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 Turutanovini, 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; Kaulfuss 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 hindwing preserved was reported to date (Shcherbakov and one specimen of Turutanoviini, and Sanmai gen. nov. 1, northeastern Brazil (Hamilton 1990); 2, England (Whalley 1985); 3, Kazakhstan (Shcherbakov and Popov 2002; Shcherbakov 2009); 4, Tajikistan (Becker-Migdisova 1949); 5, Ust'-Baley, southern Siberia (Shcherbakov 1985); 6, Myangad, western Mongolia (Shcherbakov 1986); 7, northeastern China (Wang and Zhang 2009; this study). These two taxa (Shcherbakov 2009). The Tettigarctidae sensu lato was revised in detail by Shcherbakov (2009), and it was divided into two subfamilies, Cicadoprosbolini, Architettigini and Turutanoviini, and Tettigarctinae with tribes Protabanini, Meinieriini, and Tettigaretiini, respectively. However, recent discoveries of Mesozoic tettigarctids with well-preserved body structures and complete forewings suggested that the current taxonomic system, just on basis of forewing venation, might not effectively reflect evolutionary relationships (Wang 2009; Li et al. 2012; Chen et al. 2014; this study). Based on two whole-bodied adults and one nymph from the Lower Cretaceous Crato Formation of northeastern Brazil, Hamilton (1990) described the tettigarcid genus Architettix (Architettigini) with some body and wing characters distinctly different from known extant and extinct tettigarctids: tarsi cicadellid-like and forewing with M_{3+4} unbranched. Hamilton (1990, 1996) considered that the genus shows a mixture of cicadoid and cicadellid characters, suggesting these two cicadomorph groups are closely related. Recently, some fossil tettigarctids were collected from the upper Middle–Lower Jurassic Daohugou fossil-bearing strata of Inner Mongolia, China (Fig. 1). These new tettigarctids possess an unusual forewing with M_{3+4} unbranched as in Architettigini, but their tarsus and other body structures are similar to Shuraboprosbole spp. (Turutanoviini) from the contemporaneous strata at Daohugou Village.

Although tettigarctids were rich in the Mesozoic, only 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 tettigarcid 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 branches of the media veins; ir, crossvein connecting the anterior and posterior branch 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 faunae, 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 (latest 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 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 measured from the base of tegmen to the ending of vein ScP; width of costal area measured at its widest part. 

The following standards were used for measurements: whole length measured from the apex of the vertex to the apex of the tegmen; 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 the 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


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; CuA₂ 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, Shechbakov (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 .................................................. Sanmai xuni Length/width ratio 2.5–2.7; RP fused with nodal line for a distance .............................. 2
2. RA₁ short and straight; M₁₋₂ long and curved near nodal line; u₃ elongate, about 0.3 wing length ................................ Sanmai mengi 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 streaks 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 M₁₂ and M₃₄ basal of middle of wing length. u₃ about 0.25 wing length. Vein M₁₂ short and straight, bifurcating at about basal 0.64 wing length. Vein M₁₄ 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 aedeagus 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
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 cua-cup. Stem M straight, bifurcating into M₁₂ and M₃₄ at basal 0.42 wing length. u₃ about 0.3 wing length. Vein M₁₂ long and sinuous beyond nodal line. Vein M₃₄ 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 u3, 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.** Hairy cicada *Sanmai xuni* sp. nov. from the upper Middle–lower Upper Jurassic Daohugou beds. **A.** Holotype STMN48-1803. Photograph (A\(_1\)), explanatory drawing (A\(_2\)), enlargement of head (A\(_3\)). **B.** Paratype STMN48-1804. Photograph (B\(_1\)), explanatory drawing of hind wing (B\(_2\), horizontal mirror), photomicrograph of ovipositor and pygofer (B\(_3\)). **C.** Paratype STMN48-1805. Photograph (C\(_1\)); photomicrograph of part of rostrum (C\(_2\)). Abbreviations: CuA, anterior branch of the cubitus vein; M, media vein; RA, anterior branch of the radial vein; RP, posterior branch of the radial vein.

**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; u3 about 0.26 wing length; CuA 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
longitudinal stripes. Costal area long and narrow, with ante-
rior 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, geniculate at junction with
crossvein ir, subparallel to RA1. RP sinuous 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 cua-cup. Stem M straight, bifurcating into
M1+2 and M3+4basal of middle of wing wing length. u3 about
with crossvein cua-cup. Stem M straight, bifurcating into
M1+2 and M3+4basal of middle of wing wing length. u3 about
0.26 wing length. Vein M1+2nearly straight, bifurcating at
about basal 0.66 wing length. Vein M3+4simple, connected
with M2 by crossvein im. Stem CuA long and sinuous, bi-
furcating 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. 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,
applied 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. CU A two-branched; CuA1
and CuA2 long.

**Paratype STMN48-1805:** Body 25.4 mm long including
forewing in repose. Compound eye large, nearly semicircu-
lar 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
lateralspines. Ovipositor ensiform, upcurved, adressed to
pygofer. Forewing length about 22.3 mm, width as pre-
erved 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 sin-
uous 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.

**Discussion**

**Evolutionary implications.—**The new genus seems to be
closely related to the tribes Turutanoviini and Architetittigini
of Cicadoprosbolinae, and the three taxa seem to form a
monophyletic group based on the following forewing char-
acters; most apical cells extremely long and narrow, and
nearly longitudinal, RA at most possessing three termina-
tions, and distal section of CuA2 running along wing margin.
Considering many dissimilarities of *Sanmai* gen. nov.
from the tribe Architetittigini, the M1+4 fork might be lost in
parallel in the new genus and Architetittigini. The alternative
scenario, however, can not be excluded that *Sanmai* gen. nov.
is a transitional form between widespread Turutanoviini and
specialized Architetittigini, since it possesses common body
structures as *Shuraboprosbole* spp. of Turutanoviini but
shares a simple M3+4 vein on forewing with Architetittigini.
*Sanmai* gen. nov. is provisionally assigned into the tribe
Turutanoviini herein because the new genus and the genera
of Turutanoviini share many common morphological char-
acters 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 at-
tributed to Turutanoviini (Fig. 1). *Shuraboprosbole* is very
similar to *Paraprosbole*, but differs from the latter in pos-
sessing a larger forewing with costal margin strongly arched
near wing base, and stem R and M+CuA bifurcating nearly at
the same level. Some tettigarctid fossils recently discovered
from the Daohugou Lagerstätte have filled the morpholog-
ical 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 morpholog-
ic characters. Therefore, the genus *Paraprosbole* should be
synonymized with *Shuraboprosbole*. Although the records
of Mesozoic tettigarctids are relatively rich, only fossil spec-
imens of two genera, *Shaangaextica* (forewing unknown) 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 *Tettigarctia* by
simple M1+2 and bifurcated M3+4, but very similar to that of
*Shuraboprosbole media* (unpublished specimen; see SOM:
fig. S1, Supplementary Onliine Material available at http://
app.pan.pl/SOM/app61-Chen_etal_SOM.pdf). If *Sanmai*
gen. nov. was a transitional form between Turutanoviini
and Architetittigini we can infer, based on morphological and
palaeobiogeographical data, that tettigarctids with M three-
branched on forewing (*Architetttix* 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 barier for these flying insects.

Compared to living tettigarctids, Architetttigini (*Architettix*)
possesses some distinct body structures, such as
broadly exposed mesonotum, long hind tibia, and cicadellid-
like tarsi. *Architettx* possesses elongate hind basitarsomere
with rows of plantar setae like modern cicadellids (leaf-
hoppers). Hamilton (1990, 1996) considered structures
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 (Shcherbakov 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 laterotibial spines, must be adapted to jumping (Shcherbakov 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 tettigarctids are crepuscular (hiding under loose bark during daylight hours; Moulds 1990; Shcherbakov 2009), but some structurally diverse Mesozoic tettigarctids (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 Tettigarctidae. The mottled forewings of the relict modern *Tettigactra* 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 tettigarctid specimens, e.g., *Protobanamus* (Hong 1982), *Liassocicada* (Nel 1996), and *Shuraboprosbole* (Wang and Zhang 2009). Most forewing membranes of Mesozoic tettigarctids, however, are almost monochrome (e.g., *Sunotettigarcta hirtusa*) 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 STM48-1800 of *S. kongi* sp. nov., STM48-1803 and STM48-1804 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 preservational environment. Most well-preserved tettigarctid 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 tettigarctids were arboreal and xylem feeding (Wang and Zhang 2009). Therefore, it seems that when the early tettigarctids stayed on the branch to suck xylem fluids, their folded and rooflike wings covered bodies just as extant Cicadoidea, and so the forewing color pattern was essential for tettigarctids 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 Palaeontinidae, another common large-sized arboreal cicadomorph group of Daohugou Biota. However, unlike *Sanmai*, the disruptive wing coloration of palaeontinids is transverse alternating dark and light stripes or light spots on dark membrane (Shcherbakov and Popov 2002; Wang 2009).

To date, eight species within four genera (*Shuraboprosbole*, *Sunotettigarcta*, *Tianyuprosbole*, and *Sanmai* gen. nov.) attributed to the family Tettigarctidae 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 *Sunotettigarcta* and *Tianyuprosbole* is mostly dark and lacks highly contrasting coloration patterns, and is probably crypsis 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 tettigarctids likely have evolved different mechanisms of camouflage to avoid detection by potential predators. Besides, the different styles of forewing coloration of Daohugou tettigarctids suggest that although all of them were likely arboreal, they might have occupied slightly different ecotopes to reduce inter-specific competition.

**Conclusions**

Chen, Zhang, and B. Wang) from the Middle–Upper Jurassic of northeastern China (Daohugou). The new genus might be a transitional form between Turutanovini and specialized Architettigini which suggests that tettigarctids with vein M three-branched on forewing probably originated from some *Shurapobrosole*-related tettigarctids in Laurasia in the Middle Jurassic, and then spread to Gondwana before significant extension of the Tethys Sea. The disruptive coloring of forewing, prominent on some specimens of *Sanmai*, represents a novel type to Tettigarctidae, which can effectively break up the body outline as well as surface, and so likely enabled *Sanmai* to reduce the detectability of potential predators. The high divergence of forewing coloring preserved in Daohugou tettigarctids suggests that although most of early tettigarctids were arboreal (Wang 2009), they might have occupied slightly different ecotopes.

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References


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