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A new early representative genus of Hylicellidae from the Triassic of China (Hemiptera, Cicadomorpha)

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Abstract

A new genus and species of the extinct hemipteran family Hylicellidae, *Sinohylicella sigmoidea* **gen. et sp. nov.**, is described and illustrated on the basis of a forewing specimen from the Middle-Upper Triassic Yanchang Formation of Shaanxi, northern China. The new fossil exhibits strongly curved CuA and PCu veins, peculiar characters adding to the morphological disparity of Triassic Cicadomorpha. The diagnoses of the Hylicelloidea, and its component families Hylicellidae, Mesojabloniidae, and Chiliocyclidae, are discussed.

Key words: Insecta, Hylicelloidea, systematics, fossil record, Tongchuan

Introduction

The Cicadomorpha Evans, 1946, belonging to the highly-diversified Hemiptera and encompassing froghoppers, leafhoppers, treehoppers, and cicadas, appeared during the Permian and diversified throughout the Mesozoic (Shcherbakov 1996). Their extant diversity is impressive, with more than 33,000 known species (Bartlett *et al*. 2018). Their fossil record testifies to an exceptionally high level of diversity, with numerous extinct lineages ranging from the Permian to the Cretaceous (e.g., Shcherbakov 1996; Wang *et al*. 2010).

Among these lineages, the Mesozoic superfamily Hylicelloidea Evans, 1956 is very poorly defined, considered by Wang *et al*. (2010) as a paraphyletic group. It currently comprises the four following families: Chiliocyclidae Evans, 1956, Hylicellidae Evans, 1956, and Mesojabloniidae Storozhenko, 1992, and Minlagerrontidae Chen, Szwedo & Wang, 2019 (Shcherbakov 2011; Szwedo 2018; Chen *et al.* 2019; Lambkin 2020). This superfamily exemplifies the current problematics surrounding the delimitations of many cicadomorphan lineages: poorly defined, not based on polarized character states, and lack clear synapomorphy supporting these sets of taxa. Nevertheless, Hylicelloidea are important group as they are putatively closely related to the Clypeata, a clade encompassing all extant cicadomorphan families.

The Middle Triassic Tongchuan entomofauna of northern China has yielded a notably abundant assemblage of cicadomorphan insect (Zhang *et al.* 2022; Fu *et al.* 2022; Fu & Huang 2022a,b, 2023). In particular, the description of *Vetusala maculata* Fu & Huang, 2023, from this outcrop, corresponds to the earliest record of Hylicellidae in China. Herein, we describe a second species of Hylicellidae, *Sinohylicella sigmoidea* **gen. et sp. nov.**, another early representative of its family, increasing our knowledge on the diversity of cicadomorphans in the Tongchuan entomofauna.

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Material and methods

The studied specimen (NIGP205890), consisting of part and counterpart, was preserved in greenish grey shale. It was collected from the lower section of the Middle-Upper Triassic Yanchang Formation, previously referred to as the Tongchuan Formation in earlier paleontological studies, near Hejiafang Village, Jinsuoguan Township, Yintai District, Tongchuan City, Shaanxi Province, China (detailed location of the fossil site in Fu *et al*. 2021: Fig. 1).

The studied specimen was carefully prepared using a sharp blade. Photographs were taken with a Zeiss AxioZoom V16 stereoscope and the line drawing was drafted with CorelDRAW 2018 graphic software. The specimen is deposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Systematic framework follows Szwedo (2018), and the wing venation terminology follows Nel *et al*. (2012), Bourgoin *et al*. (2015), and Lambkin (2020), as adapted by Schubnel *et al*. (2019) for the postcubitus vein. Venation abbreviations are as follows: C, costa; Pc, praecosta; ScP, subcostal posterior; RA_1, first branch of the radius anterior; RA_2, second branch of the radius anterior; RP, radius posterior; MP, media posterior; CuA_1, first branch of cubitus anterior; CuA_2, second branch of cubitus anterior; CuP, cubitus posterior; PCu, postcubitus; A1, first anal vein. Crossveins are written in lowercase, e.g. cua-cup is the crossvein between CuA and CuP.

Results

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Cicadomorpha Evans, 1946
Clade Clypeata Qadri, 1967
Superfamily Hylicelloidea Evans, 1956
Family Hylicellidae Evans, 1956

Genus *Sinohylicella* gen. nov.
Urn:lsid:zoobank.org:act:8CEC6E00-D607-4E06-9059-3251DF8ABF7C

Type species. *Sinohylicella sigmoidea* **sp. nov.**; by present designation and monotype.

Etymology. The generic name derives from Sinica, Latin name for China and the genus name *Hylicella*. Gender: feminine.

Diagnosis. Tegmen with Pc+CP long; RA_2 sinuous, with four pectinate anterior branches; stem CuA sigmoidal medially; PCu strongly curved medially, widely sigmoidal; two crossveins ir present; C3 cell elongate; only one crossvein rp-mp; and cua-cup ending at base of CuA.

***Sinohylicella sigmoidea* sp. nov.**
(Fig. 1)
Urn:lsid:zoobank.org:act:2515CC3E-41B6-45D4-A3DB-A6F5F720E921

Material. Holotype, NIGP205890, an isolated tegmen.

Etymology. The specific epithet is derived from the strongly sigmoidal stem of CuA and PCu, characteristic of the taxon.

Diagnosis. As for the genus with additional characters: tegmen with dark markings between base of CuP and base of PCu, near terminal part of PCu, and along CuA_2 and basal CuA_1; area along Pc+CP lightly darkened.

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

Description. Tegmen about 13.3 mm long, with basal half strongly punctured; costal margin arched; apical margin rounded, posterior margin straight; bScP smoothly arched; Pc+CP extending apicad of apex of ScP+RA_1; stem R smoothly arched, forked into ScP+RA and RP at basal 41% of tegmen length; ScP+RA forked basad of MP and CuA forking; RA_2 sinuous, pectinate forked, with four terminal branches; RP unbranched with basal half sinuous;

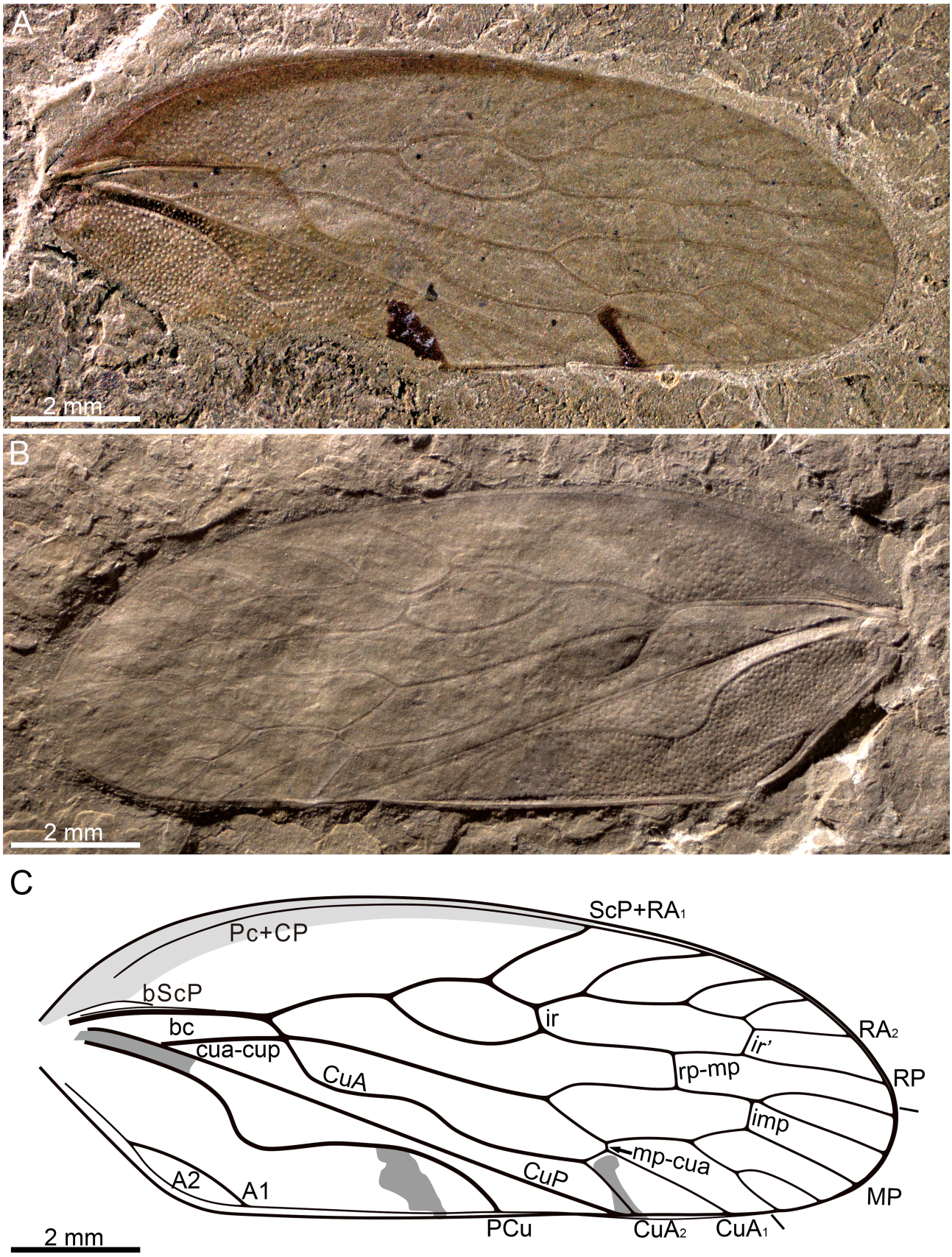

Figure 1. Photographs and line drawing of *Sinohylicella sigmoidea* **gen. et sp. nov.** from the Triassic Yanchang Formation of China. **A,** Photograph, part (NIGP205890a). **B,** Photograph, counterpart (NIGP205890b). **C,** Line drawing. Abbreviations: (bc) basal cell.

MP+CuA stalk present; stem of MP almost straight, forked basad of CuA forking, at basal 59% of tegmen length, with five terminal branches; stem CuA curved medially towards costal margin; 2nd section CuA_1 about twice as long as CuA_2; CuP straight; PCu initially straight; curving downward and forming smooth arc, extending towards CuP near wing edge, then to anal margin, creating reverse smooth arc; A1 simple. Crossvein cua-cup distally ending at point of separation between MP and CuA at a single point; two crossveins ir present, rp-mp, imp, and mp-cua single. Basal cell long and wide; postcostal cell broad, much wider than median cell and radial cell. First anal cell rather small. Tegmen with darkly pigmented patches between base of CuP and base of PCu, near terminal part of PCu, and along CuA_2 and basal CuA_1; area along Pc+CP lightly darkened. Distinctive punctures evenly distributed in basal half of postcostal cell, basal cubital cell, most of clavus, and along basal parts of stem R, MP, and Cu.

Discussion

The new fossil is considered to be a forewing of Cicadomorpha (Hemiptera) due to its tegminization with strong punctuations on the basal half part of the wing, 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). Within the Cicadomorpha, the superfamily Hylicelloidea are defined, after Shcherbakov (2011: 2) by 'Pcu and 1A likewise appear free, but the claval structure is further modified: the 1st anal space is short, closed by the 1A+2A junction, and the narrow, deflected 2nd anal space is sometimes visible along the commissural margin. The crossveins are labeled as *ir, rm, im,* and *mcu.* The surface sculpture sometimes consists of rasp-like punctures (with the side nearest to the tegmen base raised) resembling granules'. PCu and A are not free like it was previously suggested; it is clearly visible in the new fossil with A1 fused very basally with A2, then PCu fused with A, distally from the base of the forewing, in a very distal part of the clavus, almost in the anal margin of the forewing, but still retaining the classical Y-shaped claval vein present in Cicadomorpha and Fulgoromorpha. However, the new fossil has these characters, supporting an attribution of the new fossil to this group of taxa.

Lambkin (2024a: 37) proposed the following characters for the Hylicellidae: 'short lower carina at base of costal field, basal cell broad proximally then tapering distally, CuA+M and then CuA curved downward and approaching claval suture, ir present, RA_1 [ScP+RA_1] simple, RA_2 forked, RP simple, and M with four terminal branches'. All these characters are present in the new tegmen, supporting a possible attribution to this family. Originally, Evans (1956: 195) defined the Hylicellidae as follows: 'This family is created for the reception of Upper Triassic Homoptera with tegmina which resemble those of recent hylicids in having M_{3+4} in part incorporated in the same vein as Cu_1. They differ from hylicids in retaining Cu_{1a} and in having a more complete *M*'. The partial fusion of CuA_1 with posterior-most branch of MP is a character clearly insufficient to define the family, as it is present in the type genus *Hylicella* Evans, 1956, but absent in many other genera currently attributed to this family, except *Conjucella* Shcherbakov, 2012.

The affinities of the new fossil with the Mesojabloniidae can be excluded based on its unbranched RP and its cua-cup ending in the point of separation between MP and CuA (Shcherbakov, 2011). The recently described mesojabloniid genus *Allawah* Lambkin, 2024b, based on the distal part of a tegmen, strongly resembles *Vietocycla* (see Lambkin 2024b: figs 5–6). Lambkin (2024b) noted that the crucial diagnostic character of the Mesojabloniidae is the early forking of the CuA, well before the nodal level. The primary fork of CuA is at or beyond the nodal level in the other hylicelloid families (Hylicellidae, Chiliocyclidae, and Minlagerrontidae) (Lambkin 2024b). In the holotype, of *Allawah tillyardi* Lambkin, 2024b, the fork of CuA is not preserved, even if it appears to be more basal than in *Vietocycla*.

Chiliocyclidae were placed in Hylicelloidea by Shcherbakov (1992, 1992) and Szwedo (2018). However, this family was also assigned within the Scytinopteroidea Handlirsch, 1906 (Martins-Neto 2003), another paraphyletic assemblage, recently placed outside the Cicadomorpha (Szwedo 2018). Evans (1956: 209, fig. 12F) proposed the following diagnosis for the Chiliocyclidae: 'having tegmina in which an enclosed cell is formed between the arms of M_{1+2} and M_{3+4}. Cu_1 may have a basal bend or be linked with *M* by a crossvein [indeed corresponding to cua-cup ending into independent CuA or in MP+CuA], and Rs [RP] is invariably present'. This diagnosis is clearly insufficient to correctly define a family. Evans (1956) listed a series of genera in this family, but Hamilton (1992) only retained the type genus *Chiliocycla* Tillyard, 1919, without further explanation. Other genera have been placed within this family like *Argentinocicada* and *Tipuloidea* (Martins-Neto *et al*. 2023; Lara & Wang 2016) but recently placed in Scytinopteridae Handlirsch, 1906 (Lara & Bashkuev 2020; Lara *et al*. 2023). The new fossil shares with the type genus *Chiliocycla* Tillyard, 1919 the presence of a cell enclosed between the branches of MP and a simple RP, but strongly differs from it in the multi-branched RA and cua-cup not ending into the free distal part of CuA.

The Hylicellidae are currently divided into three subfamilies, viz. the Conjucellinae Shcherbakov, 2012, Hylicellinae Evans, 1956, and Vietocyclinae Shcherbakov, 1988. The Conjucellinae strongly differ from the new fossil in the RA simple, a larger first anal cell, and overall, CuA emerging from R+MP well basal to the base of MP (Shcherbakov 2012). Notice that *Conjucella* has a cell enclosed between the branches of MP as in *Chiliocycla*. The Vietocyclinae differ from the new fossil in the presence of no less than two crossveins between RP and MP (vs. only one crossvein), but this is a rather secondary character, as the presence vs. absence of the second, distal-most crossvein could be variable as in extant Cicadomorpha. Also Chen *et al.* (2022: 1128) noticed that 'Hylicellids, especially Hylicellinae and Vietocyclinae, possess a tegmen with considerable intraspecific or even intra-individual variation in venation'. The new fossil shares with *Vietocycla* Shcherbakov, 1988 and *Cycloscytina* Martynov, 1926 the cua-cup ending at point of separation of MP with CuA, while in *Reticycla* Shcherbakov, 2020, cua-cup ends into MP+CuA (Shcherbakov 2020). The new fossil further differs from *Vietocycla* in the absence of a series of veinlets in the area between ScP+R and the anterior margin of the wing (Shcherbakov 1988; Fu & Huang 2019). It differs from *Jiphara* Ren, 1995 in the absence of numerous veinlets emerging from ScP+RA_1 (Ren *et al*. 1995: figs 3–27 and 3–28). It more closely resembles *Cycloscytina*, especially in the shape of the radial and median veins and their branches, but strongly differs from it in the longer cua-cup and longer basal cell, and CuA stem distinctly sigmoidal (vs. straight) (Shcherbakov 1988: fig. 3b; Chen *et al*. 2022). Lambkin (2010: 391) indicated that 'third subfamily, Hylicellinae, lacks clear definition'. Chen *et al.* (2022) indicated that the 'known representatives of Hylicellinae possess some common tegminal features (e.g., RP single, M four-branched, and crossveins [ir, r-m, im, m-cua] single)'.

After Lambkin (2020: 526), *Crosbella* Evans, 1956 and *Triassoscelis* Evans, 1956 are assigned to the subfamily Vietocyclinae, while *Hylicella* Evans, 1956, *Mesocixiodes* Tillyard, 1922, and *Mesothymbris* Evans, 1956 are tentatively retained in the Hylicellinae. *Crosbella* has numerous veinlets emerging from ScP+R, three crossveins between RP and MP, and branches of MP (Lambkin 2020), characters that would rather belong to the Vietocyclinae, and are sufficient to separate it from the new fossil. *Hylicella* differs from the new fossil in cua-cup ending into MP+CuA, one ir crossvein and RA with only two distal branches (Lambkin 2020). *Mesocixiodes* also has only one ir crossvein and cua-cup ending into MP+CuA, but shares with the new fossil several anterior branches of RA (Lambkin 2020). *Mesothymbris* has cua-cup ending in CuA and several branches of RA, but only one ir crossvein. Also, the C3 cell is shorter than in the new fossil, and overall, CuA is simply curved instead of being sigmoidal (Lambkin 2019). *Triassoscelis* differs from the new fossil in the presence of much more anterior veinlets emerging from ScP+RA, one ir crossvein and CuA_1 branched (Lambkin, 2020). *Tychoscytina* is based on a very poor incomplete tegmen (Becker-Migdisova 1952: fig. 4). *Mesocicada* is based on the basal two-third of a tegmen (Becker-Migdisova, 1962: fig. 465). If it resembles the new fossil in the PCu sigmoidal, much less than in the new fossil, it strongly differs from it in MP and CuA emerging from R at the same point (vs. having a common stem), and probably only one crossvein ir. Interestingly, the curving of the postcubitus vein is a rather unusual character in Hylicellidae, but is present in several extinct Mesozoic cicadomorphans and scytinopteromorphans families: Hylicellidae, Archijassidae, Prosbolidae or Ipsviciidae.

The fossil differs from *Vetusala maculata*, also described in the Tongchuan entomofauna, by the following characters: RA_2 with four branches, MP with five branches, dichotomous posteriorly, medially curved CuA, and a weak cua-cup. We consider that all of the raised differences between our fossil and the enumerated genera are sufficient to create a new genus within Hylicellidae. However, we have left this genus unranked within any Hylicellidae subfamilies, as we emphasize that they are poorly defined and require revision under phylogenetic framework.

Conclusion

This new fossil expands our understanding of the morphological disparity within Hylicellidae, revealing features previously unknown in this extinct family. Furthermore, describing early representatives of Hylicellidae will be crucial for better understanding their morphological evolution. These specimens will need to undergo phylogenetic analyses alongside other families within Hylicelloidea—and possibly with the Clypeata superfamilies—to clarify the systematic delimitations of Cicadomorpha taxa.

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