

Short communication

The oldest known basal tiphiid wasp (Hymenoptera, Tiphidae) from mid-Cretaceous Burmese amber of northern Myanmar

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ABSTRACT

A new genus and species of tiphiid wasps, *Burmatiphia mandibulata* gen. et sp. nov., is described and illustrated based on a new specimen from the lowermost Cenomanian Burmese amber as forming a distinct subfamily Burmatiphiinae subfam. nov. The new taxon is characteristic of a combination of striking plesiomorphies (metasomal sterna 1 and 2 forming even surface, female metasomal apical tergum and sternum unmodified with narrow orifice for sting, and female mid and hind tibiae lacking digging adaptation) and synapomorphies (single mid and hind tibial spurs, long and sharp tibial spines, scape with long radix, possibly reduced costal space in fore wing). *Burmatiphia* gen. nov. supposedly hunted for prey within underground tunnels.

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1. Introduction

Tiphidae form a relatively small but diverse group of parasitic aculeate wasps of small to big size, with approximately 2000 described species in 120 genera distributed worldwide (Brothers, 1999; Engel et al., 2009; Gadallah and Brothers, 2020). We take the family in its traditional, morphological sense as defined by Kimsey (1991), because the novel approaches based on molecular phylogenetic evidence (Pilgrim et al., 2008; Wilson et al., 2012) not only consider Tiphidae as highly polyphyletic but propose an array of contradictory cladograms with tiphiid subfamilies assorted into several assemblages (often mixed with other vespoid families)

which lack morphological diagnoses and so are inapplicable to fossils. For instance, Pilgrim et al. (2008) propose clades (Tiphinae + Brachycistidinae + Myrmosinae [former Mutillidae]) and (remaining extant Tiphidae named Thynnidae plus a part of Bradynobaenidae), whilst remaining Bradynobaenidae are grouped with Vespidae, Rhopalosomatidae and Sierolomorphidae. Unlike this, Wilson et al. (2012) group Tiphinae and Brachycistidinae with Sierolomorphidae, other Tiphidae (= Thynnidae), again with a part of former Bradynobaenidae, and Myrmosidae join with Sapygidae. Propose a slightly different cladogram: Tiphidae s.str. + (Thynnidae + Chyphotidae (a part of former Bradynobaenidae), and Myrmosidae + Mutillidae). Until the molecular methods result in a workable system of Vespoidea, we prefer to follow Engel et al. (2009) in using the classical model of the tiphiid system.

Tiphidae are presently divided into eight subfamilies: Anthoboscinae, Brachycistidinae, Diamminae, Methochinae, Myzininae, Thynninae, Tiphinae and the extinct Thanatotiphinae which was recently erected as a new subfamily based on a male sample from

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mid-Cretaceous Burmese amber (Kimsey, 1991; Engel et al., 2009; Aguiar et al., 2013). Relations between living subfamilies were developed by Brothers (1975) and refined by Kimsey (1991) as follows: Anthoboscidae + (Diamminae + ([Tiphinae + Brachycistidinae] + [Metochinae + (Thynninae + Myzininae)])). Thanatoti-phinae are said to be synapomorphic with the clade comprising Tiphinae, Brachycistidinae, Methochinae, Thynninae and Myzininae based on their hook-like male hypopygium.

The fossil records of Tiphidae remain sparse and poorly dated. Engel et al. (2009) provide a list of 17 fossil species in 7 genera from Early Cretaceous to Miocene in Asia and N. and S. America. Herein, we describe a new subfamily, genus and species of tiphid wasp based on a unique female preserved in the mid-Cretaceous (earliest Cenomanian) Kachin amber in Myanmar, the second record of Tiphidae in Burmese amber.

2. Material and methods

The type and only specimen in the present study is a female fossil collected from the Hukawng Valley, Kachin State, northern Myanmar (26°20'N, 96°36'E). The age of Burmese amber is now considered as mid-Cretaceous, dated to the earliest Cenomanian (about 98.79 ± 0.62 Ma) based on the radiometric analyses of zircon grains (Shi et al., 2012). A late Albian–early Cenomanian age has been further proposed by ammonites (Yu et al., 2019). Significantly, some researchers seem to argue for an older age for the Burmese amber based on palaeontological dating (Mao et al., 2018; Smith and Ross, 2018).

The holotype of *B. mandibulata* gen. et sp. nov. is well preserved in a yellow and almost quadrilateral Burmese amber piece measuring $14.85 \times 12.68 \times 3.52$ mm. It is housed in the Institute of

Geology and Paleontology, Linyi University, under the collection number LYU-HY-2003, collected legally in 2015 (see “Museum Catalogue Entry” in Supplementary Material).

In order to show a better view and illustration of the morphological details, the amber piece was re-cut and manually polished. The emery paper (grit sizes of 5000–1000) and rotary polisher (Mecatech 33, France) were used to prepare the sample for study. It was further checked and photomicrographed by stereomicroscope and a Nikon D800 and examined by VHX 5000 digital microscope. Drawing line figures were illustrated with Coreldraw X7 and Adobe Photoshop CC graphics software. Measurements were made with Image J software.

3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Family Tiphidae Leach, 1815

Subfamily Burmatiphinae Zheng, Zhuo & Rasnitsyn, subfam. nov.

Type genus. *Burmatiphia* Zheng, Zhuo & Rasnitsyn, gen. nov.

Diagnosis. Female body slender, showing no distinct digging adaptations; antennal sockets open, ocelli small, antenna not modified except scape with long radix, with pedicel fully exposed; mandible long sickle-shaped with long apical and minute preapical teeth; labrum short, narrow, long spinose; epipharynx large; tegula small; mesopleural lamellae long, wide; metasternal plate triangular, intruding between mesopleural lamellae; forewing venation full (except possibly no costal space), with pterostigma ordinary but small, R very long between 1-Rs and pterostigma; cell 3r closed at wing margin near wing apex; mid and hind tibiae slender and armed with long, thick thorns on outer surface; metasoma with

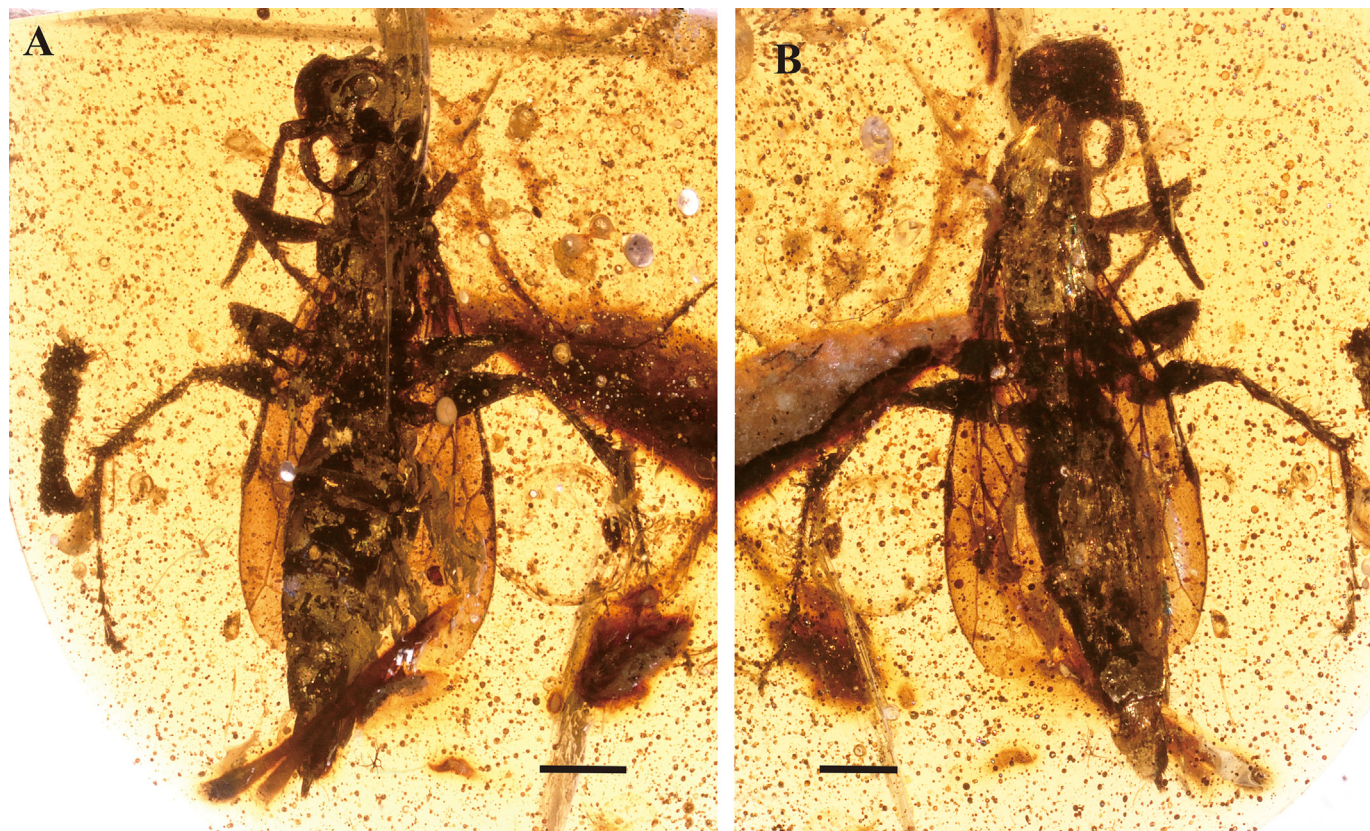


Fig. 1. *Burmatiphia mandibulata* Zheng, Zhuo & Rasnitsyn, gen. et sp. nov., holotype, LYU-HY-2003. (A), dorsal view; (B), ventral view. Scale bars = 1 mm.

basal sterna forming smooth surface, with hind margin of sternum 1 apparently straight, with apical tergum and sternum apparently not specialized and forming small subcircular opening for sting. Male unknown.

Genera included. Type genus only.

Genus ***Burmatiphia*** Zheng, Zhuo & Rasnitsyn, gen. nov.

Type species: *Burmatiphia mandibulata* Zheng, Zhuo & Rasnitsyn, gen. et sp. nov.

Diagnosis. As for subfamily because of monotypy.

Etymology. The generic name is derived from the combination of “Burma”, the old name for Myanmar) and “*Tiphia*”, type genus of the family. The name is feminine.

Species included. Type species only.

Burmatiphia mandibulata Zheng, Zhuo & Rasnitsyn, gen. et sp. nov.

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Figs 1-3

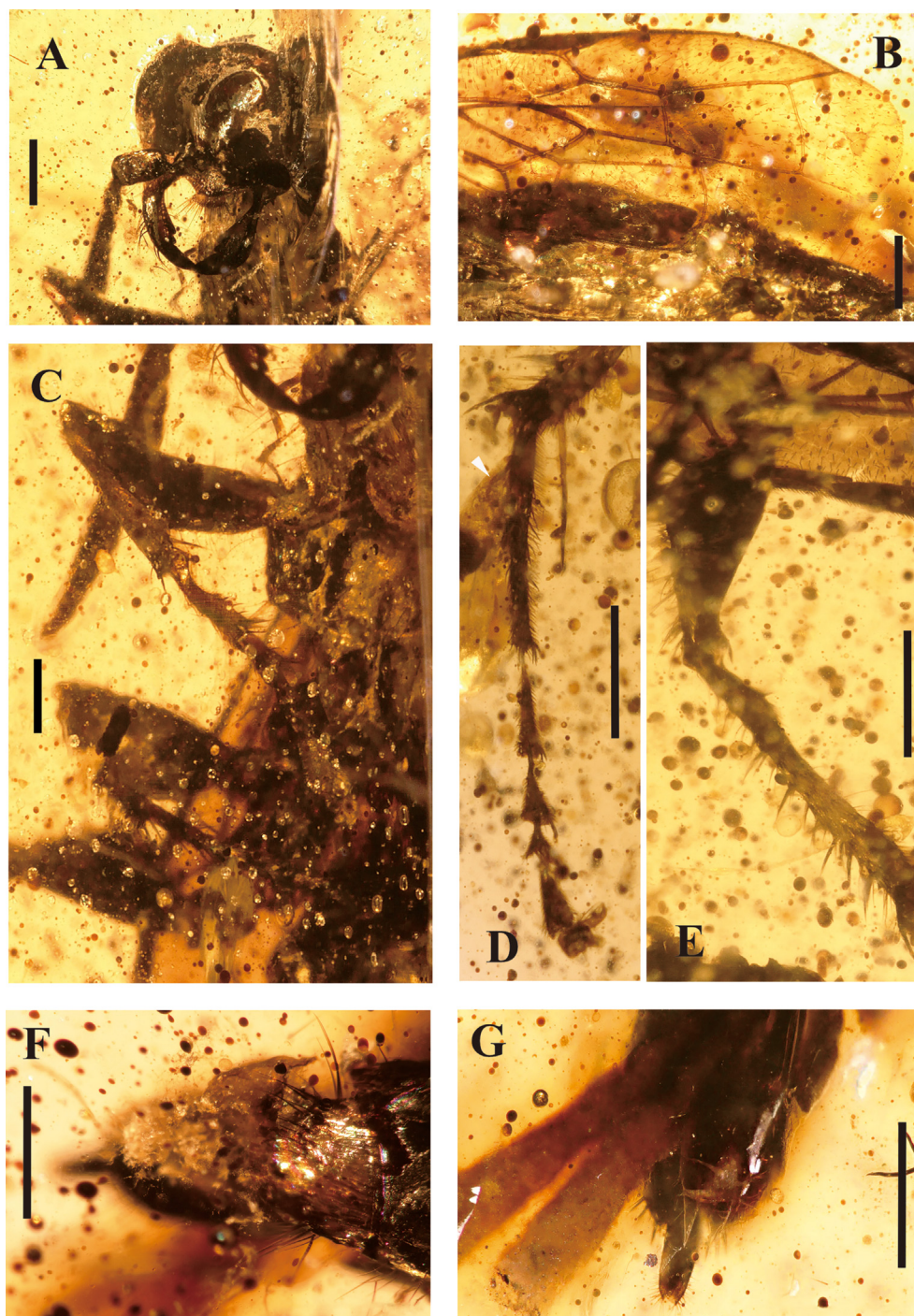


Fig. 2. *Burmatiphia mandibulata* gen. et sp. nov., holotype, details. (A), head and mouthparts, ventral view; (B) pterostigma and membrane covered with microtrichiae, dorsal view; (C), left fore and mid legs, ventral view; (D), tibial apex and tarsus with claws and arolium of left hind leg, ventral view, with arrowhead indicating minor spur; (E), left hind coxa, trochanter and femur, ventral view; (F), metasomal apex with sting, dorsal view; (G), same, ventral view. Scale bars = 0.5 mm.

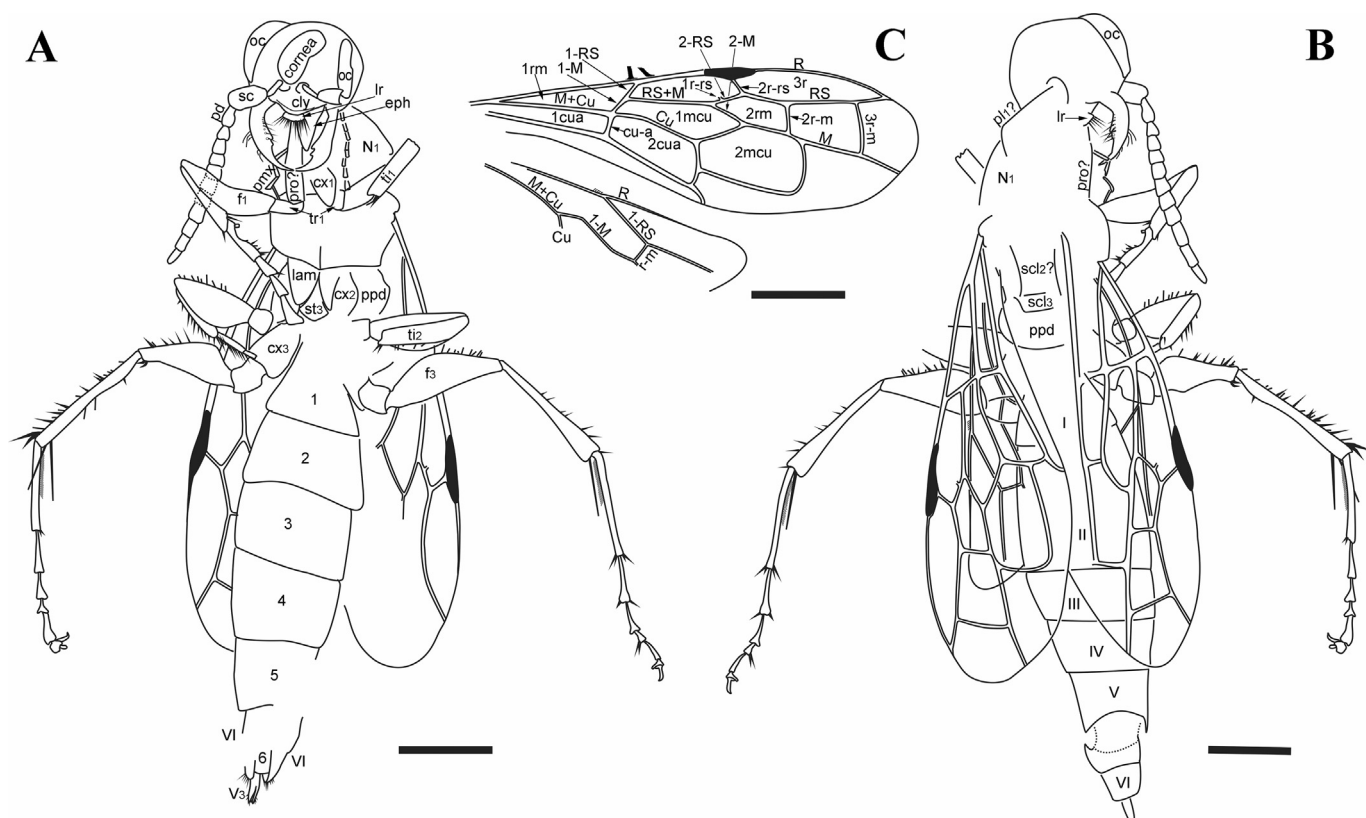


Fig. 3. Line drawings and details of holotype of *Burmatiphia mandibulata* gen. et sp. nov. (A), dorsal view; (B), ventral view; (C), wings, vein and cell names indicated. Abbreviations: oc = compound eye; sc = scape; cornea = detached cornea of left eye; pd = pedicel; lr = labrum; pmx = maxillary palp; eph = epipharynx; pro? = proboscis?; pl? = propleuron?; N₁ = pronotum; cx₁, cx₂, cx₃ = pro-, meso-, meta-coxa; tr₁ = trochanter; f₁, f₃ = fore and hind femur; ti₁, ti₂ = fore and mid tibia; lam = mesopleural lamella; st₃ = metasternum; scl₂? = mesoscutellum; scl₃ = metascutellum; ppd = propodeum; 1–6 = metasomal sterna 1–6; I–VI = metasomal terga I–VI; V₃ = sting sheath. Scale bar = 1 mm.

Etymology. The species name is from “mandibulata”, based on its murderous mandibles, the largest of all tiphiids. The name is feminine.

Holotype. Female, LYU-HY-2003, specimen within a re-cut and polished piece of amber which is housed in the Institute of Geology and Paleontology, Linyi University, Linyi, China.

Diagnosis. As for genus.

Description. Female. Body relatively small (8.37 mm long excluding antenna and ovipositor), rather slender, generally black to dark brown and covered with long, rough vestiture.

Head roundish, approximate width 0.95 mm, height 0.97 mm as visible and slightly wider than mesosoma; eyes large, at least 0.66 mm high, long oval, taking most of head sides, with margins not distinctly emarginate, glabrous; small ocelli in small equilateral triangle; antennal attachments open, distant by less than their width; clypeus transverse, with roundly triangular fore margin, with distinct smooth apical rim and densely short setose subapically; occipital region rounded, apparently without occipital carina; antenna not coiled, 12-segmented, with conspicuous erect short pilosity, scape broadened, 0.38 mm long and 0.21 mm wide, with thin radix almost as long as scape itself, pedicel half as wide as scape and about as long as scape width, flagellum widest midlength, with basal flagellomeres slightly transverse and almost subequal in length, distal flagellomeres lengthening gradually toward apex, with F₈–F₁₀ one and a half times to twice as long as wide; mandible long sickle-shaped, 0.87 mm long and 0.21 mm maximum wide, with two small preapical denticles, with row of long setae along inner margin on middle third; labrum short, abundantly long setose; epipharynx triangular, long and wide; other mouthparts apparently forming proboscis of obscure

structure, with only two long segments of each maxillary palp visible.

Mesosoma narrow, 2.78 mm long and 1.56 mm wide across tegulae; dorsal surface degraded and deformed, its structure mainly obscure, tegula apparently small (wing base exposed), mesoscutellum longer than wide, parallel-sided, metascutellum long, propodeum short and wide, rounded behind; mesopleuron short and wide ventrally, with long and wide lamellae over midcoxae; metasternum triangular with rounded hind margin, extending far between lamellae (similar to that in Tiphiinae). Fore wing membranous covered with abundant microtrichiae, about 4.78 mm in length and 1.54 mm in maximum width; venation relatively complete, with 7 closed cells; pterostigma narrow, completely sclerotized, about 0.75 mm long and 0.12 mm wide, with 2r-rs near its midlength; vein C not visibly distinct from R except for apically before pterostigma (apparently tucked down under R); basal vein straight, joining R far from pterostigma, 1-Rs slightly shorter than 1-M; 2-Rs equal to 2-M in length; 2-Rs almost straight, with short rudiment of 1r-rs; 2r-rs oblique; cell 3r almost reaching wing apex; 2r-m and 3r-m almost straight and subparallel, 3r-m near apex of cell 3r; 1m-cu straight and strongly oblique, reaching midlength of cell 2rm; 2m-cu gently curved, reaching basal quarter of cell 3rm; M reaching wing margin; cu-a interstitial; cell 2cua closed. Hind wing with 1-R more than twice as long as r-m, R near reaching wing margin, 1-M long, sinuate, cu-a postfurcal (not preserved before distinctly behind M + Cu fork).

Legs slender, hind pair long; fore and mid coxae small, hind coxae large, apparently distant from each other; fore trochanters elongate, mid and hind ones short, stout, femora widened midlength, tibiae and tarsi long, slender, fore tibia smooth dorsally and with no

spur visible (probably lost through damage because fore basitarsal cleaning device is well developed; apical tibial spines are present but as ordinary spines, being short straight and sharp and not long and modified to fit basitarsus as parts of antennal cleaner), hind tibia and tarsus very long, tibia with hairs and long thick spines dorsally, with two long, smooth straight spurs; tarsi longer than respective tibiae, with basitarsi longer than 3 middle tarsomeres combined, fore basitarsus with deep subbasal excision of cleaning apparatus, hind basitarsus subcylindric, with ventral brush of short hairs, other tarsomeres triangular, three middle ones rich in hair and spines, particularly apically; claws simple, arolium of medium size. Fore coxa 0.33 mm long, 0.27 mm wide, trochanter 0.36 mm long, 0.14 mm wide, femur 1.08 mm long, 0.28 mm wide, tibia 0.85 mm long, 0.17 mm wide, tarsomeres length ratio: 0.48:0.21:0.14:0.14:0.27; mid coxa 0.73 mm long, trochanter 0.22 mm long, 0.23 mm wide, femur 0.99 mm long, 0.38 mm wide, tibia ca. 0.94 mm long, 0.21 mm wide, tarsi not completely visible; hind coxa 0.52 mm long, 0.41 mm wide, trochanter about 0.33 mm long, 0.29 mm wide, femur 1.13 mm long, 0.40 mm wide, tibia 1.43 mm long, 0.28 mm wide, hind femoral spur 0.60 mm long, tarsomere length ratio: 1.09:0.48:0.30:0.11:0.26.

Metasoma 4.96 mm long, 1.59 mm maximum wide, slender, fusiform, apparently with six external segments (deformed with apex detached and some intersegmental boundaries obscure, particularly between terga); two basal sterna forming even surface (with no angle in-between), with hind margin of sternum 1 apparently straight; sterna 1–5 of similar length, tergal proportions obscure; apical segment narrow, with apical foramen small, roundish, apical tergum and sternum simple (apparently not specialized), sting not protruding behind sheaths.

4. Discussion

Burmatiphia gen. nov. is attributed to the family Tiphidae based primarily on the characteristic wasp appearance combined with a pair of large mesopleural lamellae overlapping much of the mid coxae (synapomorphy of the family, cf. Brothers, 1975; Kimsey, 1991), plus form of metasternum characteristic of Tiphidae and Anthoboscinae (cf. Brothers, 1975: fig. 18.1; Kimsey, 1991, fig. 10). In contrast, there are problems accommodating the new genus to a particular tiphid subfamily because of a combination of unique plesiomorphies with synapomorphies, in part unique within Vespoidea s.l. as well. The unique plesiomorphies are two basal metasterna forming an even surface (the character state lost even in Anthoboscinae, cf. Rasnitsyn, 1980, fig. 162b vs. 162a), and narrow metasomal apical orifice formed with non-modified apical tergum and sternum (unlike slit-like or further specialized metasomal apex in living tiphid taxa as described by Rasnitsyn, 1980, p. 124 and fig. 195). The synapomorphies are scape with long radix; long spines on slender mid and hind tibiae (other female Tiphidae have robust tibiae armed with short, thick, obtuse pegs used while digging to find prey, or secondarily slim and poorly armed; more similar even though thicker are the tibiae in *Diamma* Westwood that belongs to another and highly specialized branch of the family, see Introduction). Nevertheless the more evident features listed above are sufficient to justify evaluation of the fossil under description as belonging to a new subfamily. The proper position of *Burmatiphinae* within the family can hardly be defined before a better understanding of the structure of the family itself is reached (see Introduction). Preliminarily, based on the above combination of plesio- and synapomorphies, it is possible to infer that *Burmatiphinae* takes a basal position in respect to all other Tiphidae.

Direct comparison of *Burmatiphinae* with *Thanatotiphinae*, another extinct tiphid subfamily known solely from Burmese (Kachin) amber, is hardly possible because of the male sex of the

only known specimen of *Thanatotiphia nyx* Engel et al., 2009, and strong sexual dimorphism in many Tiphidae. Yet we consider their synonymy as unlikely even at subfamily level because of the uniquely reduced wing venation of *Thanatotiphia*, and the latter genus is considered as putatively monophyletic with the advanced tiphid subfamilies, synapomorphic in having the male hypopygium transformed as an upward hook, that is, all other than Anthoboscinae and Diamminae (Engel et al., 2009). Unlike that assemblage, *Burmatiphinae* putatively represent a sister to all Tiphidae including Anthoboscinae and Diamminae (see above).

The biology of *B. mandibulata* sp. nov. can be only vaguely outlined as different from what is typical of most Tiphidae with females digging through soil in search of grubs (larvae of scarab-beetle-type). Their long and sharp spines on slender mid and hind tibiae find its analogy in cockroaches and the cockroach-like *Notiothauma* McLachlan (Mecoptera), and, less closely, the wasps *Diamma* Westwood (Tiphidae) and *Larra* F. (Crabronidae), both hunting for mole crickets (Gryllotalpidae) in their tunnels. This suggests the hypothesis that *Burmatiphia* also hunt for a prey within tunnels in soil.

5. Conclusion

Burmatiphia mandibulata gen. sp. nov. represents a distinct subfamily of the family Tiphidae treated here in the traditional (morphological) sense (cf. Kimsey, 1991). The features available for the fossil suggests a basal position of *Burmatiphinae* within the family. Biologically *B. mandibulata* differs from the vast majority of living Tiphidae in that it did not practice active digging through soil when searching for prey. The newly described tiphid wasp increases the known diversity of Mesozoic lower vespoid wasps and adds more high-rank endemics to the Kachin fauna that is already famous for its incomparably high rate of endemism (Rasnitsyn and Öhm-Kühnle, 2021).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2022.105337>.