New Jurassic Tettigarctid Cicadas from China with a Novel Example of Disruptive Coloration

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New Jurassic tettigarctid cicadas from China with a novel example of disruptive coloration

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Tettigarctidae is the most primitive family of Cicadoidea, with only two relict species. Although they are relatively well known from Eurasia, Australia, Africa, and South America, their Mesozoic examples are typically preserved only as isolated forewings. Herein, a new genus Sanmai Chen, Zhang, and B. Wang with three new species (Sanmai kongi Chen, Zhang, and B. Wang, S. mengi Chen, Zhang, and B. Wang, and S. xuni Chen, Zhang, and B. Wang) are described based on fossil specimens from the Middle–Upper Jurassic of northeastern China, with well-preserved body structures, forewing and hindwing venations, making it the hitherto best known extinct tettigarctid taxon. The new genus, provisionally assigned to the tribe Turutanoviini, provides some new information about the evolution and palaeobiogeography of Mesozoic Tettigarctidae. The genus Paraprosbole is synonymized with Shuraboprosbole. In addition, the coloration pattern of forewing, prominent on some specimens of Sanmai kongi Chen, Zhang, and B. Wang sp. nov. and Sanmai xuni Chen, Zhang, and B. Wang sp. nov., represents a novel example of disruptive coloration in Tettigarctidae, which can effectively break up the body outline as well as surface, and so likely enabled these cicadas to reduce the detectability of potential predators.

Key words: Insecta, Hemiptera, Tettigarctidae, coloration pattern, Jurassic, China, Daohugou.

Introduction

The Tettigarctidae, known as hairy cicada, is the most primitive group of the superfamily Cicadoidea, comprising only two relict modern species within a sole genus (Tettigarcta tomentosa White, 1845 and T. crinita Distant, 1883) restricted to the mountains of Tasmania and South-East Australia (Moulds 1990; Shcherbakov 2009). The oldest record of Tettigarctidae is from the terminal Triassic of England (Whalley 1983; Shcherbakov and Popov 2002). The Mesozoic fossils of Tettigarctidae are relatively rich in Eurasia, Australia, Africa and South America (see Wang and Zhang 2009; Li et al. 2012; Chen et al. 2014). However, only few Cenozoic records were reported; from the Paleocene of France (Meuniera haupti; Piton 1936), the Eocene of Scotland (Eotettigarcta scotica; Zeuner 1944) and Germany (Tettigarctidae gen. et sp. indet.; Wappler 2003), and the Lower Miocene of New Zealand (Paratettigarcta zealandica; Kauffuss and Moulds 2015).

Because of high diversity but poor preservation, the Mesozoic tettigarctids have a controversial taxonomic history and their evolutionary history remains poorly understood. Cicadoprosbole Becker-Migdisova, 1947 was transferred from Prosbolidae to Tettigarctidae by Becker-Migdisova (1949), and then separated at the family level by Evans (1956). Some researchers treated Cicadoprosbolidae as independent family (e.g., Hamilton 1990, 1996), but others considered it as a subfamily of Tettigarctidae (e.g., Bouard and Nel 1990; Nel et al. 1998; Menon 2005). Because diverse Mesozoic forms fill the morphological gap, it is reasonable to synonymize...
A new genus one specimen of Turutanoviini with both forewing and hindwing preserved was reported to date (Shcherbakov and Popov 2002; Shcherbakov 2009). A new genus Sanmai with three new species are described herein based on six fossil specimens with well-preserved body structures, forewing and hindwing venations, making it the hitherto best known extinct tettigarctid taxon, and providing some new information about the evolutionary history and paleobiogeography of the Mesozoic Tettigarctidae. Additionally, we discuss herein the special disruptive coloration preserved on these new tettigarctids, which is remarkably different from that of known extinct and living tettigarctids as well as other cicadomorphs discovered in the same fossil layers of Daohugou.

Institutional abbreviations.—STMN, Shandong Tianyu Museum of Nature, Pingyi, Shandong Province, China.

Other abbreviations.—A, anal vein; CuA, anterior branch of the cubitus vein; cua-cup, crossvein connecting the anterior and posterior branches of the cubitus vein; CuP, posterior branch of the cubitus vein; im, crossvein connecting the anterior and posterior branches of the radial vein; M, media vein; m-cua, crossvein connecting the fourth branch of the media vein and the anterior branch of the cubitus vein; RA, anterior branch of the radial vein; RP, posterior branch of the radial vein; r-m, crossvein connecting the posterior branch of the radial vein and the first branch of the media vein; ScP, posterior branch of the subcosta vein; u, ulnar cell (terminology after Moulds 2005).

Material and methods

The new Mesozoic tettigarctids described herein were collected from the Daohugou fossil-bearing strata of northeastern China, and are deposited in STMN. Daohugou has yielded abundant and diverse fossil plants and animals, and is now considered to be one of the most important insect Lagerstätten (Rasnitsyn et al. 2006). The hitherto known Tettigarctidae is much more diverse in Daohugou than in any other faunas, with eight species described and attributed to four genera and some available fossils awaiting description (Wang 2009; Wang and Zhang 2009; Li et al. 2012; Chen et al. 2014). Generally, the fossil-bearing beds at Daohugou were placed within the Jiulongshan Formation of Bathonian–Callovian (late Middle Jurassic) (e.g., Wang and Zhang 2009; Chen et al. 2014; Liu et al. 2014). However, recent isotopic dating results indicated that the Daohugou beds were deposited in the geological age of 164–158 Ma (Liu et al. 2006, 2012; L. Wang et al. 2013), Callovian–Oxfordian (late Middle–earliest Late Jurassic) according to the updated International Chronostratigraphic Chart (Cohen et al. 2013; Wang et al. 2015).

There is no consensus on the interpretation of vein nomenclature in Cicadomorpha (Wang and Zhang 2009). Nel et al. (2012) proposed a new interpretation of wing venation pattern for all Paraneoptera, assuming that CuA gets fused with M+R stem at wing base and connected with CuP by a specialized crossvein cua-cup after its departure from M+R,
which is remarkably different from the traditional interpretations. The venational terminologies used herein follow Nel et al. (2012), including that the first longitudinal vein on the clavus is tentatively treated as A1 rather than Peu, that is treated as an open problem in Nel et al. (2012).

The fossil tettigarctids were examined dry or under alcohol, with details observed and microphotographed under a stereomicroscope (ZeissSterEO Discovery V8). Photographs were taken using a NikonD800 digital camera. Line drawings were prepared with image-editing software. All measurements were made using software ImageJ 1.42q (Wayne Rasband; National Institute of Health, USA). The following standards were used for measurements: whole length of the tegmen measured at the widest part; length of costal area from the base of tegmen to the ending of vein CuP; width of clavus measured at its widest part; length of tegmen measured from the base to the apex; width of tegmen measured at the widest part from costal margin to posterior margin; length of clavus measured from the base of tegmen to the ending of vein CuP; width of clavus measured at its widest part; length of costal area measured from the base of tegmen to the ending of vein ScP; width of costal area measured at its widest part.

**Systematic palaeontology**

Order Hemiptera Linnaeus, 1758  
Suborder Cicadomorpha Evans, 1946  
Superfamily Cicadoidea Latreille, 1802  
Family Tettigarctidae Distant, 1905  
Subfamily Cicadoprosbolinae Becker-Migdisova, 1947

**Genus Sanmai Chen, Zhang, and B. Wang nov.**

*Etymology:* From Mandarin san, three, and mai, branch; referring to vein M three-branched on forewing.

*Type species:* Sanmai kongi Chen, Zhang, and B. Wang, sp. nov., designated herein; see below.

*Included species:* Sanmai kongi Chen, Zhang, and B. Wang, sp. nov. (the type species); S. mengi Chen, Zhang, and B. Wang, sp. nov.; S. xuni Chen, Zhang, and B. Wang sp. nov.

*Diagnosis.*—Postclypeus swollen. Compound eye large, oval or semicircular in lateral view. Antenna with scape slightly thicker than pedicel; flagellum aristiform, with five segments. Pronotum expanded, anterior half with tiny granular protuberances and posterior area transversely rugose. Mesonotum partly exposed, with posterior one-third area transversely rugose. Femora with tiny granules (or bases of thick setae?); tibiae densely setose, with distinct ridges, hind tibia with two lateral spines; tarsidensely setose, with three tarsomeres; claws well-developed. Ovipositor ensiform, upcurved, adpressed to pygofer extended just below anal tube. Forewing with dark membrane colored with light and irregular speckles and longitudinal stripes (coloration pattern not preserved for S. mengi); apical cells eight; R bifurcating at about basal one-third wing length; RP fused with nodal line for a distance or sinuous near nodal line; M three-branched; M3+4 unbranched; CuA bifurcating just beyond nodal line; distal section of CuA2 running along wing margin. Hindwing with M three-branched and M1+2 simple.

*Remarks.*—Based on information from forewings, Shcherbakov (2009) divided Tettigarctidae into subfamilies Cicadoprosbolinae and Tettigarctinae, each with three tribes respectively. Sanmai gen. nov., possessing an elliptical forewing with broad costal area and clavus, undoubtedly belongs to the subfamily Cicadoprosbolinae. The new genus is similar to Architettix Hamilton, 1990 in having a forewing with vein M three-branched, but differs from the latter in possessing a forewing with R bifurcated far away from nodal line, RA with two terminations, and CuA2 fused with nodal line. In addition, forewing with three-branched M vein makes the new genus and Architettix different from all other fossil and extant tettigarctids.

**Stratigraphic and geographic range.**—Upper Middle–Lower Upper Jurassic Daohugou beds; Daohugou Village, Ningcheng County, Inner Mongolia, China.

*Key to species of the new genus Sanmai on forewing:*

1. Length/width ratio >3; RP sinuous near nodal line but not fused with the latter ..........................................................  
2. RA1 short and straight; M1+2 long and curved near nodal line; u3 elongate, about 0.3 wing length ....................................... Sanmai mengi  
3. RA1 long and slightly sinuous; M1+2 short and straight; u3 about 0.25 wing length ........................................ Sanmai kongi

**Sanmai kongi** Chen, Zhang, and B. Wang sp. nov.

*Fig. 2.*

*Etymology:* In reference to the family name of Confucius (Kung Futsy), the founder of Confucianism.

*Type material:* Holotype, STMN48-1800a, b (part and counterpart), well-preserved adult female in lateral aspect with overlapped wings at the top of the body. Paratype, STMN48-1801, well-preserved adult male in lateral aspect with overlapped wings at the top of the body.

*Type locality:* Daohugou Village, Ningcheng County, Inner Mongolia, China.

*Type horizon:* Upper Middle–lower Upper Jurassic Daohugou beds.

*Material:* Type material only.

*Diagnosis.*—Compound eye nearly semicircular in lateral view. Forewing length/width ratio about 2.65; RA1 long and slightly sinuous; RP fused with nodal line for a distance; M1+2 short and straight; u3 about 0.25 wing length.

*Description.*—Holotype STMN48-1800: Body 22.3 mm long including forewing in repose. Compound eye large, nearly semicircular. Antenna partly preserved, scape slightly thicker than pedicel. Pronotum expanded, anterior half with tiny granular protuberances and posterior area transversely rugose. Mesonotum partly exposed, with posterior one-third area transversely rugose. Femora with tiny granules (or bases of thick setae?); tibiae densely setose,
with distinct ridges; tarsi densely setose, with three tarsomeres. Fore femur strong; fore tibia slender, about 2/3 length of hind tibia, with one apical tooth visible; tarsus with apical tarsomere much longer than mid and basitarsomeres; one well-developed claw preserved. Mid femur as long as fore femur, but much slenderer than the latter; mid tibia largely missing. Hind femur strong, slightly shorter than fore and mid femora; hind tibia long and slender, with two extremely long lateral spines, with a row of apical teeth (six? visible); hind tarsus about 3/4 length of fore tarsus, with mid tarsomere slightly shorter than basi- and apical tarsomeres; two well-developed claws visible. Ovipositor ensiform, up-curved, adpressed to pygofer.

Forewing length about 18.8 mm, width about 7.1 mm. Dark membrane colored with light and irregular speckles and longitudinal stripes. Costal area long and narrow, with ratio of length to width about 5.2. Clavus broad and arched, with ratio of length to width about 3.9. Nodal line distinct. Eight apical cells. Stem ScP+R+M+CuA thick, bifurcating into ScP+R and M+CuA at basal 0.23 wing length. Stem ScP+R straight, bifurcating into ScP+RA and RP at basal 0.34 wing length. RA with two terminations; RA1 long and slightly sinuous; RA2 geniculate at junction with crossvein ir, subparallel to RA1, and curved apically. RP fused with nodal line for a distance, slightly curved at junction with crossvein r-m, and re-curved at junction with crossvein ir. Stem M+CuA bifurcating just beyond junction with crossvein cua-cup. Stem M straight, bifurcating into M1+2 and M3+4 basal of middle of wing length. u3 about 0.25 wing length. Vein M1+2 short and straight, bifurcating at about basal 0.64 wing length. Vein M3+4 simple, connected with M2 by crossvein im. Stem CuA long and sinuous, bifurcating into CuA1 and CuA2 just beyond nodal line. CuA1 long, geniculate at junction with crossvein m-cua. Distal section of CuA2 running along wing margin. CuP long and straight. A1 sinuous. A2 short and strongly curved.

Paratype STMN48-1801: Body length as preserved 21.7 mm long including forewing in repose. Postclypeus ornamented with distinct transverse grooves. Mid tibia slender, slightly longer than fore tibia. Pygofer largely missing, but well-developed adeagus visible. Forewing length about 17.5 mm, width about 6.6 mm; venation in general as in holotype; coloration pattern not preserved.

Remarks.—The new species is similar to S. mengi Chen, Zhang, and B. Wang sp. nov., but differs from the latter in

Fig. 2. Hairy cicada Sanmai kongi sp. nov. from the upper Middle–lower Upper Jurassic Daohugou beds. A. Holotype STMN48-1800a. Photograph under alcohol (A1), explanatory drawing (A2). Hind leg (A3). Enlargement of apical teeth set of hind tibia (A4). Photomicrograph of ovipositor (A5). B. Paratype STMN48-1801. Photograph (B1), photomicrograph of male genitalia (B2). Abbreviations: A, anal vein; CuA, anterior branch of the cubitus vein; CuP, posterior branch of the cubitus vein; M, media vein; RA, anterior branch of the radial vein; RP, posterior branch of the radial vein; ScP, posterior branch of the subcosta vein; u, uhorn cell.
possessing long and slightly sinuous RA1, short and straight M1+2, and u3 about 0.25 wing length for tegmen.

**Stratigraphic and geographic range.**—Upper Middle–lower Upper Jurassic; Daohugou Village, Ningcheng County, Inner Mongolia, China.

*Sanmai mengi* Chen, Zhang, and B. Wang sp. nov.

Fig. 3.

**Etymology**: In reference to the family name of Mencius (Meng Tsy), one of the sages of Confucianism.

**Holotype**: STMN48-1802, well-preserved adult female in lateral aspect with overlapped wings at the top of the body.

**Type locality**: Daohugou Village, Ningcheng County, Inner Mongolia, China.

**Type horizon**: Upper Middle–lower Upper Jurassic Daohugou beds.

**Diagnosis.**—Compound eye nearly oval in lateral view. Abdomen stout. Forewing with length/width ratio 2.5; RA1 short and straight; RP fused with nodal line for a distance; M1+2 long and curved near nodal line; u3 elongate, about 0.3 wing length.

**Description.**—Holotype STMN48-1802: Body length as preserved 23.6 mm including forewing in repose. Compound eye large, nearly oval in lateral view. Antenna with scape slightly thicker than pedicel, flagellum aristiform, with segments invisible. Postclypeus partly missing, convex. Rostrum extending beyond hind coxae, nearly to apex of hind femur. Pronotum expanded, anterior half with tiny granular protuberances and posterior area transversely rugose. Mesonotum partly exposed. Legs partly preserved; femora with tiny granules (or bases of thick setae?); tibiae densely setose, with distinct ridges. Abdomen stout, with nine segments visible. Ovipositor well-developed, ensiform, adpressed to pygofer. Forewing length about 19.6 mm, width about 7.8 mm. Coloration pattern not preserved. Costal area long and narrow, with ratio of length to width about 5.1. Clavus broad and arched. Nodal line distinct. Eight apical cells. Stem ScP+R+M+CuA thick, bifurcating into ScP+R and M+CuA at basal 0.22 wing length. Stem ScP+R straight. RA with two terminations; RA1 short and nearly straight; RA2 geniculate at junction with crossvein ir, then subparallel to RA1. RP fused with nodal line for a distance, slightly curved at junction with crossvein r-m, and re-curved at junction with crossvein ir. Stem M+CuA bifurcating just beyond junction with crossvein cu-aup. Stem M straight, bifurcating into M1+2 and M3+4 at basal 0.42 wing length. U3 about 0.3 wing length. Vein M1+2 long and sinuous beyond nodal line. Vein M3+4 simple, connected with M2 by crossvein im. Stem CuA long and sinuous. CuP long and straight. A1 sinuous. A2 short and strongly curved.

**Remarks.**—The new species is similar to *S. kongi* Chen, Zhang, and B. Wang sp. nov., but differs from the latter in possessing short and straight RA1; long and curved (near
nodal line) $M_{1+2}$; elongate $u_3$, about 0.3 wing length for tegmen.

Stratigraphic and geographic range.—Upper Middle–lower Upper Jurassic; Daohugou Village, Ningcheng County, Inner Mongolia, China.

Sanmai xuni Chen, Zhang, and B. Wang sp. nov.

Fig. 4.

Etymology: In reference to the family name of Xuncius (Xun Tsy), one of the sages of Confucianism.

Type material: Holotype, STMN48-1803, well-preserved adult female in lateral aspect with overlapped wings at the top of the body. Paratypes, STMN48-1804, well-preserved adult female in lateral aspect with overlapped wings at the top of the body; STMN48-1805, well-preserved adult female in lateral aspect with overlapped wings at the top of the body.

Type locality: Daohugou Village, Ningcheng County, Inner Mongolia, China.

Type horizon: Upper Middle–lower Upper Jurassic Daohugou beds.

Diagnosis.—Compound eye oval or semicircular in lateral view. Flagellum aristiform, with five segments visible. Ovipositor ensiform, upcurved, adpressed to pygofer extended just below anal tube. Forewing length/width ratio > 3; $RA_1$ long; $RP$ sinuous near nodal line but not fused with the latter; $M_{1+2}$ short and nearly straight; $u_3$ about 0.26 wing length; $CuA_1$ bifurcating just beyond nodal line; distal section of $CuA_2$ running along wing margin.

Description.—Holotype STMN48-1803: Body 25.2 mm long including forewing in repose. Compound eye large, nearly oval in lateral view. Antenna with scape slightly thicker than pedicel, flagellum aristiform, with segments invisible. Postclypeus swollen, greatly inflated. Rostrum extending beyond hind coxae, nearly to apex of hind femur. Pronotum expanded, anterior half with tiny granular protuberances and posterior area transversely rugose. Mesonotum partly exposed, with posterior one-third area transversely rugose. Femora with tiny granules (or bases of thick setae?); tibiae densely setose, with distinct ridges. Fore femur strong; fore tibia slender. Mid femur much slenderer than the latter. Hind femur strong, but slender than fore femora. Ovipositor ensiform, upcurved. Forewing length about 21.5 mm, width about 6.4 mm. Dark membrane colored with light and irregular speckles and
Discussion

Evolutionary implications.—The new genus seems to be closely related to the tribes Turutanoviini and Architettitigini of Cicadoprospolinae, and the three taxa seem to form a monophyletic group based on the following forewing characters; most apical cells extremely long and narrow, and nearly longitudinal, RA at most possessing three terminations, and distal section of CUa2 running along wing margin. Considering many dissimilarities of Sanmai gen. nov. from the tribe Architettitigini, the M1,4 fork might be lost in parallel in the new genus and Architettitigini. The alternative scenario, however, can not be excluded that Sanmai gen. nov. is a transitional form between widespread Turutanoviini and specialized Architettitigini, since it possesses common body structures as Shuraboprosbole spp. of Turutanoviini but shares a simple M3+4 vein on forewing with Architettitigini. Sanmai gen. nov. is provisionally assigned into the tribe Turutanoviini herein because the new genus and the genera of Turutanoviini share many common morphological characters besides the number of terminations of M vein.

Up to now, three genera (i.e., Turutanovia, Paraprosbole, Shuraboprosbole), with rich fossil record from the Lower Jurassic to the Upper Cretaceous of Eurasia, have been attributed to Turutanoviini (Fig. 1). Shuraboprosbole is very similar to Paraprosbole, but differs from the latter in possessing a larger forewing with costal margin strongly arched near wing base, and stem R and M+CuA bifurcating nearly at the same level. Some tettigarctic fossils recently discovered from the Daohugou Lagerstätte have filled the morphological gap between Shuraboprosbole and Paraprosbole, and some of these genus-level diagnostic differences are even intra-specific in Daohugou specimens, such as the relative bifurcating position of stem R and M+CuA in forewing of Shuraboprosbole daohouensis (Wang and Zhang 2009). These two genera do not possess distinguishable morphological characters. Therefore, the genus Paraprosbole should be synonymized with Shuraboprosbole. Although the records of Mesozoic tettigarctids are relatively rich, only fossil specimens of two genera, Shuraboprosbole and Turutanovia, preserve information of hindwing to date. The hindwing of Sanmai gen. nov. is distinctly different from that of these two genera as well as extant Tettigarcia by simple M1+2 and bifurcated M3+4, but very similar to that of Shuraboprosbole media (unpublished specimen; see SOM: fig. S1, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Chen_etal_SOM.pdf). If Sanmai gen. nov. was a transitional form between Turutanoviini and Architettitigini we can infer, based on morphological and palaeobiogeographical data, that tettigarctic genera with M three-branched on forewing (Architettitix and Sanmai) probably originated from some Shuraboprosbole-related tettigarctids in Eurasia (Laurasia) in the Middle Jurassic, and then spread to South America (Gondwana) before the expanding Tethys Ocean became a geographic barrier for these flying insects.

Compared to living tettigarctids, Architettitigini (Architettitix) possesses some distinct body structures, such as broadly exposed mesonotum, long hind tibia, and cicadellid-like tarsi. Architettitix possesses elongate hind basitarsomere with rows of plantar setae like modern cicadellids (leafhoppers). Hamilton (1990, 1996) considered structures as

longitudinal stripes. Costal area long and narrow, with anterior area partly missing. Clavus long, with ratio of length to width about 4.8. Nodal line distinct. Eight apical cells. Stem ScP+R+M+CuA thick, bifurcating into ScP+R and M+CuA at basal 0.21 wing length. Stem ScP+R straight, bifurcating into ScP+RA and RP at basal 0.32 wing length. RA with two terminations; RA1 long, RA2 genulate at junction with crossvein ir, subparallel to RA1. RP sinusous near nodal line but not fused with the latter, slightly curved at junction with crossvein ir. Stem M+CuA bifurcating just beyond junction with crossvein cu-a-cup. Stem M straight, bifurcating into M1+2 and M3+4basal of middle of wing wing length. u3 about crossvein ir. Stem M+CuA bifurcating just beyond junction about basal 0.66 wing length. Vein M 3+4 simple, connected lateral spines. Ovipositor ensiform, upcurved, adpressed to Rostrum long, with a distinct ridge. Hind tibia with two pedicel, flagellum aristiform, with five segments visible. Larva in lateral view. Antenna with scape slightly thicker than forewing in repose. Compound eye large, nearly semicircular gap between

inner area partly missing. Clavus long, with ratio of length to width about 4.8. Nodal line distinct. Eight apical cells. Stem ScP+R+M+CuA thick, bifurcating into ScP+R and M+CuA at basal 0.21 wing length. Stem ScP+R straight, bifurcating into ScP+RA and RP at basal 0.32 wing length. RA with two terminations; RA1 long, RA2 genulate at junction with crossvein ir, subparallel to RA1. RP sinusous near nodal line but not fused with the latter, slightly curved at junction with crossvein ir. Stem M+CuA bifurcating just beyond junction with crossvein cu-a-cup. Stem M straight, bifurcating into M1+2 and M3+4basal of middle of wing wing length. u3 about crossvein ir. Stem M+CuA bifurcating just beyond junction about basal 0.66 wing length. Vein M1+2 nearly straight, bifurcating at about basal 0.66 wing length. Vein M3+4 simple, connected with M2 by crossvein im. Stem CuA long and sinusous, bifurcating into CuA1 and CuA2 just beyond nodal line. CuA1 long, genulate at junction with crossvein m-cua. Distal section of CuA2 running along wing margin. CuP long and straight. A3 nearly straight. A2 short and strongly curved.

Paratype STMN48-1804: Fore tarsus with basitarsomere slightly longer than mid and apical tarsomeres; one well-developed claw visible. Ovipositor ensiform, upcurved, adpressed to pygofer, extended just below anal tube. Body length as preserved 23.5 mm including forewing in repose. Forewing length as preserved 20.9 mm, width as preserved 6.1 mm; coloration pattern and venation in general as in holotype. Hindwing venation partly preserved. RP simple, curved at junction with crossvein r-m, and recurved at junction with crossvein ir. Stem M with three terminations; M1+2 unbranched. Crossvein m-cua long, connecting M1 just beyond its departure from M3+4. CuA two-branched; CuA1 and CuA3 long.

Paratype STMN48-1805: Body 25.4 mm long including forewing in repose. Compound eye large, nearly semicircular in lateral view. Antenna with scape slightly thicker than pedicel, flagellum aristiform, with five segments visible. Rostrum long, with a distinct ridge. Hind tibia with two lateral spines. Ovipositor ensiform, upcurved, adpressed to pygofer. Forewing length about 22.3 mm, width as preserved 6.2 mm; coloration pattern and venation in general as in holotype.

Remarks.—The new species differs from S. kongi Chen, Zhang, and B. Wang sp. nov. and S. mengi Chen, Zhang, and B. Wang sp. nov. in possessing length/width ratio >3; RP sinusous near nodal line but not fused with the latter for tegmen. Stratigraphic and geographic range.—Upper Middle–lower Upper Jurassic; Daohugou Village, Ningcheng County, Inner Mongolia, China.
of “cicadellid-like tarsi” as synapomorphies linking the Membracoidea and Cicadoidea. In modern Clypeata, only leafhoppers have the elongate hind basitarsomere with rows of plantar setae, and this morphological character is considered important for high level classification of leafhoppers (Davis 1975). The present study shows that the closely related Sanmai has common tarsi similar to modern Cicadoidea (Figs. 2, 3; Emeljanov 1987). Recent molecular and fossil evidences have confirmed that modern Clypeata comprises two monophyletic clades, divided into Myerslopoidea + Membracoidea and Cicadoidea + Cercopoidea, respectively (Scherbakov and Popov 2002; Cryan and Urban 2012; Wang et al. 2012). Hence, the similarity of the tarsi between Cicadellidae and Architettigini is undoubtedly the result of convergent evolution. The specialized body structures of Architettigini are probably due to predation pressure from some early birds and insectivorous pterosaurs reported from the same formation of northeastern Brazil (Kellner 2002; Naish et al. 2007; Unwin and Martill 2007; Sayao et al. 2011; Carvalho et al. 2015). Architettigini, with long hind tibia and well-developed lateroribial spines, must be adapted to jumping (Scherbakov 2009) as modern cicadellids. Meanwhile, the huge and broadly exposed mesonotum probably suggests an improvement of flight ability, like modern singing cicadas (Cicadidae), since the forewing is connected to flight muscles in mesonotum (Yao 2012). The adults of modern tettigarcids are crepuscular (hiding under loose bark during daylight hours; Moulds 1990; Scherbakov 2009), but some structurally diverse Mesozoic tettigarcids (e.g., Architettix) with better locomotor capacity were likely diurnal.

**Coloration pattern.**—The disruptive coloration of forewing is prominent on some specimens of Sanmai gen. nov. (Figs. 2A, 4A, D), with light and irregular speckles and longitudinal stripes bold contrasting to dark membrane, and the type is new to Tettigarcidae. The mottled forewings of the relict modern Tettigarcra spp. blend with the lichen-covered eucalypt bark (Moulds 1990). The transverse alternating dark and light stripes on wings, as a common disruptive coloration type for fossil cicadas (Wang et al. 2010), were reported in some Mesozoic tettigarcid specimens, e.g., Protabanus (Hong 1982), Liassociacna (Nel 1996), and Shuraboprosbole (Wang and Zhang 2009). Most forewing membranes of Mesozoic tettigarcids, however, are almost monochrome (e.g., Sunotettigarcra hirsuta) or colorless and transparent (e.g., Turutanovia karatavica). The disruptive coloration of Sanmai gen. nov. might be an effective camouflage which enabled Sanmai. to reduce the detectability of arboreal and insectivorous predators from the same Lagerstätte, such as ancestral Avialae, gliding mammals, and rhamphorhynchoid pterosaurs.

The special disruptive coloration type seems to be an autapomorphy of Sanmai. In specimens STMN48-1800 of S. kongi sp. nov., STMN48-1803 and STMN48-1804 of S. xuni sp. nov., the coloration pattern of forewing is well preserved and similar in general: some speckles in various sizes and shapes on prenodal area and some longitudinal stripes on postnodal area. The color impression of the remaining specimens of S. kongi sp. nov. and S. xuni sp. nov. as well as the holotype of S. mengi sp. nov. is obscure or even absent, likely weakened or erased by diagenetic process. Hence, considering taphonomic factors, the presence or absence of forewing coloration is not a useful distinguishable character for Sanmai.

The Daohugou palaeolake was a low-energy preservation environment. Most well-preserved tettigarcid specimens collected from Daohugou area are preserved in the lateral position with all four wings folded (Wang and Zhang 2009; Li et al. 2012; B. Wang et al. 2013; Chen et al. 2014; this study). The large body with a greatly inflated frontoclypeus and a long rostrum indicates that the Mesozoic tettigarcids were arboreal and xylem feeding (Wang and Zhang 2009). Therefore, it seems that when the early tettigarcids stayed on the branch to suck xylem fluids, their folded and roof-like wings covered bodies just as extant Cicadoidea, and so the forewing color pattern was essential for tettigarcids to hide themselves. For Sanmai, most of the highly contrasting speckles and longitudinal stripes extend to the edge of the forewings. This disruptive coloration can effectively break up the body outline as well as surface (Cuthill et al. 2005; Schaefer and Stobbe 2006), and enabled Sanmai to hide in faint light under the cover of thick forest (see SOM: fig. S2).

Disruptive camouflage is also frequent in Palaeotiniidae, another common large-sized arboreal cicadomorph group of Daohugou Biota. However, unlike Sanmai, the disruptive wing coloration of palaeotiniids is transverse alternating dark and light stripes or light spots on dark membrane (Scherbakov and Popov 2002; Wang 2009).

To date, eight species within four genera (Shuraboprosbole, Sunotettigarcra, Tianyuprosbole, and Sanmai gen. nov.) attributed to the family Tettigarcidae have been recorded from the Daohugou beds (Wang and Zhang 2009; Li et al. 2012; Chen et al. 2014; this study). The forewing membrane in Sunotettigarcra and Tianyuprosbole is mostly dark and lacks highly contrasting coloration patterns, and is probably cryptic via background-matching. The postnodal area of Tianyuprosbole, ornamented with some thick ruffles, might be leaf mimesis (Chen et al. 2014). These well-preserved Daohugou specimens indicate that early tettigarcids likely have evolved different mechanisms of camouflage to avoid detection by potential predators. Besides, the different styles of forewing coloration of Daohugou tettigarcids suggest that although all of them were likely arboreal, they might have occupied slightly different ecotopes to reduce inter-specific competition.

**Conclusions**

We report the new genus Sanmai Chen, Zhang, and B. Wang with three new species (Sanmai kongi Chen, Zhang, and B. Wang, S. mengi Chen, Zhang, and B. Wang, and S. xuni...
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