

A new fossil family of aculeate wasp sheds light on early evolution of Apoidea (Hymenoptera)

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Abstract

In the present work, we describe a new fossil family of Apoidea supported by phylogenetic analyses involving both fossil and extant groups. †Burmasphecidae **fam.n.** is based on †*Burmasphex* Melo & Rosa, a genus described from Burmese amber. We include in this family the monotypic genus †*Decasphe* Zheng, Zhang & Rasnitsyn also from Burmese amber. Additionally, we describe two new genera and four new species in †Burmasphecidae **fam.n.**: †*Burmasphex mirabilis* **sp.n.**; †*Simplisphex* **gen.n.**, containing *S. scutellatus* **sp.n.** and †*S. burmensis* **sp.n.**; and †*Callisphex robustus* **gen. et sp.n.** In our phylogenetic study, we extended a pre-existing matrix of morphological data and analysed it under parsimony and Bayesian inference. In the Bayesian inference analyses, the morphological dataset was partitioned under a homoplasy criterion. We postulate the first phylogenetic hypotheses for the placement of †Angarosphecidae based on the type species, †*Angarosphex myrmicopterus* Rasnitsyn, plus a new Burmese amber taxon, †*A. alethes* **sp.n.** We demonstrate that †Burmasphecidae **fam.n.** clearly belongs to Apoidea and has a sister relationship with the other representatives of the superfamily. Our results indicate that †Burmasphecidae **fam.n.** and †Angarosphecidae are distinct lineages, with the second clearly more derived than the first. We discuss the phylogenetic relationships of these fossil lineages with extant groups of both Apoidea and other Aculeata, and present morphological evidence for the first time supporting the Formicidae + Apoidea clade. Finally, we indicate some considerations about the paleoenvironment and the nature of the Burmese amber biota, suggesting an alternative hypothesis to the island endemism described in previous works.

KEYWORDS

†*Angarosphex myrmicopterus*, †*Burmasphex*, ants, apoid wasps, Bayesian inference, bees, partitioning

INTRODUCTION

Among the hymenopteran insects, bees (Apidae) and ants (Formicidae) are perhaps the families best known by the general public, since they play fundamental ecological roles in ecosystems and are also present in practically all terrestrial environments (Hölldobler & Wilson, 1990; Michener, 2007). These two groups are included in the clade called Aculeata, whose main evolutionary change is the modification of the structures of the ovipositor in a stinger (Brothers, 1975). Traditionally,

this clade is subdivided into three superfamilies: Chrysidoidea, Vespoidea and Apoidea, with ants and bees included in the latter two, respectively (Brothers, 1975; Brothers, 1999; Brothers & Carpenter, 1993). However, studies based on molecular data suggest that Vespoidea is paraphyletic towards Apoidea (Branstetter et al., 2017; Debevec et al., 2012; Faircloth et al., 2014; Johnson et al., 2013; Peters et al., 2017; Pilgrim et al., 2008). In most results, ants are closer to Apoidea than any other aculeate wasp lineage (Branstetter et al., 2017; Faircloth et al., 2014; Johnson et al., 2013; Peters et al., 2017).

The Apoidea superfamily includes not only bees but also a series of predatory wasps popularly known as apoid wasps. Commonly,

apoid wasps are classified into four living families: Ampulicidae, Crabronidae, Heterogynaidae, and Sphecidae (sensu Melo, 1999). Although the monophyly of Ampulicidae, Heterogynaidae and Sphecidae is corroborated by different phylogenetic results (Alexander, 1992; Branstetter et al., 2017; Debevec et al., 2012; Melo, 1999; Peters et al., 2017; Sann et al., 2018), some studies suggest that crabronid wasps are paraphyletic in relation to bees or even polyphyletic regarding bees and sphecids (Alexander, 1992; Branstetter et al., 2017; Debevec et al., 2012; Peters et al., 2017; Sann et al., 2018). Apoidea are easily recognized by the posterolateral angle of the pronotum reduced dorsally above and anterior to the spiracular operculum, delimiting the pronotal lobe (figures 21.2 and 21.2.1 in Brothers, 1975), and the metapostnotum expanded posteromesally, forming the “propodeal triangle”. In addition to these two synapomorphies, in Apoidea, the posterior margin of the dorsal portion of the pronotum forms a specialized articulation with the anterior portion of the mesoscutum (figures 25, 26 and 45 in Melo, 1999). This zone of contact between the posterior margin of the pronotum and the anterior margin of the mesoscutum limits the movement of the pronotum, which no longer moves freely over the mesoscutum.

Regarding the origin of Apoidea, estimates based on the molecular clock indicate that the Apoidea crown group arose in the late Jurassic (~153 Mya) (Peters et al., 2017) or early Cretaceous (~134.90 Mya) (Branstetter et al., 2017) (hypotheses indicating older ages seem very unlikely, e.g., Ronquist et al., 2012 and Sann et al., 2018). The oldest fossils unequivocally attributed to Apoidea come from Lebanese amber and are estimated to be between 130 and 125.5 Mya (Poinar & Milki, 2001; Prentice, 1993, 1994). The two fossils from this deposit have been interpreted as Ampulicidae, although they have never been described (Prentice, 1993, 1994). In addition to these fossils, the fossil record of Apoidea is very extensive, with taxa described from most large insect deposits of the Cretaceous, Paleogene and Neogene (Grimaldi & Engel, 2005; Penney & Jepson, 2014; Pulawski, 2022).

The Apoidea diversified mainly during the Cretaceous, and most of the living families were already established by the end of the Early Cretaceous and the beginning of the Late Cretaceous (Branstetter et al., 2017; Peters et al., 2017; Sann et al., 2018; Rosa & Melo, 2021; Rosa & Melo, unpublished data). Even with this evident diversity of taxa during the period, most apoid wasp fossils from the Cretaceous have been traditionally described in a single family, †Angarosphecidae Rasnitsyn (Melo & Rosa, 2018; Rasnitsyn, 1975; Rasnitsyn et al., 1998, 1999; Zhang et al., 2018; Zheng et al., 2021). This family was proposed based on the lacustrine fossil †*Angarosphex myrmicopterus* Rasnitsyn from the Aptian Lagerstätte Baissa, Zaza Formation, Transbaikalia, in Russia (Rasnitsyn, 1975). Currently, about 15 genera and 50 species are included in †Angarosphecidae (Zheng et al., 2021). Several authors have already emphasized that this family comprises a paraphyletic or polyphyletic group, although a formal phylogenetic hypothesis for these taxa has never been proposed (Rasnitsyn et al., 1998, 1999; Ohl & Engel, 2007; Rosa & Melo, 2021; Rosa & Melo, unpublished data).

The systematic classification of the apoid fossils from the Cretaceous is not an easy task. In general, fossils found in sedimentary

rocks usually show low quality in preservation compared with those found in fossil resins (e.g., Penney, 2010; Penney & Jepson, 2014). Most Cretaceous apoid fossils from sedimentary rocks, even those from Konservat-Lagerstätten deposits, have fragmented preservation (e.g., Darling & Sharkey, 1990; Rasnitsyn, 1975; Rasnitsyn et al., 1998, 1999). Another peculiarity of this fauna is that many of the taxa have been described solely by forewings (e.g., Rasnitsyn et al., 1998, 1999). Furthermore, the generic diagnostic system of †Angarosphecidae is based almost exclusively on venation characters (Zheng et al., 2021). However, as discussed by Rosa and Melo (2021), a classification based solely on wing venation is unable to properly deal with the diversity of apoid lineages already present in the Cretaceous. In view of this and also due to the lack of phylogenetic efforts, the systematic position of several of these taxa, as well as their real identity, remains uncertain.

On the other hand, fossils found in amber inclusions preserve more characters for use in phylogenetic studies than those preserved in sedimentary rocks. Perhaps for this reason, the apoid wasp fauna of Burmese amber has rarely been associated with †Angarosphecidae (Antropov, 2000; Rosa & Melo, 2021). Although three Apoidea fossil families are known from this deposit—†Allommationidae Rosa & Melo, †Cirrosphecidae Antropov and †Spheciellidae Rosa & Melo—none of them are phylogenetically closely related to †Angarosphecidae (Rosa & Melo, 2021). Only a few taxa found in Burmese amber have been assigned to †Angarosphecidae: †*Burmasphex pilosus* Melo & Rosa, †*B. sulcatus* Melo & Rosa and †*Decasphex cretacicus* Zheng, Zhang & Rasnitsyn (Melo & Rosa, 2018; Zheng et al., 2021). Furthermore, Burmese amber is the richest fossil deposit for apoid wasps, with more than 29 species and seven families (Rosa & Melo, 2021). Conducting phylogenetic studies including representatives of this deposit is, therefore, the best opportunity to understand the phylogenetic relationships of Cretaceous apoid wasps associating great diversity of taxa with superb preservations.

In this work, we describe a new fossil family of apoid wasps based on taxa from Burmese amber, previously described in †Angarosphecidae. All these results are based on phylogenetic analyses under the criteria of parsimony and Bayesian inference. Additionally, we describe two more new genera and four new species in this family. We also postulate the first phylogenetic hypothesis for the placement of †Angarosphecidae based on †*A. myrmicopterus* plus a new taxon from Burmese amber. Finally, we present for the first time the morphological characters that support the Formicidae + Apoidea clade.

MATERIALS AND METHODS

Material studied

The studied amber pieces came from the Hukawng Valley, near Tanai, Kachin State, in northern Myanmar (see figure 1 in Dong et al., 2015). Burmese amber has been dated as originating in the early Cenomanian, at about 99–98 mya (Shi et al., 2012). The pieces are deposited in the Department of Zoology (DZUP) of the Universidade Federal do

Parana (UFPR) under the care of the second author. In order to have a better view of the inclusion, the amber 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 or manually trimmed with a jewellery saw and ground with wet emery paper (grit sizes of 800–3000). Final polishing was carried out in the same rotary polisher using aluminium oxide (grits of 1 and 0.3 μm) or using a sanding sponge pad (grit size of 5000), followed by rubbing in soft cloth. Also, we studied the holotype of †*Angarosphex myrmicopterus*, the type species of †*Angarosphex* Rasnitsyn, from high-resolution photographs kindly provided by Dr. Alexander P. Rasnitsyn. The holotype is deposited at the Paleontological Institute of the Russian Academy of Sciences under the number PIN 3064/629.

The general morphological terminology follows Bohart and Menke (1976) and Melo (1999). Antennal flagellomeres are indicated as F1, F2, etc.; metasomal terga and sterna, respectively, as T1–T7 and S1–S8. Proportions and measurements of head parts are provided in reference to the anterior–posterior axis. Nomenclature for wing venation follows Rosa & Melo (Rosa & Melo, 2021; see their figure 1). Length of wing cells is taken along the basal–apical axis, while the width is measured along the anterior–posterior axis, considering the wings open. The 2nd abscissa of Rs (section separating 1st and 2nd submarginal cells) takes an inflection along its trajectory (corresponding to the point in which the absent vein 1r-rs would join the Rs); we use here this inflection point to refer to basal and apical portions for this abscissa. The Apoidea classification follows Melo (1999), including crabronids and bees as single families, Crabronidae and Apidae, respectively. For subfamily-level classification of the Apidae, see details in Melo and Gonçalves (2005).

Colour images of the fossil amber specimens were taken on a Leica DFC295 camera attached to a Leica M125 stereomicroscope and processed by the software Zerene Stacker®. Artistic rendering of †*Burmasphex mirabilis* sp.n. was carried out by Gabriel Uguetto based on camera lucida drawings of the holotype. Line drawings were prepared using a camera lucida attached to a Leica M125 stereomicroscope. The following taxa had their pronotum illustrated based on camera lucida drawings of cleared disarticulated sclerites: *Pachycondyla striata* Smith (Formicidae), *Aphelotoma rufiventris* Turner (Ampulicidae), *Heterogyna fantsilotra* Day (Heterogynidae), *Stangeella cyaniventris* (Guérin-Ménéville) (Sphecidae), *Mellinus alpestris* Cameron (Crabronidae), *Calliopsis andreniformis* Smith (Apidae). Those of †*Burmasphex mirabilis* sp.n. (†Burmasphexidae fam.n.) and †*Angarosphex alethes* sp.n. (†Angarosphexidae) were drawn directly from the fossil inclusions and also using a camera lucida.

Phylogenetic analyses

In order to investigate the position of the fossil taxa, we ran a phylogenetic analysis using the dataset of Melo (1999), with addition of *Pachycondyla striata* Smith, a representative of Formicidae. Some of the original characters of Melo (1999) were reinterpreted, and eight

new characters were added (Text S1). Terminals added to those already listed by Melo (1999) are indicated in Table S1. Therefore, the new dataset contains 61 taxa and 147 characters (Matrix data S1).

The morphological data were partitioned according to the homoplasy criterion proposed by Rosa et al. (2019). In this criterion, the characters are partitioned according to their homoplasy values, therefore, the characters are organized in partitions corresponding to their values (Table S2). We measured the homoplasy values using TNT (Goloboff et al., 2008) through an implicit weighing analysis with the default concavity parameter ($k = 3$). The values are normalized between 0 and 1, with the lowest value corresponding to no homoplasy. The morphological data were modelled according to suggestions by Rosa et al. (2019), as follows: ascertainment bias as variable, branch lengths linked among-partition rate variation, equal rates among-character rate variation, and the branch length prior equal to 10. This partitioning was used in all Bayesian analyses carried out here.

The Bayesian inference was carried out in MrBayes 3.2.7 (Ronquist et al., 2012) through the CIPRES Science Gateway portal (Miller et al., 2010), using runs with 10×10^6 generations, four independent runs (four chains each) and 25% of burn-in. Convergence of the chains was checked in MrBayes 3.2.7 and Tracer 1.6 (Rambaut et al., 2013) using as references ESS (effective sample size) >200 , ASDSF (average standard deviation of split frequencies) ≤ 1 and PSRF (potential scale reduction factor) ~ 1.0 . Convergence for topologies was checked through the visualization of the trace plots generated by the function analyze.rwty in the package RWTY (Warren et al., 2017) in the R environment, and according to the analytical references suggested by Wilgenbusch et al. (2004), Nylander et al. (2008), Rambaut et al. (2013) and Warren et al. (2017). The trace plot results are shown in Appendix S2. For the trees, we applied the 50% majority rule consensus (Contype = *Halfcompat*) and the majority rule consensus with all compatible groups added (Contype = *allcompat*). For both consensus, the posterior probability was used as branch support.

In order to investigate the behaviour of the characters under parsimony, we carried out an analysis in TNT (Goloboff et al., 2008), under implied weighting with $k = 3$. The resulting tree and the unambiguous optimizations of the characters were plotted in Winclada 1.0.8 (Nixon, 2002) and edited in image processing software.

RESULTS

Phylogenetic analyses

The Bayesian inference analyses did not present difficulties in the mixing of the chains and convergence for the topologies. All four runs were successful in exploring the sample space, presenting ASDSF values below 0.005, ESS values greater than 1000 and PSRF equal to 1.0 for all parameters without exceptions (see Appendix S2 for details).

The partitioning of the morphological data under the homoplasy criterion resulted in a scheme of 19 partitions, with homoplasy values

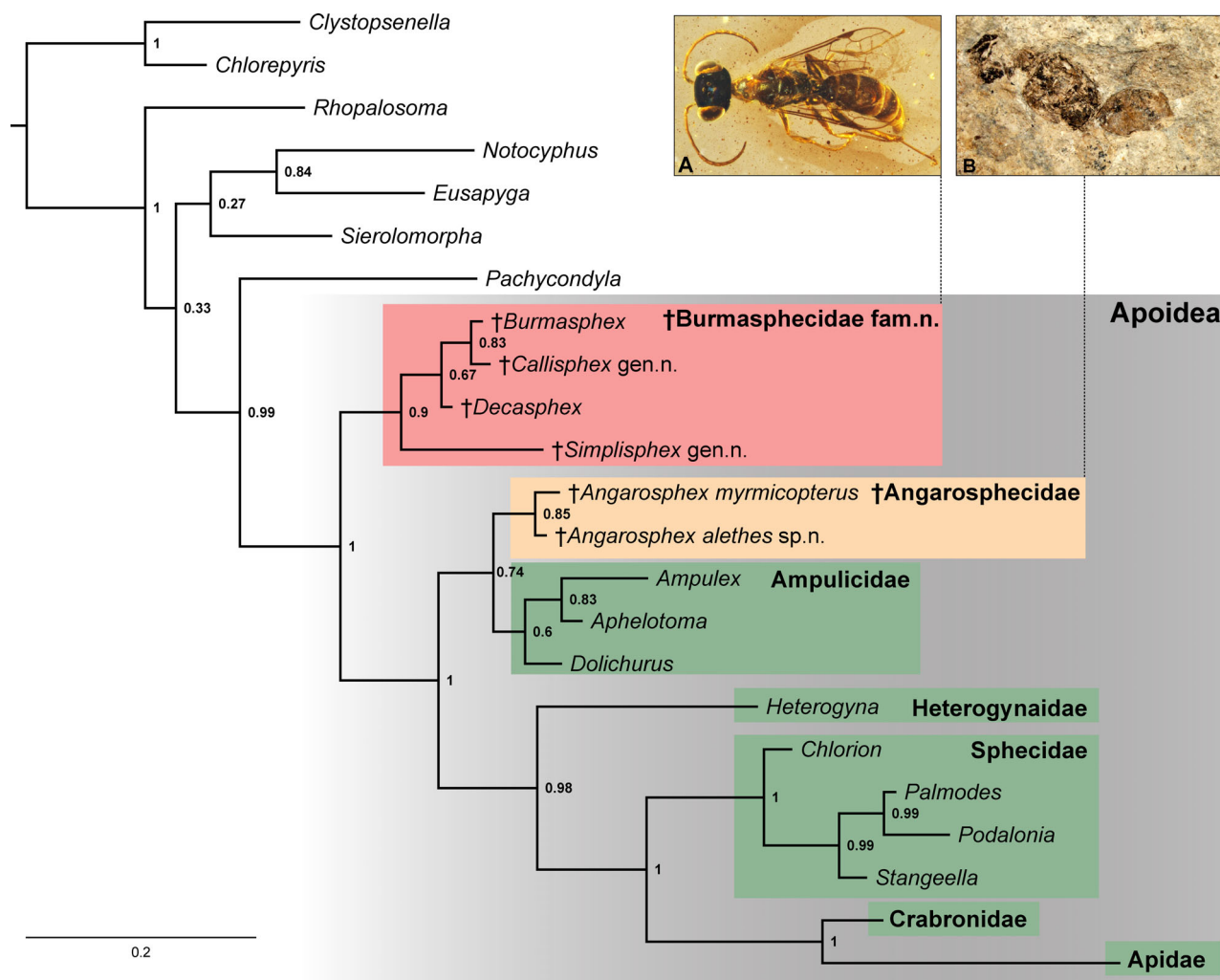


FIGURE 1 Phylogenetic relationships among the major groups of apoid hymenopterans and related aculeate wasp families. Tree resulting from a Bayesian analysis with 146 morphological characters split into 19 partitions under homoplasy criterion. Consensus tree with all compatible groups added and posterior probability as support branch. Inset a. *†Burmasphex mirabilis* sp.n. inset B. *†Angarosphex myrmicopterus* Rasnitsyn.

varying between 0 and 0.88 (Table S2). Figure 1 shows the tree resulting from the Bayesian analysis, representing a majority rule tree showing all compatible groups. In Figure S1, the same tree is shown but with the internal branches of Apoidea and Crabronidae not collapsed. A 50% majority rule tree is represented in Figure S2. In Figure S3, we show the character-state changes optimized in the parsimony tree resulting from the implicit weighting analysis (only unambiguous changes are shown).

The phylogenetic relationships involving the major clades do not differ between the trees from the Bayesian (under both consensus) and the parsimony analyses. There are a few divergences between the topologies, which are restricted either to the outgroup (although not involving the position of Formicidae) or related to some lineages within the Crabronidae. In both cases, the alternating relationships involve groups outside the scope of the present study. Given our current sampling, our phylogenetic results strongly support the position of Formicidae as sister group of the Apoidea (posterior probability = 1). At least four unambiguous transformations

are optimized in the branch leading to Formicidae + Apoidea (Figure S3).

At the base of Apoidea, we recovered a clade joining *†Burmasphex* Melo & Rosa, *†Callisphex* gen.n., *†Decasphex* Zheng, Zhang & Rasnitsyn and *†Simplisphex* gen.n., which form a monophyletic group with high branch support (pp = 0.91 in all compatible groups consensus and pp = 0.89 in the 50% majority rule consensus). The recognition of this clade as an independent lineage prompted us to propose here the *†Burmasphexidae* fam.n. The branch of Apoidea, including *†Burmasphexidae* fam.n., is strongly upheld (pp = 1) with seven unambiguous transformations optimizing on it. The clade containing the remaining Apoidea, forming the sister lineage of *†Burmasphexidae* fam.n., has strong branch support (pp = 1), with at least four unambiguous transformations (see Figure S3).

Finally, in both Bayesian and parsimony results, *†Angarosphex alethes* sp.n. came out as closely related to *†Angarosphex myrmicopterus* Rasnitsyn. These two terminals are being used here to circumscribe and position the *†Angarosphexidae*. This family is clearly placed

far apart from the †Burmasphecidae **fam.n.** and the results support an affinity with Ampulicidae. The relationship between †Angarosphecidae and Ampulicidae received relatively weak support ($pp = 0.75$ in the all compatible groups consensus and $pp = 0.7$ in the 50% majority rule consensus), with only two unambiguous transformations optimizing in the branch leading to them.

Systematics and taxonomy

Order Hymenoptera Linnaeus

Superfamily Apoidea Latreille

Diagnosis. Apoidea are easily distinguished from other Aculeata by the following synapomorphies: posterolateral angle of pronotum reduced dorsally above and anterior to spiracular operculum, thus delimiting a pronotal lobe (character 38:1 in this study); distinct constriction in the lateral portion of pronotum, between its anterior and posterior portions (40:1); metapostnotum strongly expanded posteromesally to form “propodeal triangle” (=propodeal enclosure in Bohart & Menke, 1976) (108:1). Additional synapomorphies for Apoidea, not including †Burmasphecidae **fam.n.**, are posterior margin of dorsal portion of pronotum slanted down and in distinct plane compared with adjacent anterior portion of pronotum (39:1); ventral angle of pronotum greatly produced mesad and closely approaching its counterpart midventrally (42:1); and possession of a mesepisternal clip (43:1).

Included families. †Allommationidae Rosa & Melo; Apidae Latreille sensu lato; Ampulicidae Shuckard; †Angarosphecidae Rasnitsyn; †Burmasphecidae **fam.n.**; †Cirrosphecidae Antropov; Crabronidae Latreille sensu lato; Heterogynaidae; Sphecidae Latreille; †Spheciellidae Rosa & Melo.

†Burmasphecidae **fam.n.**

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Type genus: †*Burmasphex* Melo & Rosa

Included genera: †*Burmasphex* Melo & Rosa, 2018,

†*Callisphex* **gen.n.**, †*Decasphex* Zheng et al., 2021 and

†*Simplisphex* **gen.n.**

Diagnosis. The new family is easily recognized by its slender body, broad head, mandible tridentate in both sexes, long and slender antennae, large eyes with subparallel inner orbits, long and narrow pronotum that overlays anterior portion of mesoscutum, deeply marked notauli (complete, extending to transcutal articulation), which strongly converge posteriorly, and mesal condyle of mid-coxa situated in small projection of posterior border of mesepisternum.

Description. Head. Mandibles tridentate in both sexes, with two dorsal subapical teeth and its outer ventral margin simple; mouthparts very short, less than twice as long as wide; labrum transverse, its apex entire and broadly rounded; clypeus not contacting eye orbits; antennal sockets touching upper epistomal

suture; tentorial pits situated on epistomal ridge and level with tangent to lower rims of antennal sockets; upper portion of outer rim of antennal sclerite level with lower portion, antennal alveolus directed forward; pedicel attachment eccentric; facets of compound eyes more or less uniform in size; preoccipital carina interrupted ventrally. **Mesosoma.** Pronotum much longer than wide, and overlaying anterior portion of mesoscutum posteriorly; posterior margin of dorsal portion of pronotum level with adjacent anterior portion; shape of lateral portion of pronotum exhibiting distinct constriction between anterior and posterior portions of sclerite; pronotum with lateral ridges; notauli indicated by deep sulcus and converging posteriorly (complete, extending to transcutal articulation); parapsidal lines extending to transcutal suture; ocellular carina present; medial portion of mesometepisternal suture (between midcoxae) clearly visible; mesal condyle of mid coxa situated in small projection of posterior border of mesepisternum; propodeum box-like, with a well-defined dorsal portion, whose length is subequal to its posterior surface.

Legs. Basal part of mesocoxa forming narrow pedicel (coxa pedunculate); claws with subapical tooth; midtibia with two spurs; hindcoxa with socket of mesal articulation on ventral surface; hindcoxa with well-developed posterodorsal carina but not forming lamella. **Wings.** Pterostigma flat, not conspicuously thickened; forewing with three submarginal cells or only a single one; costal cell wider than width of vein C; marginal cell longer than pterostigma (measured along vein C); M and CuA diverging at cu-a or distally; M (basal to Rs) gently curved. Hindwing vein C absent; M, when present, diverging from CuA before cu-a; clavus (= plical lobe) indicated by short incision. **Metasoma.** Metasomal petiole absent, T1 and S1 apparently not fused, separation between them clearly visible; medial longitudinal ridge on base of S1 absent; male S7 partly exposed; apical margin of male S8 broadly rounded or with parallel margins.

Key to the genera and species of †Burmasphecidae **fam.n.**

1. Forewing with one submarginal cell; forewing 2nd medial cell absent; marginal cell open along costal margin, R not extending much beyond pterostigma; scape long, at least 3.5× longer than wide; vertex relatively short, 1.2× longer than distance between anterior and posterior ocelli or less; prosternum enlarged, about as long as wide; scutellum distinctly long, longer than mesoscutum; hind tibia without any bristles; medial portion of metepisternum narrow, forming strong keel and narrowly fused to medial portion of mesokatepisternum (as in figure 59 in Melo, 1999); male S8 with parallel margins... †*Simplisphex* **gen.n.** 2
- Forewing with three submarginal cells; forewing 2nd medial cell present; marginal cell closed, R extending beyond pterostigma and meeting Rs at apex of marginal cell; scape length less than 3× its width; vertex distinctly long, 2–3× longer than distance between anterior and posterior ocelli; prosternum transverse, much wider than long; scutellum at most as long as mesoscutum; hind tibia with bristles; medial portion of metepisternum wide and flat, broadly

- fused to mesokatepisternum (as in figure 23 in Melo, 1999); male S8 forming a broad apical lobe 3
2. Scape distinctly thickened along its midlength; decrease in width of flagellomeres somewhat abrupt, F5 distinctly thinner than F3; clypeus with longitudinal carina medially; frons, vertex, mesoscutum and scutellum with dense and coarse punctation, punctures spaced apart by one-half puncture diameter; propodeum without pair of flat projections on posterior corners; body length around 3.5 mm †*S. burmensis* sp.n.
- Scape cylindrical, its width uniform along its length; flagellomeres gradually decreasing in width, F5 only slightly thinner than F3; clypeus without longitudinal carina medially; frons, vertex, mesoscutum and scutellum with fine and sparse punctation, punctures spaced apart by 1–2 puncture diameters; propodeum with pair of flat projections on posterior corners; body length over 4.0 mm †*S. scutellatus* sp.n.
3. Occipital carina complete; pronotum 2× longer than mesoscutum; 2nd segment of metasoma without constriction anteriorly; anterior portion of S2 not differentiated compared with remainder of sclerite †*Decasphegus cretacicus* Zheng, Zhang & Rasnitsyn.
- Occipital carina interrupted ventrally; pronotum at most 1.5× longer than mesoscutum; 2nd segment of metasoma with distinct constriction anteriorly; anterior portion of S2 at different level compared to remainder of sclerite, surface separating these two portions almost vertical 4
4. Forewing 3rd submarginal cell about 2.5× longer than wide (width measured along 2Rs-m vein); apical portion of 2nd abscissa of Rs (separating 1st and 2nd submarginal cells) 2.5× longer than its basal portion; 2nd medial cell about 3× longer than wide (width measured along 2 m-cu vein); 1st and 2nd cubital cells about 3× longer than wide †*Callisphegus robustus* gen. et sp.n.
- Forewing 3rd submarginal cell almost as long as wide; apical portion of 2nd abscissa of Rs (separating 1st and 2nd submarginal cells) about as long as its basal portion; 2nd medial cell almost as long as wide; 1st and 2nd cubital cells less than 1.5× longer than wide... †*Burmasphex* Melo & Rosa 5
5. Body length at least 6 mm and forewing length more than 3.5 mm; distance between posterior ocelli longer than ocello-orbital distance; pilosity mostly long and conspicuous; lateral propodeum pilosity with longest setae about as long as 5× ocellar diameter; metasoma with conspicuous erect pilosity, whose length and diameter increase towards its posterior end, longest setae about 3× as long as ocellar diameter †*B. pilosus* Melo & Rosa.
- Body length varying between 3 and 4 mm and forewing length less than 3 mm; distance between posterior ocelli shorter than ocello-orbital distance; pilosity mostly short and less conspicuous; lateral propodeum pilosity with setae about as long as 3× ocellar diameter or less; metasoma with short and inconspicuous pilosity, longest setae about 2× as long as ocellar diameter or less 6
6. Dorsal surface of propodeum with deep medial sulcus along its entire length; basal portion of 3rd tergum strongly constricted, forming marked step with tergal disc. †*B. sulcatus* Melo & Rosa.

- Dorsal surface of propodeum without sulcus, smooth; basal portion of 3rd tergum not strongly constricted..... †*B. mirabilis* sp.n.

†*Burmasphex* Melo & Rosa, 2018

Type species: †*Burmasphex sulcatus* Melo & Rosa, 2018

Included species: †*Burmasphex mirabilis* sp.n., †*B. pilosus* Melo & Rosa, 2018 and †*B. sulcatus* Melo & Rosa, 2018.

This genus was described by Melo and Rosa (2018) and included two species found in Burmese amber. It is easily recognized by the slender body, broad, transverse head (distinctly wider than long) with very long vertex, long and slender antennae, large eyes with sub-parallel inner orbits, long and narrow pronotum, and marked constriction between 1st and 2nd metasomal segments (Melo & Rosa, 2018). In the present study, we are describing a new species, †*Burmasphex mirabilis* sp.n. This new species is similar to †*B. sulcatus* and can be easily distinguished by dorsal surface of propodeum, very smooth without sulcus and basal portion of 3rd tergum not strongly constricted.

†*Burmasphex mirabilis* sp.n.

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Figs. 2, S4 and S5

Diagnosis. This species can be recognized by the distance between posterior ocelli being shorter than the ocello-orbital distance, pilosity mostly short and inconspicuous, dorsal surface of propodeum without sulcus and smooth, and basal portion of 3rd tergum not strongly constricted.

Description. Holotype male (DZUP). **Measurements (in mm).** Approximate body length, 3.22; maximum head width, 0.96; forewing length, 2.08; maximum width of T2, 0.57. **Coloration.** Head mostly dark metallic blue, with some purplish reflexes; clypeus, antennae, mandibles except for the dark brown teeth, and mouthparts light reddish brown. Pronotum light reddish brown with very faint greenish reflexes; mesoscutum, scutellum, metanotum, metapostnotum, metapleura and propodeum mostly dark brown with dark metallic bluish green reflexes; mesopleura mostly light reddish brown, except for a brown band on its upper portion; legs light reddish brown. Wing membrane hyaline, veins and pterostigma dark reddish brown. Metasomal terga 1–3 mostly dark brown with weak metallic green reflexes, their marginal zone light reddish brown; disc of T4 dark brown with basal portion and marginal zone reddish brown; remaining apical terga light reddish brown; sterna 1–3 mostly dark brown, their marginal zone light reddish brown; S4 mostly reddish brown except for a transverse dark brown band crossing the entire sclerite; S5–S7 light reddish brown; S8 dark reddish brown. **Pilosity.** Mostly very short and inconspicuous; upper portion of gena with some very thin setae, their length subequal to diameter of ocelli; pronotum with similar setae,

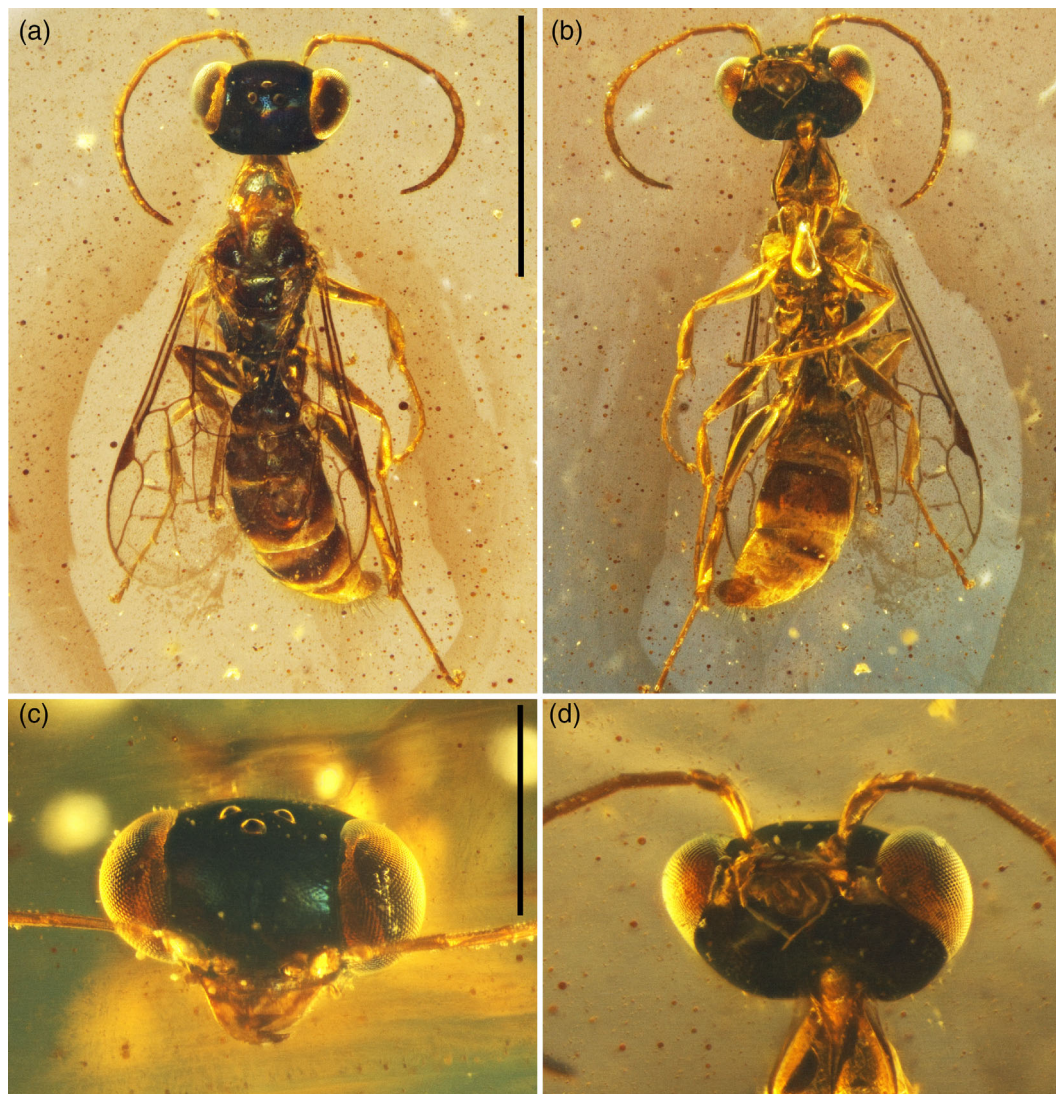


FIGURE 2 †*Burmasphex mirabilis* sp.n. (mid-cretaceous, Burmese amber; male holotype – DZUP bur-017a). (a) dorsal habitus; (b) ventral habitus; (c) head, frontal view; (d) head, ventral view. (Scale bars = a, b, 1 mm; c,d, 0.5 mm).

longest ones about as long as $2\times$ ocellar diameter; terga 3–7 with conspicuous erect pilosity, whose length and diameter increase towards apex of metasoma, longest setae almost $3\times$ as long as ocellar diameter; sterna 4–5 also with erect pilosity; ventral surface of sternum 8 with abundant long pilosity, apical margin with a loose fringe of very long setae, their length over $3\times$ ocellar diameter. **Integumental surface.** Mostly smooth and shiny; frons and vertex with conspicuous punctation, punctures spaced apart by 1–2 puncture diameter; punctation on pronotum, mesoscutum and scutellum much sparser. Propodeum with a strong transverse carina separating dorsal and posterior surfaces, carina extending ventral and separating lateral surfaces from posterior surface as well; a pair of longitudinal carinae connects the transverse carina to the spiracles. **Structure (measurements in mm).** Head transverse in frontal view, about $1.4\times$ wider than long (0.95:0.65); malar space as long as ocellar diameter (0.06:0.06); clypeus very short, $5\times$ wider than long (0.4:0.08); interalveolar distance about $2\times$ alveolus diameter (0.15:0.07). Scape short, about $2.7\times$

longer than wide (0.22:0.08); F1–F3 slender, respectively about 5.7, 5.3 and $4.5\times$ longer than wide (0.23:0.04; 0.21:0.04; 0.18:0.04); F4–F10 progressively decreasing in length, with increasing diameter from F4 to F6 and then decreasing again. Inner orbits subparallel, upper and lower interorbital distances subequal (0.49:0.5); eye, in lateral view, about $1.5\times$ as long as its maximum width (0.5:0.33); distance between posterior ocelli shorter than ocello-orbital distance (0.09:0.13). Prosternum relatively short, about $1.6\times$ wider than long (0.11:0.07). Legs slender, femur of hind leg as long as tibia (0.65:0.65). Dorsal surface of propodeum rectangular, about $2\times$ as wide as long (0.43:0.21). Wing venation as in Figures 2 and S5. Sternum 8 with apical half forming a broad spatulate lobe.

Type material. Holotype male, in amber piece DZUP Bur-017a. The specimen is superbly well preserved and fully articulated.

Etymology. The species name is a Latin adjective, *mirabilis* (wonderful), in reference to the state of preservation of the holotype. The larger amber piece, which contained the holotype, also

had a fragmentary dryinid wasp, two small dipterans and one psocopteran.

Locality and horizon. Hukawng Valley, near Tanai, Kachin State, northern Myanmar; lowermost Cenomanian (Late Cretaceous).

†*Callisphex* gen.n.

urn:lsid:zoobank.org:act:280B58B5-B819-44DE-83A4-D8C6FE7F55E3

Fig. 3

Type species: †*Callisphex robustus* sp.n.

Diagnosis. See above key to genera and species of †Burmasphecidae fam.n.

Description. Same as †Burmasphecidae fam.n. including the following features. **Head.** Epistomal suture (between antennal sockets) below transverse median line across antennal sockets. Scape short, about 2.5× longer than wide. Vertex long, 2× longer than distance between anterior and posterior ocelli. **Mesosoma.** Prosternum relatively short, about 1.4× wider than long. Scutellum shorter than mesoscutum, anterior depression forming a transverse groove. Hind tibia with spiniform bristles. Medial portion of metepisternum wide and flat, broadly fused to mesokatepisternum. **Wings.** Forewing with three submarginal cells (1st larger than 2nd and 3rd, 2nd smaller than 3rd), 2nd cubital, 1st and 2nd medial cells; apical portion of 2nd abscissa of Rs (separating 1st and 2nd submarginal cells) 3× longer than its basal portion; vein 1 m-cu ending at Rs and vein 2 m-cu ending at 3rd submarginal cell; veins M and CuA diverging distal to cu-a; 2nd abscissa of M + CuA shorter than cu-a. Hindwing vein M diverging from CuA before cu-a. **Metasoma.** 2nd segment of metasoma with distinct constriction anteriorly; anterior portion of S2 at different height compared to remainder of sclerite, surface separating these two portions almost vertical.

Etymology. The genus name combines a Latinized form of the Greek word *kallos* (beautiful), referring to the astonishing preservation of the holotype and *Sphex*, the type genus of the apoid family Sphecidae. The name is masculine.

†*Callisphex robustus* sp.n.

urn:lsid:zoobank.org:act:A36E4A68-FC02-49BD-978C-31A0CFC1AF24

Fig. 3

Diagnosis. This species can be recognized by its forewing 3rd submarginal cell being about 2.5× longer than wide (width measured along 2rs-m vein), apical portion of 2nd abscissa of Rs (separating 1st and 2nd submarginal cells) 2.5× longer than its basal portion, 2nd medial cell about 3× longer than wide (width measured along 2m-cu vein) and 1st and 2nd cubital cells about 3× longer than wide.

Description. Holotype female (DZUP). **Measurements (in mm).** Approximate body length, 5.78 (without part of metasoma, see below); maximum head width, 1.49; forewing length, 3.80; maximum width of T2, 1.32. **Coloration.** Head mostly dark metallic blue, with some purplish reflexes; mesosoma mostly brown, with some metallic

light brown reflexes; metasoma mostly brown with posterior margin of segments light brown. Wing membrane hyaline, veins and pterostigma brown. **Pilosity.** Head mostly glabrous with short and silvery setae on lower frons, setae shorter than half ocellus diameter; legs, meso- and metasoma with very short, silvery and velvet pubescence. **Integumental surface.** Head mostly smooth and shiny, frons and vertex with shallow and inconspicuous punctation, punctures spaced apart by 3–4 puncture diameter. Meso- and metasoma mostly dull, without apparent punctation. Dorsal surface of propodeum with deep medial sulcus along entire surface. **Structure (measurements in mm).** Head about 1.3× wider than long (1.49:1.16); malar space shorter than ocellar diameter (0.09:0.12); clypeus very short, 3.3× wider than long (0.85:0.26); interalveolar distance as long as alveolus diameter (0.15:0.15). Scape short, about 2.5× longer than wide (0.25:0.1); F1–F3 slender, respectively about 6.1, 4.8 and 3.8× longer than wide (0.43:0.07; 0.34:0.07; 0.27:0.07); F4 to F10 progressively decreasing in length. Inner orbits subparallel, upper and lower interorbital distances subequal (0.8:0.9); eye, in lateral view, about 2.1× as long as its maximum width (1.02:0.49); distance between posterior ocelli shorter than ocello-orbital distance (0.02:0.09). Prosternum relatively short, about 1.4× wider than long (0.13:0.09). Legs slender, femur of hind leg almost as long as tibia (1.52:1.36). Dorsal surface of the propodeum rectangular much wider than long. Wing venation as in Figure 3b.

Type material. Holotype female, in amber piece DZUP Bur-1346a. The specimen is very well preserved, head and propleura disarticulated from the remainder of body but present; forelegs missing; posterior portion of metasoma missing after 2nd segment. Syninclusions include some debris and many disarticulated parts of other insects.

Etymology. The species name is a Latin adjective, *robustus* (robust), in reference to the robust body in contrast to the graceful habits of the other species of †Burmasphecidae fam.n.

Locality and horizon. Hukawng Valley, near Tanai, Kachin State, northern Myanmar; lowermost Cenomanian (Late Cretaceous).

†*Simplisphex* gen.n.

urn:lsid:zoobank.org:act:538BB1FB-75F0-4917-ADB9-B03E7BA4370E

Fig. 4

Type species: †*Simplisphex scutellatus* sp.n.

Included species: †*Simplisphex burmensis* sp.n. and †*Simplisphex scutellatus* sp.n.

Diagnosis. See above key to genera and species of †Burmasphecidae fam.n.

Description. Small wasps, 3.4–4.3 mm in length. Same as †Burmasphecidae fam.n. including the following features: **Head.** Epistomal suture (between antennal sockets) above transverse median line across antennal sockets; vertex short, 1.1× longer than distance between anterior and posterior ocelli. Antenna relatively long, F1 distinctly longer than wide and 2× longer than F2, remaining flagellomeres with about the same size. **Mesosoma.** Prosternum enlarged,

about as long as wide. Scutellum very long, longer than mesoscutum, anterior depression broad, semilunar in shape. Hind tibia without any bristles; medial portion of metepisternum narrow, forming strong keel and narrowly fused to medial portion of mesokatepisternum. **Wings.** Forewing with one submarginal cell (veins Rs + M, 2 M and 2rs-m tubular; veins 2Rs, 3rs-m and M beyond submarginal cell absent), 2nd cubital and 1st medial cell present, 2nd medial cell absent; marginal cell very long, $1.5\times$ longer than pterostigma, its apex acute not touching the wing margin (marginal cell open); costal cell slightly wider than width of vein C; veins M and CuA diverging at cu-a. Hindwing clavus indicated posterodistally by moderate incision; jugal lobe small and indicated by distinct incision; veins on the hindwing apparently totally absent (we suspect that it may be an artefact caused by diagenesis). **Metasoma.** Apical margin of male S8 with parallel margins and rectangular apex.

Etymology. The genus is named after *simplex*, *simplicicus*, in reference to the simpler wing venation compared with the other genera, and *Sphex*, the type genus of the apoid family Sphecidae. The name is masculine.

†*Simplisphex scutellatus* sp.n.

urn:lsid:zoobank.org:act:6A3B27C9-29E8-4CF5-9E46-

B666CBDD514A

Fig. 4a, c and e

Diagnosis. This species can be recognized by the scape being cylindrical, its width uniform along its length, flagellomeres gradually decreasing in width (F5 only slightly thinner than F3), clypeus without longitudinal carina medially, frons, vertex, mesoscutum and scutellum with fine and sparse punctation (punctures spaced apart by 1–2 puncture diameters), propodeum with pair of flat projections on posterior corners and body length over 4.0 mm.

Description. Holotype male (DZUP). **Measurements (in mm).** Approximate body length, 4.3; maximum head width, 0.95; forewing length, 2.6; maximum width of T2, 0.6. **Coloration.** Head and mesosoma mostly dark. Pronotum brown with mandibles brown with dark apex. Scape dark, flagellomeres brown to light brown. Legs brown to light brown. Wing membrane hyaline, veins and pterostigma brown to light brown. Metasoma dark brown to light brown. **Pilosity.** Mostly light, erect, dense and short, setae shorter than ocellar diameter. **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. Metanotum areolate. Propodeum with transverse carina separating dorsal and posterior surfaces, and forming a pair of pointed projections on posterior corners; dorsal surface of propodeum with deep medial longitudinal sulcus along entire surface, interrupting transverse carina and apparently extending on to posterior surface; anterior margin of propodeum with deep transverse areolate sulcus. **Structure (measurements in mm).** Scape very long, about $4.3\times$ longer than wide (0.39:0.09); F1 very slender, about $4.4\times$ longer than wide (0.29:0.06); F2 about $2.8\times$ longer than wide (0.18:0.06); F3–F4 about

$2\times$ longer than wide (0.13:0.06); F5–F8 about $1.8\times$ longer than wide (0.12:0.06); F9–F10 about $2\times$ longer than wide (0.10:0.05); F11 about $2.3\times$ longer than wide (0.12:0.05). Distance between posterior ocelli shorter than ocello-orbital distance (0.06:0.13). Prosternum enlarged, about as long as wide (0.25:0.22). Legs slender, femur of hind leg as long as tibia (0.71:0.65). Dorsal surface of the propodeum rectangular, about $2.5\times$ as wide as long (0.44:0.23). Wing venation as in Figure 4e.

Type material. Holotype male, in amber piece DZUP Bur-036. The specimen is very well preserved except for the left antenna, which is slightly deformed. Syninclusions include some debris, plant stellate trichomes, a dipteran and an orthopteran.

Etymology. The species name *scutellatus* refers to the peculiar form of the scutellum.

Locality and horizon. Hukawng Valley, near Tanai, Kachin State, northern Myanmar; lowermost Cenomanian (Late Cretaceous).

†*Simplisphex burmensis* sp.n.

urn:lsid:zoobank.org:act:307417B5-B08A-49CB-

BD43-BF472D3DDD56

Fig. 4b, d and f

Diagnosis. This species can be recognized by the scape distinctly thickened along its mid length, decrease in width of flagellomeres somewhat abrupt (F5 distinctly thinner than F3), clypeus with longitudinal carina medially, frons, vertex, mesoscutum and scutellum with dense and coarse punctation (punctures spaced apart by one-half puncture diameter), propodeum without pair of flat projections on posterior corners and body length around 3.5 mm.

Description. Holotype male (DZUP). **Measurements (in mm).** Approximate body length, 3.4; maximum head width, 0.9; forewing length, 2.3; maximum width of T2, 0.6. **Coloration.** Antennae, head, mesosoma and metasoma mostly dark. Mandibles dark brown. Legs mostly dark, basitarsus and tarsus brown. Wing membrane hyaline, veins and pterostigma dark brown. **Pilosity.** Mostly dark, erect, dense and short, setae shorter than ocellar diameter. **Integumental surface.** Frons, vertex, mesoscutum and scutellum with dense and thick punctation, punctures spaced apart by 0.5 puncture diameter. Clypeus with longitudinal carina medially. Propodeum with transverse carina separating dorsal and posterior surfaces. **Structure (measurements in mm).** Head transverse in frontal view, about $2\times$ wider than long (0.79:0.39); malar space as long as ocellar diameter (0.06:0.06); clypeus short, $3\times$ wider than long (0.39:0.13), convex medially with free margin slightly projected and truncated; interalveolar distance about $2.3\times$ alveolus diameter (0.09:0.04). Scape very long, about $3.6\times$ longer than wide (0.32:0.09); F1 slender, about $3.6\times$ longer than wide (0.32:0.09); F2–F4 and F5–F7 about $1.7\times$ longer than wide (0.13:0.08; 0.09:0.05 respectively); F8–F10 about $2\times$ longer than wide (0.08:0.04), F11 very slender, about $3\times$ longer than wide (0.12:0.04). Inner orbits subparallel, upper and lower interorbital distances subequal (0.45:0.47); eye, in frontal view, about $2.3\times$ as long as its maximum width (0.39:0.17); distance between posterior ocelli

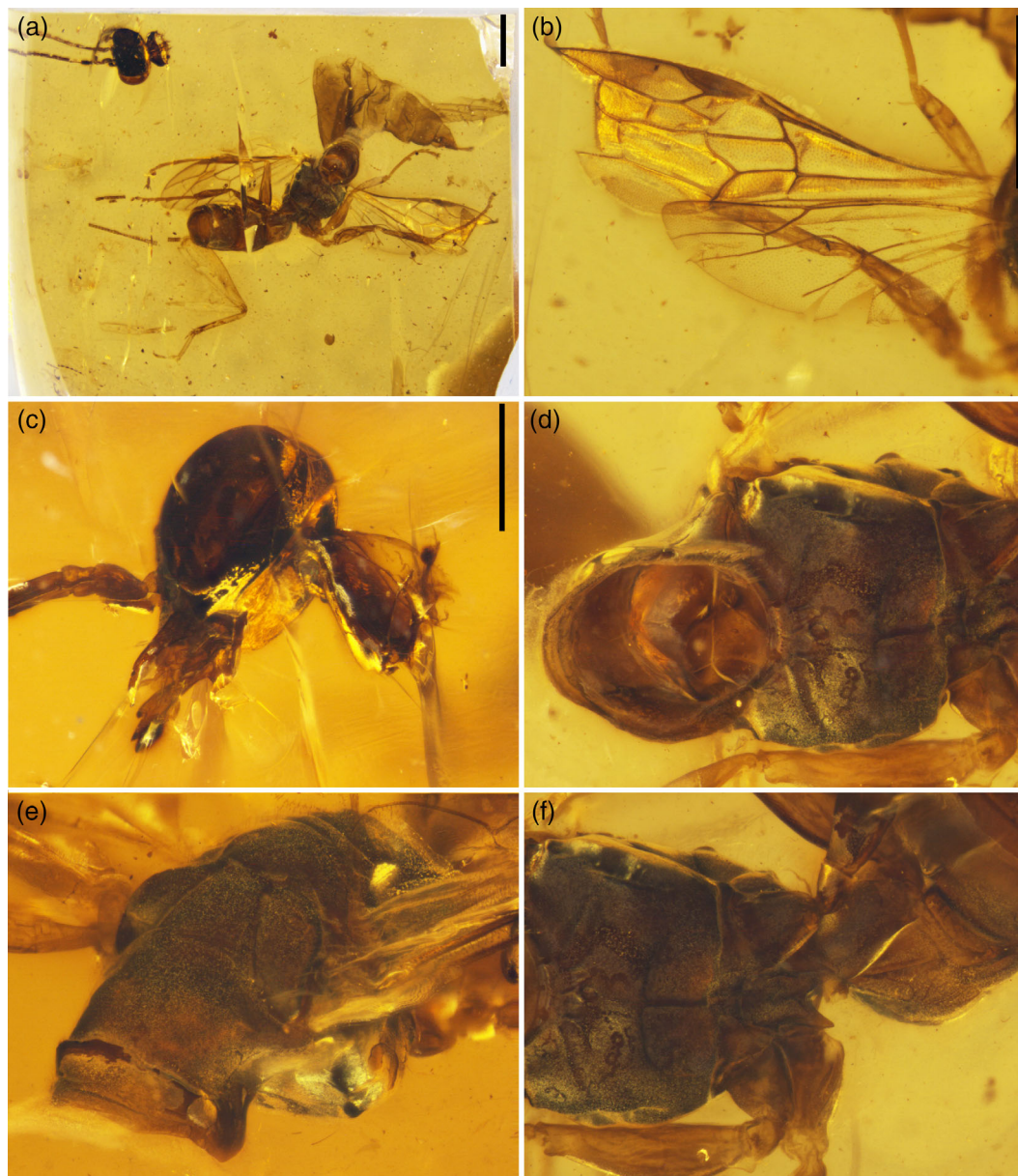


FIGURE 3 †*Callisphex robustus* sp.n. (mid-cretaceous, Burmese amber; female holotype – DZUP bur-1346a). (a) head dorsal habitus and body ventral habitus; (b) fore and hind wings; (c) head, lateral view; (d) anterior portion of mesosoma, ventral view; (e) mesosoma, latero-dorsal view; (f) posterior portion of mesosoma, ventral view. (scale bars = a, 1 mm; B, 1 mm; c–f, 0.5 mm).

shorter than ocello-orbital distance (0.06:0.12). Prosternum enlarged, about as long as wide (0.23:0.20). Legs slender, femur of hind leg as long as tibia (0.65:0.61). Dorsal surface of the propodeum rectangular, about 2.5× as wide as long (0.45:0.18).

Type material. Holotype male, in amber piece DZUP Bur-589. The specimen is very well preserved, but apical portion of wings wrapped over the metasoma (although not obstructing visibility of main veins).

Etymology. The species name *burmensis* refers to the former name of the country from which the amber originated.

Locality and horizon. Hukawng Valley, near Tanai, Kachin State, northern Myanmar; lowermost Cenomanian (Late Cretaceous).

†*Decasphe* Zheng et al., 2021

Type species: †*Decasphe cretacicus* Zheng et al., 2021.

Included species: †*Decasphe cretacicus* Zheng et al., 2021.

†*Decasphe* was described from Burmese amber based on a single species. The main features that support the inclusion of †*Decasphe* in †Burmasphecidae fam.n. are the tridentate mandibles, the distinctly long vertex (2–3× longer than distance between anterior and posterior ocelli) (Figure 2a in Zheng et al., 2021), the shape of the pronotum, and the wide and flat medial portion of metepisternum, with medial portion is broadly fused to mesokatepisternum (Figure 2f in

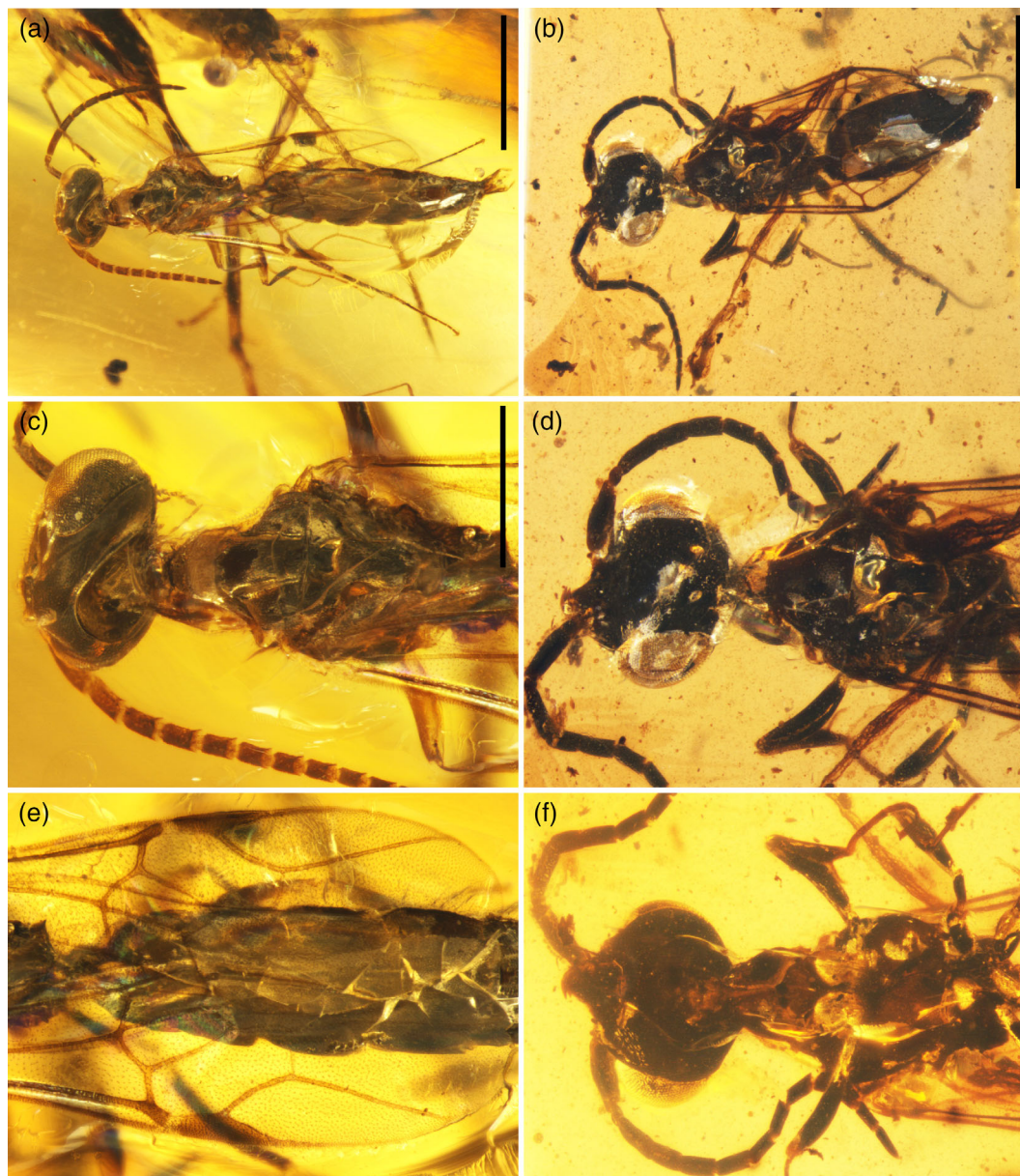


FIGURE 4 †*Simplisphex* gen.n. (mid-cretaceous, Burmese amber). †*Simplisphex scutellatus* sp.n. (male holotype – DZUP Bur-036) (a, c, e). (a) dorsal habitus; (c) head and mesosoma, dorsal view; (e) fore wings. †*Simplisphex burmensis* sp.n. (male holotype – DZUP Bur-589) (b, d, f). (b) dorsal habitus; (d) head and mesosoma, dorsal view; (f) head and mesosoma, dorsal view. (scale bars = a, 1 mm; b, 1 mm; c–f, 0.5 mm).

Zheng et al., 2021). This genus is easily distinguishable from the other genera of †Burmasphecidae by pronotum 2× longer than mesoscutum, preoccipital carina complete, 2nd segment of metasoma without constriction anteriorly and anterior portion of S2 not differentiated compared with remainder of sclerite.

Zheng et al. (2021) point out that †*D. cretacicus* has eight flagellomeres instead of the usual 10 flagellomeres found in female apooid wasps. The reduction in the number of flagellomeres in Apoidea is quite uncommon and is present only in Crabronidae and Apidae. This condition appears in Crabroninae, specifically in some species of the tribes: Crabronini, Miscophini Fox and Trypoxylini Lepeletier (Bohart & Menke, 1976). In bees, this reduction is present in some species of the tribes Ammobatini Handlirsch, Ammobatoidini Michener, Biastini

Linsley & Michener, Augochlorini Beebe, Rophitini Schenck and Meganomiini Michener (Michener, 2007). The missing flagellomeres of the holotype (LYHY-013) appear to have been disarticulated during the taphonomic process or even before the wasp was wrapped by the resin. In this latter case, the wasp was probably already dead and dry before having had contact with the resin. Until another new specimen of †*D. cretacicus* is discovered, it is prudent to assume that this reduction is a preservation artefact.

†Angarosphecidae Rasnitsyn.

Type genus: †*Angarosphex* Rasnitsyn, 1975

Included genera: See Pulawski (2022) and Table 1 in Zheng et al. (2021) (the title of their table is written as

“fossils of Ampulicidae”, where the correct would be “fossils of †Angarosphecidae”).

In order to have a proper delimitation of the †Angarosphecidae, we reinvestigate here the fossil †*Angarosphex myrmicopterus*, the type species of the genus †*Angarosphex*. This fossil family has a convoluted taxonomy and currently contains a multitude of taxa that clearly do not constitute a monophyletic group, with many of them not even belonging to Apoidea (Rosa & Melo, unpublished data). Our reinterpretation of the †Angarosphecidae is also based on a newly described species of †*Angarosphex*, from Burmese amber, which resembles †*A. myrmicopterus* in many details and to which it is phylogenetically related.

†Angarosphecidae, as conceived here in its narrow sense, came out as sister-group of Ampulicidae (see phylogenetic results below), and perhaps could be included in it as a subfamily. We defer from changing the current classification and maintain it with family status until further studies, with a broader representation, are carried out. Inclusion of †*Angarosphex* in our phylogenetic analyses has shown that †*Burmasphex* and its closely related genera clearly constitute an independent main lineage of the Apoidea, recognized here as a separate family, the †Burmasphecidae fam.n.

†*Angarosphex* Rasnitsyn, 1975

Type species: †*Angarosphex myrmicopterus* Rasnitsyn, 1975

Synonymic list: See Pulawski (2022).

Included species: See Pulawski (2022) and Table 1 in Zheng et al. (2021) (table title erroneously cited as “Ampulicidae fossils”).

We do not attempt here to diagnose or redescribe †*Angarosphex*. As currently conceived, the genus is clearly polyphyletic resulting in a very heterogeneous assemblage. There are 15 species included in this genus, in addition to five genus-group synonyms (Pulawski, 2022; Zheng et al., 2021). Species as well as generic synonyms included in †*Angarosphex* should be reviewed on a case-by-case basis and preferably be included in broader phylogenetic analyses involving other clades of Aculeata. The treatment of these taxa as well as a new definition of the genus is beyond the scope of the present study. Some of these taxa are already being studied and will be treated in forthcoming publications (Rosa & Melo, unpublished data).

†*Angarosphex myrmicopterus* Rasnitsyn, 1975

Fig. 5

Redescription. Holotype sex unknown (PIN). **Measurements (in mm).** Approximate body length, 8.0; maximum head width, 1.68; forewing length, 5.5; maximum width of T2, 1.52. **Head.** Ventral surface exposed, well preserved; mandibles, mouthparts and left compound eye not discernible. Head wider than long; hypostomal carina and midventral line present; hypostomal bridge slightly longer than oral fossa; occipital carina complete; right compound eye apparently

occupying more than half of entire lateral surface of head. **Mesosoma.** Dorsal surface exposed; pronotum mostly preserved with right portion slightly disarticulated from mesothorax; mesoscutum, scutellum, metanotum and propodeum well preserved; left portion of scutellum somewhat sunk under the metanotum; upper portion of left mesepisternum exposed; tegulae apparently preserved. Pronotum longer than wide; posterior margin of pronotum abutting mesoscutum, not overlying its anterior portion, and raised in relation to anterior portion, delimiting a pronotal collar; pronotal collar broader than long, shorter than mesoscutum, somewhat high and with short shallow sulcus medially; lateral pronotal ridge apparently indicated; anterior portion of mesoscutum with a straight transverse step, separating the disc posteriorly from a lowered anterior portion onto which the pronotum fits; notauli indicated by deep sulcus and converging posteriorly; parapsidal lines apparently preserved and extending to transcutal suture; scutellum wider than long, disc delimited laterally by low carina or step; anterior groove of scutellum 4× wider than long; metanotum apparently areolate; propodeum box-like, with well-defined dorsal surface, almost as long as wide; dorsal surface of propodeum clearly with large areolation and with deep medial sulcus along entire surface. **Legs.** In general, not preserved or not exposed; left hind coxae and part of femur (?) very poorly preserved, mostly not discernible. **Wings.** Right forewing and left hindwing exposed, poorly preserved; left forewing apparently missing. 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 1 m-cu ending at Rs and vein 2 m-cu ending at 3rd submarginal cell; 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 vein M diverging from CuA before cu-a. **Metasoma.** Latero-ventral surface exposed, poorly preserved, terga and sterna mostly not discernible.

Type material. Holotype (sex unknown), in mould/impression lacustrine fossil PIN n°3064/629. Specimen conditions along the redescription. Material studied through high-resolution photographs.

Locality and horizon. Baissa, Buryatia, Transbaikalia, Russia; Zaza formation, Aptian (Early Cretaceous).

†*Angarosphex alethes* sp.n.

urn:lsid:zoobank.org:act:E2C049A8-B1D4-47D1-8A49-5BBF3F16BB52

Figs. 6 and S6

Diagnosis. This species can be recognized by very short and inconspicuous pilosity (setal length shorter than half of ocellar diameter), propodeum with strong transverse carina separating dorsal and posterior surfaces, carina extending ventrally and separating lateral surfaces from posterior surface as well, dorsal surface of propodeum transversally areolate and posterior surface of propodeum divided medially by distinct carina ending near propodeal foramen.

Description. Holotype male (DZUP). **Measurements (in mm).** Approximate body length, 2.5 (without metasoma); maximum head width, 1.16; forewing length, 2.8. **Coloration.** Not well preserved, lower inner orbits, frons just above antennal sockets, mesoscutum



FIGURE 5 †*Angarosphex myrmicopterus* Rasnitsyn (†Angarosphecidae Rasnitsyn, early cretaceous, Zaza formation; male? Holotype – PIN n°3064/629). Top, photograph of holotype (assembly of two separate images in higher magnification; right image, with metasoma and fore wing, slightly rotated counterclockwise in relation to left image); middle, line drawing with interpretation of main morphological structures; bottom, line drawing superimposed on lower magnification photograph showing the entire holotype. Scale bar = 2 mm.

and metanotum with dark metallic red areas preserved, with some reddish reflexes; scutellum and propodeum apparently weakly metallic, with some greenish reflexes; legs brown to light brown; wing membrane hyaline, veins and pterostigma brown to light brown. **Pilosity.** Mostly glabrous; mesoscutum, scutellum and mesepisternum with very short and inconspicuous pilosity, setal length

shorter than half of ocellar diameter. **Integumental surface.** Mostly smooth and shiny; frons and vertex with conspicuous punctation, punctures spaced apart by 1–2 puncture diameter; punctation on pronotum, mesoscutum and scutellum much sparser; punctation of mesepisternum and metepisternum thicker than head punctation, laterally punctures spaced apart by 2–3 puncture diameters,

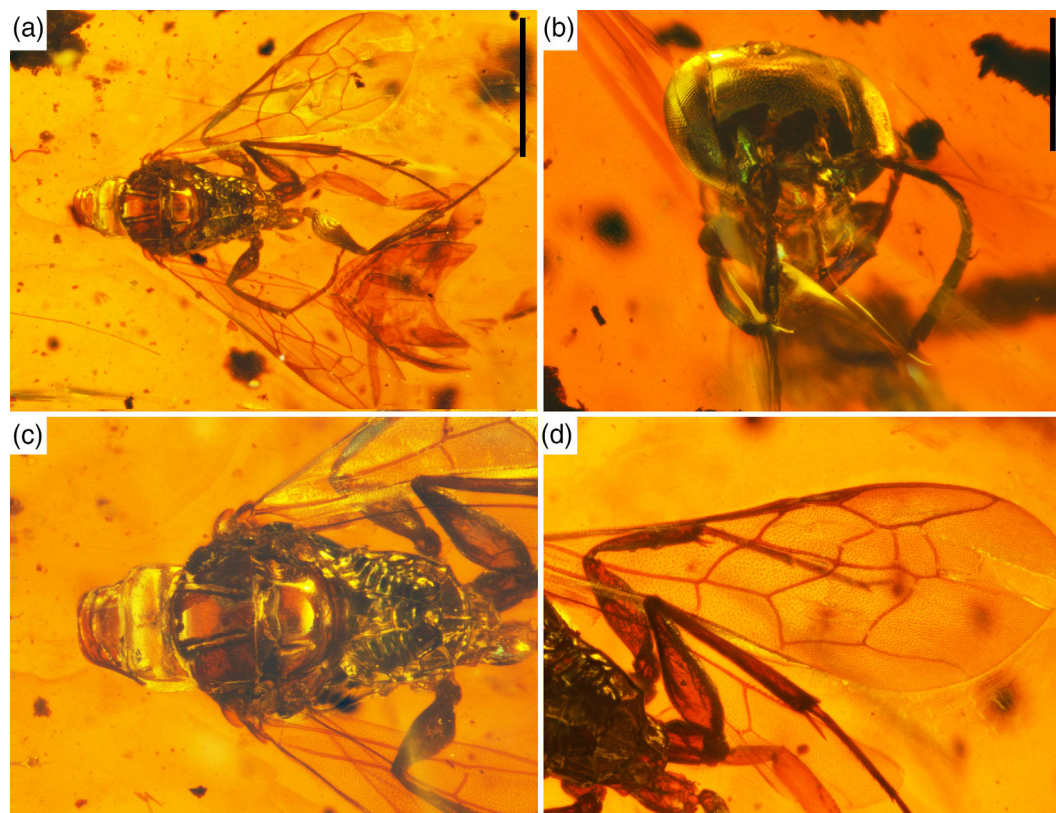


FIGURE 6 †*Angarosphex alethes* sp.n. (†Angarosphecidae Rasnitsyn, mid-cretaceous, Burmese amber; male holotype – DZUP Bur-1429). (a) dorsal habitus; (b) head, frontal view; (c) mesosoma, dorsal view; (d) fore wing. (scale bars = a, 1 mm; b–d, 0.5 mm).

ventrally punctures spaced apart by 0.5–1 puncture diameter. Propodeum with strong transverse carina separating dorsal and posterior surfaces, carina extending ventrally and separating lateral surfaces from posterior surface as well; dorsal surface of propodeum transversally areolate; metapostnotum apparently extending as large areolate sulcus medially in dorsal surface; posterior surface of propodeum divided medially by distinct carina ending near propodeal foramen. **Structure (measurements in mm).** Head transverse in frontal view, about $1.26\times$ wider than long (1.16:0.92); malar space $1.3\times$ longer than ocellar diameter (0.09:0.07); clypeus very short, $2.1\times$ wider than long (0.51:0.24); interalveolar distance shorter than alveolus diameter (0.09:0.14). Antenna about $2.5\times$ longer than maximum head height. Inner orbits subparallel, upper and lower interorbital distances subequal (0.61:0.6); eye, in lateral view, about $2.7\times$ as long as its maximum width (0.73:0.27); distance between posterior ocelli $1.66\times$ longer than diameter of posterior ocellus (0.15:0.09). Legs slender, hind tibia $1.2\times$ longer than hind femur (1.02:0.85). Wing venation as in Figure 6d. Dorsal surface of propodeum $1.4\times$ longer than wide (0.68:0.48).

Type material. Holotype male, in amber piece DZUP Bur-1429a. The specimen is very well preserved and partly disarticulated, with head, propleura and forelegs separated from the rest of the body; right antenna lacking F9–F11, left antenna lacking F10 and major part of F11; entire metasoma lacking. Syninclusions include some debris, plant stellate trichomes, an auchenorhynchous hemipteran and an exuvia of an unidentified arthropod.

Etymology. The species name is a Greek adjective *alethes* (true), in reference that it is the only true †*Angarosphex* Rasnitsyn known from Burmese amber.

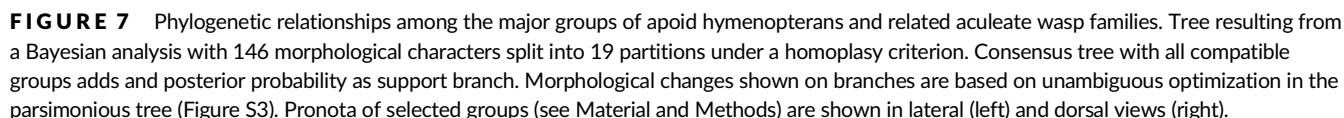
Locality and horizon. Hukawng Valley, near Tanai, Kachin State, northern Myanmar; lower most Cenomanian (Late Cretaceous).

Remarks. The recognition of this species at this moment is taking into account only the venation of the forewings as well as the entire classification of †*Angarosphex*, since we have not reviewed this taxon as a whole. According to the species key presented in Rasnitsyn et al. (1998), †*A. alethes* sp.n. has a venation similar to that of †*A. niger* Rasnitsyn, 1990. Likewise, the venation of †*A. alethes* sp.n. resembles that of †*A. saxosus* Zhang et al., 2018, a taxon described more recently. However, †*A. alethes* sp.n. differs from †*A. niger* and †*A. saxosus* for having the vein 1 m-cu ending at Rs instead of ending in the 2nd submarginal cell.

DISCUSSION

Phylogenetic position of Apoidea and relationships of its fossil lineages

Our results support the monophyly of the clade formed by Apoidea + Formicidae found in previous studies based on molecular data (Branstetter et al., 2017; Faircloth et al., 2014; Johnson et al., 2013; Peters et al., 2017). This is the first time that this clade has been



Another important synapomorphy for the Apoidea + Formicidae clade is the ventrolateral fusion between meso- and metapleura

Our results also confirm monophyly of the Apoidea as found in previous studies (Alexander, 1992; Branstetter et al., 2017; Debevec et al., 2012; Melo, 1999; Peters et al., 2017; Sann et al., 2018). †Burmasphecidae **fam.n.** is clearly included in Apoidea, and this relationship was found in all topologies (Figures 1, 7, S1–S3). In our results, this clade has high branch support (pp = 1; Figures 1, S1 and

S3) and is supported by seven unambiguous changes (Figures 7 and S3). In Figure 7, the main changes associated with the pronotum are illustrated. Indicated in blue is the posterolateral angle of the pronotum, which in Apoidea is reduced dorsally above and anterior to the spiracular operculum, where it is also differentiated and forms the pronotal lobe (38:1; in blue in Figure 7; see also Figures S4b and S5f for details in †*Burmasphex*). This condition of the pronotum, together with the metapostnotum expanded posteromesally, forming the “propodeal triangle” (108:1) (see S4c and S5a for details in †*Burmasphex*), are undoubtedly the most characteristic synapomorphies of Apoidea. Additionally, we introduce a new character to describe a specialized condition in the shape of the lateral portions of the pronotum exhibited by the Apoidea, which characterizes an additional synapomorphy for this clade (40:1). In this lineage, the lateral portions of the pronotum are compressed and form an evident strangulation immediately anterior to the pronotal lobes (40:1; in red in Figure 7; see also Figures S4c and S5a for details in †*Burmasphex*).

†*Burmasphexidae* **fam.n.** exhibit all the synapomorphies discussed above, and our results show that it has a sister relationship with the remaining Apoidea (Figure 1). The recognition of this lineage sheds light on our understanding of the early morphological evolution of the Apoidea. In Apoidea, excluding †*Burmasphexidae* **fam.n.**, the posterior margin of the dorsal portion of the pronotum is part of a specialized joint between the pronotum and the mesoscutum. The pronotum has its posterior margin sloping downwards towards the mesoscutum, and at the same time, the anterior margin of the mesoscutum has a step along its entire length into which the pronotal margin fits (39:1; green in Figure 7). Therefore, the contact zone between the posterior margin of the pronotum and the anterior margin of the mesoscutum is rigidly articulated. In †*Burmasphexidae* **fam.n.** on the other hand, the posterior margin of the pronotum extends over the anterior margin of the mesoscutum and does not slant downwards, a condition reminiscent of that found in the rest of Aculeata (39:0; black in Figure 7; see also Figures S4c and S5a for details in †*Burmasphex*).

Additionally, we introduce a new character to describe a specialized articulation in the anterior margin of the mesepisternum, referred here as the mesepisternal clip (43:1). The clip projects over the posterior margin of the pronotum ventrally under the pronotal lobe (Figure S7). This articulation seems to be related to the limitation of movement of the pronotum, acting as an additional lock for this sclerite. This condition is found in all Apoidea except †*Burmasphexidae* **fam.n.** (Figures S2, S3). Although the shape of this clip is quite variable in different lineages, our hypothesis is that this articulation appeared only once and is homologous throughout the entire clade. In general, this character could be examined in the studied fossil specimens, especially in those in which the head, propleura and forelegs are disarticulated from the rest of the body as in †*Callisphex robustus* **gen. et sp.n.** (†*Burmasphexidae* **fam.n.**) and in †*Angarosphex alethes* **gen. et sp.n.** (†*Angarosphexidae*). Recognition of this character is fundamental for our understanding of the evolution within the Apoidea. The presence of this articulation in †*Angarosphexidae*, for example, as well as of other characters discussed so

far, categorically shows that this group is more derived than †*Burmasphexidae* **fam.n.**

Our study is pioneering in including †*Angarosphexidae* and other apoid wasp fossil lineages in a formal phylogenetic analysis. Traditionally, the vast majority of fossil apoid wasps from the Cretaceous period have been described in †*Angarosphexidae* (Melo & Rosa, 2018; Rasnitsyn, 1975; Rasnitsyn et al., 1998, 1999; Zhang et al., 2018; Zheng et al., 2021). However, our results show that †*Angarosphexidae* in this sense is strongly polyphyletic. Classifying most Cretaceous apoid wasps into a single family clearly does not reflect the true diversity of these lineages. It must be emphasized that the circumscription of †*Angarosphexidae* being used in our study is based on †*Angarosphex myrmicopterus*, the species that bears the family name, and also in †*A. alethes* **sp.n.**, which according to our results is phylogenetically related to the type species. However, the taxon “†*Angarosphexidae*” as used by other authors, with about 13 genera and 47 species (updating the numbers from Zheng et al., 2021), remains a very heterogeneous assemblage and its constituent taxa should be investigated phylogenetically in future works, a task beyond the scope of the present study.

Our results show that †*Angarosphexidae*, in its narrow sense, is nested within the Apoidea, thus occupying a more derived phylogenetic position than †*Burmasphexidae* **fam.n.** (Figure 1). Closer examination of the holotype of †*A. myrmicopterus* revealed that its pronotum was preserved slightly disarticulated from the remainder of the mesosoma (more pronounced in its right side), showing a depressed margin along the posterior edge (Figure 5). This indicates that the posterior dorsal margin of the pronotum articulated directly with the mesoscutum (39:1) and did not overlap its anterior portion, as in †*Burmasphexidae* (39:0). Likewise, the condition of the mesoscutum of †*A. myrmicopterus*, whose anterior portion has a straight transverse step, separating the disc posteriorly from a lowered anterior portion onto which the pronotum fits (Figure 5), provides additional evidence for presence of a specialized dorsal articulation between the pronotum and the mesoscutum. It is also noticeable that the dorsal portion of its pronotum shows evidence of forming a raised surface, therefore characterizing possession of a pronotal collar (41:1; Figure 5). The phylogenetic hypotheses resulting from our study show that †*Angarosphexidae* *sensu stricto* is closely related to Ampulicidae. Although branch support was not as high (pp = 0.75 / 0.70), this clade was recovered in all of our analyses (Figures 1, S1, S2 and S3). This relatively low branch support results probably from the large amount of missing data associated with the specimen of †*A. myrmicopterus*.

Diversity and natural history of †*Burmasphexidae* **fam.n.**

Recognition of †*Burmasphexidae* **fam.n.** as one of the early offshoots of the Apoidea offers a rare glimpse into better understanding the behaviour exhibited by these ancient wasps. Males of burmasphexids, especially †*Burmasphex*, are small, slender and delicate, resembling males of ampulicid or even some groups of ants. †*Burmasphex mirabilis* **sp.n.** is unique in that it is exquisitely preserved, with all the structural



FIGURE 8 Artistic reconstruction by Gabriel Uguetto of the mid-Cretaceous apoid wasp †*Burmasphex mirabilis* sp.n. (†Burmasphexidae fam.n., Burmese amber).

details of the integument preserved, including its metallic colours (Figures 2 and S4). These males must have surely roamed the foliage of the ancient Burma forests looking for sugary liquid food (including droplets of honeydew) and probably females to mate with (Figure 8). In addition to a slender and delicate body, males of †*Simplisphex* gen. n., above all, have clearly derived characters, such as the reduction of veins on the forewing (Figure 4e), indicating that the burmasphexids were already a diverse group in the Cenomanian as a result of a long history of diversification by the end of the Early Cretaceous.

The disparity in morphology among genera also suggests a pronounced diversification with different types of morphological specializations, and consequently, somewhat distinct habits. The female of †*Callisphex* gen.n. is quite large (the largest known burmasphexid) reaching over 5.5 mm in length, with a robust body (Figure 3), relatively strong legs (Figure 3a) and quite long, thick mandibles (Figure 3c). On the other hand, the female of †*Decasphex* is slender, with delicate mandibles provided with thin, specialized apical teeth, in addition of being very small, measuring less than 3 mm in length (the smallest known burmasphexid).

Based on living groups, Melo et al. (2011) inferred that the switch from an aculeate ancestor behaving as an idiobiont parasitoid of beetle larvae to a predator of orthopteroid insects (in particular Blattodea), happened very early in the evolutionary history of Apoidea. The behaviour of acting as a predator, with relocation of the host from the place in which it was stung to a preexisting niche or a newly-built nest, was attributed by Melo et al. (2011) to the groundplan of Apoidea. This scenario becomes more complex with corroboration of a sister-group relationship between Formicidae and Apoidea. It is well known that ants also feed their larvae with prey that is captured outside and then relocated to the nest. Therefore, prey relocation might have evolved in the common ancestor of Formicidae + Apoidea, or even earlier depending on what is going to be found when the biology of both Bradynobaenidae and the scoliid *Proscolia* becomes known. Considering that females of these two groups have not been

observed dragging their hosts around, they likely behave as the remainder of the Scoliidae, which at most move their beetle host larvae underground (see references in Melo et al., 2011).

Inferring biological features of fossil extinct lineages is quite challenging, but considering its phylogenetic position, it is reasonable to suggest that †Burmasphexidae fam.n. may have preyed on orthopteroids and possibly relocated their prey by walking, as the extant Ampulicidae still do. The fauna of cockroaches known from Burmese amber is quite diverse, with 37 described species from 11 families (Chen et al. 2021), and female burmasphexids may have hunted them. Regardless of the prey group used by †*Callisphex* gen.n. and †*Decasphex*, the two burmasphexid genera with known females, it is reasonable to suggest that their biology could differ from one another considering their morphological differences, including body size. A good comparative approximation can be made between the living genera of Ampulicidae, which although all prey on cockroaches, the taxonomic groups (i.e., families and genera) as well as the size of individuals are quite different between them (see Gess, 1984; Krombein, 1979).

Paleoenvironment and composition of the Burmese amber biota

Comparisons between †Burmasphexidae fam.n. and Ampulicidae are also relevant to understand the paleoenvironment occupied by Apoidea during the beginning of their diversification. Based on the fauna of apoid wasps preserved in Burmese amber, Rosa and Melo (2021) suggest that the paleoenvironment of this deposit was not temporally or geographically entirely homogeneous, and likely was represented by a mosaic of vegetation types and more dynamic environmental conditions, with alternating humid and more arid periods, either along the geological time or yearly in a monsoon-type climate. In any case, considering their morphological features, including possession of metallic coloration, the †Burmasphexidae fam.n., like ampulicids, were probably associated with forested environments. Even more than the †Burmasphexidae fam.n., the Ampulicidae present in Burmese amber are diverse, demonstrating a long association with these archaic forests (Rosa & Melo, unpublished data). Therefore, all this evidence points to a scenario in which the initial radiation of the Apoidea probably took place in gymnosperm-dominated humid forests throughout the Early Cretaceous.

Recognition here of a new lineage with family-status, the †Burmasphexidae fam.n., also provides an opportunity to discuss the hypotheses that have been advanced to explain the composition of the Burmese amber biota. Taking examples from Hymenoptera, many higher taxa that have been proposed in the last few years, such as the †Aptenoperissidae, †Myanmarinidae, †Burmorussidae, †Ohlhoiffidae, †Othniodellithidae, †Burmusculidae and †Panguidae, have been considered as endemic elements that evolved while the Burma terrane was isolated from other landmasses (e.g. Jouault et al., 2021; Rasnitsyn & Öhm-Kühnle, 2018, 2021; Zhang et al., 2018). Under an alternative hypothesis, as advocated recently by Lepeco and Melo (2021)

for †Holopsenellidae, most of these taxa simply seem to represent archaic lineages, belonging to a once-widespread biota, that somehow survived to the end of the Early Cretaceous in the Burma terrane.

Our phylogenetic results for the Apoidea support the latter hypothesis, in which the elements placed in †Burmasphecidae **fam.n.** represent one of stem groups of the first radiations within this clade that survived at least to the mid-Cretaceous. Based on molecular clock estimates we can suggest that burmasphecids diverged from the other apoid lineages either in the late Jurassic or early Cretaceous, ~153 Mya (based on Peters et al., 2017) or ~134.90 Mya (based on Branstetter et al., 2017), respectively. Considering this ancient age of divergence and the expressive richness of burmasphecids found in Burmese amber, it seems safe to suggest that the diversity of this lineage was even greater long before the beginning of the Cenomanian. Although some burmasphecid genera may in fact be endemic to the Burma terrane, the distribution of this lineage throughout the Early Cretaceous certainly must have been much wider.

In the case of apoid wasps, the fauna of this deposit is composed of ancient, relict lineages such as the †Burmasphecidae **fam.n.**; lineages that likely represent truly endemics, most probably restricted to genus-level elements; and lineages related to groups with wide geographic distribution during the period of deposit formation, as is the case of the †Angarosphecidae, Ampulicidae and Crabronidae. Therefore, as an alternative to the insular endemism hypothesis, the Burmese amber biota may have resulted from a more complex combination of historical patterns and events, and contained archaic elements, derived lineages at the beginning of their diversification and perhaps a few truly endemic groups.

CONCLUSION

The present study is a pioneer in the inclusion of apoid wasp fossil lineages in a comprehensive phylogenetic framework. Our results based on morphological data strongly support the sister group relationship between ants and apoids. We present for the first time the morphological characters that support the clade Formicidae + Apoidea. Our results support that †Burmasphecidae **fam.n.** clearly belongs to Apoidea occupying position as a sister group of this lineage.

The †Angarosphecidae are much more closely related to the other apoids than to †Burmasphecidae **fam.n.**, thus occupying a derived phylogenetic position. Plus, our results also suggest that †Angarosphecidae is strongly related to Ampulicidae. However, “†Angarosphecidae”, remains a very heterogeneous set and its taxa included currently should be reviewed on a case-by-case basis and preferably be included in broader phylogenetic analyses involving other clades of Aculeata.

Recognition of †Burmasphecidae **fam.n.** offers a rare glimpse into better understanding the behaviour exhibited by the early apoids and also provides new insights to explain the composition of the Burmese amber biota. The evidence gathered in our study suggests that the first apoid lineages were probably already associated with archaic forest environments during their diversification throughout the Early

Cretaceous. At the same time, the Burmese amber biota may have been a combination of much more complex historical patterns and events containing archaic elements, derived lineages and effectively endemic groups.

AUTHOR CONTRIBUTIONS

Brunno B. Rosa: Conceptualization; methodology; data curation; investigation; validation; formal analysis; funding acquisition; project administration; writing – original draft; writing – review and editing; resources; visualization. **Gabriel A. R. Melo:** Conceptualization; methodology; data curation; investigation; validation; formal analysis; funding acquisition; project administration; writing – original draft; writing – review and editing; resources; visualization.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The matrix, trees and files of the Bayesian analyses from this study can be accessed from Zenodo, DOI: <https://doi.org/10.5281/zenodo.7432813>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supporting Information.

Appendix S2. Supporting Information.

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