

Short communication

New genus of falsiformicid wasps (Hymenoptera, Vespoidea: Falsiformicidae) with brachypterous male from middle Cretaceous Kachin amber in Myanmar

Qi Zhang ^{a,*}, Ning Jia ^a, Yizheng Li ^a, Jianxun Wang ^b, Alexander P. Rasnitsyn ^{c,d,**}

^a School of Geography and Tourism, Qufu Normal University, Rizhao 276826, China

^b School of Life Sciences, Qufu Normal University, Qufu 273165, China

^c A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow 117647, Russia

^d Natural History Museum, Cromwell Road, London SW7 5BD, UK

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ABSTRACT

Falsiformicidae is a poorly known extinct family of aculeate wasps. It is known only as inclusions in various Cretaceous ambers. Brachypterous male *Falsiformix pedestris* Zhang and Rasnitsyn gen. et sp. nov. is described in the family Falsiformicidae based on a unique fossil from the middle Cretaceous Kachin amber. Occurrence and meaning of the male flightlessness in Hymenoptera is discussed. A combination of the flightless males with flying females occurs when mating takes place shortly after the eclosion, before adults disperse from confined space where they developed. An equally rare even if less exotic strategy with males and females both being flightless depends on the female pedestrian habits rather than on the pre-dispersal mating. Wide spatial (Angara Land, Laurussia Land and Gondwana Land) and narrow temporal distribution (Cenomanian and Turonian ages only) indicate Falsiformicidae as a possibly important stratigraphical indicator.

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1. Introduction

Falsiformicidae is an insufficiently known extinct family of aculeate wasps known so far exclusively as inclusions in various Cretaceous ambers. The first description has appeared half century ago (Rasnitsyn, 1975) based on a pair of incomplete male and female in the amber of Nizhnaya Agapa (Taimyr Peninsula, northern Siberia) in deposits of the Dolgan Formation (Cenomanian, Late Cretaceous). Originally, the new family was attributed to the superfamily of Scolioidea (now a part of Vespoidea), even though not without doubts because of incomplete preservation of the fossils available and some character incompatibilities (particularly, chrysidoid-like wing venation).

The next record, unfortunately unnamed yet, has been published more than three decades later in the Cenomanian amber of

Charente in SW France (Lak et al., 2008, fig. 5), the process produces a 3D segmentation result for phase contrast microtomographic data assigned to the wasp family Falsiformicidae (in the original text, the word was incorrectly entered as Falciformicidae). Then Perrichot et al. (2014) published a conference abstract announcing evidence of the chrysidoid affinities of Falsiformicidae: the very evidence not followed yet until a similar idea is proposed by Engel (2022). Meantime the aculeate wasps have been discovered in the middle Cretaceous (earliest Cenomanian) Kachin amber of Myanmar (Cocks and McKellar, 2016) that were attributed to Falsiformicidae in the following description of Falsiformicidae in the Burmese amber (Rasnitsyn et al., 2020). *Burmomyrma rossi* assigned to Formicidae proposed originally by Blusky (1996), the initial specimen was poorly preserved and could not be assigned to exact systematic position with confidence, particularly as the wing venation described is not shared by other known aneuretines and with the head missing. But now *Burmomyrma rossi* was said likely to belong to the Falsiformicidae (Lucena and Melo., 2018, Boudinot et al., 2020). The mentioned paper by Engel (2022) added to the family a new genus and species from the Turonian amber of New Jersey, USA.

* Corresponding author.

** Corresponding author. A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow 117647, Russia.

E-mail addresses: zhqi1105@126.com (Q. Zhang), alex.rasnitsyn@gmail.com (A.P. Rasnitsyn).

The present publication is aimed to present a description of an uncommon fossil, a brachypterous male falsiformicid. This is not to say that flightless females are unique or exceptional in any way: both chrysidoid (Plumariidae, Sclerogibbidae, many Dryinidae, Embolemidae, some Bethyidae) and vespoid wasps (many Tiphidae, Bradynobaenidae, worker ants) exhibit this feature. However, the occurrence of apterous and brachypterous males is rare, particularly among fossils.

The Kachin (Burmese) amber is found to be an unfathomable source of knowledge about the middle Cretaceous biodiversity, with endless new taxa and life forms, often strange, unexpected and highly endemic (Zhang et al., 2018; Rasnitsyn and Öhm-Kühnle, 2021): the present fossil adds some hue to that bright picture as well.

2. Material and methods

The Kachin amber specimen, which contains a species belonging to the family Falsiformicidae, was obtained from amber mines in the Hukawng Valley of Kachin State, Myanmar (26°29'N, 96°35'E) (Figure 1). The Hukawng Valley is located in the northern state of Kachin in Myanmar which is a flat alluvial plain surrounded by mountains, measuring approximately 80 km in length from north to south and 50 km in width from east to west. The age of Kachin amber was determined to be 98.79 ± 0.62 Ma based on U–Pb zircon dating of the volcanoclastic matrix, an ammonite trapped in amber also supported this result, so the insect inclusions in the amber are considered to be of the Cenomanian within Cretaceous (Shi et al., 2012; Yu et al., 2019). A total of 70 families, 202 genera and 350 species in Hymenoptera are identified in the checklist of Kachin amber till the end of 2023 (Ross, 2024). The amber studied were legally collected by the first author in 2016 and legally acquired prior to the closure of the Kachin amber mine by

the Burmese military in November 2017, and were not involved in armed conflict or ethnic strife in Myanmar.

The amber pieces have been trimmed, polished and photographed by Dr. Dmitry D. Vorontsov (PIN RAS, Moscow). The fossil was subjected to examination using a Leica M165C stereomicroscope equipped with a Leica DFC 420 camera. Imaging was conducted using a compound microscope Nikon E–800 with dry ($4\times$, $10\times$, $20\times$) and water-dipping optics ($40\times$ and $60\times$) was used. The specimen was imaged with a combination of brightfield and incident illumination. Stacks of images, comprising multiple focal planes, were acquired using an Olympus OM-D E-M10II camera. Stacks were processed with Helicon Focus version using mostly algorithm B. The morphological terminology in this study is based on the approach developed by Rasnitsyn et al. (2020). The type material is stored in the School of Geography and Tourism, Qufu Normal University, China. All taxonomic acts established herein have been registered in ZooBank (see below), together with the electronic publication LSID urn: lsid: zoobank.org: pub: 3F4905F2-AFA2-4238-BC4D-170916B34435.

3. Systematic paleontology

Order Hymenoptera Linnaeus, 1758
Superfamily Vespoidea Laicharting, 1781
Family Falsiformicidae Rasnitsyn, 1975

Genus *Falsiformix* Zhang and Rasnitsyn gen. nov.
LSID urn:lsid:zoobank.org:act:62CFB9C8-581E-4E02-90FE-5A06A91FBB57
Type species. *Falsiformix pedestris* Zhang and Rasnitsyn sp. nov.

Diagnosis (male only). Male flightless, brachypterous, with forewing about as long as mesosoma (supposedly, female also flightless). Scape slightly longer than pedicel. Propodeum very short, with

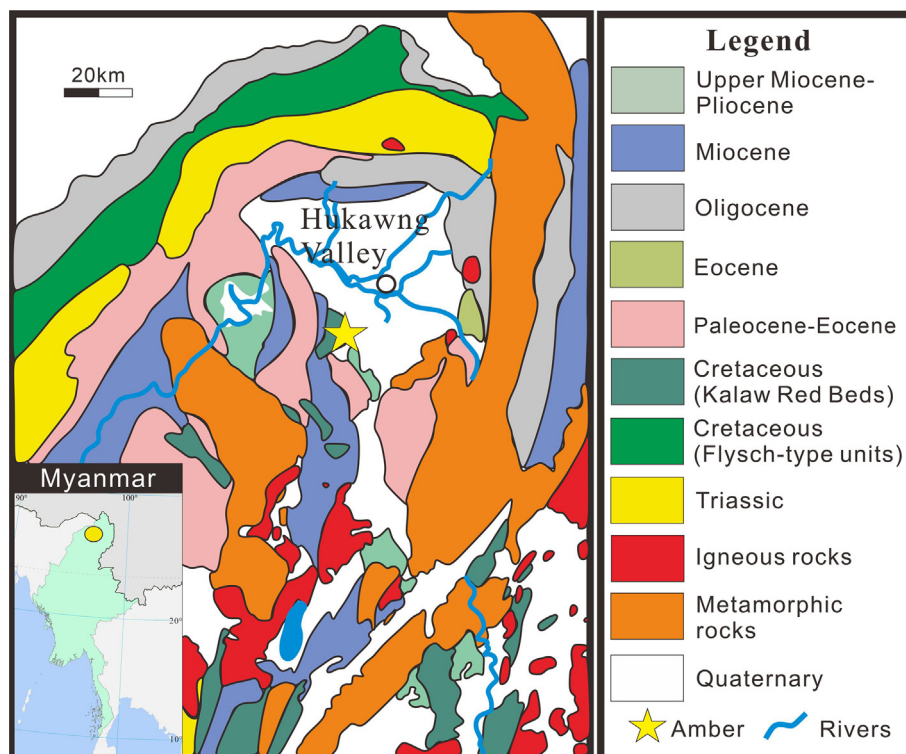


Fig. 1. Location (26°29'N, 96°35'E) of specimen in Kachin, Myanmar (modified from Yu et al., 2019).

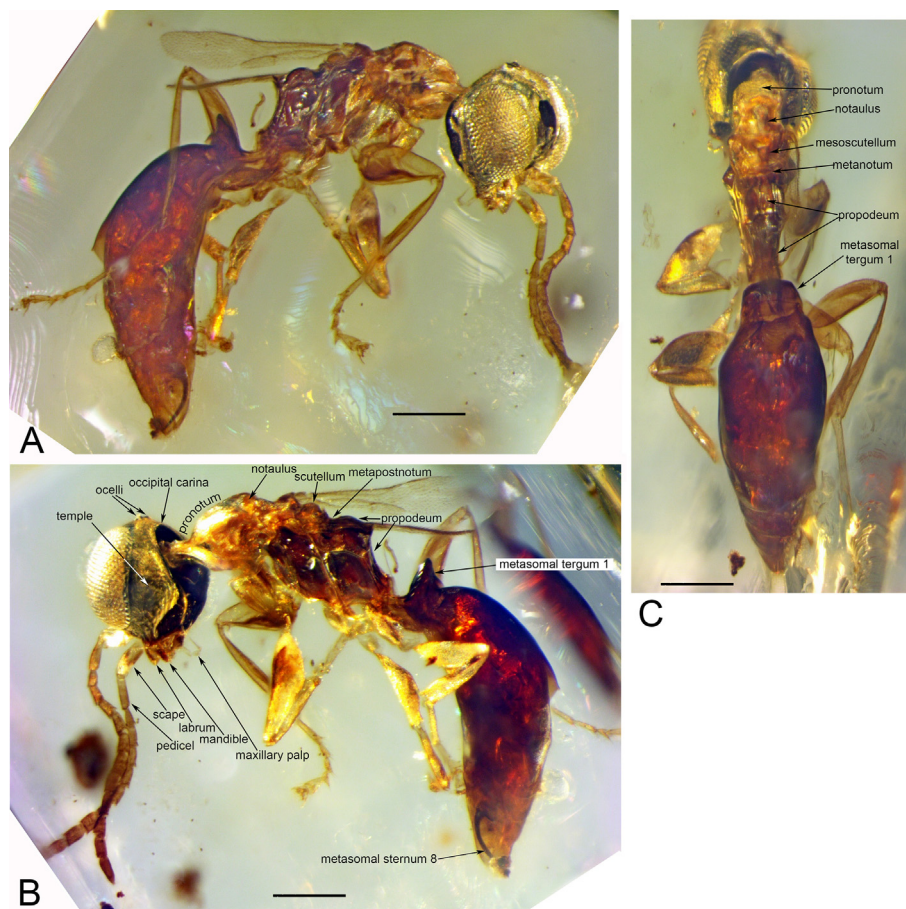


Fig. 2. *Falsiformix pedestris* Zhang and Rasnitsyn sp. nov., male holotype QFD16201. (A), Right lateral aspect. (B), Left lateral aspect. (C), Dorsal aspect. All scale-bars = 0.2 mm.

dorsal length at most $0.5 \times$ of declivity length, with declivity distinctly concave. Claws simple.

Species included. Type only.

Remarks. New genus differs from other genera in male brachyptery (female putatively also brachypterous or apterous) and in having propodeum very short (dorsal length at most half as long as declivity length, with declivity distinctly concave).

Etymology. Genus name is a modified name of the related genus *Falsiformica*. The gender is feminine.

Falsiformix pedestris Zhang and Rasnitsyn sp. nov.

LSID: zoobank.org:act: 4777DE97-DFC2-4A79-BCFD-1A06C9B8 365A

(Fig. 2).

Holotype. QFD16201. Male. Kachin amber, middle Cretaceous. Completely preserved wasp originally in a flat ovoid piece of amber, trimmed in a polished rectangular block $1.8 \times 1.8 \times 1.2$ mm, not well seen in some aspects, particularly in dorsal, ventral and frontal, because of irregularities of amber texture.

Etymology. Species name *pedestris* is the Latin for pedestrian because of the flightlessness of the species.

Diagnosis as for genus because of monotypy.

Description. Body moderately slim. Metasoma and head dark; propodeum and meso- and metapleura laterally less dark; prothorax, mesonotum and appendages rather pale except antenna slightly darkened and femora irregularly darkened (irregularity apparently preservationally caused, originally femora could be predominantly darkened); surface microsculpture and vestiture not discernible.

Head large, transverse, slightly longer than high, with big eyes occupying most of its sides (reaching occiput level and almost reaching mandibular bases). Ocelli not enlarged, apparently in isosceles triangle. Antennal attachment at clypeal margin. Clypeus moderately short, convex, with fore margin more or less straight. Malar space much shorter than mandible basal width. Temple angularly widened near midheight. Postoccipital bridge almost as long as each half of hypostomal margin. Occipital carina complete. Labrum long and wide (almost clypeus-wide), oval. Antenna with scape longer and wider than other segments, pedicel thin, almost as long as scape, longer than any flagellomere, basal flagellomere shortest, apical one longest, middle and apical segments slightly wider than pedicel and basal flagellar segments. Mandible short, bidentate, with teeth short, subequal, placed in plane of mandibular base. Maxillary palp with four segments visible, all elongate, basal ones thicker, terminal segment longest, thin and acute. Labial palp not clear.

Pronotum longer than high, attenuate rostrally into distinct neck, posterolateral angle elongate and form flat lobe reaching tegula, lower angle short, rounded. Mesonotum distorted, mesoscutellum narrow triangular, prescutellar fossa long and deep, axillae wide. Metanotum short, not clearly differentiated, metapostnotum wide transverse trough traversed with five carinae. Meso- and metapleura with no carination. Propodeum with carinae bordering short distinctly convex dorsal surface and two times longer and strongly concave declivity, dorsal area with two complete sublateral and incomplete medial carina, with short teeth at junction of lateral dorsal and posterior (declivity) carinae. Fore coxa largest, mid one smallest, mid coxa with narrow basal articulation. Trochanters narrow, not elongate, trochantelli not distinct. Femora looking differently

depending on aspect (probably much flattened preservationally), originally probably all rather wide, more so subbasally. Tibiae narrow, fore one shorter and hind one longer than respective femur, fore tibial spur thin, gently bent, acute, mid and hind tibia with one spur visible (possibly because of improper position of tibiae). Basitarsus longer than three following segments combined in fore leg, subequal to these in hind one, fourth segment of hind tarsus dorsally half as long as ventrally, fifth one as long as third, claws simple, arolium small as preserved. Forewing as long as mesosoma dorsally (except neck and propodeal declivity), with only R and narrow pterostigma present, hind wing half as long as forewing, with no distinct veins visible. Metasoma smooth, fusiform except for node, with seven segments visible. First segment with petiole distinct but not long, scale triangular, higher than long, with fore declivity slightly convex and hind one slightly concave. Second segment longest, following gradually shorter. Long curved horns of eighth sternum visible inside metasomal apex.

Measurements in mm. Body length 1.7, head length 0.26, height 0.42, antenna length 0.80, mesosoma length 0.62, height 0.27, length of fore femur 0.32, tibia 0.29, tarsal segments 1–5 (the latter without claws and arolium) 0.15, 0.05, 0.04, 0.03, 0.07, hind femur 0.34, tibia 0.41, tarsal segments 1–5 0.18, 0.09, 0.06, 0.04, 0.07, forewing 0.51, hind wing 0.27, metasoma 0.87.

4. Discussion

Falsiformicidae appear as a stratigraphically important group with wide space (Figure 3) and narrow time distribution (Table 1).

Their four fossil sites are widely spread geographically (northern Siberia, SE France, NE USA and northern Myanmar) and vary climatically from warm temperate (Agapa, N. Siberia; based on data for the most similar deposits of New Siberia IIs., Herman et al., 2019) to highly thermophilic (Burmese amber with velvet worms, numerous webspinners, termites, etc.) that fall respectively either into Baeomorpha Realm (Siberian ambers) or Isoptera Realm (Burmese, Charente and New Jersey ambers) sensu Gumovsky et al. (2018). At the same time, falsiformicid fossil sites are chronologically limited within the Cenomanian (Burmese, Charente and Agapa amber) and Turonian (New Jersey amber). Undoubtedly, a new material could easily falsify the above inference, but for the present we are to consider Falsiformicidae as a perspective candidate to the position of an important stratigraphical indicator.

In Hymenoptera, flightless males (those with brachyptery, microptery or aptery) might combine with females either able or unable to fly. Flightless males with their females able to fly occur when mating takes place before dispersal from the confined space where their eclosion happened. This combination is more characteristic of various parasitic wasps, including the pollinating and some non-pollinating fig wasps (e.g., Cook, 2021) as well as other chalcidoid wasps *Trichogramma* (Kurosui, 1985) and *Monodontomerophagus* (Schauff, 1986); highly reduced males *Dicopomorpha eschmepterigis* Mockford, 1997 (Mymaridae) probably fall here as well (Polilov, 2015). Sometimes these males are dimorphic, winged or wingless depending on different mating strategies, when winged males disperse before mating whilst flightless males start mating immediately (e.g., Cook, 2021).

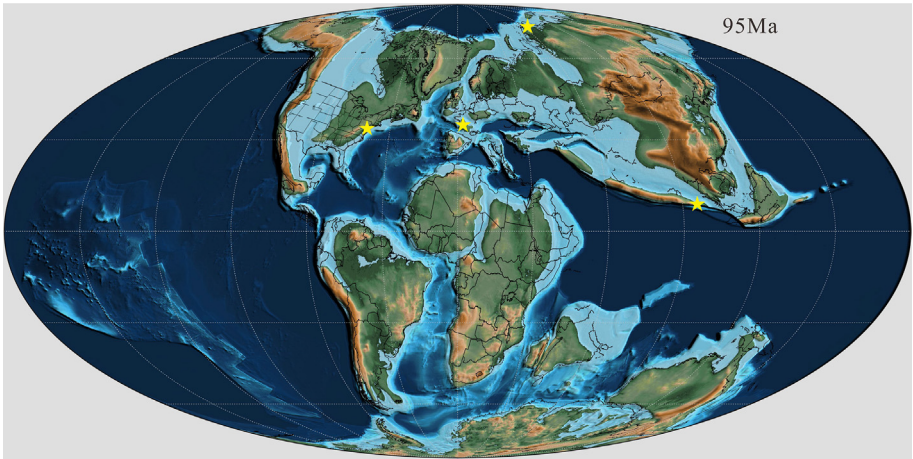


Fig. 3. World distribution of the Falsiformicidae in the Cenomanian (star represents the position of the specimen, modified from Scotese et al., 2024).

Table 1
The checklist of genus and species in Falsiformicidae.

Genus	Species	Locality	Age	References
<i>Falsiformica</i>	<i>Falsiformica cretacea</i>	Siberia, Russia	Cenomanian	Rasnitsyn, 1975
<i>Burmomyrma</i>	<i>Burmomyrma rossi</i>	Myanmar	Cenomanian	Dlussky, 1996, Lucena and Melo. (2018) Lak et al. (2008)
Unknown	Unnamed	France	Cenomanian	Cockx and McKellar. (2016)
<i>Siccibythus</i>	<i>Siccibythus musculosus</i>	Myanmar	Cenomanian	Rasnitsyn et al. (2020)
	<i>Siccibythus martynovae</i>	Myanmar	Cenomanian	Rasnitsyn et al. (2020)
	<i>Siccibythus oculatus</i>	Myanmar	Cenomanian	Rasnitsyn et al. (2020)
	<i>Siccibythus ohmkuhnlei</i>	Myanmar	Cenomanian	Rasnitsyn et al. (2020)
	<i>Siccibythus pallidus</i>	Myanmar	Cenomanian	Rasnitsyn et al. (2020)
	<i>Siccibythus paulus</i>	Myanmar	Cenomanian	Rasnitsyn et al. (2020)
<i>Neophenax</i>	<i>Neophenax orcus</i>	USA	Turonian	Engel, 2022
<i>Falsiformix</i>	<i>Falsiformix pedestris</i>	Myanmar	Cenomanian	This research

An alternative population structure with the wingless males combined with equally flightless females represents a less exotic even though equally uncommon strategy. It usually realizes when both sexes similarly rely on a hidden or at least pedestrian way of life. This kind of flightlessness is known in aculeate wasps including some Bethyridae, Dryinidae, Rhopalosomatidae (Goulet and Huber, 1993), Mutillidae (particularly among Myrmillinae; Brothers and Lelej, 2017) and ergatomorph male ants (Wilson and Hölldobler, 1990).

The new species is captured into a resin trap on a tree: evidently, the male under description has left its place of eclosion whatever it could be, and most probably it has dispersed from there seeking for a potential mating partner rather than to be destined to concealed habits and mating with siblings in a narrow space of eclosion. That is why it looks reasonable to attribute it to the second category of flightless males with the equally flightless females. The characteristic form of propodeum of the present fossil may leave us a hope to identify the respective female in a happy occasion while screening an inconceivable diversity of wasps buried in the Kachin amber.

5. Conclusion

The present find of a brachypterous male wasp from the insufficiently known strictly Cretaceous family Falsiformicidae of debatable taxonomic position highlights a well-known potential of the middle Cretaceous amber of Myanmar as a plethora of the insect diversity. It demonstrates us, among others, rare phenomena of insect evolution like the flightless wasp males. In the contemporary world, to collect in a field a flightless male wasp as a viable rather than abnormal insect is a very rare occasion even for experienced entomologist, unless you are engaged in a respective special research. Insects of Kachin amber from Myanmar are now a subject of a quarter-of-century-long unprecedentedly intensive study (Ross, 2024). Yet the flow of amazing new discoveries does not even slow down.

CRediT authorship contribution statement

Qi Zhang: Writing – original draft, Resources, Funding acquisition. **Ning Jia:** Writing – review & editing, Formal analysis. **Yizheng Li:** Writing – review & editing, Visualization, Methodology. **Jianxun Wang:** Methodology, Formal analysis. **Alexander P. Rasnitsyn:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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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.2024.106057>.