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A new record of Scytinopteridae from the Middle Triassic Tongchuan entomofauna of China

MARINA HAKIM^{1,3} & YAN-ZHE FU^{1,2,4*}

¹State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

²Ludwig-Maximilians-Universität München, Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

³✉ marina@nigpas.ac.cn; <https://orcid.org/0000-0003-4398-6140>

⁴✉ yzfu@nigpas.ac.cn; <https://orcid.org/0000-0002-7819-1703>

*Corresponding author

Abstract

A new species of the extinct hemipteran family Scytinopteridae, *Scytinoptera minusculata* **sp. nov.**, is described and illustrated based on a forewing specimen from the Middle to Upper Triassic Yanchang Formation of Tongchuan, northern China. The new fossil differs from *Scytinoptera tongchuanensis* by its extremely short common stem MP+CuA, strongly curved R vein, and distinct colour pattern. This finding represents the third record of Scytinopteridae in the Tongchuan entomofauna, enhancing the species richness of cicadomorphan insects in the fauna. Additionally, the diagnosis of *Scytinoptera tongchuanensis* is emended, with a supplemental description provided based on seven new specimens from the same locality of the Yanchang Formation as *S. minusculata*.

Key words: Insecta; Scytinopteroidea; *Scytinoptera*; Triassic; Tongchuan

Introduction

The extinct superfamily Scytinopteroidea Handlirsch, 1906 is a hemipteran group typically assigned to the infraorder Cicadomorpha, although Szwedó (2018) proposed an alternative classification in which Scytinopteroidea is placed within the paraphyletic group Scytinopteromorpha. Scytinopteroidea includes seven families: Granulidae Hong, 1980, Ipsviciidae Tillyard, 1919, Paraknightiidae Evans, 1950, Saaloscytinidae Brauckmann, Martins-Neto & Gallego, 2006 (Martins-Neto *et al.* 2006), Scytinopteridae Handlirsch, 1906, Serpentinae Shcherbakov, 1984, and Stenoviciidae Evans, 1956. The taxonomic placement of the Granulidae as a separate family within Scytinopteroidea is acknowledged and adopted by some hemipteran researchers (Szwedó 2018; Zhang *et al.* 2021a; Fu *et al.* 2022; Lara *et al.* 2023), though it remains questionable to others (Lambkin 2020). The Scytinopteroidea is suggested to form a paraphyletic group (Szwedó 2018; Lara *et al.* 2023), indicating a need for taxonomic revision (Prokop *et al.* 2015). In fact, the taxonomic placement of some taxa within the Scytinopteroidea remains uncertain, e.g., *Doryscarta xialiaoensis* Lin, 1982 (Lin 1982a), and *Shaanxioscarta juxta* Lin, 1982 (Lin 1982b) due to the lack of necessary information to support their current placements or justify their transfers (Lambkin 2020). In this work, no attempts are made to discuss or revise any of these classifications.

Representatives attributed to the Scytinopteridae are known from the Permian of France, Russia, Kazakhstan, Mongolia, Australia, and Mexico (e.g., Handlirsch 1904; Martynov 1928; Carpenter & Miller 1937; Davis 1942; Becker-Migdisova 1948, 1961; Prokop *et al.* 2015; Shcherbakov 1984, 2022, 2024), and from the Triassic of Russia, China, Australia, Argentina, and South Africa (e.g., Tillyard 1919, 1922; Riek 1976; Lin 1986; Martins-Neto & Gallego 1999, 2003; Lara & Wang 2016; Lara & Bashkuev 2020; Lambkin 2016, 2020; Lara *et al.* 2021, 2023; Zhang *et al.* 2021b; Shcherbakov 2024). Records of Scytinopteridae from China are scarce, including only *Apheloscyta xiangdongensis* Lin, 1986, *Dytoscytina ejuncida* Lin, 1986, *Mesoscytina tongchuanensis* Zhang, Du & Zhang, 2024,

and *Scytinoptera tongchuanensis* Zhang, Zheng & Zhang, 2021 (Zhang *et al.* 2021b). Lambkin (2020) also proposed that *Disivicia tianshanensis* Lin, 1992 belongs to Scytinopteridae based on the characteristics of its tegmen. In addition to these species, other taxa attributed to the Scytinopteroidea from Chinese deposits include *Doryscarta xialiaoensis* Lin, 1982 and *Shaanxioscarta juxta* Lin, 1982 in Ipsviciidae, and *Granulus tongchuanensis* Hong, 1980, *Sinogranulus jinsuoguanensis* Fu & Huang, 2022 and *Sinogranulus qishuiheensis* Zhang, Chen & Zhang, 2021 in Granulidae.

Herein, we describe the new species *Scytinoptera minusculata* **sp. nov.**, representing the third record of the family from the Triassic Tongchuan entomofauna, and update the diagnosis of *Scytinoptera tongchuanensis* based on the newly discovered material.

Material and methods

The holotype of *Scytinoptera minusculata* **sp. nov.** (NIGP205891) and seven newly discovered specimens of *Scytinoptera tongchuanensis* (NIGP205892–205894, 206003–206006) were collected from greenish grey shale in the lower part of the Yanchang Formation (formerly referred to as the Tongchuan Formation in earlier palaeontological studies) at the Hejiafang Village, Jinsuoguan Township, Yintai District, Tongchuan City, Shaanxi Province, northwestern China (for a map of the fossil locality see Fu *et al.* 2021: fig.1).

The specimens were carefully cleaned and prepared for observation by removing sediments covering them with a small sharp blade. The material was later examined and photographed with a Zeiss AxioZoom V16 stereomicroscope. Photographs were stacked using Helicon Focus 6 software and the line drawings were prepared from photographs using Adobe Photoshop CC 2019 software. The holotype of *Scytinoptera tongchuanensis* was re-examined for comparison with the new specimens. The studied material is deposited at the Nanjing Institute of Geology and Palaeontology (NIGPAS), Chinese Academy of Sciences, Nanjing, China.

Lara *et al.* (2023) mentioned that no clear consensus exists at the moment for vein homology and nomenclature in our group of interest, thus we mostly adopted herein the terminology of Nel *et al.* (2012) for Acercaria, modified after Schubnel *et al.* (2020) for the presence of the PCu vein in the Neoptera, which is mainly followed in recent studies on Scytinopteridae. Wing venation abbreviations: bc, basal cell; cf, costal fracture; Pc+CP, praecosta + costa posterior; R, radius; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; cua-cup, cubitus anterior-cubitus posterior specialized crossvein; PCu, postcubitus; A1, first anal vein; A2, second anal vein.

Results

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Infraorder Cicadomorpha Evans, 1946

Superfamily Scytinopteroidea Handlirsch, 1906

Family Scytinopteridae Handlirsch, 1906

Genus *Scytinoptera* Handlirsch, 1904

Type species. *Scytinoptera kokeni* Handlirsch, 1904

***Scytinoptera tongchuanensis* Zhang, Zheng, Teng & Zhang, 2021**

Figs 1–3

Additional material. NIGP205892a and NIGP205892b (part and counterpart, respectively), completely preserved tegmen; NIGP205893a and NIGP205893b (part and counterpart), completely preserved tegmen; NIGP205894, completely preserved tegmen; NIGP206003 mostly complete tegmen missing anterior basal section; NIGP206004, incomplete tegmen missing clavus; NIGP206005 and NIGP206006, incomplete tegmen missing clavus and basal section. All material is deposited at the Nanjing Institute of Geology and Palaeontology, CAS.

Locality and horizon. Hejiafang Village, Jinsuoguan Township, Yintai District, Tongchuan City, Shaanxi Province, China; Yanchang Formation; Middle Triassic.



Figure 1. Tegmen of *Scytinoptera tongchuanensis*, photographs. **A**, NIGP205892a; **B**, NIGP205892b; Scale bars= 2 mm.

Emended diagnosis. Based on the newly available material, we make the following corrections: tegmen with common stem MP+CuA relatively long; R almost straight or slightly arched; tegmen with transverse, light-coloured stripe almost across anterior and posterior margins of wing at about 1/3 of wing base.

Remarks. *Scytinoptera tongchuanensis* was established based on a complete tegmen from the Middle Triassic Tongchuan entomofauna (Zhang *et al.* 2021b). In the new material, the main veins are very faint and/or indistinct at their distal sections, as in the type specimen. The branches and crossveins are not clearly visible in the new specimens but probably present. Additionally, the colour pattern appears consistent in the new specimens with the illustration of the type material: tegmen darkish in colour with a wide vertical light-coloured stripe around basal third section of the wing, upper distal zone with speckled colouration, and potential small discoloured zone near the area where CuP reaches posterior margin. The tegmen size is also comparable with the type material (length between 8.7–9.1 mm in complete specimens, and over 6 mm in incomplete specimens). Therefore, we consider it reasonable to assign the new specimens to the co-occurring species *Scytinoptera tongchuanensis*.

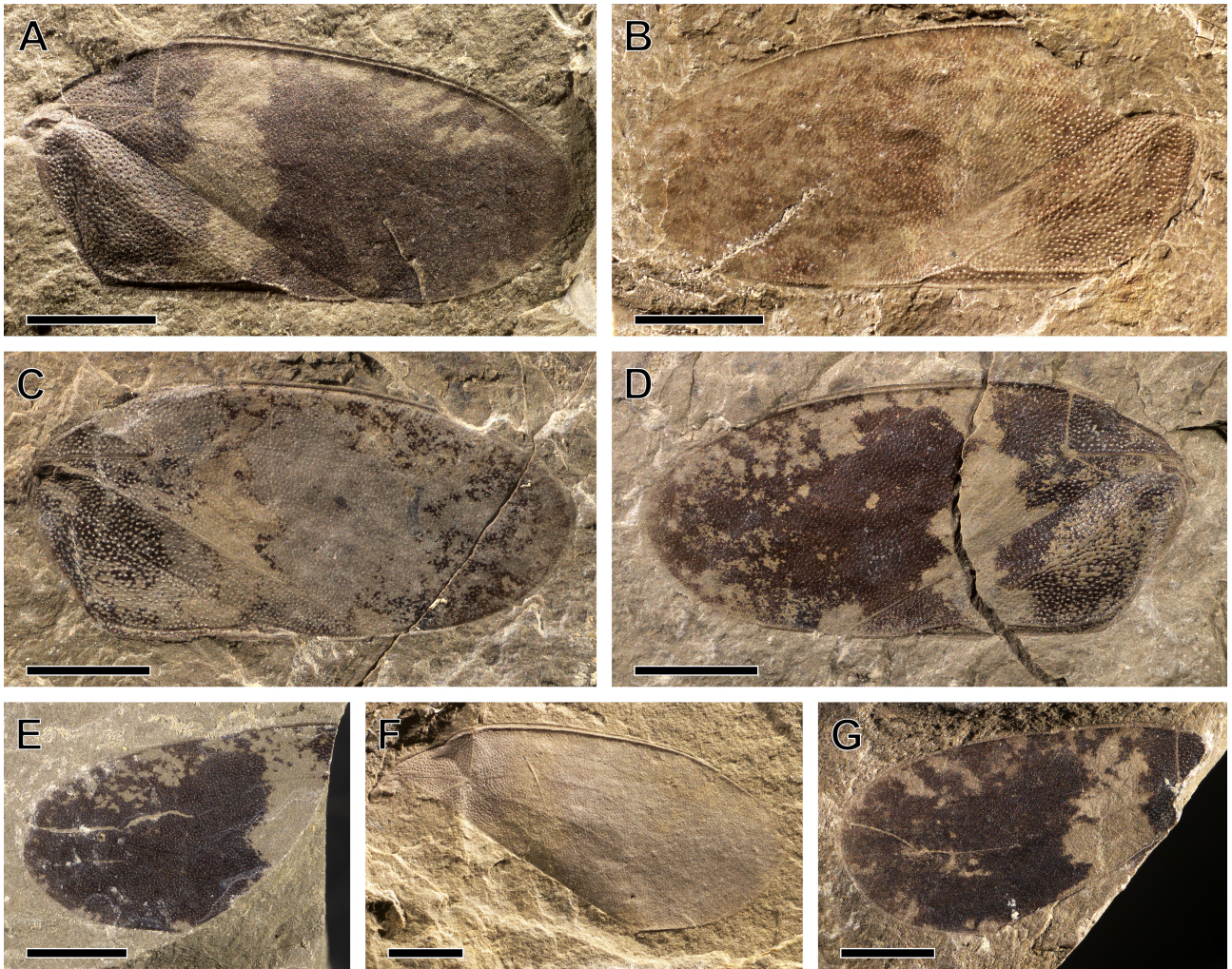


Figure 2. Tegmen of *Scytinoptera tongchuanensis*. **A**, NIGP205894; **B**, NIGP206003; **C**, NIGP205893a; **D**, NIGP205893b; **E**, NIGP206005; **F**, NIGP206004; **G**, NIGP206006. Scale bars= 2 mm.

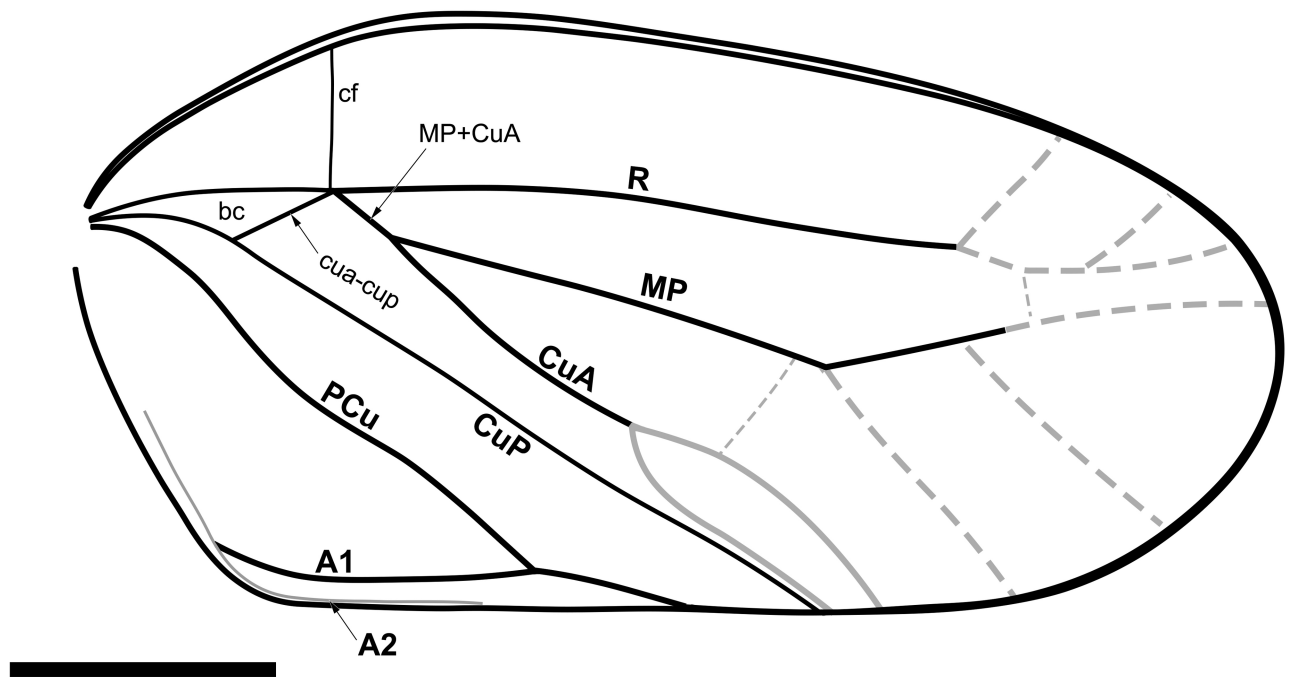


Figure 3. Reconstructed line drawing of *Scytinoptera tongchuanensis* based on the new specimens combined (full grey lines represent faint but observed veins; dotted grey lines represent uncertain but potential veins). Scale bar= 2 mm.

Zhang *et al.* (2021b) described and illustrated the claval veins PCu and A1 junction at the midpoint of A1; however, the new material and a re-examination of the holotype show that common stem PCu+A1 is shorter than originally interpreted, at about half the length of A1 (not as long as A1). Zhang *et al.* (2021b) considered both anal veins (A1 and A2) present but not joining distally. It is noteworthy that a basal division of A into A1 and A2, which later join again before fusing with PCu, is a common occurrence in Hemiptera. If such a pattern exists in this species, it is too faint to be clearly detected in the new specimens. Additionally, the basal sections of MP and CuA are not visible in the type specimen. The new specimens share the consistent characteristic of a relatively long common stem of MP+CuA, which is clearly visible in specimens NIGP205892, NIGP205893, and NIGP205894 (Figs 1, 2A–C, F).

Scytinoptera minusculata sp. nov.

(Fig. 4)

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Type material. Holotype NIGP205891, completely preserved forewing (tegmen), deposited at the Nanjing Institute of Geology and Palaeontology, CAS.

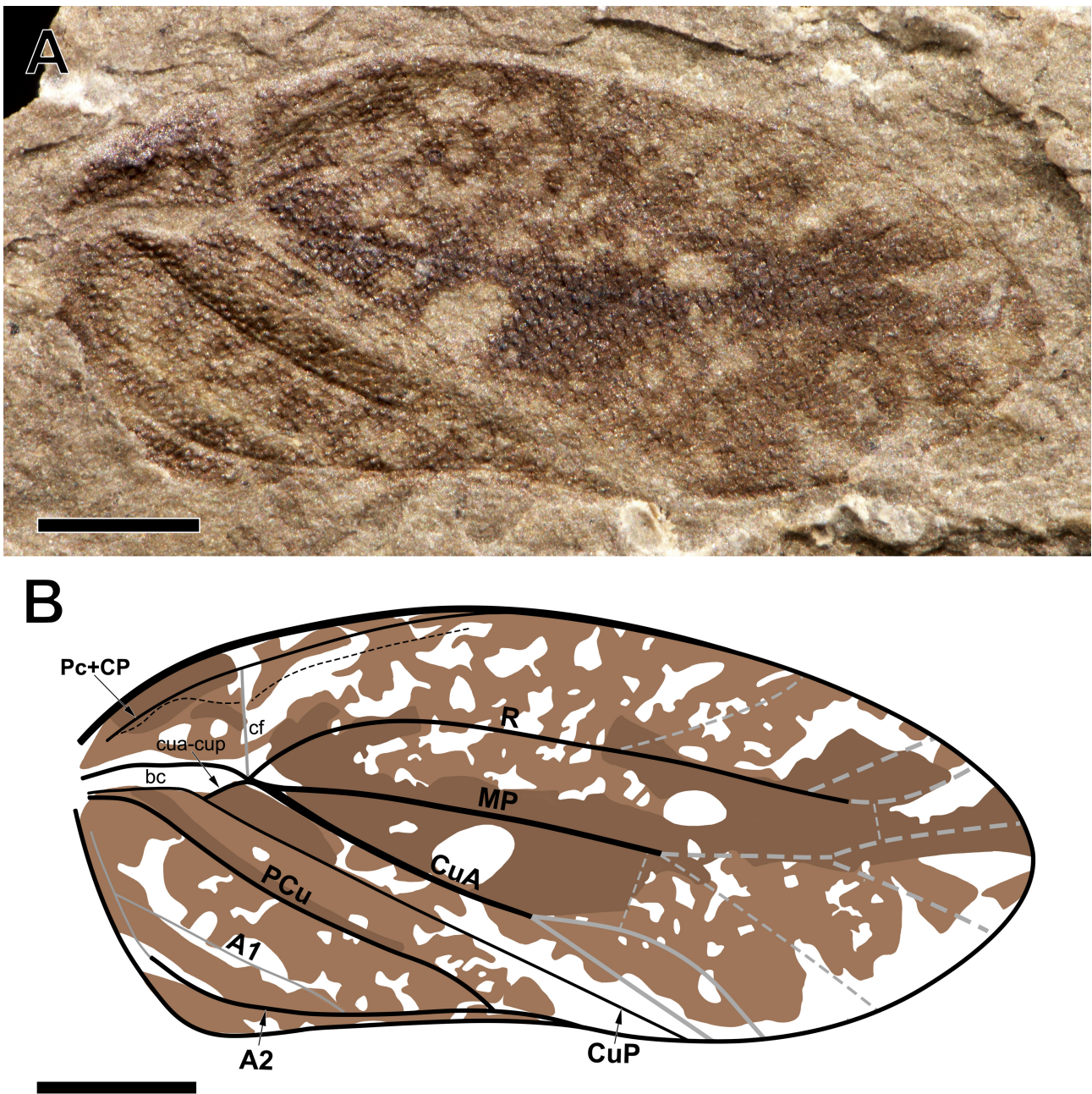


Figure 4. Tegmen of *Scytinoptera minusculata* sp. nov., holotype NIGP205891, photographs. **A**, Venation detail and potential colouration pattern; **B**, Line drawing (full grey lines represent faint but observed veins; dotted grey lines represent uncertain but potential veins). Scale bars= 0.5 mm.

Locality and horizon. Hejiafang Village, Jinsuoguan Township, Yintai District, Tongchuan City, Shaanxi Province, China; Yanchang Formation; Middle Triassic.

Etymology. The specific epithet is derived from the Latin word for “minuscule”, in reference to the species’ small tegmen size.

Diagnosis. Tegmen approximately 3 mm in length, broadest at mid-length; main veins strongly delimited basally but indistinct distally; branches and crossveins indistinct in distal half; R strongly curved basally; common stem MP+CuA very short; tegmen with mottled pattern, light pigmentation interspersed, lacking distinct light-coloured stripe as in *Scytinoptera tongchuanensis* (Fig. 4).

Description. Tegmen elongate, 3.1 mm long, 1.3 mm wide, length/width ratio 2.4:1. Tegmen widest near mid-length, with asymmetrically rounded apex and large clavus. Costal margin convex, thickened basally; posterior margin concave before the claval suture; cf subvertical, emerging from apex of bc, and weakly delimited; bc closed distally, semi-triangular. Main veins strongly delimited basally but very faint and unclear distally; main branches and crossveins indistinct in distal half. Veins R, MP and CuA fused near base, at apex of basal cell. R strongly curved basally. Common stem MP+CuA very short. MP mostly straight. CuA curved, forking in its distal third into two very faint but visible branches; CuA₁ strongly curved, CuA₂ straight. Crossvein cua-cup present. CuP curved basally, then straight across most length, simple. PCu single, weakly sinusoidal. A1 possibly present, weakly defined, distally fused with A2; A2 distinct, close to wing margin. PCu connected near posterior margin to A and forming large Y-claval vein; common stem PCu+A under half (around 25%) the total length of A2. Wing surface covered with punctures, punctures bigger and more distinct in tegmen basal half and less clear in distal half. Potential colouration pattern with dark sclerotized zone in anterior basal area near costal margin and across central area of tegmen; two moderately large unsclerotized circular zones in center; lighter colouration speckled across wing surface.

Discussion

The new taxon displays affinities to Cicadomorpha in the tegminized forewing with strong punctuations at the basal half part of the wing, the main and secondary veins forming large cells all over the forewing, and the presence of an elongated cua-cup closing a long basal cell (Shcherbakov 1984). It further relates to the Scytinopteroidea by the strongly convex hyposubcostal carina (= base of Sc), the distinct costal fracture at the apex of the basal cell and a reduced nodal flexion line (Shcherbakov 1996).

Determining the accurate taxonomic placement of the new species is problematic due to the difficulty in observing the venation pattern in the distal half of the tegmen, which hinders any attempted comparisons with other described scytinopterids. Zhang *et al.* (2021b) revised the diagnosis of *Scytinoptera* Handlirsch, 1904 after Martynov (1928). The characteristics of the new fossil (NIGP205891) are consistent with this diagnosis and it can be assigned to this genus based on the following diagnostic characters (Zhang *et al.* 2021b): 1) tegmen convex with apex asymmetrical, and base comparatively broader; 2) veins R, MP, and CuA fused or very close at tegminal base; 3) CuA two-branched; 4) clavus large with posterior margin bent downwards, and anal angle around 120°; 5) tegminal surface punctured, punctures becoming gradually smaller apically; and 6) colouration present, albeit this character is weak for generic diagnosis in Cicadomorpha as colour on the tegmen is quite frequent.

As mentioned previously, the main veins of both *Scytinoptera tongchuanensis* and *Scytinoptera minusculata* **sp. nov.** are indistinct in their distal sections, with branches and crossveins not clearly visible for a confident interpretation. This trait remains consistent in *S. tongchuanensis* after the discovery of additional material. Consequently, it appears to be a common characteristic observed in these two described scytinopterid species originating from the Tongchuan entomofauna. One likely implication of this observation is that the veins are morphologically weaker distally—after they start branching—than they are basally, which, combined with the taphonomy behind their preservation, is probably causing them to become indistinguishable in the compressions. The illustration by Zhang *et al.* (2024, fig. 1A) of *Mesoscytina tongchuanensis* also shows somewhat faint distal veins, albeit more discernible when compared to *S. minusculata* **sp. nov.** and *S. tongchuanensis*. Further discoveries of new specimens from the Tongchuan outcrops, including new material belonging to *Scytinoptera minusculata* **sp. nov.**, will help determine the stability and causes of this feature in the taxa, solidify the diagnostic characters and their phylogenetic values, and clarify whether *S. tongchuanensis* and the new species should be kept in *Scytinoptera* or moved to a new separate genus. At present, we tentatively follow the taxonomic assignation of Zhang *et al.* (2021b) and attribute the new species to *Scytinoptera*.

Lambkin (2016) defined the distinguishing tegminal characters of Scytinoptera, after Shcherbakov (1984), as: ‘the shape of the basal cell [basal cell short, gradually narrowing beyond the middle part in Shcherbakov (1984)], the presence of uniformly punctate or slightly rasp-like macrosculpture, a single r-m, a very weak or absent nodal groove, and in Triassic genera M bent strongly towards CuA at the level of an absent nodal groove and without an accompanying m-cu’. *Scytinoptera tongchuanensis* and *S. minusculata* **sp. nov.** exhibit a similar basal cell shape and punctate tegmen; however, vein MP appears to be straight rather than bent strongly towards CuA. It is noteworthy that *Duraznoscytinum* Lara, Cariglino & Zavattieri, 2023 also displays a clearly straight vein MP; this characteristic should be re-evaluated in light of these recent discoveries.

Scytinoptera includes nineteen species, of which fifteen are known from the Permian and only three from the Triassic. The Triassic species comprise *Scytinoptera distorta* Riek, 1976 originating from South Africa, and *S. tongchuanensis* and *S. minusculata* **sp. nov.** from China (Tongchuan entomofauna). Interestingly, *S. distorta* also does not seem to exhibit a bend of MP towards CuA. The new species differs from the other two by the tegmen length (*S. minusculata* **sp. nov.** around one third of the tegmen length of *S. tongchuanensis* and around half of the tegmen length of *S. distorta*) and vein R strongly curved basally (vs. semi-straight). The new species *S. minusculata* **sp. nov.** further differs from *S. tongchuanensis* by the shape of the anterior costal margin (maximum curvature at mid-length in *S. minusculata* **sp. nov.** vs. at basal quarter in *S. tongchuanensis*), the common stem MP+CuA very short (less than half the length of *S. tongchuanensis*), a different colour pattern, and potentially a different anal vein pattern. The new species further differs from *S. distorta* by the latter having clear and distinguishable veins all across the tegmen. Riek (1976, fig. 13) described and illustrated the common stem MP+CuA as absent, with the two veins connected by a short crossvein instead; however, the photo of the specimen (Riek, 1976, plate 1, fig. 7) is very blurry and the status of the veins at base cannot be confirmed. Our findings suggest that the length of the common stem MP+CuA varies among species within a genus.

The strongly curved vein R at the base is regarded as one of the diagnostic characteristics of the Triassic genus *Mesoscytina* Tillyard, 1919 (Lambkin 2016). Zhang *et al.* (2024) described a new scytinopteroid species from the Tongchuan entomofauna and assigned it to *Mesoscytina* Tillyard, 1919 by the apically forked vein R, the curved vein MP with three terminal branches, and the punctate tegmen (Zhang *et al.* 2024). The vein R of *Mesoscytina tongchuanensis* is slightly arched and lacks the strongly curved base characteristic. Additionally, *M. tongchuanensis* possesses a long common stem MP+CuA, a less curved MP with a different branching pattern (two-branched, MP₁₊₂ with two terminals) compared to other *Mesoscytina* species. Re-evaluations of the family Scytinoptera and its genera, particularly *Scytinoptera* and *Mesoscytina*, might be necessary for establishing clear definitions. Nonetheless, *Scytinoptera minusculata* **sp. nov.** differs from *M. tongchuanensis* in the length of the tegmen (less than or equal to half the length), and several variations to the venation pattern, mainly: stem of R with strong arch at base; stems of M and CuA with longer branches; and stem of M lacking a curve distally (Zhang *et al.* 2024).

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