Rosa and Melo (2021), a series of morphological characters support their close relationship with bees, including mid tibia with one spur and possession of a basitibial plate in the hind tibia of female Cirrosphecinae. With removal of Melittosphecidae from Apoidea (see Rosa and Melo, 2021), Cirrosphecidae constitutes the closest known relatives of bees among the apoid wasps.

The Myanmar amber biota, comprising 8 classes, 66 orders, 596 families, 1357 genera and 2059 species of arthropods (Ross, 2021), is the most diverse and well-preserved in the Mesozoic. In recent years, many well-preserved hymenopteran fossils have been reported from Myanmar amber, e.g., Evanioidea (Li et al., 2015, 2018b; Shih et al., 2019), Pelecinidae (Guo et al., 2016), Ichneumonidae (Li et al., 2017a, 2019b), Stephanoidea (Li et al., 2017b; Jouault et al., 2021), Braconidae (Chen et al., 2021; Li et al., 2021), Myanmarinidae (Zhang et al., 2018; Li et al., 2018a), Panguidae (Li et al., 2019a), Embolemidae (Perkovsky et al., 2020), Bethylidae (Jouault et al., 2021), as well as the apoid families Allommationidae, Cirrosphecidae, Crabronidae and Spheciellidae (Rosa and Melo, 2021). Herein, we describe a new amber wasp: *Heterosphex wuni* Li, Rosa, Melo and Shih gen. et sp. nov. in Cirrosphecidae based on one well-preserved Myanmar amber specimen. The new taxon can be accommodated within the classification proposed recently by Rosa and Melo (2021), with few adjustments, and represent an important addition to the knowledge of the subfamily Cirrosphecinae.

2. Material and methods

The male holotype specimen described herein was legally acquired before June 2017. It was collected from deposits in the

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Hukawng Valley of Kachin State, in northern Myanmar, approximately 100 km southwest of the Village of Tanai. Based on palynology and ammonoid zonation within the surrounding rock units, and insect taxa preserved within Myanmar amber, age estimates have ranged from Albian to Cenomanian. Considering other factors (e.g., radiometric dates obtained from the volcanic clasts present within the amber-bearing sediments), an age of the earliest Cenomanian (98.79 ± 0.62 Ma) has been established for the Myanmar (Burmese) amber (burmite) (Cruickshank and Ko, 2003; Shi et al., 2012). Now, the type specimen is housed in the Institute of Vertebrate Paleontology, College of Life Science and Technology, Gansu Agricultural University, Lanzhou City, Gansu Province, China. A detailed statement was appended in Supplementary Material (see Statement-GAU-HYM-MA-2016001-Museum Catalogue Entry in Supplementary Material). The specimen was examined and photographed by using a Nikon SMZ 25 dissecting microscope with an attached Nikon DS-Ri2 digital camera system. The figures were drawn using Adobe Photoshop CS5. Morphological terminology follows that of Bohart and Menke (1976) with modifications proposed by Melo (1999). Antennal flagellomeres are indicated as F1 to F10 in females and F1 to F11 in males; metasomal terga as T1 to T6 in females and T1 to T7 in males; metasomal sterna as S1 to S6 in females and S1 to S8 in males. The wing venation nomenclature follows Rosa and Melo (2021). Proportions and measurements of head parts are provided in reference to the anterior-posterior axis.

3. Systematic paleontology

Order Hymenoptera Linnaeus, 1758
Superfamily Apoidea Latreille, 1802
Family Cirrosphecidae Antropov, 2000
Subfamily Cirrosphecinae Antropov, 2000

Genus ***Heterosphex*** Li, Rosa, Melo and Shih gen. nov.
Type species: *Heterosphex wuni* Li, Rosa, Melo and Shih sp. nov.

Diagnosis. Heterosphex Li, Rosa, Melo and Shih gen. nov. is recognized by its long antenna, male with conspicuous modification of F7 to F11, large eye, clypeus distinctly wider than long, mandible large and falciform with one subapical tooth, pronotum distinctly elongated, claw with one subapical tooth, forewing vein 1m-cu ending at 1st submarginal cell and 2m-cu ending at 3rd submarginal cell.
Description. Head. Head distinctly wider than long; vertex short, its length approximately equivalent to distance between anterior and posterior ocelli. Maxillary palp slender and relatively long, its length not surpassing eye height; palpal formula apparently 6−4. Male mandible large and falciform, apparently with only one subapical tooth. Clypeus distinctly wider than high. Eye contacting clypeus, their contact extending for half of antennal socket diameter. Antennal socket distant from clypeus, their distance equaling socket diameter. Antenna long, 1.5 x head width; male scape as long as F1+F2+F3, F1 conical and longer than F2, F2−F6 as wide as long and with same length and width, F7−F9 and F11 slightly concave ventrally, F10 strongly concave ventrally. Eye large, occupying more than half of entire lateral surface of head; eye close to posterior ocellus above; inner orbits concave, distinctly angled on upper portion; eye bare, male with slightly enlarged frontal facets. Occipital carina apparently complete. Mesosoma. Pronotum elongate, distinctly longer than wide; pronotal collar distinctly delimited. Notaulus not indicated. Scutellum large, much longer than wide, and distinctly convex with posterior margin rounded, axilla shortened. Metanotum almost vertical, its anterior margin forming a semi-circle behind scutellum. Mesepisternal sulcus complete, reaching body's midline ventrally; omaular sulcus and omaular carina absent. Propodeum relatively short, with rounded edges and distinctly slanted; metapostnotum extending as a narrow triangle on to posterior surface of propodeum. Legs. Femora enlarged, posterior basitarsus very long and slender; plantulae apparently absent; claw with one subapical tooth; mid tibia with one spur; mid leg with some thin and spiniform setae; basal part of mesocoxa continuous with rest of coxa (coxa not pedunculate); mesocoxal carina present; male outer condyle of hind femur without spatulated process; male hind tibia with thin and long bristles; male without basitibial plate. Wings. Forewing with three submarginal cells (1st larger than 2nd and 3rd, 3rd and 2nd straight), 2nd cubital, 1st and 2nd medial cells; vein 1m-cu ending at 1st and vein 2m-cu ending at 3rd submarginal cell; marginal cell longer than pterostigma with acute apex touching wing margin; veins M and CuA diverging distal to cu-a; 2nd abscissa of M+CuA shorter than 1cu-a. Hind wing vein C present, and six hamuli; vein M diverging from CuA before cu-a. Metasoma. Anterior portion of T1 not forming a petiole; male pygidial plate absent; male S8 rounded apically, its margin with fringe of short setae.
Etymology. The generic name is a combination of the Greek '*hetero-*' meaning different, and the Greek word '*Sphex*' for wasp. Gender masculine.

Heterosphex wuni Li, Rosa, Melo and Shih sp. nov. (Figs.1−2)
LSID urn:lsid:zoobank.org:act: BA9A5C16-1277-43C7-B4FD-35F4A60C3D14

Description. Holotype male. Measurements (in mm). Approximate body length, 4.63; maximum head width, 1.21; forewing length, 3.33, maximum width of T2, 0.87. Coloration. Integument color not well-preserved; antennae and legs apparently lighter; metasoma apparently darker than mesosoma and head; wings hyaline with light brown veins. Pilosity. Frons, clypeus and lower paraocular area with conspicuous and decumbent pilosity; flagellum with a few erect isolated setae in addition to short pilosity; mesosoma, especially mesepisternum laterally and ventrally, with conspicuous, sparse and decumbent pilosity; mid tibia with some spiniform bristles at apex; outer margin of hind tibia with very sparse, thin and long spiniform bristles; metasoma covered with pubescence very short and slightly decumbent, T5−T6 apically and T7 with bristles longer and thicker than remaining metasomal pilosity. Integumental surface. Head and mesosoma mostly smooth and shiny, metasoma finely reticulate punctulate. Structure. Head transverse, wider than long. Clypeus large, 3 x as wide as long. Frons slightly prominent. Antenna long, about 1.5 x as long as maximum head width; ocello-orbital distance about 1.5 x as long as mid ocellus diameter. Head maximum width about 2 x as wide as intertegular distance; pronotum longer than wide; mesoscutum and scutellum much longer than wide. Legs elongated, fore femur fusiform, mid and hind femora elongated slightly swollen at base to middle; basitibial plate absent. Wing venation as for the genus. Male S8 rounded apically. Pygidial plate absent.
Etymology. The specific name is in honor of Vincent Wun for his guidance, advice and friendship to C. K. Shih, his business accomplishments and his assistance for insect fossil research.
Type material. Holotype male, in amber piece GAU-HYM-MA-2016001. The specimen is well-preserved.
Locality and horizon. Hukawng Valley, near Tanai, Kachin state, northern Myanmar; lowermost Cenomanian (mid-Cretaceous).
Systematic remarks. Heterosphex gen. nov. differs from the other genera of Cirrosphecidae Antropov, 2000 by having the pronotum considerably more elongated and the recurrent veins ending

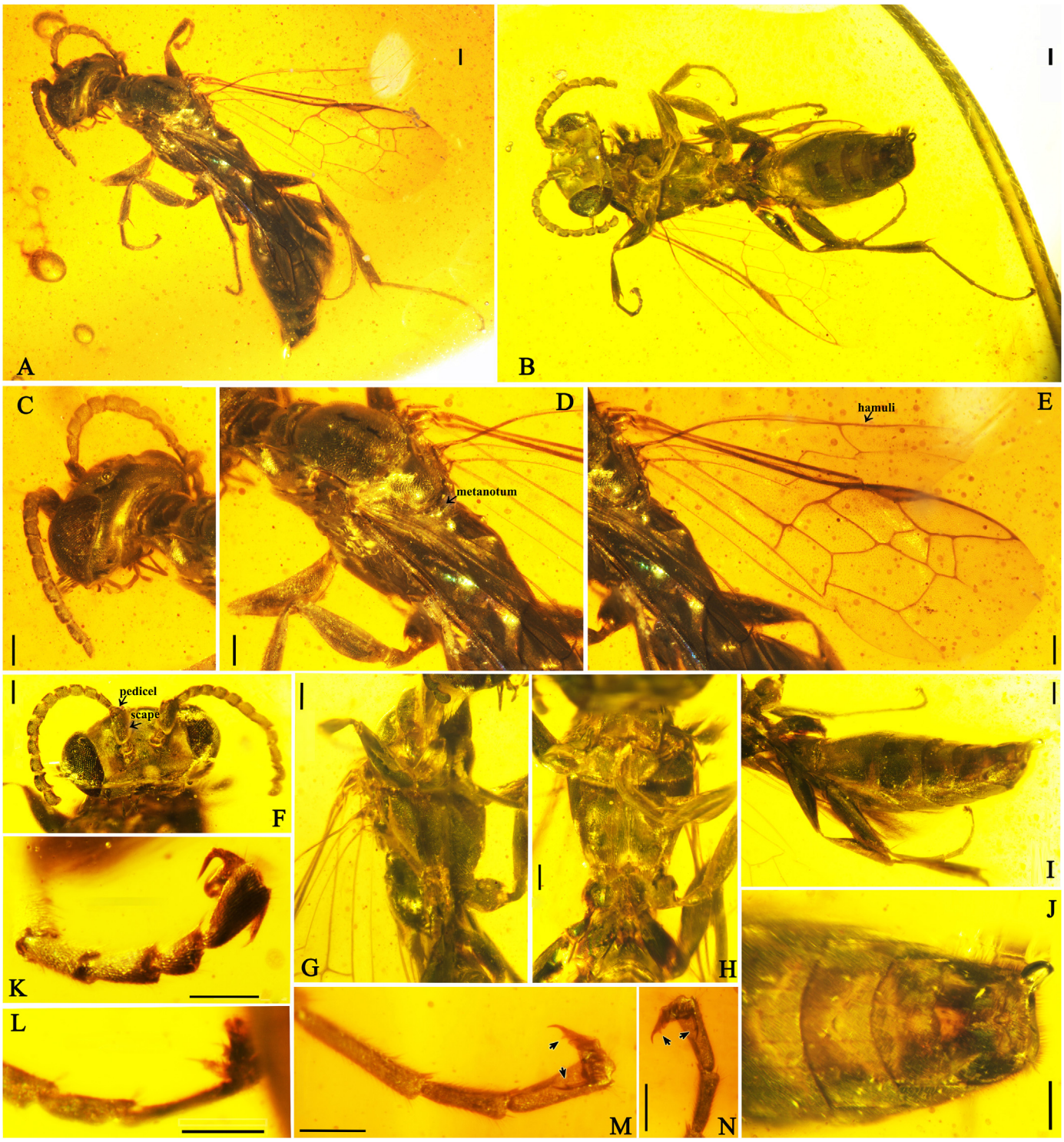

Fig. 1. Photographs of *Heterosphex wuni* gen. et sp. nov. Holotype. GAU-HYM-MA-2016001. (A) Habitus in dorsal view. (B) Habitus in ventral view. (C) Head in dorsal view. (D) Mesosoma in dorsal view. (E) Wings. (F) Head in frontal view. (G) Mesosoma in lateral view. (H) Mesosoma in ventral view. (I) Metasoma in ventral view. (J) Posterior portion of metasoma, ventral view. (K) Claws of fore leg. (L) Claws of mid leg. (M) and (N) Claws of hind leg, arrows referring to the teeth of claws. Scale bars = 0.2 mm (A–J); 0.1 mm (K–N).

respectively at 1st and 3rd submarginal cells. This new genus also differs from *Glenocephalus* Rosa and Melo, 2021 by having a mandible with very elongated apex, a visibly shorter vertex and by not having projections on the fore coxa and on sides of the pronotum. Furthermore, it differs from *Cirrosphex* Antropov, 2000 by having the clypeus considerably wider; in the male flagellum, the F10–F11 are also concave, not just the F7–F9; and finally, also in males, the S8 of metasoma is rounded apically. Additionally, *Heterosphex* gen. nov. differs from *Haptodioctes* Rosa and Melo, 2021 by having the antenna clearly longer (*Heterosphex* with antennae more than 2 times as long as head length vs. *Haptodioctes* with antennae nearly as long as head length).

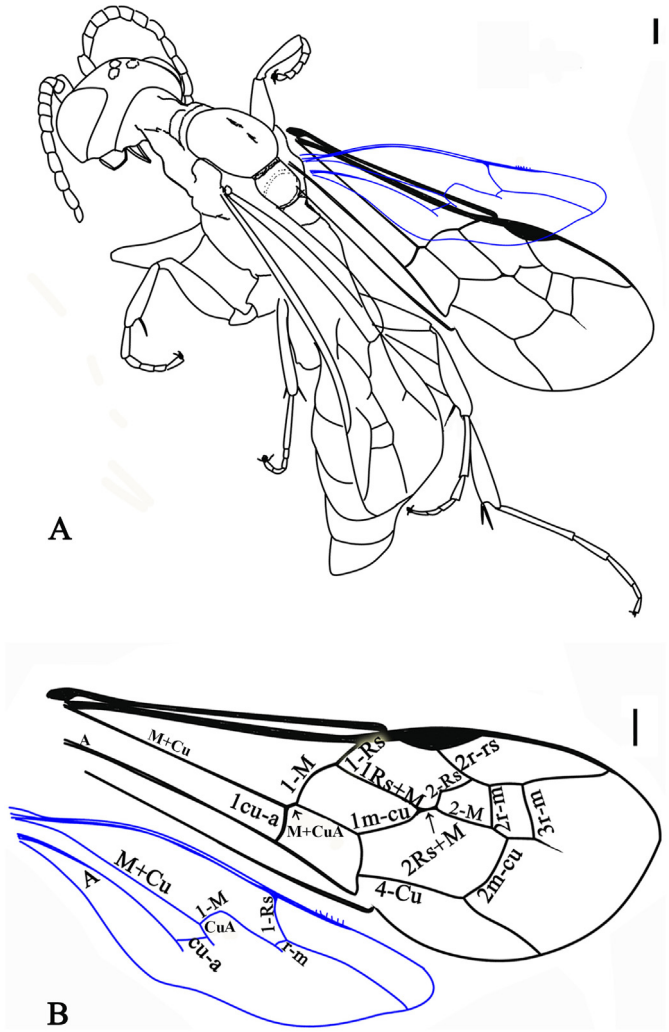

Fig. 2. Line drawings of *Heterosphex wuni* gen. et sp. nov. Holotype. GAU-HYM-MA-2016001. (A) Habitus in dorsal view. (B) Wings. Scale bars = 0.2 mm.

Key to the genera of Cirrosphecidae (modified from Rosa and Melo, 2021)

1. Head slightly wider than long; fore coxa with a lateral spiniform process; lateral corners of pronotal collar projected..... Glenocephalinae Rosa .....& Melo, *Glenocephalus* Rosa and Melo
—. Head distinctly wider than long; fore coxa unmodified, without lateral expansion; pronotal collar unmodified, without projections..... Cirrosphecinae Antropov..... 2
2. Forewing with vein 1m-cu ending at 1st submarginal cell (therefore delimiting the abscissas 1Rs+M and 2Rs+M) and 2m-cu ending at 3rd submarginal cell (Fig. 3A) ..... *Heterosphex* gen. nov.
—. Forewing with vein 1m-cu ending at 2nd submarginal cell, while vein 2m-cu ends at 2nd or 3rd submarginal cell 3
3. Forewing veins 1m-cu and 2m-cu ending at 2nd submarginal cell (Fig. 3B) ..... *Cirrosphex* Antropov
—. Forewing vein 1m-cu ending at 2nd submarginal cell and vein 2m-cu ending at 3rd submarginal cell..... ..... *Haptodioctes* Rosa and Melo

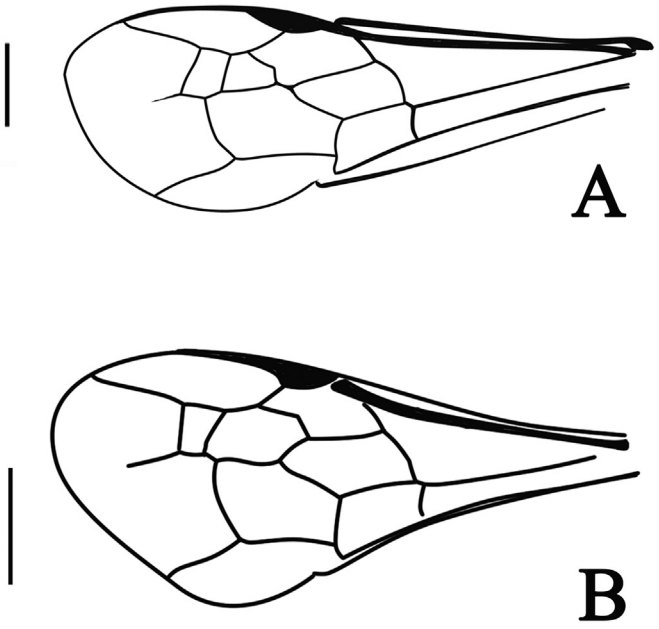

Fig. 3. Line drawings of the forewings of Cirrosphecidae. (A) *Heterosphex wuni* gen. et sp. nov. (B) *Cirrosphex admirabilis* Antropov, 2000. Scale bars = 0.5 mm.

4. Discussion

Heterosphex gen. nov., belongs to Cirrosphecidae for having the metanotum swollen and prominent medially with its anterior margin surrounding the scutellum, the omaular sulcus and omaular carina absent, propodeum short, with rounded edges and distinctly slanted, metapostnotum extending as a narrow triangle onto posterior surface of propodeum, notaulus not indicated, claws with subapical teeth, and mid tibia with one spur.

Among the genera of Cirrosphecidae, *Heterosphex* gen. nov. seems to be most closely related to *Cirrosphex*, based mainly on modifications of the male flagellum. However, these two taxa exhibit many morphological differences. The clypeus in *Heterosphex* gen. nov., approximately 3 x as wide as long, is noticeably shorter compared to that of *Cirrosphex*. The color of the clypeus also differs between the two genera, i.e., entirely discolored in *Cirrosphex* (perhaps it was yellow in live specimens), while in *Heterosphex* gen. nov., it seems uniformly brown (with a circular spot at the center of the clypeus likely representing a small calcite granule).

The mandibles of *Heterosphex* gen. nov. also differ from those of *Cirrosphex*. The mandibles in both genera are large and falciform, each with a very elongated apex. However, *Heterospex* gen. nov. has a subapical tooth, which is absent in *Cirrosphex*. In addition, what certainly draws attention between the two genera are the modifications of the male flagellum. In both genera, the flagellomeres VII, VIII and IX are modified ventrally, forming a concave surface. In *Heterospex* gen. nov., these modifications also extend to flagellomeres X and XI. Furthermore, the ventral surfaces of flagellomeres X and XI are even more modified, each forming a clearly stronger concavity.

Description of a new genus of Cirrosphecidae provides evidence that this family was relatively diverse during the mid-Cretaceous, and it is expected that future studies of inclusions to be found in Myanmar amber and in other coeval deposits are likely to reveal new representatives of this intriguing apoid family. However, the entire family seemed to become extinct at some point in the Late

Cretaceous and left no direct descendants in the extant Hymenoptera. The position of Cirrosphecidae within Apoidea was discussed recently by Rosa and Melo (2021), who argued for a close relationship with the lineage that gave rise to the bees. Although the external morphological characters of Cirrosphecidae do not closely match with those of extant modern bees, detailed future studies of new findings of the Cirrosphecidae will certainly provide further clues to the origin of this important hymenopteran lineage and perhaps shed light on their early evolution.

5. Concluding remarks

We enhance the known diversity of the apoid family Cirrosphecidae with the description of *Heterosphex wuni* gen. et sp. nov. from mid-Cretaceous Myanmar (Burmese) amber, which represents the 30th fossil apoid species known from Myanmar amber. The new taxon with well-preserved new morphological characters provides an important addition to the knowledge of the subfamily Cirrosphecinae. Description of a new genus of Cirrosphecidae provides evidence that this family and other apoid wasps were relatively diverse during the mid-Cretaceous. However, the entire family seemed to become extinct at some point in the Late Cretaceous and left no direct descendants in the extant Hymenoptera. It is expected that future studies of inclusions in Myanmar amber will certainly continue to reveal important findings of this intriguing apoid family.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2022.105333.