



# A new *Jaculistilus* species of Mimarachnidae (Hemiptera: Fulgoromorpha) from mid-Cretaceous Kachin amber of northern Myanmar, with geometric morphometric analysis of the mimarachnid genera

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## ABSTRACT

Mimarachnidae is a Mesozoic planthopper family, with high palaeodiversity at generic and species levels during Cretaceous. Herein, geometric morphometric analysis of mimarachnid forewings was executed. Our results of principal component and cluster analyses show that *Dachibangus formosus* and *D. hui* are morphologically distinct from the type species of *Dachibangus*. Therefore, *Xiaochibangus* gen. nov. is erected, and those two species are transferred to this new genus, resulting in new combinations – *Xiaochibangus formosus* comb. nov. and *X. hui* comb. nov. Besides, *Jaculistilus xixuanae* sp. nov., the second species of *Jaculistilus* with well-preserved 12 eyespots on tegmina, is described here from mid-Cretaceous Kachin amber of northern Myanmar, adding novel knowledge on the palaeodiversity of Mimarachnidae.

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## 1. Introduction

The Mimarachnidae Shcherbakov, 2007, as an extinct Fulgoromorpha family established by Shcherbakov (2007), comprises taxa with quite peculiar features, including mesonotum with two longitudinal median carinae, sensory pits retained in the adults, tegmina with basal cell weak or absent, both tegmina and hind wings with simplified longitudinal venation and polygonal meshwork of veinlets (Shcherbakov, 2007; Jiang et al., 2018; Zhang et al., 2018, 2021). To date, 14 genera and 22 species have been reported and ascribed to this family, together with some yet undescribed specimens (Table 1).

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All known species of this family present tegminal information, except for *Nipponoridium matsuoii* (Fujiyama, 1978), which was erected solely based upon an isolated hind wing (Fujiyama, 1978; Szewo, 2008). The current classification framework of Mimarachnidae is established mainly on information of fossil tegmina. The adpressions of forewings, the tegmina, originally used to establish this family, have typical mimicry features, including eye spots and color pattern; and so, they were thought to be mimicking spiders (Shcherbakov, 2007). Eyespots are important in mimicry, aposematism, deflection, and even may in intraspecific recognition and sexual selection, and their presence and crypsis are thought to be a trade-off between crypsis and the presence of distinct eyespot (Stevens, 2005; Parchem et al., 2007; Wittkoppa and Beldade, 2009). Eyespots on fossilized insect wings have been reported mainly in Neuroptera and a few groups of Hemiptera (Shcherbakov, 2002, 2007; Liu et al., 2013, 2018; Shih et al., 2019). Mimarachnidae is one of the few hemipteran

groups with distinctive eyespots reported (e.g., Shcherbakov, 2002, 2007); such pattern of tegminal coloration is present e.g. among modern representatives of the families Derbidae, Eurybrachidae, Fulgoridae. With the increased specimens were discovered, eye spots are not considered the required feature of this family; the presence of eyespots and color patterns, however, is still important for the discrimination of different mimarachnid taxa.

Geometric morphometric analysis (GMA) has widely been used in the study of phenetic relationships for extinct organisms, but its

application on fossil insects are few (e.g., Michez et al., 2009; De Meulemeester et al., 2012; Wappler et al., 2012; Shih et al., 2017; Dehon et al., 2019; Herrera-Flórez et al., 2020; Chen et al., 2022). We herein use GMA to elucidate the systematic relationships of Mesozoic Mimarachnidae. In addition, we report a new species *Jaculistilus xixuanae* sp. nov. from mid-Cretaceous Kachin amber. The new mimarachnid has six eyespots and complex patterns on each tegmen, likely indicating broader ecological implications of eyespots in this family.

**Table 1**  
Checklist of species in Mimarachnidae.

Species	Age (Ma)	Horizon	Locality	Reference
<i>Saltissus fennahi</i> Luo, Liu et Jarzembowski, 2021	ca. 128	Lower Cretaceous, lower Barremian	Smokejacks brickworks, England	Luo et al. (2021)
<i>Mimarachne mikhailovi</i> Shcherbakov, 2007	125–113	Lower Cretaceous, Aptian	Zaza Formation, Baissa, Buryatia, Russia	Shcherbakov (2007)
<i>Saltissus eskovi</i> Shcherbakov, 2007	125–113	Lower Cretaceous, Aptian	Zaza Formation, Baissa, Buryatia, Russia	Shcherbakov (2007)
<i>Nipponoridium matsuii</i> (Fujiyama, 1978)	125–113	Lower Cretaceous, Aptian	Kuwajima Formation; Kaseki-kabe Hakusan City, Ishikawa Prefecture, Japan	Szwedo (2008)
<i>Mimamontsecia cretacea</i> Szwedo et Ansorge, 2015	130.0–125.5	Lower Cretaceous, lower Barremian	La Pedrera de Rubies Formation, Noguera, Lleida, Catalonia, Spain	Szwedo and Ansorge (2015)
<i>Chalicoridulum montsecensis</i> Szwedo et Ansorge, 2015	130.0–125.5	Lower Cretaceous, lower Barremian	La Pedrera de Rubies Formation, Noguera, Lleida, Catalonia, Spain	Szwedo and Ansorge (2015)
<i>Burmessus raunoi</i> Shcherbakov, 2017	98.79 ± 0.62	'mid-Cretaceous', lower Cenomanian	Kachin amber, Myanmar	Shcherbakov (2017)
<i>Burmessus latimaculatus</i> Fu et Huang, 2020	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Fu and Huang (2020)
<i>Burmessus szwedoi</i> Luo et al., 2020	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Luo et al. (2020)
<i>Dachibangus trimaculatus</i> Jiang et al., 2018,	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Jiang et al. (2018)
<i>Xiaochibangus formosus</i> (Fu et al., 2019)	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Fu et al. (2019)
<i>Xiaochibangus hui</i> (Zhang, Yao et Pang, 2021)	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Zhang et al. (2021)
<i>Jaculistilus oligotrichus</i> Zhang et al., 2018	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Zhang et al. (2018)
<i>Jaculistilus xixuanae</i> sp. nov.	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	In this work
<i>Mimaplax ekrypsan</i> Jiang et al., 2019	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Zhang et al. (2018)
<i>Ayaimatum trilobatum</i> Jiang et Szwedo, 2020	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Jiang et al., 2020
<i>Ayaimatum minutum</i> Fu et Huang, 2021	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Fu and Huang, 2021
<i>Cretodorus angustus</i> Fu et Huang, 2020	98.79 ± 0.62	mid-Cretaceous' lower Cenomanian	Kachin amber, Myanmar	Fu and Huang (2020)
<i>Cretodorus granulatus</i> Fu et Huang, 2020	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Fu and Huang (2020)
<i>Cretodorus rostellatus</i> Zhang, Yao et Pang, 2021	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Zhang et al. (2021)
<i>Mimaeurypterus burmiticus</i> Fu et Huang, 2021	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Fu and Huang, 2021
<i>Multistria orthotropa</i> Zhang, Yao et Pang, 2021	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	Zhang et al. (2021)
<i>Tenebricosus coriaceus</i> He, Jiang et Szwedo	98.79 ± 0.62	mid-Cretaceous, lower Cenomanian	Kachin amber, Myanmar	He et al. (2022)
Undescribed specimens	145 ± 4.0–132.9 ± 2.0	Berriasian–Valanginian, Lower Cretaceous	Turga, Chita Region, East Transbaikalia, Russia	Shcherbakov (2007)
Undescribed specimens	125–113	Lower Cretaceous, Aptian	Bon Tsagaan, Bayanhongor Province, Mongolia;	Shcherbakov (2007)
Undescribed specimen	93.9–89.8	Upper Cretaceous, Turonian	Khetana River, Khabarovsk Krai, Russia	Shcherbakov (2007)
Undescribed specimen	93.9–89.8	UpperCretaceous, Turonian	Kzyl-Zhar Locality, Shieli, Kyzylorda Region, Kazakhstan	Shcherbakov (2007)

## 2. Materials and methods

The amber piece NIGPAS-Z101 trapping the new planthopper specimen described herein is permanently deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS) (see Supplementary statement – ‘Museum Catalogue entry’). It was collected from the Angbamo site, Tanai Township, Myitkyina District, Kachin Province of northern Myanmar. The maximum age of amber is  $98.8 \pm 0.6$  million years (earliest Cenomanian), according to U–Pb dating of zircons from the volcanoclastic matrix (Shi et al., 2012). The amber piece was collected from 2013 to 2016, before the Myanmar army closed the Kachin amber mines in November 2017 (see Supplementary statement – ‘Museum Catalogue entry’). The fossil was acquired in full compliance with the laws of Myanmar. All authors declare that the specimen reported in this study is not involved in armed conflict and ethnic strife in Myanmar. The specimen representing new species is deposited permanently in public museums in full compliance with the International Code of Zoological Nomenclature (ICZN 1999), the indications of the International Palaeontological Society (Szwedo et al., 2020), and policies proposed by Haug et al. (2020). Reflected light micrographs were acquired using a Zeiss AXIO ZoomV16 stereo microscope system. Each image is digitally superimposed from approximately 40–60 images taken in separate focal planes, and combined using Helicon Focus 7 software. Data acquisition and data analysis for morphometrics used TpsDig232, OriginPro 2020 and PAST3.15. In this paper, hierarchical clustering analysis was used, and the UPGMA algorithm and Euclidean Distance were as the methods of the similarity measure.

## 3. Systematic palaeontology

Order: Hemiptera Linnaeus, 1758

Suborder: Fulgoromorpha Evans, 1946

Superfamily: Fulgoroidea Latreille, 1807

Family: Mimarachnidae Shcherbakov, 2007

Genus: *Jaculistilus* Zhang, Ren et Yao, 2018

Type species: *Jaculistilus oligotrichus* Zhang, Ren et Yao, 2018; by original designation and monotypy.

### *Jaculistilus xixuanae* sp. nov

(Figs. 1, 2)

Zoobank LSID: zoobank.org:pub:BC297EF3-1B43-421F-A79C-DBDE1565CA05.

**Etymology.** The specific name is from the first name of Xixuan Han, who is the first author's childhood friend. Name the fossil after her and wish her a happy birthday.

**Material.** Holotype, NIGP200044, housed in the in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing. Burmese amber, Kachin State, northern Myanmar, collected before 2016, gender unknown, quite well-preserved specimen with head and prothorax largely destroyed, abdomen unclear.

**Diagnosis.** Stem MP bent at about half of its length to outline the large eyespot (stem MP straight along in *J. oligotrichus*); MP with four terminals,  $MP_{1+2}$  forked apicad of  $MP_{3+4}$  forking (both forks  $MP_{1+2}$  and  $MP_{3+4}$  at same level in *J. oligotrichus*). Two dominating eyespots placed horizontal and located in the middle of tegmen, at about  $\frac{1}{3}$  and  $\frac{2}{3}$  of its length, and the other four lateral eye spots located longitudinally in pairs at wing base, at about  $\frac{1}{8}$  of tegmen length and on membrane, at about  $\frac{7}{8}$  of tegmen length (no such coloration in *J. oligotrichus*). Posterior margin of pronotum

shallowly concave (more roundly concave in *J. oligotrichus*). Metatibio-metatarsal formula: 6: 6: 7 (6(6): 7(7): 7(7) in *J. oligotrichus*).

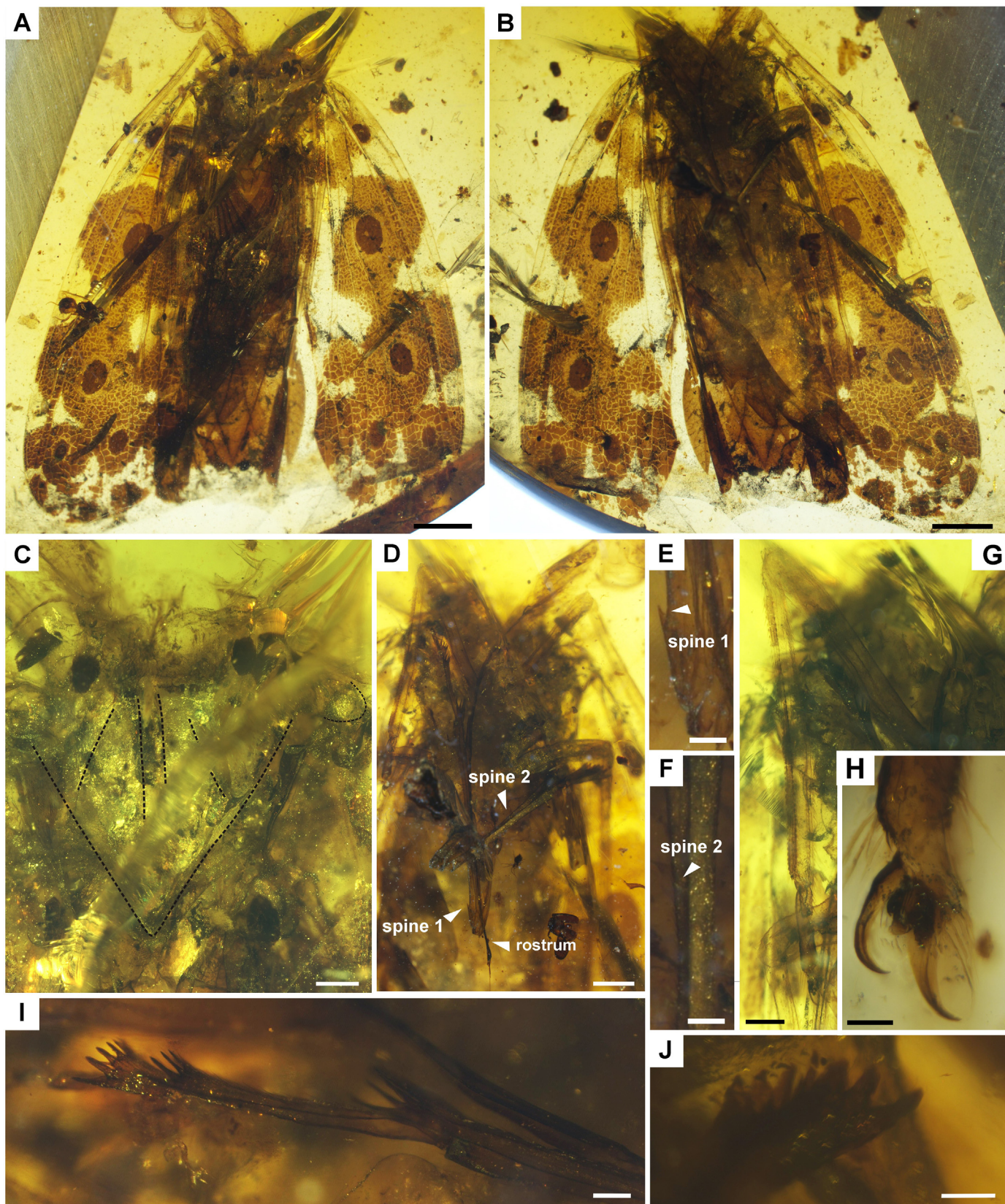
**Description.** The preserved part of body length 13.36 mm (without wings); preserved part with tegmina 18.86 mm (with wings). Head missing, only rostrum preserved in ventral view; rostrum elongate, reaching far beyond the meta coxae, about 6.99 mm long.

**Prothorax** seriously damaged, posterior margin of pronotum shallowly concave medially. Mesonotum 3.28 mm in length, 3.14 mm in width, with a pair of parallel median carinae, lateral carinae nearly straight, diverging posteriad. Tegula distinct.

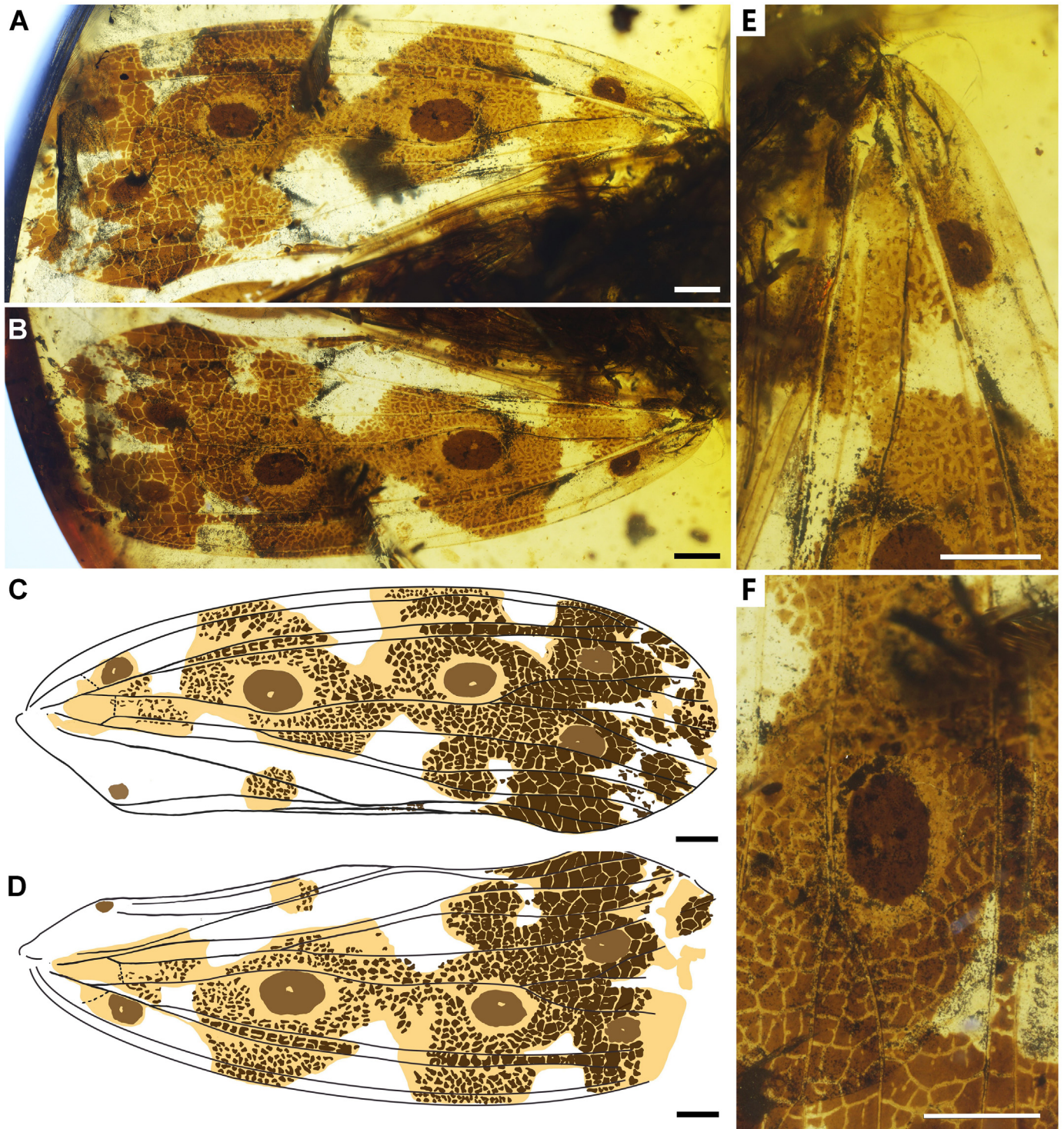
**Tegmen** membranous, 15.48 mm long, 5.39 mm wide, length/width ratio about 2.87, with distinct coloration six eyespots, large colored patterns around eyespots, membrane with slightly darker coloration. Two dominant eyespots placed horizontally along MP stem and located in the middle of tegmen, two smaller pairs at base, at about  $\frac{1}{8}$  of tegmen length, not surrounded by distinct colored area and on membrane, at about  $\frac{7}{8}$  of tegmen length, surrounded by darker colored areas; two lighter, subtriangular areas at about half of tegmen length, and less regular lighter patches on membrane near margin and apex. Meshwork of veinlets lighter. Costal margin slightly curved at base, then arcuate to widely arcuate anteroapical angle, apex rounded (damaged), posteroapical angle widely arcuate, tornus long, since the level of MP forking, convex, claval margin straight. Basal cell weak, arculus weak, stem Pc + CP almost parallel to costal margin. Costal area narrow and long, narrowing toward tegminal apex. Common stem ScP + R + MP (+CuA) thickened, stem ScP + R leaving basal cell anteriad from basal, weakened section of CuA ('arculus'), stem ScP + R about as long as common stem ScP + R + MP (+CuA); ScP + RA and RP single, almost parallel to each other since the separation, stem ScP + R subparallel to costal margin, apically fused with Pc + CP. Stem MP straight, diverging mediad at base, then arcuately bent, to omit first large eyespot, then subparallel to costal margin, forked apically, apicad of widest point of cubitoanterior cell, branch  $MP_{1+2}$  shorter than terminals  $MP_3$  and  $MP_4$ , forked apicad of branch  $MP_{3+4}$  forking, marginal distances between terminals  $MP_1$ ,  $MP_2$ ,  $MP_3$  and  $MP_4$  subequal. Very basal section of CuA ('arculus') weakened, stem CuA straight, parallel to basal portion of CuP, forked basad of claval veins junction, branch  $CuA_1$  arcuate, branch  $CuA_2$  sinuate. CuP straight at base, then slightly sinuate apicad of claval veins junction, since level of MP fork. Claval veins Pcu and A1 fused well basad of half of tegmen length, fused vein Pcu + A1 slightly arcuate, reaching margin at posteroapical angle. Irregular meshwork of veinlets between longitudinal veins distinct. Radial cell long, narrow, about as wide as costal area; medial cell long, in apical portion of equal width; anteroapical cell widest slightly basad of middle, narrowing apicad, cubitoanterior cell narrow in basal  $\frac{2}{3}$  then widened; cubitoposterior cell widest in the middle, then tapered and again widening apicad; anal cell narrow, elongate reaching to posteroapical angle.

**Hind wing** membranous, shorter than tegmen, with irregular meshwork of veinlets between longitudinal veins.

**Legs** elongate, tibiae subquadrate in cross section, with rows of shore setae along carinate margins. Profemur slightly longer than mesofemur and metafemur, about 3.13 mm long, 1.64 mm long, 2.27 mm long, respectively. Protibia shorter than mesotibia, about 4.05 mm long and 4.22 mm long, respectively. Pro- and mesoleg basitarsomeres much shorter than apical tarsomeres. Length of protarsomeres: I 0.30 mm, II 0.98 mm, the length of mesotarsomeres: I 0.38 mm, II 0.90 mm; basal claws distinct, sickle-like, arolium large, bilobate. Metatibia 5.58 mm long, carinate, with a small subgenual spine (spine 1 in Figs. 1D, E) and at least a lateral small spine (spine 2 in Figs. 1D, F), and row of 6 apical teeth, lacking subapical setae; basimetatarsomere the longest, 1.49 mm long, longer than



**Fig. 1.** *Jaculistilus xixuanae* sp. nov., holotype NIGP200044, photograph. (A) Dorsal view. (B) Ventral view. (C) Showing mesonotum in dorsal view. (D) Showing long rostrum. (E) Showing magnified of the small subgenual spine (spine 1) of metatibia from (D). (F) Showing magnified of a small lateral spine (spine 2) of metatibia from (D). (G) Showing foreleg. (H) Showing pretarsus of midleg. (I) Showing right metatibio-metatarsal structures. (J) Showing magnified of 6 apical teeth of left metatibia. Scale bars = 2 mm (A, B), =1 mm (D), =0.5 mm (C, G), =0.2 mm (E, F, I, J), =0.1 mm (H).



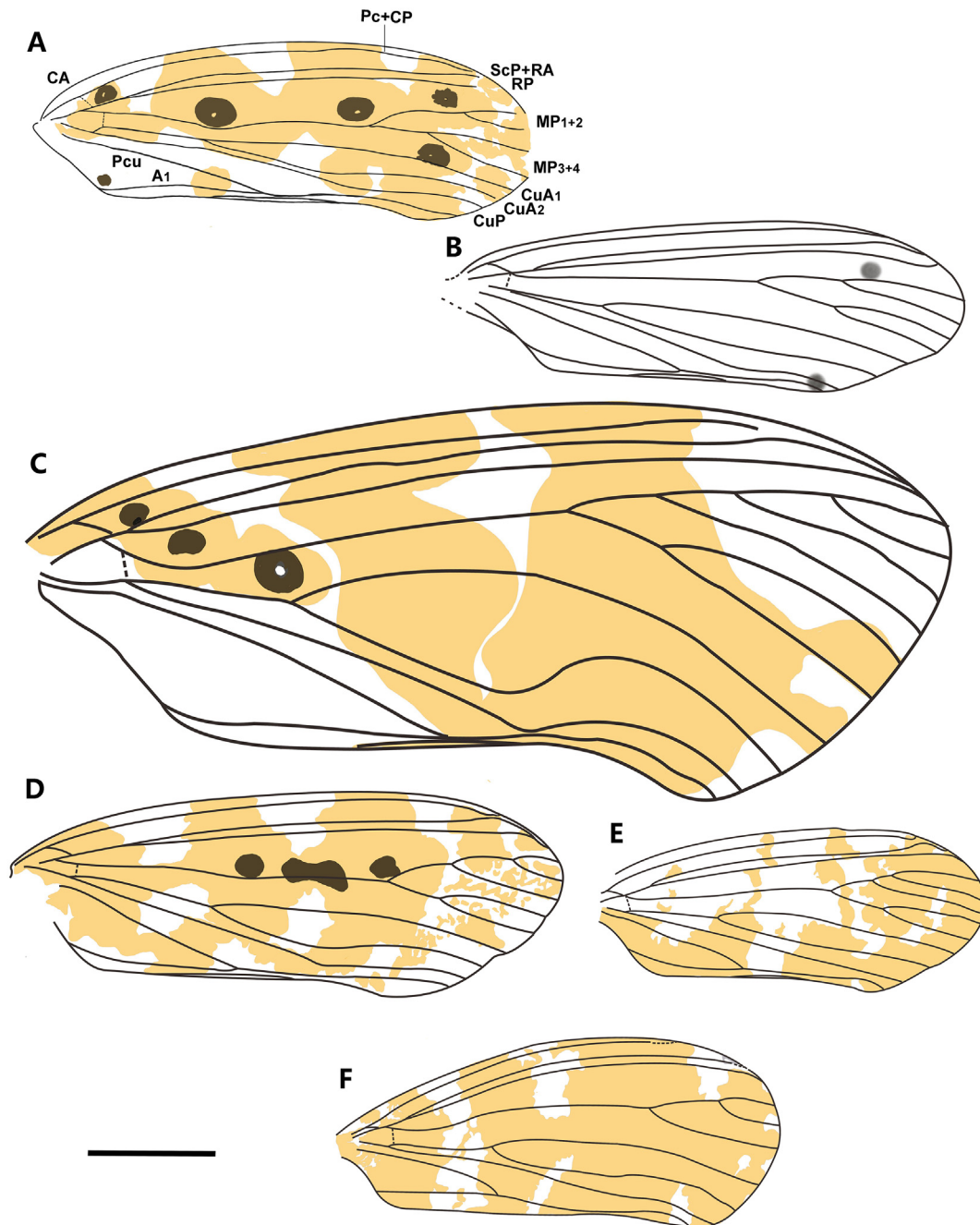
**Fig. 2.** Forewing of *Jaculistilus xixuanae* sp. nov., holotype NIGP200044. (A) and (B) Photograph, showing the left and right forewings, respectively. (C) and (D) Drawing, showing right and left forewings, respectively. (E) Showing magnified of anterior section of forewing from (B). (F) Showing magnified of anterior section of eye spot from (B). Scale bars = 1 mm (A–F).

combined length of mid- and apical metatarsomere, with 6 apical teeth in row, midmetatarsomere 0.47 mm long, with seven apical teeth, lacking subapical setae, widely fan-like dispersed, apical tarsomere elongate, longer than midmetatarsomere, tarsal claws large, sickle-like, arolium bilobate (see Fig. 1H–J). Abdominal structures not preserved.

*Horizon and occurrence.* Upper Cretaceous, earliest Cenomanian ('mid-Cretaceous' auct.); Angbamo site, Tanai Township, Myitkyina District, Kachin State, northern Myanmar.

***Xiaochibangus* gen. nov**

Zoobank LSID: zoobank.org:pub:BC297EF3-1B43-421F-A79C-DBDE1565CA05.



**Fig. 3.** Drawings for comparison. (A) *Jaculistilus xixuanae* sp. nov. (B) *Jaculistilus oligotrichus* Zhang et al., 2018. (C) *Dachibangus trimaculatus* Jiang et al., 2018. (D) *Xiaochibangus formosus* (Fu et al., 2019) comb. nov. (E) *Xiaochibangus hui* (Zhang, Yao and Pang, 2021) comb. nov. (F) *Multistria orthotropa* Zhang, Yao et Pang, 2021. Scale bars = 4 mm (A–F).

**Type species.** *Dachibangus formosus* Fu et al., 2019; by present designation.

**Etymology.** The generic name is derived from Chinese words ‘xiao chi bang’ meaning “small wing”. Gender: masculine.

**Diagnosis.** Pronotum with posterior area rugulose (not rugulose in *Dachibangus*); tegminal costal area narrow, exceeding  $\frac{2}{3}$  tegmen-length, termini of Pc + CP, ScP + RA and RP reaching margin separately; ScP + RA and RP single, close to each other, subparallel; stem MP slightly shifted anterior of median tegminal axis (stem MP distinctly shifted anterior of median axis – costalization in *Dachibangus*), MP with five terminals, MP<sub>1+2</sub> forked into three terminals (4 terminals of MP<sub>1+2</sub> in *Dachibangus*); CuA<sub>2</sub> slightly arcuate to

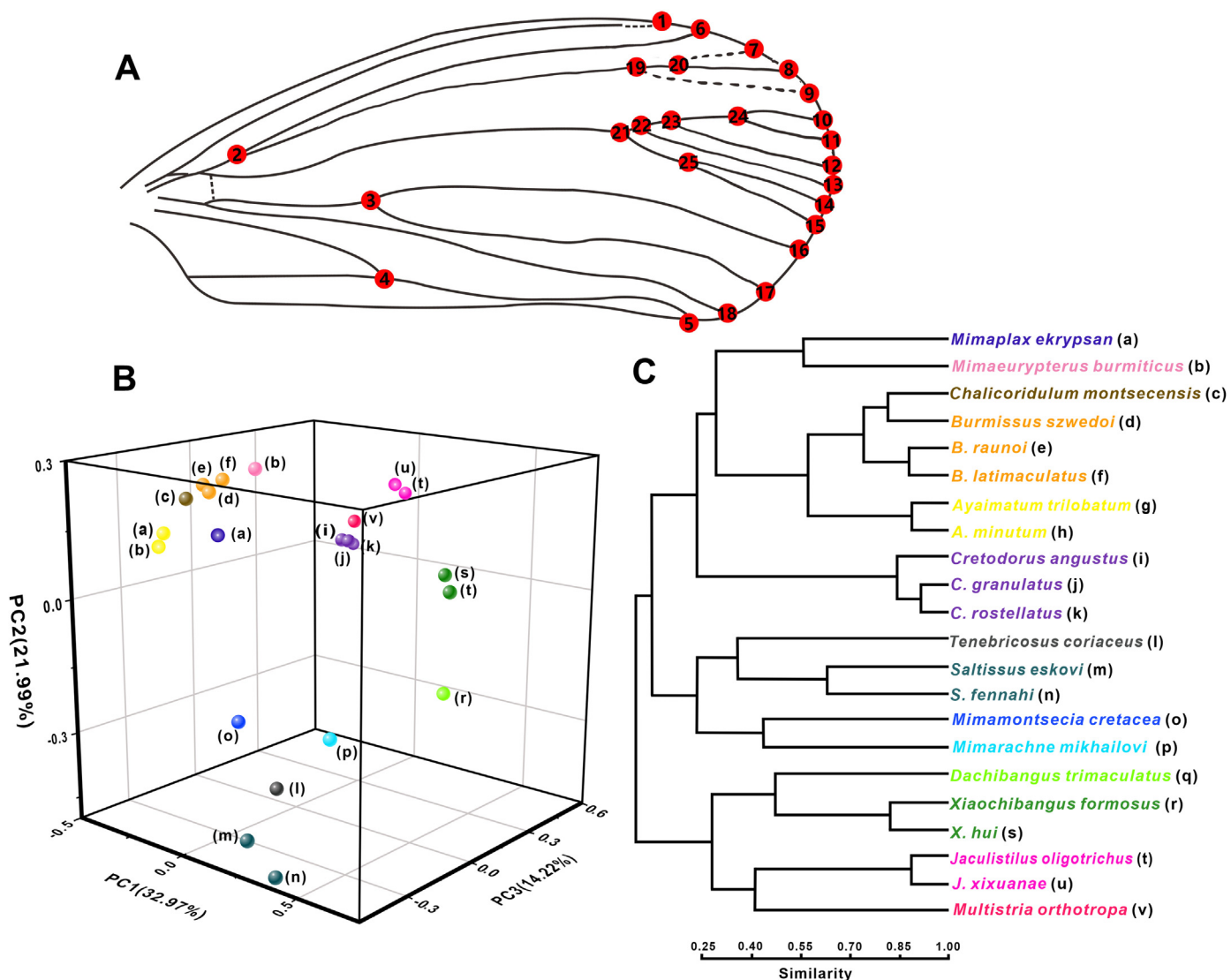
sinuate (CuA<sub>2</sub> distinctly arcuately bent in *Dachibangus*); entire tegmen with distinct meshwork of veinlets, whether or not the area of tegmen with pigmentation.

**Composition.** *Xiaochibangus formosus* comb. nov., *Xiaochibangus hui* comb. nov.

**Horizon and occurrence.** ‘mid-Cretaceous’, lowermost Cenomanian; Hukawng Valley, Kachin State, northern Myanmar.

#### 4. Discussion

The new species *J. xixuanae* sp. nov. can be assigned to the family Mimarachnidae and the genus *Jaculistilus* Zhang, Ren et Yao, 2018



**Fig. 4.** Geometric morphometrics analysis of the forewing of species in Mimarachnidae. (A) Landmarks of the modelling of the forewing of Mimarachnidae, showing 25 landmarks associated with the vein difference of the forewings of 21 mimarachnid species. (B) Result of g principal component analysis, showing principal components 1, 2 and 3. (C) Result of cluster analysis, with red square representing the species with discernible eyespots. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

based on the combination of the following characters: mesonotum with double median carina, basal cell weak, arculus weak; tegmina with simplified venation and irregular polygonal meshwork of veinlets, costal area long and narrow MP with four terminals, torus distinct; marginal membrane absent; and, metatibia with a small subgenual spine. The results of morphometric analysis and cluster analysis support that *J. xixuanae* sp. nov. is very similar to *J. oligotrichus* (Fig. 4).

Here we selected 25 landmarks associated with the vein difference of the forewings of 21 mimarachnid species for PCA and cluster analysis (Fig. 4A), to determine the similarity between the veins and thus speculate on the similarity of species. The first three PCs account for 32.97%, 21.99%, and 14.22% of the variation, and the cumulative variation explains 69.19% of the total wing shape variance, which could reflect the main variation pattern of forewing vein difference to a certain extent (Fig. 4B and Table 3). According to the analysis of eigenvalues and eigenvector matrix (Tables 3 and 4), the main characteristics that can be used to distinguish the

differences of the veins are quantitatively summarized, including the number and the position of the branchings of  $MP_{1+2}$ ,  $MP_{3+4}$  and RP, as well as the position of the end of Pc + CP. The similarity between wings can be judged by the distance between the scatterplots. But it's important to note that incomplete veins of wings can affect the results; for example, the scatterplot distance between *Saltissus eskovi* and *S. fennahi* of the same genus is greater than the distance between the other species of the same genus with complete wings (Fig. 4B). Hierarchical Cluster analysis was used here and Euclidean Distance was used as the method of the similarity measure (Fig. 4C). PCA analysis and clustering results together showed similarities among species.

Within Mimarachnidae, the genus *Jaculistilus* in tegminal venation appears similar to genera *Dachibangus* Jiang et al., 2018 and *Multistria* Zhang, Yao et Pang, 2021 (Fig. 3): they all present tegmen with long and narrow costal area, reaching more than  $\frac{2}{3}$  of tegmen length, ScP + RA and RP single, MP forked with no less than three terminals, common portion Pcu + A1 elongate and reaching

**Table 2**  
The meaning of each landmark referring to Fig. 4A.

Number	Position	Number	Position
1	The end of Pc + CP	14–15	The ends of branchings of MP <sub>3+4</sub>
2	The fork of ScP + RA	16–17	The ends of CuA <sub>1</sub> , CuA <sub>2</sub>
3	The fork of CuA	18	The end of CuP
4	The connection of Pcu + A <sub>1</sub>	19	The fork of RP <sub>1+2</sub> and RP <sub>3</sub>
5	The end of common stem of Pcu + A <sub>1</sub>	20	The fork of RP <sub>1+2</sub>
6	The end of ScP + RA	21	The fork of MP <sub>1+2</sub>
7–9	The ends of RP <sub>1</sub> –RP <sub>3</sub>	22–24	The forks of branchings of MP <sub>1+2</sub>
10–13	The ends of branchings of MP <sub>1+2</sub>	25	The forks of branchings of MP <sub>3+4</sub>

**Table 3**  
Eigenvalues and contributions of the first six principal components of landmarks.

Principal Component Number	Eigenvalue	Percentage of Variance (%)	Cumulative (%)
1	0.11988	32.97	32.97
2	0.07996	21.99	54.97
3	0.05171	14.22	69.19
4	0.04188	11.52	80.71
5	0.02357	6.48	87.19
6	0.01447	3.98	91.17

margin close to posteroapical angle, in proximity of CuP terminus. Besides, taxa of all these genera present eyespots or distinct color patterns. However, based on the line diagram of all the species in these three genera (Fig. 3), we found that the original three species in *Dachibangus* vary significantly in size, the number of terminals of MP and some other features. As result of features analysis and support from morphometric analysis the new genus *Xiaochibangus* gen. nov. can be established. Two species formerly placed in *Dachibangus*, could be placed within it, resulting in new nomenclatorial and taxonomic combinations: *X. formosus* (Fu et al., 2019) comb. nov. and *X. hui* (Zhang, Yao et Pang, 2021) comb. nov. Both species appear close in size, and their tegminal MP are with five terminals and both MP<sub>1+2</sub> are with three terminals. Tegmen of *D. trimaculatus* is very large in size, and almost twice as long as in *X. formosus* comb. nov.; its MP stem gives six terminals, with MP<sub>1+2</sub> is with four terminals. Through the principal component and cluster analyses based on landmarks of the forewings we selected (Fig. 4 and Table 2), we found the discrepancy between *D. trimaculatus* and *X. formosus* comb. nov. plus *X. hui* comb. nov. is much greater than the interspecific differences between other genera, and even greater than the differences between some genera. Among the features we selected preliminarily, for example, the location where Pc + CP reaches the wing margin, whether MP forks, the number and location of forks, and the location of forks and branches of CuA, are all features of importance, affecting the classification results. The statement is further supported by a distinct grid of veinlets, whether or not a color-patterned area presented by *Xiaochibangus* gen. nov.

In addition, from GMA results (Fig. 4), we also find that the genus *Burmissus* Shcherbakov, 2017 is superficially similar to the genus *Chalicoridulum* Szwedo et Ansorge, 2015. They all have the same number of longitudinal veins and similar pattern of venation distribution. However, no taxonomic and nomenclatorial changes are proposed here in respect to these taxa, as they seem to be well separated by other morphological characters, viz., metalegs armature and different geographic and chronological position. In any case, further examination and more specimens are required. Other phenomena, as morphological deformation due to taphonomic biases, must be considered as well. With the increase of specimens, the data selection and

operation methods of morphometry also need to be further improved and adjusted.

The most striking feature of the species described above – *J. xixuanae* sp. nov. is the presence of six eyespots on each tegmen and four smaller eyespots surrounded by dark color patterns accompanied by a variable grid pattern of veinlets, which is distinctly different from its congeneric species *J. oligotrichus*. Eyespots are often assumed to intimidate enemies or to divert their attack position (e.g., Stevens, 2005). Mimarachnidae was initially thought to be group mimicking spiders, typically by their dark silhouette on the wing, dark abdomen, and dark eyespots with central pupil on the apical and subapical part of the wing. The difference in color pattern between *Mimarachne mikhailovi* Shcherbakov, 2007 and *J. xixuanae* sp. nov. lies in eyespots of the latter distributed on whole tegmen area, with two, large principal ‘eyes’ in the middle. If we hypothesize that such color pattern is mimicking a spider, *J. xixuanae* sp. nov. seems to mimic the spider’s prosoma with eyes in front. Shcherbakov (2007) suggested the pattern with eyes mimicking ‘face’ of spider as present in jumping spiders Salticidae or wolf spiders Lycosidae, but jumping spiders and wolf spiders have not been found in the Mesozoic. However, there are reports of spiders with large frontal eyes, as Lagonomegopidae Eskov et Wunderlich, 1995 or Salticoididae Wunderlich, 2008 (Penney and Selden, 2011; Magalhaes et al., 2020). If this planthopper family mimicked spiders, it likely suggests that spiders with eyes of highly stereoscopic visual abilities existed and were widely distributed during the Cretaceous. Mimicking spiders habitus with color pattern or other morphological structures is known among some recent planthoppers, e.g. in nymphs of Fulgoridae (Zolnerowich, 1992), imagines of Derbidae (Floren and Otto, 2001) and Issidae (Gnezdilov and Fletcher, 2010; Meng et al., 2016).

Another possibility to explain such phenomenon is assumption that the color and veinlets patterns surrounding each eyespot, the color patterns with polygonal grids of veinlets around the eyes likely mimic scales, seeming like lizard eye. This assumption could be supported by rich and diversified finding of small lizards as inclusions in Burmese amber (Arnold and Poinar, 2008; Daza et al., 2014, 2016, 2018, 2020; Fontanarrosa et al., 2018; Xing et al., 2020a, b; Bolet et al., 2020, 2021; Wang and Xing, 2020; Wagner et al., 2021; Černanský et al., 2022) as well as small other proving these creatures commonly penetrate bark surface on which mimarachnid planthoppers were present too. There were a variety of eyespots in the mimarachnids, such as patches of a single color and a concentric ring with a pupil (Fig. 3). These patterns are summarized to appear in Mesozoic kalligrammatids corresponding to Type 5 and Type 6 patterns (Labandeira et al., 2016). Eyespots are very common among insects, and the eyespots of different insects can be obtained by convergent evolution (e.g., Monteiro, 2008), and the eyespots in mimarachnids may also represent an independent evolution.



**Table 4**  
Eigenvector matrix of the principal components 1, 2 and 3 of the forewings with 25 landmarks of 21 mimarachnid species.

Number	PC1 (32.97%)	PC2 (21.99%)	PC3 (14.22%)	Number	PC1 (32.97%)	PC2 (21.99%)	PC3 (14.22%)
X1	0.02	0.11	0.55	Y13	0.00	0.02	0.00
Y1	-0.05	0.04	0.03	X14	-0.06	0.12	-0.55
X2	-0.15	0.05	-0.07	Y14	0.00	-0.04	0.02
Y2	-0.01	0.08	0.01	X15	0.38	0.19	-0.18
X3	-0.19	0.07	-0.01	Y15	-0.04	-0.01	0.02
Y3	0.02	0.05	0.00	X16	-0.19	0.14	0.08
X4	-0.16	0.07	0.00	Y16	0.01	-0.05	0.01
Y4	0.00	0.01	0.01	X17	-0.18	0.12	0.08
X5	-0.13	0.17	0.04	Y17	0.01	-0.04	0.00
Y5	-0.03	-0.03	0.01	X18	-0.17	0.10	0.07
X6	-0.15	0.15	0.09	Y18	0.00	-0.04	-0.01
Y6	-0.03	-0.01	-0.03	X19	-0.08	-0.44	0.01
X7	-0.18	0.22	0.12	Y19	0.01	-0.02	0.00
Y7	0.00	0.00	0.01	X20	-0.05	-0.30	-0.02
X8	-0.04	-0.38	-0.07	Y20	0.01	-0.01	0.00
Y8	0.02	-0.03	-0.02	X21	-0.08	0.08	-0.47
X9	-0.08	-0.49	0.00	Y21	0.02	0.01	-0.05
Y9	0.01	0.01	0.00	X22	0.38	0.02	0.13
X10	-0.17	0.16	0.07	Y22	0.04	0.02	0.01
Y10	0.01	-0.03	-0.01	X23	0.21	-0.07	0.05
X11	0.43	0.03	0.13	Y23	0.02	0.02	0.01
Y11	-0.03	0.00	0.00	X24	0.04	-0.11	0.03
X12	0.23	-0.07	0.05	Y24	0.01	0.02	0.00
Y12	-0.02	0.01	0.00	X25	0.34	0.17	-0.17
X13	0.04	-0.11	0.03	Y25	0.02	0.02	0.01

Traditionally, in both the popular and scientific literature, wing spots are repeatedly assumed to mimic the eyes of the predator's own enemies and their role as antipredator mechanisms has been discussed since the 19th Century (Ruxton et al., 2004; Stevens, 2005; Stevens et al., 2008). Two broad hypotheses explain how eyespots may be effective against predation. Large, conspicuous eyespots are considered to be intimidating for the predator thereby decreasing the chances of attack – the “Intimidation Hypothesis”, whereas smaller eyespots closer to the wing margin are thought to attract attention toward themselves thus deflecting predatory attacks away from the more vital parts of the prey – the “Deflection Hypothesis” (Mukherjee and Kodandaramaiah, 2015). Eyespots could either intimidating predators or deflecting predator attacks towards less important parts of the prey's body, but their effectiveness is dependent on multiple factors (Lyytinen et al., 2003; Stevens, 2005; Kodandaramaiah 2011; Prudic et al., 2015; Skelhorn et al., 2016; Ho et al., 2016; Chan et al., 2021). The number of eyespots has also been considered to be correlated with activity levels and behavioral patterns (Van Dyck et al., 1997; Stevens, 2005; Mukherjee and Kodandaramaiah, 2015; De Bona et al., 2015). The eyespots in the front and middle of the wing in *J. xixuanae* sp. nov., *D. trimaculatus* and *X. formosus* (Fu et al., 2019) comb. nov., could be explained by both mechanisms (however the best studied on butterflies), the conspicuousness of the eyespots, may have caused aversion due to sensory biases, neophobia or sensory overloads to the predators. In a word, the new species *J. xixuanae* sp. nov. adds not only a new taxonomic diversity data, but also new points to the evolutionary mechanisms, disparity and diversity of mimetic eyespots in the Hemiptera.

## 5. Conclusion

A new species of *Jaculistilus* in Mimarachinidae, *Jaculistilus xixuanae* sp. nov., is described from mid-Cretaceous Kachin amber. The forewing coloration pattern is typically characterized by six eye spots on each tegmen and with total 12 eyespots, showing new information of color patterns adding new data to disparity and diversity of Mimarachinidae. Results of GMA principal component

and cluster analyses of forewing venation patterns allowed to propose a new genus and offer new taxonomic and nomenclatorial combinations: *Xiaochibangus formosus* comb. nov. and *Xiaochibangus hui* comb. nov., and indicated morphometrics as a useful tool in palaeoentomologists toolbox.

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## Data availability

Data will be made available on request.

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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.2022.105368>.