

Short communication

A new genus and species of Praeaulacidae (Hymenoptera: Evanioidea) from Upper Cretaceous Myanmar amber

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ABSTRACT

A new fossil praeaulacid wasp, *Habraulacus zhaoi* **gen. et sp. nov.**, is described and figured from Upper Cretaceous Myanmar amber. The new genus is established based on the following characters: mesosoma stout, metasoma elongated ellipse with the first metasomal segment very thin and tubular (like a petiole), forewing with pterostigma long and narrow, and both veins Rs+M and 1m-cu very long, forming a long cell 1mcu. Species of Praeaulacidae demonstrate a distinct evolutionary trend, which consists of miniaturization, venational reduction and enlargement of pterostigma, and reduction of number of the antennal segments from the Jurassic to Cretaceous. However, except for the miniaturization, this hardly concerns *Habraulacus*.

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1. Introduction

Praeaulacidae, together with Evaniidae, Aulacidae, Gasteruptiidae and Anomopterellidae form the superfamily Evanioidea, and are united in the possession of a typical evanoid wasp-waist. The distinctive “waist” is formed as a result of a putative synapomorphy – the metasoma is attached high on the propodeum and far away from the hind coxae, rather than articulating in a ventral position and near the hind coxae. Monophyly of Evanioidea is strongly supported by molecular and morphological data analyses (Heraty et al., 2011; Sharkey et al., 2012; Klopstein et al., 2013). The Praeaulacidae, an extinct group with complete wing venation (except for some species of the subfamily Cretocleistogastrinae), have been considered as the ancestral group of Evanioidea (Rasnitsyn, 1988; Li et al., 2013a). To date, there are three subfamilies, Cretocleistogastrinae Rasnitsyn, 1990 with four genera *Cretocleistogaster* Rasnitsyn, 1975, *Westratia* Jell & Duncan, 1986, *Miniwestratia* Rasnitsyn, 1990, and *Nanowestratia* Rasnitsyn, 1990 (Jell & Duncan, 1986; Rasnitsyn, 1990a,b); Praeaulacinae Rasnitsyn, 1972 with eleven genera: *Aulacogastrinus* Rasnitsyn, 1983, *Eosaulacus* Zhang & Rasnitsyn, 2008, *Evaniops*, *Evanigaster*, *Praeaulacinus*, *Praeaulacites*, *Praeaulacon*, *Praeaulacops* and

Praeaulacus were all established by Rasnitsyn in 1972, *Gulgonga* Oberprieler, Rasnitsyn & Brothers, 2012 (Oberprieler et al., 2012), and *Archaulacus* Li, Shih & Ren, 2014 (Rasnitsyn, 1972, 1973, 1983; Zhang & Rasnitsyn, 2008; Li et al., 2014; Li & Shih, 2014); and *Nevaniinae* Zhang & Rasnitsyn, 2007 with two genera: *Nevania* Zhang & Rasnitsyn, 2007 and *Eonevania* Rasnitsyn & Zhang, 2010 (Zhang & Rasnitsyn, 2007; Rasnitsyn & Zhang, 2010; Li et al., 2013b).

Myanmar amber, from northern Myanmar and also known as “burmite”, has been used in carvings and jewelry by the Chinese for at least two thousand years. Only about a century ago, Myanmar amber was studied scientifically for the first time (Cockerell, 1916, 1917a, 1917b, 1920a, 1920b; Burn, 1918), due to well-preserved inclusions of diverse plants and animals. Recently, study of Myanmar amber has become more active (Zherikhin & Ross, 2000; Grimaldi et al., 2002; Ross et al., 2010; Boucot & Poinar, 2011; Labandeira, 2014). However, to date, only six amber species of this deposit in Evanioidea have been reported: *Electrofoenus gracilipes* Cockerell, 1917, *Hyptiogastrites electrinus* Cockerell, 1917, *Protofoenus swinhoei* Cockerell, 1917, *Mesevania swinhoei* Basibuyuk & Rasnitsyn, 2000, *Sorellevania deansi* Engel, 2006 and *Cretevania bechlyi* Jennings, Krogmanm & Mew, 2013 (Ross & York, 2000; Basibuyuk et al., 2000; Engel, 2006; Jennings et al., 2004; Jennings et al., 2013). Based on palynology and ammonoid zonation within the surrounding rock units, and insect taxa preserved within Myanmar

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amber, age estimates have ranged from Albian to Cenomanian. Considering other factors (e.g. radiometric dates obtained from the volcanic clasts present within the amber-bearing sediments), an age of the earliest Cenomanian (98.79 ± 0.62 Ma) has recently been established for the burmite (Cruickshank & Ko, 2003; Shi et al., 2012).

Herein, we report a new genus with a new species, *Habraulacus zhaoi* gen. et sp. nov., preserved in the Upper Cretaceous amber from Myanmar, and briefly discuss the miniaturization, venational

reduction and enlargement of pterostigma, and reduction of number of the antennal segments from the Jurassic to Cretaceous in Praeaulacidae.

2. Materials and methods

The type fossil specimen studied below derives from amber deposits in Kachin (Hukawng Valley) of northern Myanmar, approximately 100 km southwest of the Village of Tanai (Fig. 1)

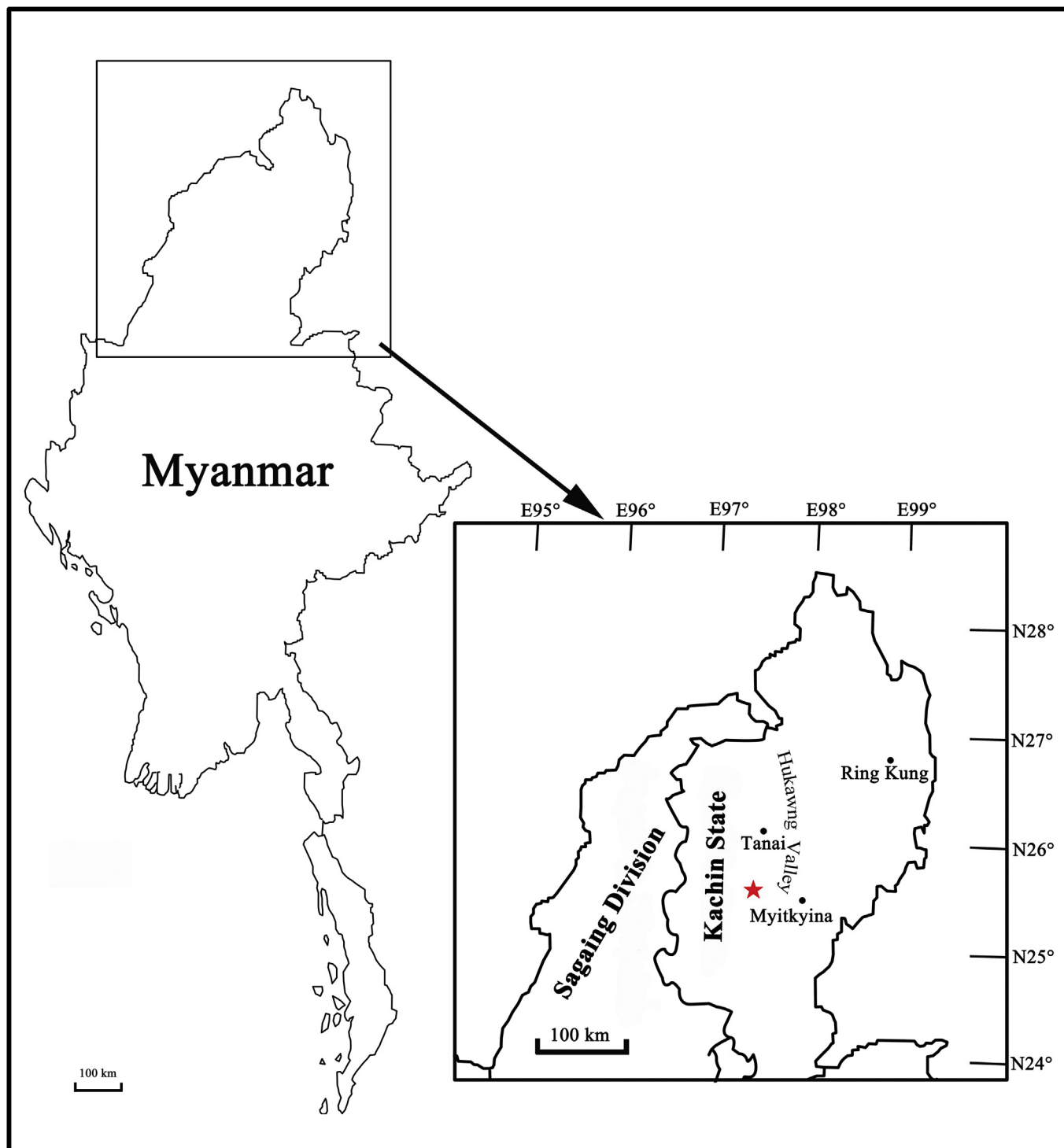


Fig. 1. Map of the amber locality near Tanai Village in Hukawng Valley (after Dong et al., 2015).

(Dong et al., 2015). This material is housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China. The specimen was examined and photographed under a Leica MZ 16.5 dissecting microscope (Leica, Wetzlar, Germany), with an attached Leica DFC500 digital camera system. The specimen was illustrated with the aid of a camera lucida attached to the microscope. The figures were composed with CorelDraw 12.0 and Adobe Photoshop CS5 software. The wing venation terminology used here follows Zhang & Rasnitsyn (2008).

3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Suborder Apocrita Gerstaecker, 1867
Superfamily Evanioidea Latreille, 1802
Family Praeaulacidae Rasnitsyn, 1972
Subfamily Praeaulacinae Rasnitsyn, 1972
Genus *Habraulacus* gen. nov.

Type species. *Habraulacus zhaoi* sp. nov.

Etymology. The generic name is a combination of the Greek term “habros” (meaning “graceful”) and the type genus name “*Aulacus*” as a suffix. Gender is masculine.

Diagnosis. Head large. Antenna with 30 or more antennomeres. Mesosoma moderately stout, with scutellum elevated high about

propodeum, metanotum probably subvertical, propodeum with dorsal surface about a quarter as long as posterior one. Legs long and thin. Forewing with venation complete; pterostigma narrow and wedge-shaped; 1-Rs more than twice as long as 1-M, removed from pterostigma by about 0.7 of its own length; 2r-rs meeting Rs halfway between Rs and base of 3r-m; Rs+M nearly as long as 1-Rs and 1-M together; 2-M (between Rs+M and 1m-cu) long (slightly shorter than 1-M); 1m-cu distinctly longer than 3-M; 1mcu cell twice as long as 2cua; 2m-cu crossvein positioned approximately midway between 1m-cu and 3r-m; cu-a interstitial. Hind wing with R, Rs, M+Cu, M, Cu, A, r-m, and cu-a all present; 1-RS shorter than r-m, position of M+Cu fork more basal than cu-a. Male narrow and roundish in cross-section (only slightly longer than combined length of head plus mesosoma and hind coxae), with the first segment long and narrow, only slightly broadening posteriorly, attached high on propodeum, distant from propodeal base.

Remarks. *Habraulacus* gen. nov. is assigned to Praeaulacidae based on hind wing venation with Rs, r-m and cu-a present (only R, M+Cu and A are present in remaining Evanioidea), supported by the high number (30 or more) of antennomeres (less than 20 antennomeres in remaining Evanioidea). Attribution to Praeaulacinae is based on differences from Nevaniinae that include the one-segmented petiole (vs. two-segmented), and forewing vein M+Cu long (vs. subequal to combined length of 1-Rs and 1-M); distinctions from Cretocleistogastrinae is based on the narrow pterostigma (vs. wide in the latter, and variable but never wide in Praeaulacinae), forewing crossvein 3r-m completely preserved (vs. completely lost; but always present in Praeaulacinae), 2-M well-developed (vs. never present; but often present in Praeaulacinae), and the first metasomal segment tubular (vs. never tubular; but variable in Praeaulacinae). The new genus differs from all other Praeaulacinae in having 1mcu cell twice as long as 2cua (vs. subequal in length), and from their majority (except for *Evanigaster* Rasnitsyn, 1972 and *Evanigaster* Rasnitsyn, 1972) also in having the first metasomal segment long and thin (narrow conical). It differs from the two latter genera additionally in small size (forewing length below 3.5 mm vs. 6 mm or more).

Habraulacus zhaoi gen. et sp. nov. (Figs. 2–4)

Etymology. The specific name is dedicated to Renhao Zhao for his generous donation of the amber fossil for scientific research.

Type material. Holotype, CNU-HYM-MA-2014001, male, well-preserved.

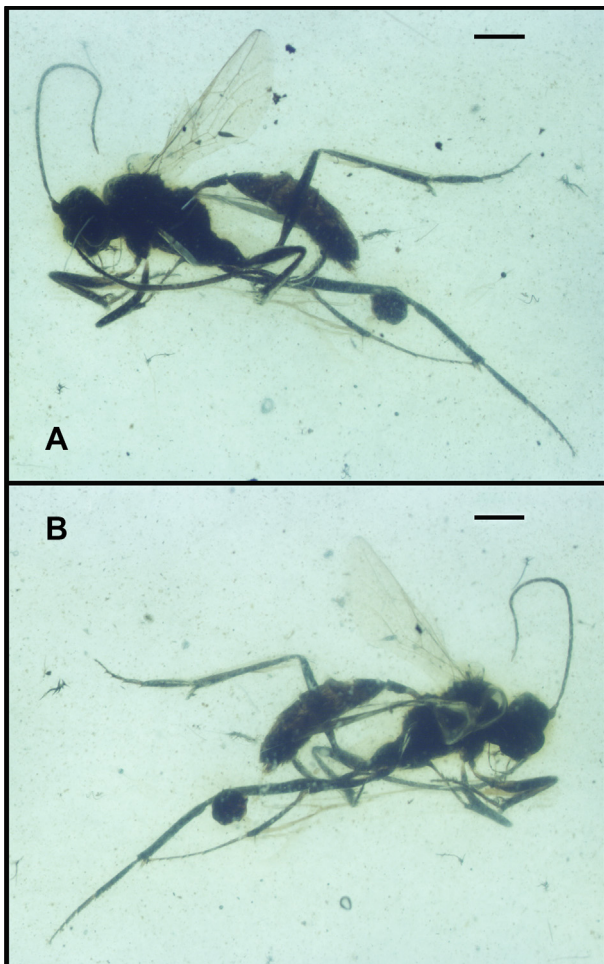


Fig. 2. Photographs of *Habraulacus zhaoi* gen. et sp. nov. Holotype CNU-HYM-MA-2014001. (A), (B) Lateral habitus. Scale bars = 1 mm.

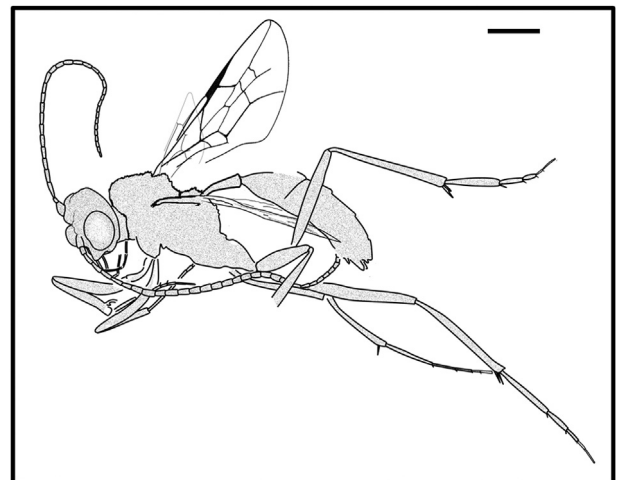


Fig. 3. Line drawing of *Habraulacus zhaoi* gen. et sp. nov. Holotype CNU-HYM-MA-2014001. Scale bars = 1 mm.

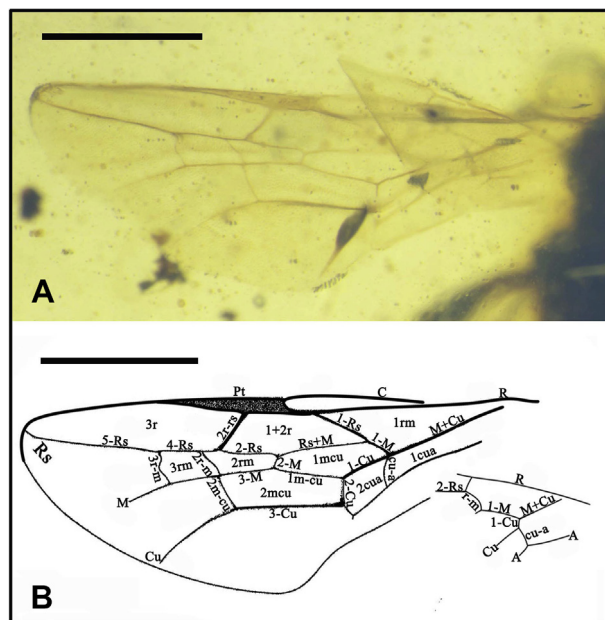


Fig. 4. Wings of *Habraulacus zhaoi* gen. et sp. nov. Holotype CNU-HYM-MA-2014001. A, Photograph. B, line drawings, with trace of visible venation in hind wing. Scale bars = 1 mm.

Locality and horizon. Hukawng Village, Kachin State, Northern Myanmar; Upper Cretaceous [Cenomanian].

Diagnosis. As for the genus, by monotypy.

Description. Adult male, body length about 5.6 mm excluding antennae (Figs. 2–3).

Head large, transverse, nearly 1.3 times as wide as long (length 1.0 mm width 1.3 mm). Antenna filiform, thin and long, with more than 30 antennomeres, about 5 mm long, with scape distinctly swollen and wider than pedicel, pedicel short and narrow, and other antennomeres decreasing in length from base to apex (Fig. 3).

Mesosoma short and stout, only can see the contour lines (Fig. 3).

Legs slender, mesocoxae contacting metacoxae, both of which are far removed from procoxae. Hind legs distinctly longer than fore and mid legs. Both mid legs and hind legs clearly preserved tarsus with five tarsal segments, and the first tarsal segment nearly as long as remaining four together; hind tibia with two spurs, tarsal segments with strong apical setae (Fig. 3).

Metasoma elongate with first segment ca. five times as long as its maximum width, apparently attached near propodeal posterior. Remaining metasomal segments rather uniform in length (second metasomal segment longest), forming curved, elongate oval; hypopygium short; cerci short, male genitalia elongate and narrow in side view (Fig. 3).

Table 1
Fossil species of Praeaulacinae Rasnitsyn, 1972 in the world, updated from Zhang & Rasnitsyn, 2008.

Species	Country	Period	Reference
<i>Habraulacus zhaoi</i> sp. nov.	Myanmar	Upper Cretaceous	This study
<i>Praeaulacus patiens</i> Rasnitsyn, 2008	Mongolia	Lower Cretaceous	Rasnitsyn, 2008
<i>Praeaulacus sharteg</i> Rasnitsyn, 2008	Mongolia	Lower Cretaceous	Rasnitsyn, 2008
<i>Aulacogastrinus ater</i> Rasnitsyn, 1983	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972, 1983
<i>Evanips rostratus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Evanigaster petiolatus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Gulgonga beattiel</i> Oberprieler, Rasnitsyn & Brothers, 2012	Australia	Upper Jurassic	Oberprieler et al., 2012
<i>Praeaulacinus crassipes</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacinus minor</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacinus parvus</i> Rasnitsyn, 1973	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972, 1973
<i>Praeaulacites medius</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacites minimus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacites nigripes</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacites pachygaster</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacites subniger</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacon caudatus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacon coniventer</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacon elongatus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacon tenuis</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacops lucidus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacus cubocephalus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacus elegans</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacus leptogaster</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacus magnus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacus obscurus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Praeaulacus ramosus</i> Rasnitsyn, 1972	Kazakhstan	Upper Jurassic	Rasnitsyn, 1972
<i>Archaulacus probus</i> Li, Shih & Ren, 2014	China	Middle Jurassic	Li et al., 2014
<i>Aulacogastrinus hebeiensis</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Aulacogastrinus insculptus</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Aulacogastrinus longaciculatus</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Eosaulacus giganteus</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Praeaulacus afflatus</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Praeaulacus douchugouensis</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Praeaulacus exquisitus</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Praeaulacus orientalis</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Praeaulacus robustus</i> Zhang & Rasnitsyn, 2008	China	Middle Jurassic	Zhang & Rasnitsyn, 2008
<i>Praeaulacus subrhombus</i> Li, Shih & Ren, 2014	China	Middle Jurassic	Li et al., 2014
<i>Praeaulacus tenellus</i> Li, Shih & Ren, 2014	China	Middle Jurassic	Li et al., 2014
<i>Praeaulacus obtutus</i> Li & Shih, 2014	China	Middle Jurassic	Li & Shih, 2014

Wings well-preserved, with one forewing folded and indiscernible, while other forewing out-stretched with clear and discernible venation. Forewing length 3.31 mm, width 1.31 mm; pterostigma long and narrow, about 7 times as long as wide; 1-Rs arising at a distance from pterostigma (equal to approximately one-half of length of 1-Rs), 1-Rs significantly inclined toward wing base, about 2.6 times as long as 1-M (1-Rs 0.36 mm, 1-M 0.14 mm); cu-a interstitial and distinctly curved, nearly as long as 1-M; both Rs+M and 1m-cu very long; Rs+M nearly as long as 1-Rs and 1-M together, 1m-cu distinctly longer than 3-M; cell 1mcu about 2 times as long as cua; 2r-rs arising from basal one-third of pterostigma, directed slightly oblique apicad, and about 3 times as long as the width of pterostigma, cell 3r about 2 times as long as 1+2r; both 2r-m and 3r-m present well, 2r-m slightly basal than 2m-cu; 3r-m longer than 2r-m, V- like bent; cell 2rm longer and narrower than 3rm; cell 2rm in long contact with 1mcu; 2m-cu nearly in line with 2r-m; cell 2mcu long and narrow, nearly 3 times as long as wide. Hind wing with veins R, Rs, M, Cu, A, r-m and cu-a; 1-RS short, almost vertical, 2-RS short (cell r open), r-m oblique, longer than 1-RS, 1-M straight, 2-M very short, 1-Cu half as long as cu-a, 2-Cu and 2-A present (Fig. 4).

4. Discussion

Praeaulacinae Rasnitsyn, 1972, as a subfamily of Praeaulacidae, has now 12 genera with 39 described species as listed in Table 1 (Rasnitsyn, 1972, 1973, 1983, 2008; Zhang & Rasnitsyn, 2008; Li et al., 2014; Li & Shih, 2014). The majority of these species are distributed in the Middle Jurassic of China and the Upper Jurassic of Kazakhstan, while only *Habraulacus zhaoi* gen. et sp. nov. is from the Upper Cretaceous in Myanmar. This new species with well-preserved venation and body structures not only extends the fossil record from the Middle Jurassic to the Upper Cretaceous, but also provides comprehensive understanding of the trend of change for the wing and body structures in this subfamily, and the family Praeaulacidae.

For easy comparison, we examined four species representing three subfamilies of Praeaulacidae, from three epochs: *Nevania exquisita* Zhang & Rasnitsyn, 2007 of Nevaniinae (Fig. 5A) and *Praeaulacus daohugouensis* Zhang & Rasnitsyn, 2008 of Praeaulacinae (Fig. 5B), both of these two species from the Middle Jurassic; *Westratia curtipes* Rasnitsyn, 1990 of Cretocleistogastrinae (Fig. 5C) from the Lower Cretaceous; and *Habraulacus zhaoi* gen. et sp. nov. (Fig. 5D) from the Upper Cretaceous. By comparing wing venation of these four species, we can draw the following inferences:

Characteristic of the predominantly Jurassic subfamilies Praeaulacinae and Nevaniinae is the complete wing venation (Fig. 5A, B) and comparatively large body size (with forewing length rarely less than 4 mm). Of them, Praeaulacinae are mainly left plesiomorphic, except for simple loss of 2A (in parallel of the great majority of other Apocrita). In contrast, Nevaniinae are highly specialized in acquiring a very mobile metasoma with two-segmented petiole which implies an unusual even if unknown in detail parasitizing adaptation, as well as a venational specialization, also of unknown functional meaning, in having M+Cu short. Unlike these more old taxa, the entirely Lower Cretaceous Cretocleistogastrinae have acquired small body size (forewing length 4 mm or less), reduced wing venation (Fig. 5C) and expanded pterostigma. As a result, the previously known Praeaulacidae demonstrate a distinct evolutionary trend at a transition from the Jurassic to Cretaceous. That trend consists of miniaturization, venational reduction and enlargement of pterostigma, and reduction of number of the antennal segments. These processes often occur jointly to form a morphological syndrome characteristic of moderately small Hymenoptera (very small ones often have

pterostigma lost; for more information about effect of miniaturization on the wing venation see Rasnitsyn, 1969, on the number of antennal segments, Rasnitsyn, 1980).

In view of the above observations, we could expect *Habraulacus* demonstrating at least a partial syndrome of miniaturization. This is not the case: even if being small (forewing length 3.3 mm), it keeps antenna polymerous, all characteristic veins present and pterostigma narrow (Fig. 5D). Of course the venation is modified in *Habraulacus*, but this concerns vein displacement rather than loss. Miniaturization has particularly affected the hind wing there, so as the veins shifted towards wing base and lost distal parts of RS, M and Cu. Again, this is a usual effect of miniaturization in the hymenopteran hind wings (Rasnitsyn, 1969).

Worth mentioning here is also the abdominal structure of *Habraulacus* and particularly its long petiole which is uncommon in Praeaulacinae in contrast to many other Evaniioidea including Nevaniinae, Evaniidae and advanced Gasteruptiidae (Aulacinae and Gasteruptiinae). Long petiolate metasoma is generally uncommon

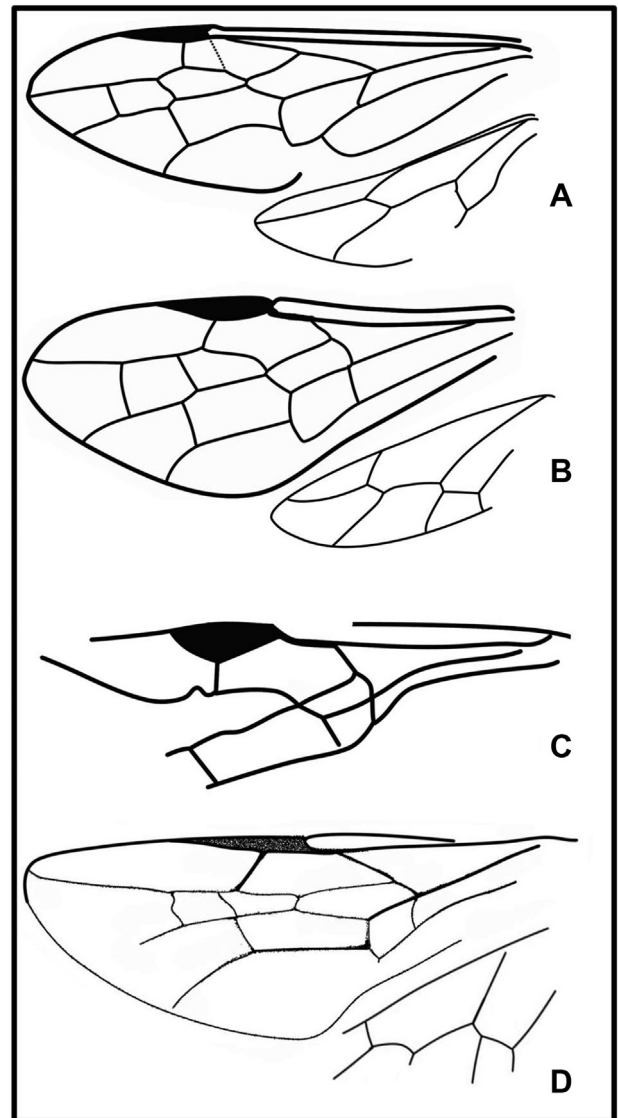


Fig. 5. Line drawings of wings of species in Praeaulacidae. A, *Nevania exquisita* (after Zhang & Rasnitsyn, 2007). B, *Praeaulacus daohugouensis* (after Rasnitsyn & Zhang, 2008). C, *Westratia curtipes* (after Rasnitsyn, 1990a). D, *Habraulacus zhaoi* gen. et sp. nov.

in Jurassic Hymenoptera in contrast to the Cretaceous and Cenozoic ones which acquire it independently many times. In that respect *Habraulacus* lies perfectly into the general hymenopteran trend.

5. Conclusion

Habraulacus zhaoi gen. et sp. nov., is described and figured from the Upper Cretaceous Myanmar amber, which not only extends the fossil record from the Middle Jurassic to the Upper Cretaceous, but also provide insight into the changes that took place within wing and body structures in Praeaulacidae. The previously known Praeaulacidae demonstrate a distinct evolutionary trend, which consists of miniaturization, venational reduction and enlargement of pterostigma, and reduction of number of the antennal segments from the Jurassic to Cretaceous. Unexpectedly, *H. zhaoi* gen. et sp. nov. does not follow this trend in spite of a rather small body size. *H. zhaoi* displays a first metasomal segment that is thin and tubular which agrees with the general hymenopteran trend for the long petiolate metasoma is generally uncommon in Jurassic Hymenoptera in contrast to the Cretaceous and Cenozoic ones which acquire it independently many times to make metasomal movements more free and precise at host paralyzation.

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