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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.

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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. *Cicadoprosole* 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 Cicadoprosole as independent family (e.g., Hamilton 1990, 1996), but others considered it as a subfamily of Tettigarctidae (e.g., Boulard and Nel 1990; Nel et al. 1998; Menon 2005). Because diverse Mesozoic forms fill the morphological gap, it is reasonable to synonymize

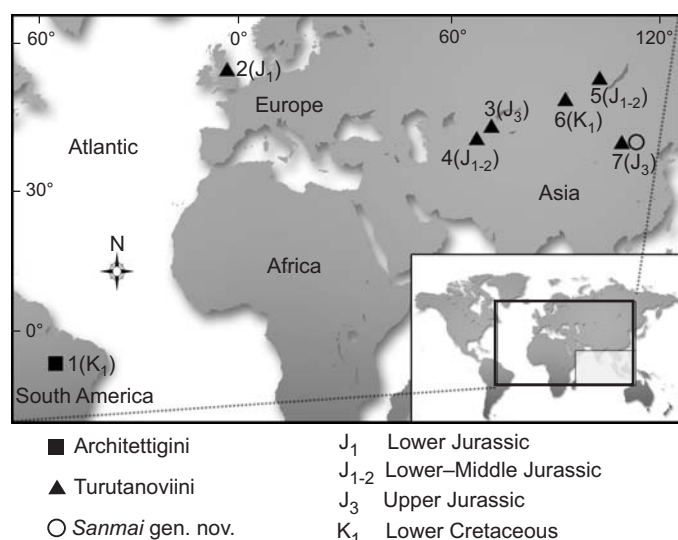


Fig. 1. Distribution of the localities and strata of *Architettigini*, *Turutanoviini*, and *Sanmai* gen. nov. 1, northeastern Brazil (Hamilton 1990); 2, England (Whalley 1985); 3, Kazakhstan (Shcherbakov and Popov 2002; Shcherbakov 2009); 4, Tajikistan (Becker-Migdisova 1949); 5, Ust'-Balei, southern 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, Cicadoprobolinae with tribes Cicadoprobolini, *Architettigini* and *Turutanoviini*, and Tettigarctinae with tribes Protabanini, Meunierini, and Tettigarctini, 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 tettigarctid 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 Upper 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 *Shuraboprobole* 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 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 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 A_1 rather than Pcu , 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 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 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 Cicadoprosobolinae 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; M_{3+4} unbranched; CuA bifurcating just beyond nodal line; distal section of CuA_2 running along wing margin. Hindwing with M three-branched and M_{1+2} simple.

Remarks.—Based on information from forewings, Shcherbakov (2009) divided Tettigarctidae into subfamilies Cicadoprosobolinae 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 Cicadoprosobolinae. 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 CuA_2 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. RA_1 short and straight; M_{1+2} long and curved near nodal line; u_3 elongate, about 0.3 wing length *Sanmai mengi*
 RA_1 long and slightly sinuous; M_{1+2} short and straight; u_3 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 Fu-Tsy), 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; RA_1 long and slightly sinuous; RP fused with nodal line for a distance; M_{1+2} short and straight; u_3 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,

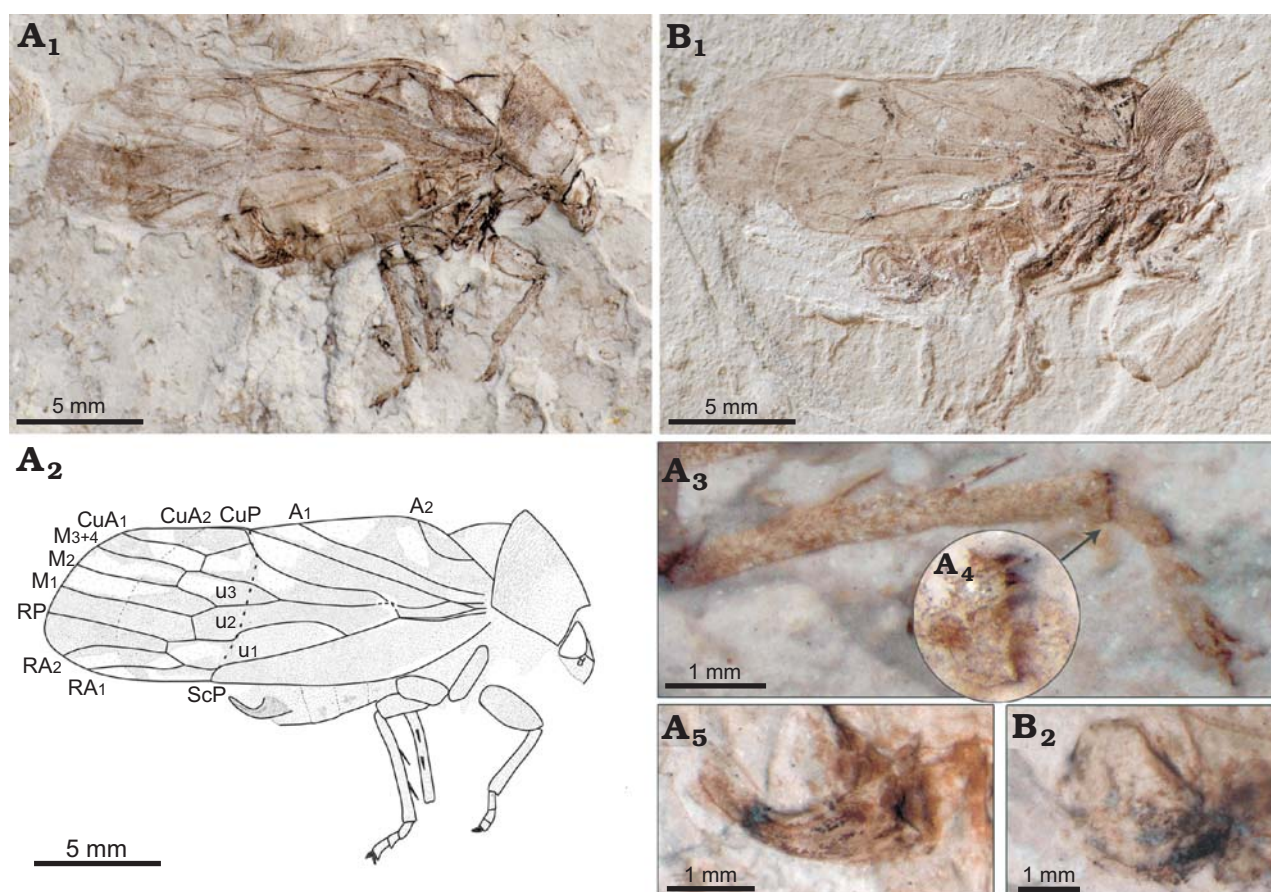


Fig. 2. Hairy cicada *Sanmai kongi* sp. nov. from the upper Middle–lower Upper Jurassic Daohugou beds. **A.** Holotype STMN48-1800a. Photograph under alcohol (A₁), explanatory drawing (A₂). Hind leg (A₃). Enlargement of apical teeth set of hind tibia (A₄). Photomicrograph of ovipositor (A₅). **B.** Paratype 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, ulnar cell.

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 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

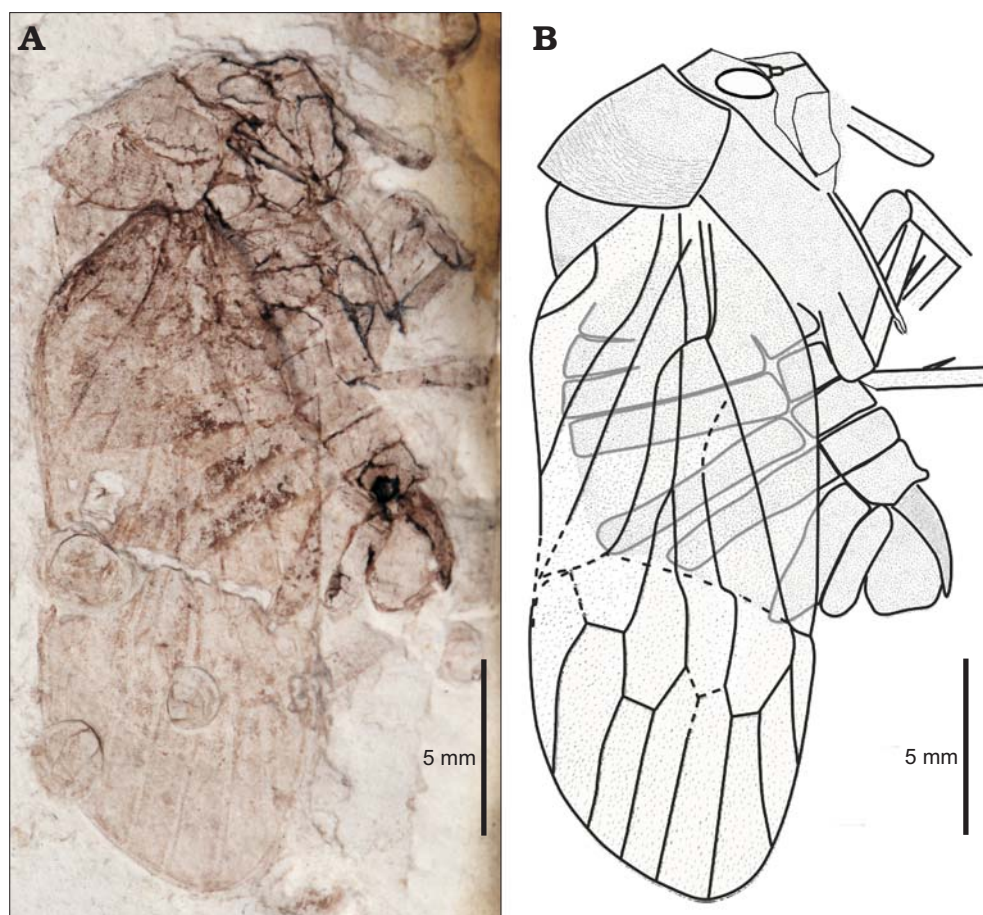


Fig. 3. Hairy cicada *Sanmai mengi* sp. nov., holotype (STMN48-1802) from the upper Middle–lower Upper Jurassic Daohugou beds. Photograph (A), explanatory drawing (B).

possessing long and slightly sinuous RA_1 , short and straight M_{1+2} , and u_3 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; RA_1 short and straight; RP fused with nodal line for a distance; M_{1+2} long and curved near nodal line; u_3 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; RA_1 short and nearly straight; RA_2 geniculate at junction with crossvein ir , then subparallel to RA_1 . 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 M_{1+2} and M_{3+4} at basal 0.42 wing length. u_3 about 0.3 wing length. Vein M_{1+2} long and sinuous beyond nodal line. Vein M_{3+4} simple, connected with M_2 by crossvein im . Stem CuA long and sinuous. CuP long and straight. A_1 sinuous. A_2 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 RA_1 ; long and curved (near

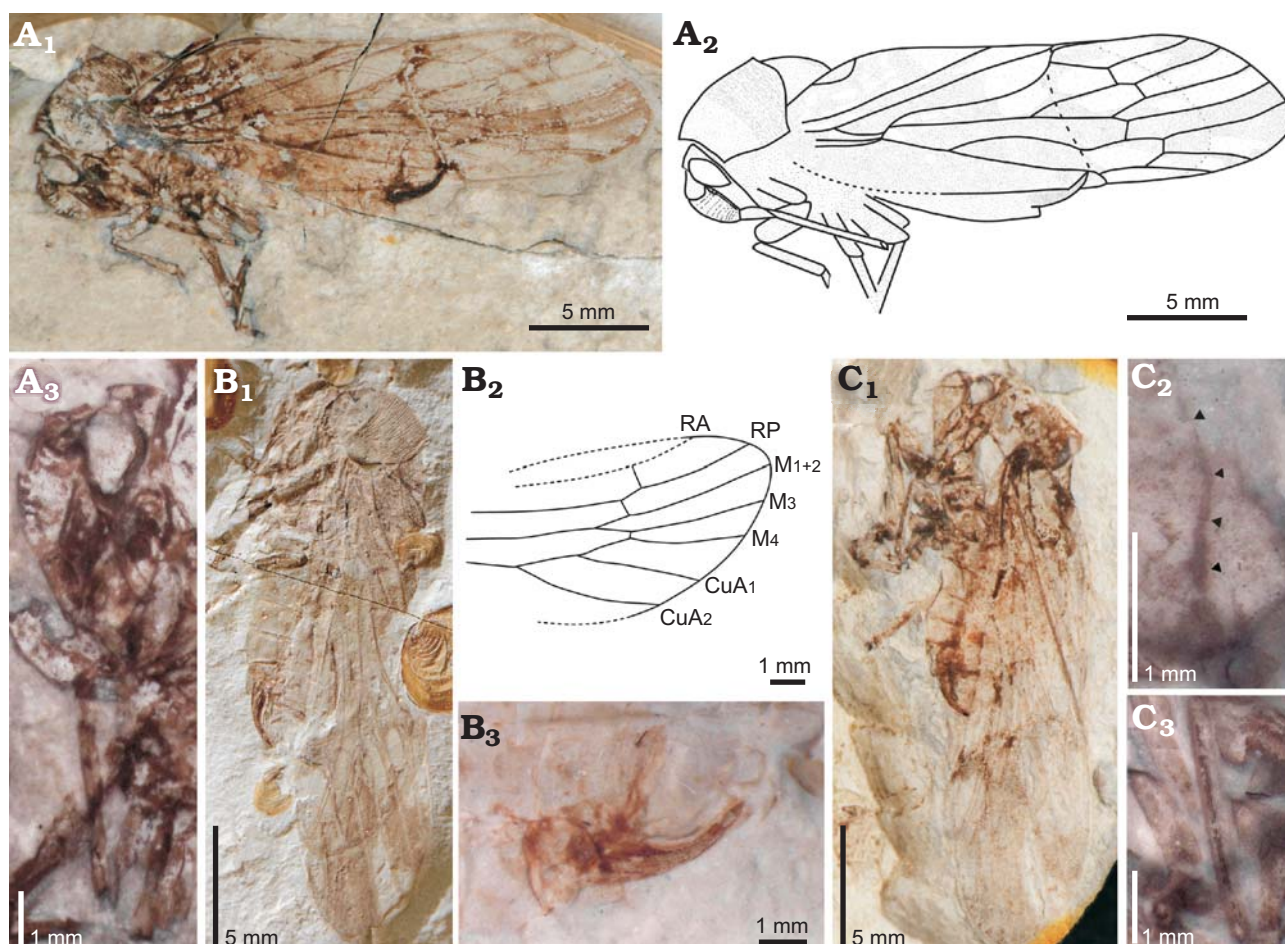


Fig. 4. Hairy cicada *Sanmai xuni* sp. nov. from the upper Middle–lower Upper Jurassic Daohugou beds. **A.** Holotype STMN48-1803. Photograph (A₁), explanatory drawing (A₂), enlargement of head (A₃). **B.** Paratype STMN48-1804. Photograph (B₁), explanatory drawing of hind wing (B₂, horizontal mirror), photomicrograph of ovipositor and pygofer (B₃). **C.** Paratype STMN48-1805. Photograph (C₁); photomicrograph of antenna, showing segments of flagellum (arrowheads) (C₂); photomicrograph of part of rostrum (C₃). 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.

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 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 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 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₊₄ basal of middle of wing wing length. u3 about 0.26 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 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 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 M₄ just beyond its departure from M₃₊₄. CuA two-branched; CuA₁ and CuA₂ 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 sinuous 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 Architettigini of Cicadoprosobolinae, 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 Architettigini, the M₃₊₄ fork might be lost in parallel in the new genus and Architettigini. The alternative scenario, however, can not be excluded that *Sanmai* gen. nov. is a transitional form between widespread Turutanoviini and specialized Architettigini, since it possesses common body structures as *Shuraboprosobole* spp. of Turutanoviini but shares a simple M₃₊₄ vein on forewing with Architettigini. *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*, *Shuraboprosobole*), with rich fossil record from the Lower Jurassic to the Upper Cretaceous of Eurasia, have been attributed to Turutanoviini (Fig. 1). *Shuraboprosobole* 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 tettigarctid fossils recently discovered from the Daohugou Lagerstätte have filled the morphological gap between *Shuraboprosobole* 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 *Shuraboprosobole daohugouensis* (Wang and Zhang 2009). These two genera do not possess distinguishable morphological characters. Therefore, the genus *Paraprosbole* should be synonymized with *Shuraboprosobole*. Although the records of Mesozoic tettigarctids are relatively rich, only fossil specimens of two genera, *Shaanxiarcta* (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 *Tettigarcta* by simple M₁₊₂ and bifurcated M₃₊₄, but very similar to that of *Shuraboprosobole 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 Architettigini we can infer, based on morphological and palaeobiogeographical data, that tettigarctids with M three-branched on forewing (*Architettix* and *Sanmai*) probably originated from some *Shuraboprosobole*-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, Architettigini (*Architettix*) possesses some distinct body structures, such as broadly exposed mesonotum, long hind tibia, and cicadellid-like tarsi. *Architettix* possesses elongate hind basitarsomere with rows of plantar setae like modern cicadellids (leafhoppers). 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 Architetigini is undoubtedly the result of convergent evolution. The specialized body structures of Architetigini 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). Architetigini, 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., *Architetix*) 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 *Tettigarcta* 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., *Protabanus* (Hong 1982), *Liassocicada* (Nel 1996), and *Shuraboprosbole* (Wang and Zhang 2009). Most forewing membranes of Mesozoic tettigarctids, however, are almost monochrome (e.g., *Sunotettigarcta 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 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 roof-like 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

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*

Chen, Zhang, and B. Wang) from the Middle–Upper Jurassic of northeastern China (Daohugou). The new genus might be a transitional form between Turutanoviini and specialized Architetigini which suggests that tettigarctids with vein M three-branched on forewing probably originated from some *Shuraboprosbole*-related tettigarctids in Laurasia in the Middle Jurassic, and then spread to Gondwana before significant extension of the Tethys Sea. The disruptive coloration 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 coloration 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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