

Systematics, Morphology and Biogeography

## New genus of fossil apooid wasps (Hymenoptera, Apoidea) from the Cretaceous amber of Myanmar

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### ABSTRACT

The new genus †*Burmasphex* is proposed for two fossil species, †*Burmasphex sulcatus* sp. nov. and †*Burmasphex pilosus* sp. nov., described from Myanmar Cretaceous amber. It exhibits many plesiomorphic features in relation to the extant Apoidea and is here provisionally allocated in the extinct family †Angarosphecidae.

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### Introduction

The Apoidea is one of the most distinct groups within the Aculeata, the clade of Hymenoptera containing the stinging wasps, bees and ants. Currently this superfamily is divided in the wasp families Ampulicidae, Heterogynaidae, Sphecidae and Crabronidae, and in Apidae, the family containing the bees (Melo, 1999; Pulawski, 2018). The monophyly of Apoidea is strongly supported by several morphological characters (reviewed in Melo, 1999), as well as by molecular evidence (e.g. Peters et al., 2017; Branstetter et al., 2017).

The group as a whole contains over 27,000 living described species (Michener, 2007; Pulawski, 2018) and possesses a rich fossil record (Ohl, 2004; Grimaldi and Engel, 2005). The oldest fossils attributed to the Apoidea are from rock impressions dated from the Early Cretaceous (Rasnitsyn, 1975; Rasnitsyn et al., 1998, 1999). These taxa have been assembled in the †Angarosphecidae, a heterogeneous group proposed originally as a family of Scolioidea (Rasnitsyn, 1975) and currently containing 14 valid genera (Pulawski, 2018). Due to the nature of their preservation, little can be studied of the external morphology of these fossils beyond their venation pattern. Therefore, the current classification system adopted for the †Angarosphecidae is based mostly in the shape of the wing veins (e.g. Rasnitsyn et al., 1998).

The oldest apooid fossils whose body shape has been well-preserved and can be examined alongside their wing venation come

from the Cretaceous amber from Myanmar, also known as Burmese amber. The age of Burmese amber has been estimated as about 99–98 million years, originating in the early Cenomanian (Shi et al., 2012). A total of nine genera and 10 species of apooid wasps have been described from Burmese amber (Antropov, 2000; Cockx and McKellar, 2018). Some of them represent lineages that are still extant, while others have no living counterparts and therefore have been described in extinct higher taxa.

As part of a revisionary work of the apooid wasps from the Cretaceous amber of Myanmar, we describe here a new genus likely representing a stem lineage within Apoidea considering the many plesiomorphies that it exhibits. A specimen belonging to this new genus has been recently illustrated in the review published by Zhang et al. (2018).

### Material and methods

The studied amber pieces came from the Hukawng Valley, near Tanai, Kachin state, in northern Myanmar. They are deposited in the Department of Zoology (DZUP) of the Universidade Federal do Paraná (UFPR) under care of the first author. In order to have a better view of the inclusion the pieces were trimmed with a precision diamond-wire saw (Well model 3032-4, USA) and ground with wet emery paper in a rotary polisher (Aropol model VV200PU, Brazil) at the facilities of UFPR's Microscopy Center. Final polishing was carried out in the same rotary polisher using aluminum oxide (grits of 1 and 0.3 μm).

The general morphological terminology follows Bohart and Menke (1976) and Melo (1999). Antennal flagellomeres are indicated as F1, F2, etc. Measurements were taken at an angle that

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provided the most accurate view of the structure being measured; in the case of body length, when necessary, separate measurements for head, mesosoma and metasoma were summed up to provide the total value. Color images of the fossil specimens were taken on a Leica DFC295 camera attached to a Leica M125 stereomicroscope and processed by the software Zerene Stacker®.

## Taxonomy

Hymenoptera Linnaeus  
Apoidea Latreille  
†Angarosphecidae Rasnitsyn

### †*Burmasphex* gen. nov.

urn:lsid:zoobank.org:act:0933E16B-7E65-4C18-BBB3-AE0F5E1AF058

Type species: †*Burmasphex sulcatus* sp. nov.

**Diagnosis.** This group is easily recognized by its slender body shape, a broad, transverse head (distinctly wider than long) with a very long vertex, long and slender antennae, large eyes with subparallel inner orbits, a long and narrow pronotum that overlays the anterior portion of the mesoscutum, deeply marked notauli, and a marked constriction between the 1st and 2nd metasomal segments.

**Description.** Small wasps, 3.5–6.5 mm in length. Body pilosity relatively long, sparse and erect; integumental surface smooth and shiny. **Head.** Distinctly wider than long in frontal view; vertex very large, 3× longer than distance between anterior and posterior ocelli. Maxillary palpus slender and relatively long, its length not surpassing eye length. Male mandible tridentate, with two dorsal subapical teeth. Clypeus very short, much wider than long. Antenna relatively long, F1–F3 slender, distinctly longer than wide, remaining flagellomeres progressively decreasing in length and width. Eye large, occupying more than half of entire lateral surface of head; inner orbits subparallel; eye bare, facets uniform in size. Occipital carina almost complete, with short ventral interruption. **Mesosoma.** Pronotum elongate, much longer than wide, and overlaying anterior portion of mesoscutum posteriorly; posterior margin of its dorsal portion level with adjacent anterior portion; lateral surface with constriction between anterior and posterior portions; lateral ridge present, relatively short and inconspicuous; posterolateral angle reduced dorsally above and anteriorly to differentiated spiracular operculum forming small pronotal lobe. Notaulus indicated by deep sulcus; parapsidal line extending to posterior margin of mesoscutum. Mesepisternal sulcus absent; omaular carina present. Condyle of mesal articulation of mid coxa located in small projection of posterior margin of mesepisternum; ventral portion of metepisternum wide and flat, broadly fused to mesokatepisternum; medial portion of mesometepisternal suture, between midcoxae, clearly visible. Propodeum box-like, with well-defined dorsal surface, whose length is subequal to its posterior surface; dorsal and posterior surfaces set apart by transverse carina. Legs slender; claws with subapical tooth; midtibia with two spurs; basal part of mesocoxa forming narrow pedicel (coxa pedunculate); mesocoxal carina absent. **Wings.** Forewing with three submarginal cells (1st larger than 2nd and 3rd, 2nd and 3rd subequal in size), 2nd cubital, and 1st and 2nd medial cells; vein 1m-cu touches M near its bifurcation with Rs (slightly after or slightly before) and vein 2m-cu touches M at 3rd submarginal cell. Marginal cell longer than pterostigma, its apex acute; costal cell slightly wider than width of vein C; veins M and CuA diverging distal to cu-a; 2nd abscissa of M+CuA shorter than cu-a. Hindwing C absent; vein M diverging from CuA at cu-a. **Metasoma.** Anterior portion of 1st segment narrow but not forming a petiole; 2nd segment with distinct constriction anteri-

orly. Anterior portion of 2nd sternum at different height compared to remainder of sclerite, surface separating these two portions almost vertical. Male sternum 8 expanded posteriorly and forming relatively broad lobe, its margin with fringe of long setae. Females unknown.

**Etymology.** The genus is named after Burma, the former name of the country from which the amber originated, and *Sphex*, the type genus of the apoidea family Sphecidae. The name is masculine.

**Included species.** †*Burmasphex sulcatus* sp. nov. and †*Burmasphex pilosus* sp. nov.

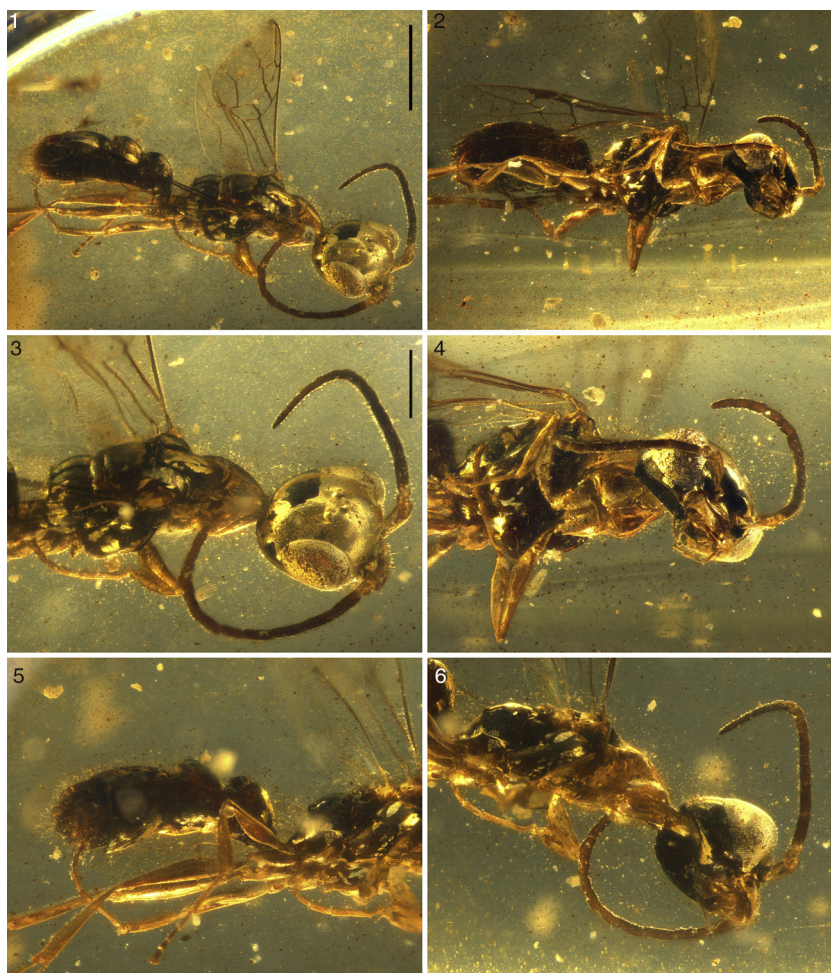
### †*Burmasphex sulcatus* sp. nov.

urn:lsid:zoobank.org:act:F66B68B3-B80E-4AB3-9806-D234E5F2EFEC

(Figs. 1–6)

**Diagnosis and remarks.** This species differs from †*Burmasphex pilosus* sp. nov. by its smaller body size, shorter and less conspicuous pilosity, especially in the first two terga, the proportions of the basal flagellomeres, the distance between posterior ocelli shorter than the ocello-orbital distance, the position of 1m-cu in the forewing (touching M+Rs basal to their bifurcation), the interrupted transverse carina of the propodeum, and a marked constriction at the base of the 3rd tergum.

**Description.** Holotype male. **Measurements (in mm).** Approximate body length, 3.8; maximum head width, 1.1; forewing length, 2.6; maximum width of T2, 0.85. **Coloration.** Head mostly dark; clypeus, antennae, mandible except for the dark brown teeth, and mouthparts light brown. Pronotum light brown; mesoscutum, scutellum, metanotum, metapostnotum, metapleura and propodeum mostly dark brown; legs light reddish brown. Wing membrane hyaline, veins and pterostigma dark brown. Metasoma mostly brown to dark brown. **Pilosity.** Mostly sparse and conspicuous; upper portion of gena with relatively long setae, their length between 1.5 and 2× diameter of anterior ocellus; pronotum with similar setae, longest ones about as long as 2× ocellar diameter; terga 3–7 with conspicuous erect pilosity, whose length and diameter increase toward apex of metasoma, longest setae almost 3× as long as ocellar diameter; sterna 4–5 also with erect pilosity. **Integumental surface.** Frons and vertex with conspicuous fine punctation, punctures spaced apart by 1–2 puncture diameters; punctation on pronotum, mesoscutum and scutellum much sparser. Propodeum with transverse carina separating dorsal and posterior surfaces, carina extending ventrally and separating lateral surface from posterior surface as well; dorsal surface bordered laterally by weak longitudinal carina; dorsal surface of propodeum with a deep medial sulcus along entire surface, interrupting transverse carina and extending on to posterior surface. **Structure (measurements in mm).** Head transverse in frontal view, about 1.7× wider than long (1.1:0.65); malar space as long as ocellar diameter (0.05:0.05); clypeus very short, about 5× wider than long (0.47:0.10); interalveolar distance about 1.6× alveolus diameter (0.11:0.07). F1–F3 slender, respectively about 4.8, 4.4 and 4.0× longer than wide (0.24:0.05; 0.22:0.05; 0.20:0.05); F4 to F10 progressively decreasing in length and in diameter. Inner orbits subparallel, upper and lower interorbital distances subequal (0.41:0.42); eye about 1.4× as long as its maximum width in lateral view (0.73:0.53); distance between posterior ocelli shorter than ocello-orbital distance (0.09:0.14). Legs slender, femur of hind leg slightly longer than tibia (0.64:0.59). Wing venation as for genus, except for vein 1m-cu touching M+Rs basal to their bifurcation. Dorsal surface of propodeum rectangular, about 2× as wide as long (0.43:0.22). Basal portion of 3rd tergum strongly constricted, forming marked step with tergal disc.



**Figs. 1–6.** †*Burmasphex sulcatus* gen. et sp. nov. from Cretaceous amber from Myanmar; male holotype (DZUP Bur-503). 1, Dorsal habitus; 2, Ventral habitus; 3, Head and mesosoma, dorsal view; 4, Head and mesosoma, ventral view; 5, Metasoma, lateral view; 6, Head and mesosoma, ventrolateral view. Scale bars: 1 mm (Figs. 1–2); 0.5 mm (Figs. 3–6).

**Type material.** Holotype male, in amber piece DZUP Bur-503. Small, complete, fully winged, well-preserved specimen. The piece has been trimmed to a small size (approximately  $7 \times 5 \times 4$  mm). A partial specimen (right wings and hind leg, and part of the abdomen) of a small mayfly is preserved in the same piece.

**Etymology.** The species is named for the deep medial sulcus on its propodeum, from the Latin *sulcus*, furrow, and *-atus*, provided with.

†*Burmasphex pilosus* sp. nov.

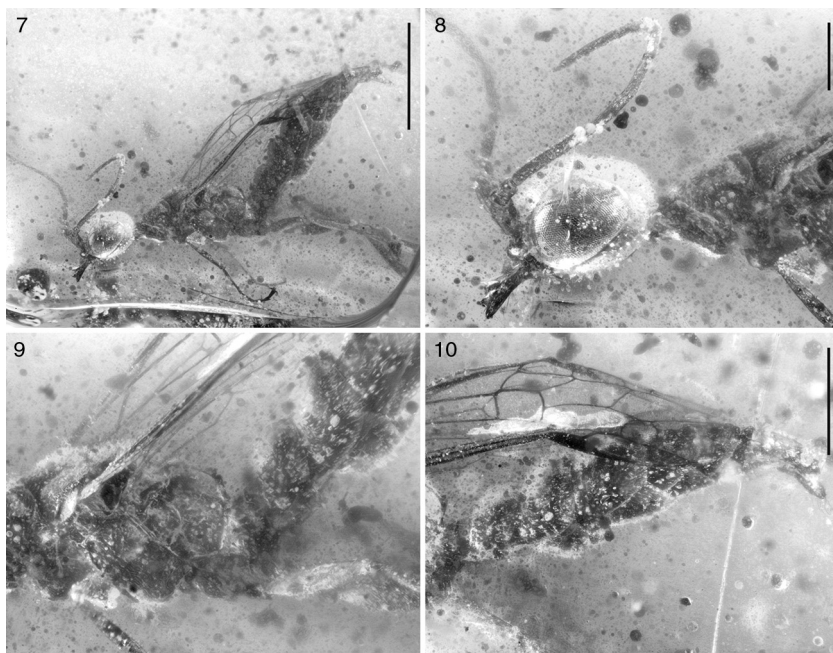
urn:lsid:zoobank.org:act:583665C0-5FFA-4B7A-A8DA-63E31D6357CD  
(Figs. 7–14)

**Diagnosis and remarks.** Diagnostic features for separating the two species described in †*Burmasphex* gen. nov. are presented above in the description of †*Burmasphex sulcatus* sp. nov.

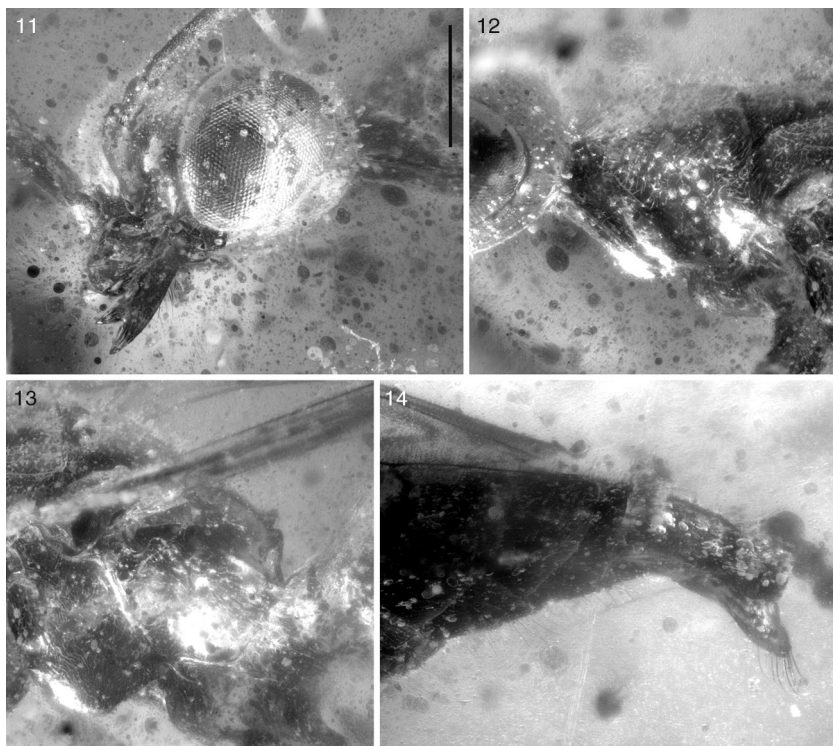
**Description.** Holotype male. **Measurements (in mm).** Approximate body length, 6.2; maximum head width, 1.2; forewing length, 3.6. Similar to †*Burmasphex sulcatus* sp. nov. except as follows: **Coloration.** Head mostly dark brown; clypeus, antennae, mandibles and mouthparts dark reddish brown. Pronotum, fore legs, mesoscutum, scutellum, metanotum, metapostnotum, metapleura and propodeum mostly dark brown; mid and hind legs

reddish brown. Wing membrane hyaline, veins and pterostigma dark. Metasoma mostly dark; sternum 8 dark reddish brown. **Pilosity.** Mostly short, dense and conspicuous; upper portion of gena with short pubescence; pronotum with dense pubescence, longest setae about as long as  $3 \times$  ocellar diameter; lateral propodeum with conspicuous erect pilosity, longest setae about as long as  $5 \times$  ocellar diameter; metasoma with conspicuous erect pilosity, whose length and diameter increase toward apex of metasoma, longest setae about  $3 \times$  as long as ocellar diameter; sterna with erect pilosity; posterior margin of sternum 8 with loose fringe of very long setae, their length over  $4 \times$  ocellar diameter. **Integumental surface.** Transverse carina separating dorsal and posterior surfaces of propodeum with a gap medially, the portions surrounding the gap raised and forming a lobe; medial sulcus on dorsal surface shallow; lateral carina of dorsal surface prominent. **Structure (measurements in mm).** Head transverse in frontal view, about  $1.7 \times$  wider than long ( $1.2:0.70$ ); malar space slightly shorter than ocellar diameter ( $0.04:0.05$ ); clypeus very short, almost  $6 \times$  wider than long ( $0.65:0.11$ ); interalveolar distance slightly longer than alveolus diameter ( $0.13:0.11$ ). F1–F3 slender, respectively about 4.1, 4.6 and  $4.4 \times$  longer than wide ( $0.33:0.08$ ;  $0.37:0.08$ ;  $0.35:0.08$ ); F4–F10 progressively decreasing in length; eye about  $1.4 \times$  as long as its maximum width in lateral view ( $0.67:0.47$ ); distance between posterior ocelli longer than ocello-orbital distance. Legs slender, femur of hind leg longer than tibia ( $0.96:0.87$ ). Wing venation as for genus,





**Figs. 7–10.** †*Burmasphex pilosus* gen. et sp. nov. from Cretaceous amber from Myanmar; male holotype (DZUP Bur-448). 7, Lateral habitus; 8, Head and mesosoma, lateral view; 9, Mesosoma, lateral view; 10, Metasoma, lateral view. Scale bars: 2 mm (Fig. 7); 0.5 mm (Figs. 8–9); 1 mm (Fig. 10).



**Figs. 11–14.** †*Burmasphex pilosus* gen. et sp. nov. from Cretaceous amber from Myanmar; male holotype (DZUP Bur-448). 11, Head, frontolateral view; 12, Pronotum, lateral view; 13, Mesopleura and propodeum, lateral view; 14, Apex of metasoma, lateral view. Scale bar: 0.5 mm.

except for vein 1m-cu touching M slightly apically to its bifurcation with Rs. Constriction at base of 3rd tergum less strong than that at base of 2nd tergum.

**Type material.** Holotype male, a small, complete, fully winged, well-preserved specimen in amber piece DZUP Bur-448. The piece has abundant particulate material in the matrix

that partially hinders the visibility of the specimen. Except for a very small mite and plant hairs, there are no other syninclusions.

**Etymology.** The species is named for its abundant pubescence, from the Latin *pilus*, hair, felt, and *-osus*, having the nature or quality of.

## Discussion

At first glance, the general body shape of the specimens described here as a new genus of Apoidea, with their broad head and slender meso- and metasomata, does not suggest any of the current known groups in this superfamily. There is no doubt, however, that the new genus belongs in the Apoidea based on morphological features of its pronotum, propodeum and wing venation. The conditions exhibited by †*Burmasphex* gen. nov., especially in relation to the shape of the pronotum and its articulation with the mesoscutum, are quite plesiomorphic and exclude it from any living group. Indeed, the specimen of †*Burmasphex* gen. nov. illustrated by Zhang et al. (2018) was referred by them as an “undescribed Angarosphexidae”.

Among the fossil taxa attributed to the stem lineages of Apoidea, the wing venation of †*Burmasphex* gen. nov. resembles most the pattern found in †*Angarosphex* Rasnitsyn, †*Calobaissodes* Zhang and †*Trigampulex* Antropov, in which the 1st recurrent vein (1m-cu) touches M near its bifurcation with Rs, the 2nd recurrent vein (2m-cu) touches M at the 3rd submarginal cell, and the 2nd submarginal cell is relatively small. In addition to having their type species described from Aptian rock fossils, the wing venation of both †*Angarosphex* and †*Calobaissodes* differs from that of †*Burmasphex* gen. nov. in some details, such as the larger size of the 1st and 3rd submarginal cells in †*Calobaissodes* and the longer prestigma and the larger 1st medial cell in *Angarosphex*. Also, the 1st abscissa of M in the hindwing of the type species of †*Angarosphex*, †*A. myrmicopterus* Rasnitsyn, is strongly curved basally and forms an almost right angle with M+Cu, a condition not observed in †*Burmasphex* gen. nov.

Compared to †*Trigampulex*, which has also been described from Burmese amber, the wing venation of †*Burmasphex* gen. nov. is even more distinct. In the forewing of †*Trigampulex* the 3rd submarginal cell is smaller and placed more basally in relation to the marginal cell, the 1st medial cell is distinctly longer (easily seen comparing the lengths of the 1st abscissa of M and of 1m-cu) and the 2nd medial cell is also quite elongate (see Antropov, 2000). Further comparisons with †*Trigampulex* are hampered by the fragmentary condition of its type specimen, whose most part of the mesosoma and the entire head are lacking.

†*Burmasphex* gen. nov. undoubtedly constitutes a distinct lineage of Apoidea and future studies should evaluate its relationships based on a formal phylogenetic analysis. Ideally the two fossil species described here should have their external morphology thoroughly examined in order to include them as terminals in an analysis containing a broader representation of other Apoidea lineages. Such an investigation is beyond our current scope and will be carried out in forthcoming work.

## Conflicts of interest

The authors declare no conflicts of interest.

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