A new genus and species of Tettigarctidae from the Mesozoic of northeastern China (Insecta, Hemiptera, Cicadoidea)

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Abstract
A new genus *Maculaprosbole* of Tettigarctidae with a new species *M. zhengi* is described based on a complete fossil forewing from the Mesozoic of northeastern China. Due to its broad costal area and clavus, *Maculaprosbole zhengi gen. et sp. n.* can be attributed to the subfamily Cicadoprosbolinae. This genus is similar to the genera *Sanmai* and *Hirtaprosbole* in coloration pattern and forewing venation, respectively. However, it differs from *Hirtaprosbole* in crossvein *r-m* absent and apical CuA section strongly curved, running along the nodal line for a distance, and *Sanmai* in transverse coloration mainly focusing on the postnodal area. Herein, the prominent coloration pattern of this new taxon is discussed.

Keywords
Coloration pattern, Daohugou, Tettigarctidae, taxonomy

Introduction
Tettigarctidae, the most primitive family of Cicadoidea, is now relict with only two modern species attributed into one genus (Moulds 1990, 2012, Shcherbakov 2009). The taxonomy of the Tettigarctidae is based mainly on the fore- and hindwing venation (Shcherbakov 2009, Li et al. 2012), and this family is divided into two subfamilies...
based on forewing features: Cicadoprosbolinae Evans, 1956 and Tettigarctinae Distant, 1905 (Wang B and Zhang 2009, Li et al. 2012). The fossils records of the Mesozoic Tettigarctidae are rather diverse (Nel 1996, Nel et al. 1998, Dietrich 2002, Menon 2005, Moulds 2005, Wang B and Zhang 2009, Wang B et al. 2013). The earliest Tettigarctidae appeared in the earliest Jurassic and terminal Triassic (ca. 200 Myr) of Eurasia (Shcherbakov 2009). The Paratettigarcta zealandica at around 23 ~ 16 Ma is known as the youngest Tettigarctidae fossil (Kaulfuss and Moulds 2015). Up to now, 27 genera and 40 extinct species (Liu et al. 2015, Kaulfuss and Moulds 2015, Chen and Wang B 2016, Chen et al. 2016) of Tettigarctidae have been reported from all over the world, ranging from the Late Triassic to the Eocene, and are distributed from Northern Hemisphere to Southern Hemisphere, Eurasia, Australia, Africa, and England, etc (Shcherbakov and Popov 2002, Martins-Neto et al. 2003, Wappler 2003, Shcherbakov 2009). Beyond that, two living species within one genus of Tettigarctidae are restricted to high altitude habitat in continental South Australia and Tasmania (Carver et al. 1992, Moulds 1990, Moulds 2005, Li et al. 2012, Liu et al. 2016).

A large number of fossils, especially the highly diverse array of insects, have been well-known and described from Daohugou based on the exceptionally well-preserved materials, showing sharp details of morphology, taxonomy and evolution (Rasnitsyn et al. 2006, Pott et al. 2012, Wang B et al. 2013, Chen et al. 2014, Wang H et al. 2015). To date, 25 insect orders have been reported from the Daohugou Biota (Huang 2010, Li et al. 2010, 2013, Wang B et al. 2013). In Tettigarctidae, eleven species within seven genera had been described from Daohugou to date (Wang B and Zhang 2009, Li et al. 2012, Chen et al. 2014, Chen et al. 2016, Chen and Wang B 2016, this study). The Tettigarctidae, in fact, is a particular group which is known to be much more rich in Daohugou than in any other fauna (Wang B and Zhang 2009, Wang B et al. 2013, Chen et al. 2016). However, their systematic position is still not very clear (Wang B and Zhang 2009, Li et al. 2012, Liu et al. 2016).

In this paper, a new fossil genus is confirmed and described, with a new species of the Tettigarctidae from Daohugou in northeast China.

**Material and methods**

The fossil specimen studied herein was collected from the Middle Jurassic Daohugou deposits (41°18.31’N; 119°13.18’E) in Ningcheng Country, Chifeng City, Inner Mongolia of China. Very recently some studies indicate Daohugou is enjoyed a humid and warm-temperate climate in the Middle Jurassic based on the palaeoenvironmental reconstructions (Ren and Krzeminski 2002, Wang B et al. 2013, Na et al. 2015). This type fossil is preserved as impressions on the surface of grey tuffaceous siltstones. The material described in this paper is deposited in Shandong Tianyu Museum of Nature at Pingyi, Shandong province, China.

The fossil was examined and then photographed with the Nikon D800 digital camera and the Photomicrographs were taken with a Nikon SMZ1000 stereomicro-
scope. The line drawing was created using Adobe Illustrator CS3 and Adobe Photoshop CS5. The quantitatively measure of forewing used NIH ImageJ software (http://rsb.info.nih.gov/ij/). The terminologies of wing venation and cell nomenclature used in herein are modified after Chen et al. (2015). Venation symbols: main longitudinal veins are SC, ScP, RA, RP, M, CuA, CuP and A; crossveins are ir, im, m-cu; cells are a1 ~ a11. The norms of measurements for the wing were following: the wing length measured from the base to the apex and the width measured at the widest part (Li et al. 2012).

Systematic paleontology

Order Hemiptera L., 1758
Suborder Cicadomorpha Evans, 1946
Superfamily Cicadoidea Latreille, 1802
Family Tettigarctidae Distant, 1905
Subfamily Cicadoprosbolinae Evans, 1956

Maculaprosbole gen. n.
http://zoobank.org/947E0D09-5577-417A-A191-5E12A3A9CBE0

Type species. Maculaprosbole zhengi new species, designated herein (Fig 1). No other species are currently included in the genus.

Etymology. The generic name is a composition of the Latin “macula”, meaning spots and stripes, and the suffix of the genus of Cicadoprosbole Becker-Migdisova, 1947.

Diagnosis. Forewing large-sized, relatively wide and with oblique apical margin. Wing membrane with distinct color patterns. Clavus and costal area long. Nodal line at the middle of wing. Nodus distinct. RA with three branches; crossvein ir halfway from nodal line to wing tip; vein RP single and extended upward along the nodal line; vein M four-branched; M1+2 branched beyond M3+4; M1+2 fork into M1 and M2 with a right angle, and M1 fused with RP for a distance, then nearly parallel to M2; crossvein r-m absent; crossvein m nearly straight, almost perpendicular to M2; vein CuA strongly downward along nodal line, branching into CuA1 and CuA2 just after nodal line; vein CuP almost straight, ending at about 2/5 of wing.

Remarks. The new genus undoubtedly belongs to the family Tettigarctidae based on the following diagnostic characteristics of the forewing: nodal line clearly visible; vein RA three-branched; intercostal area widest beyond nodal line; vein RP single and strongly bowed; vein M four-branched. The stem of M is shorter than ScP+R. Maculaprosbole gen. n. is assigned to the subfamily Cicadoprosbolinae based on the forewing features: costal area broad, basal cell narrow; clavus arched; branch CuA2 long, sinuous and near S-shaped. This genus is most similar in coloration pattern of forewing (such as dark or light speckles, longitudinal stripes) with Sanmai Chen, Zhang & Wang B 2016, but differs from Sanmai in the transverse coloration mainly focusing on the
postnodal area. *Maculaprosbole* shares some features in forewing venation with that of *Hirtaprosbole* Liu, Li & Yao, 2015: nodal line at middle of forewing, RA three-branched; stem ScP+R longer than stem M; CuP straight; cell a6 nearly quadrate; cell a8 subequal to cell a10 in length. However, it differs from *Hirtaprosbole* in the following characters: stem ScP+RA separated at the nodal line, ScP ending beyond the middle of anterior margin M_1 fused with RP for a distance and crossvein r-m absent (vs. r-m is located between M_1 and RP); apical CuA section strongly curved, running along nodal line for a distance (vs. CuA slightly sigmoidal, not along nodal line).

*M. zhengi* sp. n.

http://zoobank.org/F16A76A5-C78B-40C4-AC9A-3169B02046CF

Fig. 1

**Diagnosis.** As for genus.

**Description.** Forewing long and elongate apically and relatively wide, with oblique apical margin, near triangular in the tip, with distinctly dark or gray pigmented transverse bands, irregular speckles and longitudinal stripes, mainly behind the nodal line and postnodal area. Length about 34.04 mm, width about 14.54 mm, with the ratio of length/width approximately 2.34; costal margin broad, length about 21.36 mm; clavus arched, small and broad (length 15.06 mm, maximum width 4.55 mm), with conspicuous light pigmented bands. Nodal line situated in the middle of forewing. Crossvein r-m absent; branched into ScP+R and M at basal 0.17 wing length. Stem ScP+R bifurcated into ScP+RA and RP at basal 0.47 wing length; vein ScP forked with RA at nodal line, and terminating at nodus; RA with three branches, RA_1 short and nearly straight, RA_2 and RA_3 long and slightly sinuous, RA_2 parallel to RA_3; branch RA_3 connected with vein RP by the crossvein ir. Crossvein ir at the middle of nodal line and outer margin. Vein RP strongly curved, running along the nodal line for a distance; vein M_1 strongly curved and fused with RP for a distance, then subparallel to M_2; stem ScP+R relatively shorter than stem M. Stem M forked into M_1+2 and M_3+4 at basal 0.15 wing length, and at different level. M_1+2 branched into M_1 and M_2 at basal 0.33 wing length; M_3+4 bifurcated into M_3 and M_4 at basal 0.21 wing length; stem CuA long and initially sinuous, fusing with nodal line and running along with nodal line for a distance, then branched into CuA_1 and CuA_2 just beyond nodal line. CuA_1 long and relatively straight; CuA_2 short and obviously sinuous; CuP long and straight. A_1 sinuous. A_2 short and strongly curved; eleven apical cells.

**Etymology.** The species name refers to Prof. Xiaoting Zheng, who is the founder of Shandong Tianyu Museum of Nature and donated the type material.

**Type specimen.** Holotype STMN48-1813, complete forewing; housed in Shandong Tianyu Museum of Nature.

**Locality and age.** Middle Jurassic; Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.
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Figure 1. Holotype of Maculaprosbole zhengi gen. et sp. n. A Photograph B Line drawing.

Discussion

The Daohugou palaeolake was a low-energy preservational environment (Wang B et al. 2009, Chen et al. 2014, 2016). A large number of insect fossils have been found with well-preserved body structure and wing impression in the fossil beds (Ren et al. 2002, Wang B et al. 2013). Wang B et al. (2013) reported approximately 9% Mesozoic cicadomorph fossils designated as Jurassic tettigarctids. Tettigarctidae is quite abundant and morphologically diversified in the Daohugou area (Wang B and Zhang 2009, Chen et al. 2016, Chen and Wang B 2016). To date, one species within the genus Sunotettigarcta of the subfamily Tettigarctinae and nine species within five genera (Macrosettigarcta, Shuraboprosbole, Tianyuprosbole, Hirtaprosbole and Sanmai) assigned to the subfamily Cicadoprosbolinae have been described and illustrated (Wang B and Zhang 2009, Li et al. 2012, Chen et al. 2014, 2016, Chen and Wang B 2016). Those fossils provide new insights into the evolution, ecology, and behavior of tettigarctids.
We herein attribute a new genus *Maculaprosbole* to the family Tettigarctidae. Material of *Maculaprosbole* is undoubtedly identified as a new taxon and distinctly differs from other tettigarctids in possessing these forewing characters: nodal line at the middle of wing; vein RA divided into three branches; vein RP running along the nodal line for a distance and fused with M₁ for a long distance; CuA strongly curved, fused with nodal line for a distance and forked into CuA₁ and CuA₂ just beyond it. This study brings new insights to improve our knowledge of the biodiversity and wing structure diversification of the Mesozoic Tettigarctidae.

Nowadays, the prominent color pattern on wings, with dark or light stripes and conspicuous transverse longitudinal bands, is a topic that has been known in many insect fossils (Cott 1940, Wang Y et al. 2010, Chen et al. 2016). The color patterns on wings provide camouflage by strongly contrasting markings such as spots or stripes to hide themselves or frighten predators (Stevens et al. 2006; Stevens and Merilaita 2009; Seymoure and Aiello 2015), and are also attributed to sexual selection on visual signals (Wang B et al. 2006, Punzalan et al. 2008, Hilfert-Rüppell and Rüppell 2013).

In Mesozoic tettigarctids, eight species with four genera (*Sanmai*, *Protabanus*, *Li-associada* and *Shuraboprosbole*) have been reported possessing a color pattern with dark or light stripes and irregularly colored bands (Hong 1982, Nel 1996, Wang B and Zhang 2009, Kaulfuss and Moulds 2015, Chen et al. 2016). The disruptive coloration of the forewing seems be an autapomorphy of *Maculaprosbole*. The new fossil has prominent disruptive coloration of the type with dark or light speckles and longitudinal stripes on the forewing membrane, which is remarkably different from most Mesozoic tettigarctids. However, this disruptive coloration pattern seems to be similar to *Sanmai* in the Daohugou beds. The stripes and spots on the forewings of *Sanmai* and *Maculaprosbole* might be effective color camouflage and break up the body outline as well as the surface (Cuthill et al. 2005, Schaefer and Stobbe 2006, Chen et al. 2016).

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