

## Short communication

## First hairy cicadas in mid-Cretaceous amber from northern Myanmar (Hemiptera: Cicadoidea: Tettigarctidae)

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## ABSTRACT

Two new genera and two new species of Tettigarctidae, *Cretotettigarcta burmensis* gen. et sp. nov., and *Vetuprosbole parallelica* gen. et sp. nov., are described and illustrated based on two well-preserved specimens from the mid-Cretaceous amber of northern Myanmar. *C. burmensis* is assigned to the subfamily Tettigarctinae, providing several peculiar features that are not found in the extant representatives of Tettigarctinae: apex of fore femur armed with distal conical spine; hind tibia armed with three lateral spines; ScP + R branching distinctly after MP branching; MP<sub>3+4</sub> connecting CuA<sub>1</sub> by cross vein m-cu. The other species *V. parallelica* is tentatively assigned to the tribe Turutanoviini of Cicadoprosobolinae. *C. burmensis* resembles *Sunotettigarcta hirsuta* from the Middle–Upper Jurassic of Daohugou beds (northeastern China) in its general characters of wing venation and pronotum, which suggests a close relationship between the Daohugou and Burmese amber biotas. It likely reveals a range shift southwards after the Daohugou palaeoecosystem collapsed during the Late Jurassic in north China. Our discovery represents the first record of amber-entombed Tettigarctidae from the Mesozoic, which greatly widens the biogeographic distribution and increases the palaeodiversity of the Mesozoic tettigarctids. It also provides new insights into the morphological diversification and early evolutionary history of tettigarctids.

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## 1. Introduction

The family Tettigarctidae, also known as the hairy cicadas, is considered as a sister group of Cicadidae (singing cicadas) as evidenced by phylogenetic studies based on both morphology and molecular data (Duffels, 1993; Cryan, 2005; Moulds, 2005). Tettigarctids differ from other cicadas in many important features, including greatly expanded pronotum, fully developed nodal line on the forewing, and nymphs bearing nine antennal segments (Evans, 1941; Moulds, 1990; Nel, 1996). Due to a lack of tympanal auditory organs, tettigarctids are not capable of producing the characteristic sound of singing cicadas (Claridge et al., 1999). Unlike the extant cicadids, adults of living Tettigarctidae are nocturnal, avoiding strong

light during daylight hours (Evans, 1941; Wang and Zhang, 2009). Tettigarctids first appeared in the terminal Triassic (Rhaetian) of England, representing the most basal lineage of Cicadoidea (Whalley, 1983). Tettigarctidae is currently a relictual group, with only two extant species attributed to a single genus, i.e., *Tettigarcta tomentosa* White, 1845 from Tasmania and *T. crinita* Distant, 1883 (Fig. 1) from southeastern Australia (Whalley, 1983; Shcherbakov, 2009). Both species are restricted largely to high altitudes or frosty areas in Australia (Evans, 1941; Carver et al., 1992). Most *T. crinita* have been captured at an altitude of ca. 1600 m in summer and *T. tomentosa* occurs at an altitude of ca. 800 m in winter (Evans, 1941; Liu et al., 2016). They have a greatly expanded pronotum, a tegmen dotted with reddish-brown spots or otherwise dull, and more strikingly, the characteristic extreme hairiness of the body (Evans, 1941).

To date, fossil tettigarctids comprise 22 genera and 37 extinct species attributed into two subfamilies, Tettigarctinae Distant, 1905 and Cicadoprosobolinae Becker-Migdisova, 1947 with three tribes respectively, occurring from the Upper Triassic to Miocene

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**Fig. 1.** General habitus of two extant tettigarctid species. A, male of *Tettigarcta crinite* Distant, 1883, dorsal view; B, same as A, ventral view. ©Australian National Insect Collection, CSIRO. Scale bar: 5 mm.

(Shcherbakov, 2009; Sanborn, 2014; Moulds, 2018). Fossil tettigarctids are distributed principally in the Northern Hemisphere, and only four monotypic genera are known from the Lower Cretaceous (Aptian) in Brazil, Tunisia, and the early Miocene of New Zealand, complementing the meager record from Gondwana (Hamilton, 1990; Nel et al., 1998; Menon, 2005; Kaulfuss and Moulds, 2015). Tettigarctids flourished especially during the Jurassic to the Early Cretaceous. They are currently only confined to the middle to high latitudes areas of the North Hemisphere during the Jurassic, and distributed worldwide in the Early Cretaceous. By contrast, they are very rare as fossils from the mid-Cretaceous to the Cenozoic, with one sole nymph being reported from the Late Cretaceous in New Jersey and four monotypic genera from the Cenozoic of France, Scotland, Germany and New Zealand (Piton, 1940; Zeuner, 1944; Wappler, 2003; Kaulfuss and Moulds, 2015). The decline of Tettigarctids is probably due to the angiosperm floristic revolution and the competitive displacement with singing cicadas (Wang and Zhang, 2009).

Here we report two new genera and two species of Tettigarctidae from the mid-Cretaceous Burmese amber, representing the first fossil record of the family from the Burmese amber.

## 2. Material and methods

The two new genera and species are described based on two adult specimens (NIGP167304, NIGP168021). One specimen (NIGP167304) is preserved in a piece of relatively opaque amber; the insect is laterally compressed with overlapped wings and it displays many fine details such as antenna, ocellus, rostrum, legs, tegmen and hind wings. The other specimen (NIGP168021) is preserved in a relatively clear yellowish amber, comprising a forewing and a hind wing. Both specimens are derived from amber deposits in the Hukawng Valley of Kachin Province in northern Myanmar (Yin et al., 2018; fig. 1A). The re-deposition age of Burmese amber was considered to be the earliest Cenomanian ( $98.79 \pm 0.62$  Ma; Shi et al., 2012), but biostratigraphic studies of the amber-bearing layers indicated an age of late Albian (Cruickshank and Ko, 2003), which is adopted in this paper. Amber pieces used for photomicrography were cut using a handheld

engraving tool, and polished using emery papers of different grain sizes and rare earth polishing powder. Observations and photographs were made using a Zeiss Discovery V16 stereoscope; photomicrographs with green background are taken using green fluorescence as light source attached to a Zeiss Axio Imager 2 light microscope; stacked using CombineZP software; line drawings were drafted with CorelDRAW X7 graphic software and optimized using Photoshop CS6. The material studied here is deposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

The venation terminologies and cell nomenclature used herein largely follow Nel et al. (2012) and Moulds (2005) with slight modifications and reference to the standardized terminology of the forewing venation in Fulgoromorpha (Bourgoin et al., 2015). The nomenclatural acts established herein are registered under ZooBank LSID urn:lsid:zoobank.org:pub:C639437F-AFAE-4FEF-9B95-6AB8221781B6.

## 3. Systematic palaeontology

Order: Hemiptera Linnaeus, 1758  
 Suborder: Cicadomorpha Evans, 1946  
 Superfamily: Cicadoidea Latreille, 1802  
 Family: Tettigarctidae Distant, 1905  
 Subfamily: Tettigarctinae Distant, 1905

Genus: *Cretotettigarcta* gen. nov.

Type species: *Cretotettigarcta burmensis* gen. et sp. nov.

*Etymology.* The genus name is composed of the prefix *Creto-* derived from the Cretaceous and the extant genus *Tettigarcta*. The genus is registered under LSID urn:lsid:zoobank.org:act:8F6E92F6-B316-4E93-BCCA-B5D2152E51E8.

*Diagnosis.* The genus is characterized by the antennae bearing at least six elongate segments; tegmen small-sized, length about 8.2 mm; basal of MP and CuA connecting by a short cross vein; ScP + R branching into ScP + RA and RP distinctly after MP branching; MP<sub>1+2</sub> connecting MP<sub>3</sub> by cross vein im; MP<sub>3+4</sub> connecting CuA<sub>1</sub> by cross vein m-cu; hind wings, a6 cell wider than a5 cell and more than twice as wide as other cells; apex of fore femur armed with a distal conical spine; hind tibia armed with 3 lateral spines.

*Remarks.* The new genus resembles *Sunotettigarcta* Li et al., 2013 from the Middle to Upper Jurassic Daohugou beds (Inner Mongolia, China) by some distinct body structures and wing venation. However, it differs from the latter by the following characters: 1) body small, about 10.2 mm long (body length near 50 mm in *Sunotettigarcta*); 2) ScP + R branching distinctly after MP branching (ScP + R branching basal of MP branching in *Sunotettigarcta*); 3) MP<sub>1+2</sub> connecting MP<sub>3</sub> by cross vein im and MP<sub>3+4</sub> connecting CuA<sub>1</sub> by cross vein m-cu (MP<sub>2</sub> connecting MP<sub>3</sub> by cross vein im and MP<sub>4</sub> connecting CuA<sub>1</sub> by cross vein m-cu in *Sunotettigarcta*); and 4) apex of fore femur armed with a sole distal conical spine, hind tibia armed with three lateral spines (apex of fore femur lacking spine and hind tibia armed with two spines in *Sunotettigarcta*).

*Cretotettigarcta burmensis* sp. nov.

Figs. 2–4

*Etymology.* The specific epithet is derived from “Burma”, from where the specimen was discovered. The species is registered under LSID urn:lsid:zoobank.org:act: C639437F-AFAE-4FEF-9B95-6AB8221781B6.

*Holotype.* NIGP167304, male; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.





**Fig. 2.** Microphotographs of holotype (NIGP167304) of *Cretotettigarcta burmensis* gen. et sp. nov. from the mid-Cretaceous Burmese amber. A. lateral view, under normal reflected light; B. dorsal view, under normal reflected light. Scale bars: 2 mm.

**Locality and horizon.** Burmese amber, from deposits near the Tanai Village in the Hukawng Valley of northern Myanmar. Upper Albian.

**Diagnosis.** As for the genus (*vide supra*).

**Description.** Body covered with pubescence, total length 10.2 mm long (Fig. 2A and B); tegmen 8.2 mm long and 2.8 mm wide (Fig. 4A).

Head small, rounded apically with tiny granular protuberances. Compound eyes large, located laterally, ovoid (Fig. 3A). Antenna 1.3 mm long, scape hardly visible, pedicel broad but short, flagellum bears at least four elongate segments (Fig. 3C). Three ocelli present (Fig. 3A), ocellar triangle distinct, median ocellus oval, occur on the border of the frons, lateral ocelli globular, ecdysial suture convex. Postclypeus bulge, with a longitudinal impression (Fig. 3B), ca 1.7 mm long and 0.7 mm wide; anteclypeus ca 1.0 mm long and 0.5 mm wide. Rostrum three segments, ca 3.4 mm long with setae, reach to basal hind coxae and nearly to the apex of hind femora, basal segment short, and the third segment nearly twice as long as the second.

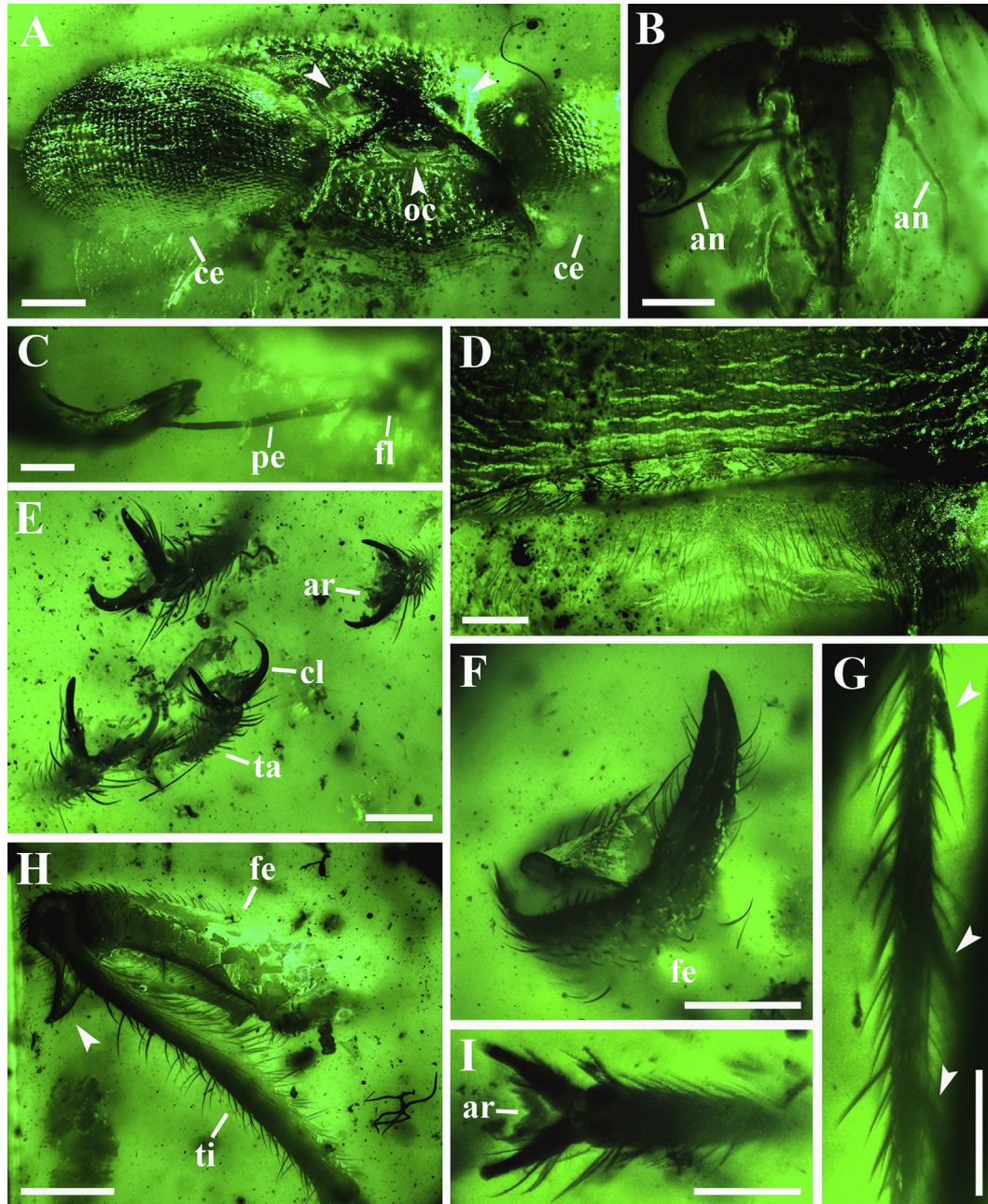
Pronotum greatly expanded, irregular hexagonal, nearly twice as wide as head, with anterior two-third tiny granular protuberances, posterior area transversely rugose and covered with dense pilosity (Fig. 3D); anterior margin nearly straight; posterior margin distinctly concave medially; posterior angles rounded; lateral margins diverging posteriad. Mesonotum greatly concealed, partly exposed, covered with dense pilosity (Fig. 3D).

Tegmen with length/width ratio about 2.9 (Fig. 4A), costal margin convex at about mid-wing; clavus reduced; basal cell

1.5 mm long and 0.3 mm wide; branch ScP + RA slightly longer than ScP + R; ScP + R branching into ScP + RA and RP reaching 0.41 of tegmen length, distinctly after MP branching; ScP nearly straight, after nodal line; RA with 2 branches, connecting RP by cross vein ir reaching 0.80 of tegmen length, RA<sub>1</sub> straight, almost parallel to RA<sub>2</sub>; RP single and straight, connecting MP<sub>1</sub> by cross vein r-m; MP with 4 branches, branching into MP<sub>1+2</sub> and MP<sub>3+4</sub> distinctly basal of nodal line; MP<sub>1+2</sub> connecting MP<sub>3</sub> by cross vein im; MP<sub>3+4</sub> connecting CuA<sub>1</sub> by cross vein m-cu and branching into MP<sub>3</sub> and MP<sub>4</sub> basal of MP<sub>1+2</sub> branching; CuA curved anteriorly, branching into CuA<sub>1</sub> and CuA<sub>2</sub> and connecting nodal line reaching 0.52 of tegmen length; CuA<sub>2</sub> sinuous, distinctly shorter than CuA<sub>1</sub>; cross vein m-cu longer than other cross veins; CuP nearly straight, fused with PCu at base of tegmen and then nearly straight, connecting posterior end of nodal line; nodal line at about half wing length, anterior end of nodal line connecting apex of ScP and then crossing MP<sub>1+2</sub> and MP<sub>3+4</sub>, base of CuA<sub>2</sub> along posterior end of nodal line. Hind wings (Fig. 4B) with marginal membrane, distinctly shorter than tegmen; RA single; RP single and straight, connecting RA by cross vein ir; MP with 3 branches; CuA branching into CuA<sub>1</sub> and CuA<sub>2</sub> basal of MP branching; MP<sub>3</sub> connecting CuA<sub>1</sub> by cross vein m-cu; m-cu 1.3 times longer than r-m and 2.5 times longer than ir; cell a6 trapezoidal in shape, slightly wider than cell a5 and more than twice as wide as other cells.

Legs covered with setae, especially tibiae; fore coxae enlarged, ca 1.2 mm long and 0.6 mm wide; fore trochanter cylindrical in shape, ca 0.24 mm long and 0.34 mm wide; fore femur robust (Fig. 3H), ca 1.7 mm long and 0.5 mm wide, apex of fore femur





**Fig. 3.** Enlargements of holotype (NIGP167304) of *Cretotettigarcta burmensis* gen. et sp. nov. under green fluorescence. A. enlargement of head, showing compound eyes and three ocelli (white arrows); B. showing details of clypeus and antenna; C. showing details of left antenna; D. posterior part of pronotum and mesonotum, showing transverse rugose and setae; E. claws; F. apex of fore femur, showing details of strong spine; G. hind tibia, showing three lateral spines (white arrows) and dense setae; H. showing details of fore leg; I. showing details of claw with arolium. Scale bars: 200  $\mu$ m in A, C–F, I; 500  $\mu$ m in B, G, H.

armed with a strong conical spine (Fig. 3F), ca 0.4 mm long; fore tibia slender (Fig. 3H), ca 1.5 times as long as fore femur; middle femur more slender than fore femur; middle tibia ca 2.7 mm long, slightly longer than fore tibia; hind tibia longer and thinner than other tibiae, with three lateral spines (Fig. 3G); all tarsi 3-segmented (Fig. 3E, I); hind tarsus nearly twice as long as fore tarsus, basal tarsomere as long as third tarsomere and longer than second tarsomere; tarsal claws sharp apically, short and robust; arolium present, relatively large (Fig. 3I).

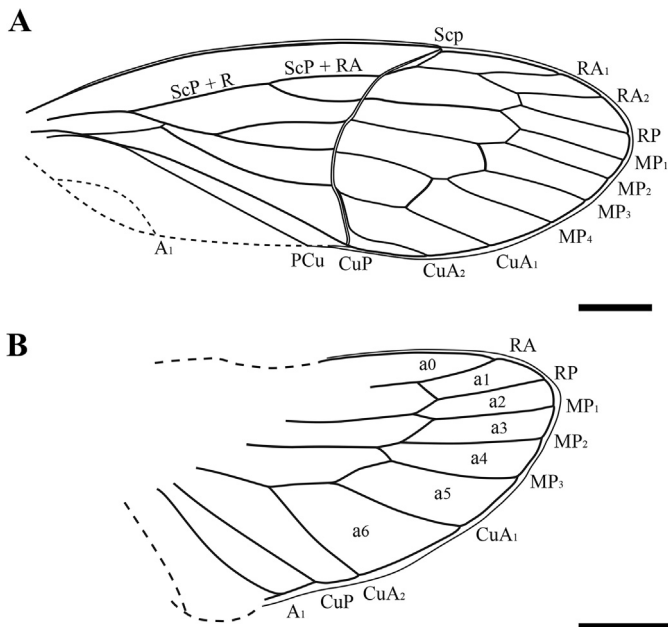
Subfamily: ? Cicadoprosobolinae Becker-Migdisova, 1947  
Tribe: ? Cicadoprosobolini Evans, 1956

Genus: ***Vetuprosobole*** gen. nov.

Type species: *Vetuprosobole parallelica* gen. et sp. nov.

**Etymology.** The genus-group name is a combination of Latin *vetus*, meaning 'old', and the suffix of the genus of *Cicadoprosobole*. The genus is registered under LSID urn:lsid:zoobank.org:act:2C79090B-5281-4BA3-B3FB-CB32CA50211C.

**Diagnosis.** The genus is characterized by tegmen medium-sized, length about 23 mm, terminal venation almost parallel; basal of MP and CuA connecting by a short cross vein; ScP + R short; MP branching nearer basal cell than nodal line; CuA branching at front half of tegmen; apical cells long; CuP fused with PCu at base; hind



**Fig. 4.** Line drawings of tegmen and hind wing of *Cretotettigarcta burmensis* gen. et sp. nov. A. left tegmen. B. hind wing. Scale bars: 1 mm.

wings, CuA branching into CuA<sub>1</sub> and CuA<sub>2</sub> at proximal one third of hind wings; cell a0 slightly wider than cell a1.

**Remarks.** Due to lacking critical characters of the apex of the tegmen, *Vetuprosbole parallelica* is tentatively assigned to the tribe Turutanoviini of Cicadoprosobolinae based on the following forewing characters: costal area wider than intercubital one; basal cell tapered towards apex; apical cell behind CuA<sub>2</sub> narrower than other cells. The new genus differs distinctly from other known genera in Turutanoviini by: 1) costal area with dark coloured bands, slightly arched (costal area without coloured bands, distinctly arched in other genera); 2) basal of MP and CuA connecting by a short cross vein (basal of MP and CuA coalescent directly in other genera); 3) CuP fused with PCu at base (CuP separating from PCu at base in other genera).

*V. parallelica* resembles species of *Sanmai* Chen et al., 2016 from the Daohugou beds by sharing a similar venation of the hind wing. However, it differs from the latter by cell a0 being slightly wider than cell a1, CuA branching nearer to base and cross veins transverse to inclined.

***Vetuprosbole parallelica* sp. nov.**

Figs. 5 and 6

**Etymology.** The specific epithet is derived from “parallel”, which indicates parallel venations of tegmen. The species is registered under LSID urn:lsid:zoobank.org:act:9B492FD1-46A7-456F-9554-C647051D862B.

**Holotype.** NIGP168021, sex unknown, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

**Locality and horizon.** Hukawng Valley, northern Myanmar. Upper Albian.

**Diagnosis.** As for the genus (*vide supra*).

**Description.** Tegmen about 23 mm long and 8.6 mm wide (Figs. 4A and 5A), with small setae on apical margin and posterior margin; costal area slightly arched, covered with punctate and dark coloured bands; apical margin unknown; basal cell tapered towards apex; branch ScP + R branching into ScP + RA and RP basal of MP

branching reaching 0.29 of tegmen length; ScP + RA 3.5 times longer than ScP + R; ScP curved; RA with 2 branches; RP single; MP with 4 parallel branches; branching into MP<sub>1+2</sub> and MP<sub>3+4</sub> distinctly basal of nodal line reaching 0.31 of hind wings length; MP<sub>3+4</sub> branching into MP<sub>3</sub> and MP<sub>4</sub> distinctly basal of MP<sub>1+2</sub> branching into MP<sub>1</sub> and MP<sub>2</sub> reaching 0.55 of tegmen length; MP<sub>2</sub> connecting MP<sub>3</sub> by cross vein im; MP<sub>4</sub> connecting CuA<sub>1</sub> by cross vein m-cu reaching 0.61 of tegmen length; CuA nearly straight, branching into CuA<sub>1</sub> and CuA<sub>2</sub> reaching 0.45 of tegmen length; CuA<sub>1</sub> almost parallel to CuA<sub>2</sub> and 1.6 times longer than CuA<sub>2</sub>; cross vein im longer than other cross veins; CuP fused with PCu at base of tegmen and connecting posterior end of nodal line; A<sub>1</sub> slightly arched at base, terminating at inner margin nearly as the same level as R + M branching; anterior portion of nodal line fused with base of ScP and then separated, basal of CuA<sub>2</sub> along posterior end of nodal line.

Hind wings (Figs. 4B and 5B) with small setae on apical margin and posterior margin, triangular in shape, with marginal membrane; branch ScP + R branching into ScP + RA and RP reaching 0.18 of hind wings length; ScP + RA branching into ScP and RA reaching 0.51 of hind wings length; RA and RP single; MP with 3 branches; CuA branching into CuA<sub>1</sub> and CuA<sub>2</sub> reaching 0.29 of hind wings length; MP<sub>1</sub> connecting MP<sub>2</sub> by cross-vein m; MP<sub>3</sub> connecting CuA<sub>1</sub> by cross vein m-cu; cross vein r-m more than twice longer than m-cu and slightly longer than other cross veins; cell a0 relatively large, slightly wider than cell a1, cell a1 nearly subequal to cell a5 in width, cell a6 longer and wider than other cells.

#### 4. Discussion

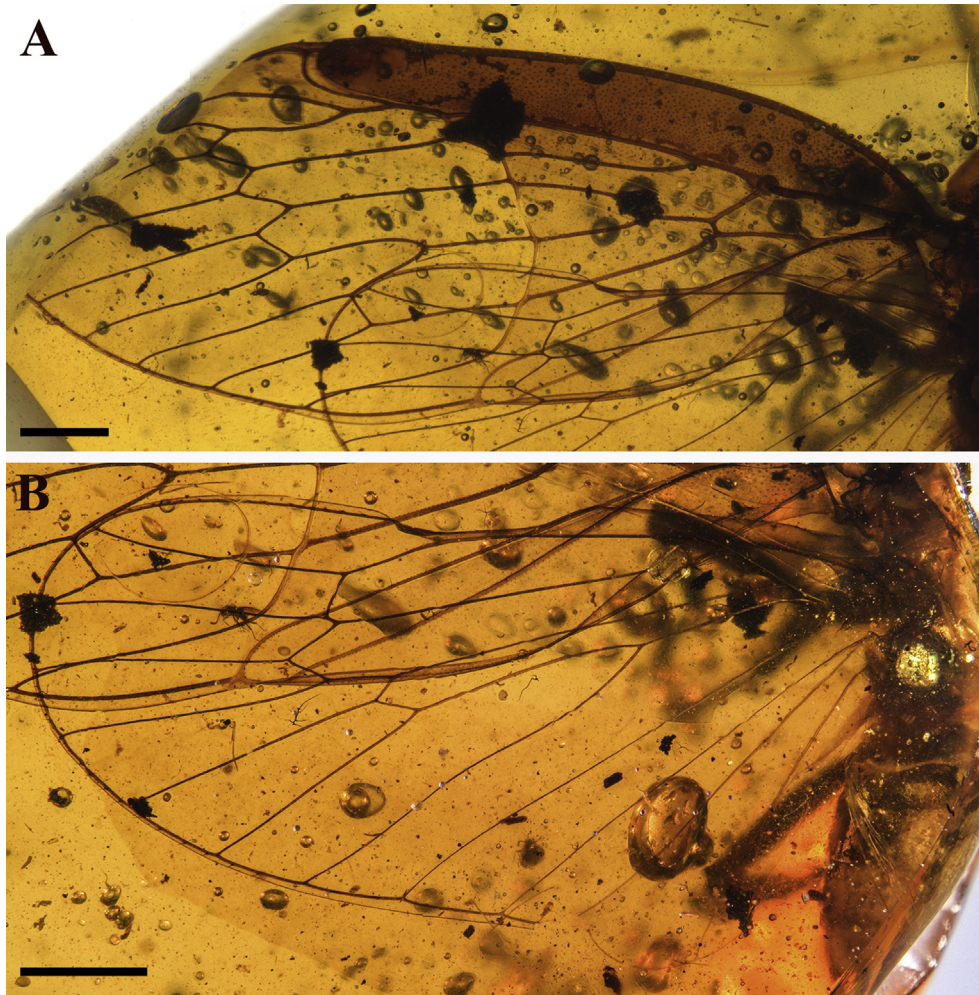
Little is known about the systematic position, early evolution, palaeoecology and palaeobiogeography of Tettigarctidae (Nel et al., 1998). Since more than half of the described fossil tettigarctids are described based only on tegmen fragments (e.g., *Paratettigarcta*), or hind wings (e.g., *Eotettigarcta*). So far, the generic classification of Mesozoic tettigarctids has been largely based on the tegmen venation. Many of these fossils lack diagnostic characters of the body parts, making it difficult to compare with other genera. The concept of classification for the Tettigarctinae and Cicadoprosobolinae used here follows Moulds (2005) and Shcherbakov (2009).

*Cretotettigarcta burmensis* gen. et sp. nov. described here exhibit wing venation patterns and body structures, and it can be placed in the subfamily Tettigarctinae based on the following apomorphic characters: costal area relatively narrow, as wide as intercubital one; basal of MP and CuA not coalescent directly, connecting by a short cross vein; cross vein ir nearer to wing tip than to nodal line; hind wings, anterior-most apical cell (a0 cell) distinctly narrower than posterior-most one (a6 cell).

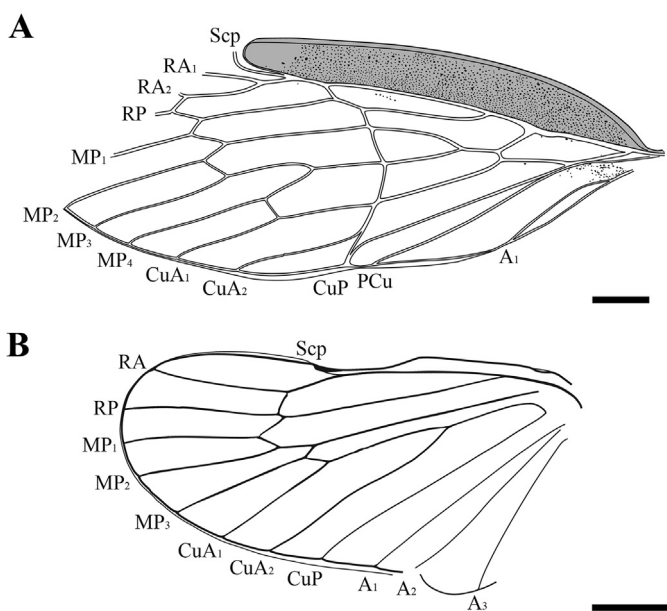
*Cretotettigarcta* gen. nov. is probably related to the members of the extant Protabanini and Meunierini. It shares with Protabanini the distal CuA<sub>2</sub> diverging from nodal line, anterior-most cell narrow triangular, and nodal line beyond or at mid-wing, and it shares with Meunierini the MP branching near basal cell, basal of MP and CuA connecting by a short cross vein. However, *Cretotettigarcta* can be ruled out from Protabanini by MP branching far away from nodal line, ScP + R long, MP and CuA connecting by a short cross vein, and from Meunierini by costal margin not arched, RA branching at the same level as cross vein im, and nodal line after mid-wing.

Interestingly, *Cretotettigarcta* bears a combination of characters previously rare known in Tettigarctinae: 1) apex of fore femur armed with a strong spine in contrast to apex of fore femur lacking spine in other genera; 2) hind tibia armed with three lateral spines in contrast to hind tibia armed with four spines in *Tettigarcta* and less than two spines in other extinct genera; 3) stem MP very short,





**Fig. 5.** Microphotographs of holotype (NIGP168021) of *Vetuprosbole parallelica* gen. et sp. nov. from the mid-Cretaceous Burmese amber. A. tegmen, under normal reflected light; B. hind wing, under normal reflected light. Scale bars: 2 mm in A, B.



**Fig. 6.** Line drawings of tegmen and hind wing of *Vetuprosbole parallelica* gen. et sp. nov. A. tegmen. B. hind wing. Scale bars: 2 mm.

ScP + R branching distinctly after MP branching in contrast to ScP + R branching basal of MP branching in other genera; 4) CuA<sub>1</sub> connecting MP<sub>3+4</sub> by cross vein m-cu in contrast to CuA<sub>1</sub> connecting MP<sub>4</sub> in other genera. A combination of these characters make it difficult to assign *Cretotettigarcta* to any known tribe of Tettigarctinae. *Cretotettigarcta* is likely an ancestor form that gives rise to the members of Protabanini and Meunierini.

*Cretotettigarcta burmensis* shares several critical characters with *Sunotettigarcta hirsuta* Li et al., 2012 from the Middle-Upper Jurassic (ca. 165 Ma) Daohugou beds (Yanliao biota, northeastern China), including short haired body; rostrum long, extending to or beyond hind coxae; expanded and hexagonal pronotum, with posterior area transversely rugose; hind tibia armed with at least two lateral spines; reduced clavus and slightly arched costal margin on tegmen. In particular, they share a similar wing venation, including tegmen bearing eight apical cell and four subapical cells; basal of MP and CuA not coalescent directly; RA with 2 branches, RP single, MP with 4 branches; nodal line at about half tegmen length; m-cu being the longest cross vein. These similarities indicate that some taxa from the Jurassic Yanliao biota persisted to a period when the mid-Cretaceous Myanmar amber produced, some 65 million years later. It is notable that no fossil tettigarctids have been reported from the Lower Cretaceous of Jehol Group in north China. Similar to tettigarctids, some particular groups from the Middle-Upper Jurassic Yanliao biota also dramatically appeared in the Burmese

amber such as Archipsyllidae, Geinitziidae, Progonomicidae and Isolitaphidae (Huang, 2015, 2016). This temporal persistence likely reveals a range shift southwards after the palaeoecosystem collapsed during the Late Jurassic in north China, which eventually formed residual groups of the Yanliao biota from the Middle Cretaceous in South Asia.

## 5. Conclusions

Our discovery of two monotypic genera of tettigarctids from the mid-Cretaceous Burmese amber represents the first record of Tettigarctidae in Mesozoic ambers. These Cretaceous fossils provide detailed morphological features that have never been previously observed in tettigarctids, adding valuable information about our knowledge of the palaeodiversity and morphological disparity of tettigarctids. Additionally, this find greatly increases the biogeographic distribution of Mesozoic tettigarctids, which provides new evidence for understanding the early evolution of this peculiar hemipteran family.

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