



<https://doi.org/10.12976/jib/2024.60.1.11>

<http://zoobank.org/urn:lsid:zoobank.org:pub:43D6B99B-D265-4A36-ADEE-15EE99BB9EF0>

New Cicadomorpha from the Triassic of China raise questions on the systematics of Archijassidae

DOLEV FABRIKANT^{1,4}, DI-YING HUANG^{2,5}, ANDRÉ NEL^{3,6} & YAN-ZHE FU^{1,2,7*}

¹Ludwig-Maximilians-Universität München, Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

²State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Palaeoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

³Institut de Systématique, Évolution, Biodiversité (UMR 7205), MNHN, CNRS, SU, EPHE-PSL, UA, CP50, 57 Rue Cuvier, 75005 Paris, France

⁴✉ dolev.fabrikant@campus.lmu.de; <https://orcid.org/0009-0004-4388-4026>

⁵✉ dyhuang@nigpas.ac.cn; <https://orcid.org/0000-0002-5637-4867>

⁶✉ anel@mnhn.fr; <https://orcid.org/0000-0002-4241-7651>

⁷✉ yzfu@nigpas.ac.cn; <https://orcid.org/0000-0002-7819-1703>

*Corresponding author

Abstract

The fossil record of Cicadomorpha is fragmentary, and mostly based on isolated tegmina. Here, we describe and illustrate a new genus and species, *Triasalus chromatus* **gen. et sp. nov.**, from the Middle–Upper Triassic Yanchang Formation of Tongchuan City, northern China. The new specimen exhibits features similar to those of the two early cicadomorphan families, Hylcellidae and Archijassidae, preventing a secure assignment to either group. The classification history of Hylcellidae and Archijassidae is reviewed and the morphological characters currently used to distinguish the two families are discussed.

Key words: Archijassidae, Hylcellidae, taxonomy, fossil, Tongchuan

Introduction

The Cicadomorpha Evans, 1946, is arguably the most diverse group of Hemiptera, containing 33,000 known species, representing a substantial portion of plant-feeding insects and encompassing cicadas, treehoppers, leafhoppers, and froghoppers (Bartlett *et al.* 2018). The Cicadomorpha first appeared in the Permian and underwent significant diversification during the Mesozoic (Shcherbakov 1996). The early fossil record of this group mainly consists of extinct lineages and, despite being relatively diverse, remains problematic due to the partial preservation of specimens and the lack of robust synapomorphies supporting the groups (Shcherbakov 1996).

The Middle–Upper Triassic Yanchang Formation of the Ordos Basin, northern China, has yielded an abundance of cicadomorphan insects, but the species richness remains underestimated. Up to now, The Cicadomorpha reported from the Yanchang Formation of the Ordos Basin include representatives of Archijassidae Becker-Migdisova, 1962, Curvicutitidae Hong, 1984, Dymorphoptilidae Handlirsch, 1906, Granulidae Hong, 1980, Hylcellidae Evans, 1956, Maguviopseidae Shcherbakov, 2011, Prosolidae Handlirsch, 1906, and Scytinopteridae Handlirsch, 1906 (Fu & Huang 2022a,b, 2023; Fu *et al.* 2021, 2022; Zhang *et al.* 2021, 2022a,b).

Herein, we describe and illustrate a new cicadomorphan insect record based on a specimen with part and counterpart from the Middle–Upper Triassic Yanchang Formation at Hejiafang Village, Jinsuoguan Township, Tongchuan City, Shaanxi Province, China. The new specimen shares similarities with both Hylcellidae and Archijassidae, yet its placement remains uncertain due to the problematic definitions and distinctions between both groups.

Material and methods

The holotype, consisting of part and counterpart (NIGP206018a,b), was collected from greenish grey shale in the lower part of the Yanchang Formation, previously referred to as the Tongchuan Formation in earlier paleontological studies. The specimen was found at Hejiafang Village, Jinsuoguan Township, Yintai District, Tongchuan City, Shaanxi Province, China. For a detailed location of the fossil site, see Fu *et al.* 2021: fig. 1.

The studied specimen was carefully prepared by using a needle to remove the sediment covering it. Photographs were taken using a Zeiss AxioZoom V16 stereoscope. The line drawing was drafted with CorelDRAW 2018 graphic software, and the colour pattern reconstruction was drawn in Procreate 5.3.9. The specimen is deposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Wing venation terminology follows Nel *et al.* (2012), Shcherbakov (2012a), Lambkin (2020a), and Bourgoïn *et al.* (2015). The costal space is defined the combination of costal area and subcostal cell, and the arculus refers to the zigzag portion of CuA reemerging from M+CuA and distally bordering the basal cell, plus the cua-cup crossvein.

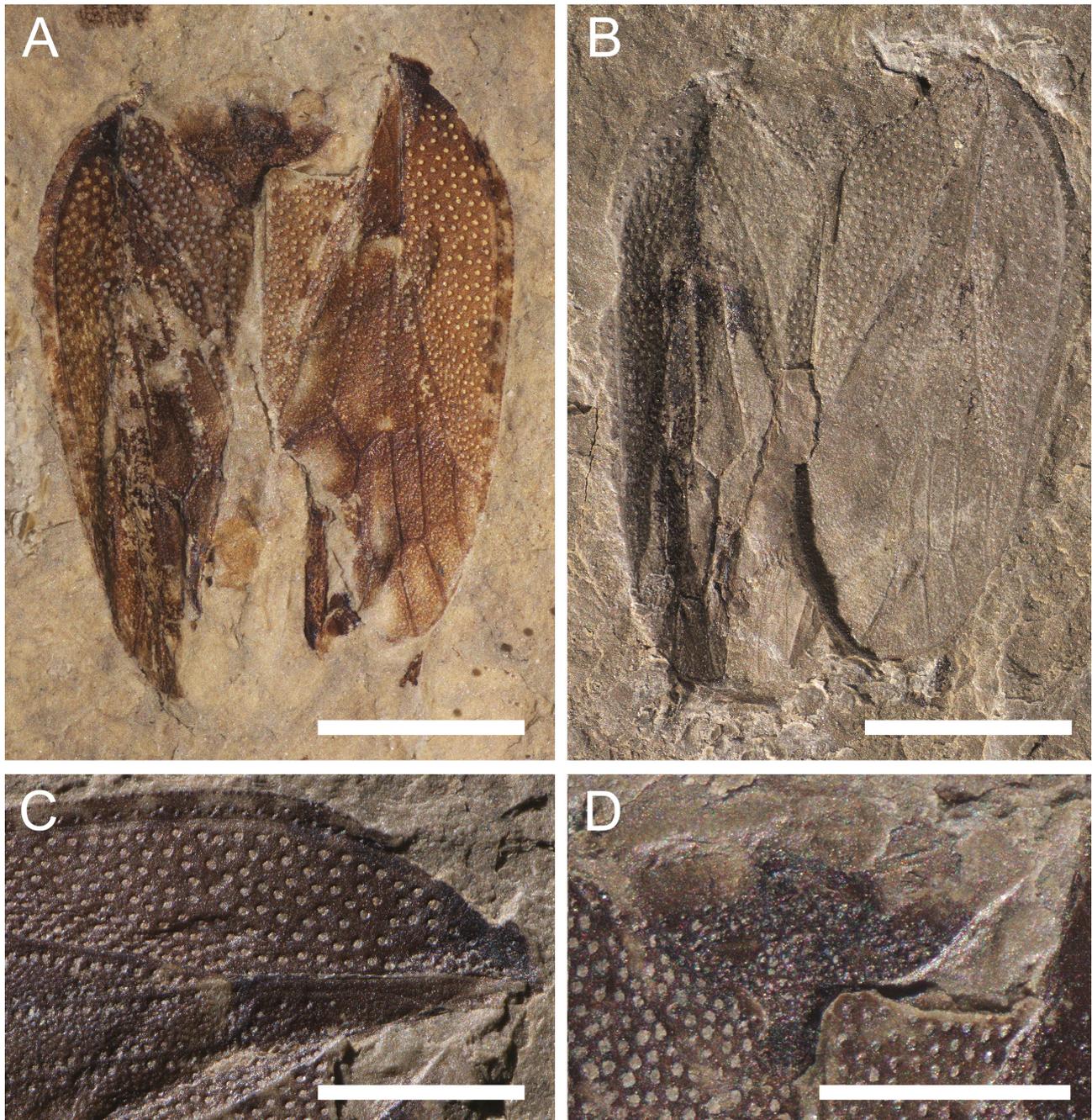


Figure 1. *Triasalus chromatus* gen. et sp. nov. Photographs of holotype. **A**, NIGP206018a (part) moistened with 70% ethanol; **B**, NIGP206018b (counterpart); **C**, Details of basal cell; **D**, Details of mesonotum. Scale bars =2 mm **A, B**; 1 mm in **C, D**.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Infraorder Cicadomorpha Evans, 1946

Genus *Triasalus* gen. nov.

urn:lsid:zoobank.org:act:4F795523-5FC6-4A6C-9660-4CD4A8C8A16A

Type species. *Triasalus chromatus* sp. nov.; by present designation and monotypy.

Etymology. The generic name is derived from the Triassic and the Latin word ‘*ala*’ (wing). Gender: masculine.

Diagnosis. Tegmen broad; costal space basally broad; costal space and clavus coarsely punctate; Pc+CP extending to tegmen apex; common stem ScP+R+M present, relatively short; stem M short, three-branched; base of stem CuA strongly curved; CuA₁ strongly arched, connecting to M₃₊₄ by fusing into common portion instead of crossvein m-cua. Basal cell small and narrow, with blunt apex; cell C5 large, subequal in length and width.

Triasalus chromatus sp. nov.

(Figs 1, 2)

urn:lsid:zoobank.org:act:99D754D7-99C6-4084-B792-E09CFE3B6276

Type material. Holotype, NIGP206538a,b, partial specimen preserving tegmen and mesonotum; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Etymology. The specific epithet means coloured maculae, referring to the complex colouration and maculae present.

Diagnosis. As for the genus. Also, tegmen mostly brown, apical and subapical cells in medial area light.

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

Description. Mesonotum subtriangular, lateral margins sinuate forming a constriction near apex. Tegmen about 5.80 mm long and 2.43 mm wide; basal half broader than apical half; costal margin arched basally, with apical half subparallel to anal margin; anteroapical angle nearly rounded; posterior margin straight; venation distinct. Pc+CP curving around costal margin to apex of RA₁; bScP very faint, reaching about midline of basal cell; stem ScP+R+M almost straight, slightly arched anteriorly; common stem ScP+R+M short, forking at about basal of 0.3 tegmen length; ScP+R forking earlier than M; RP simple; M and CuA forked at about the same level, about basal 0.6 of tegmen length; M three-branched, enclosed cell between M₁₊₂ and M₃₊₄; base of stem CuA strongly curved posteriorly, then nearly straight; CuA₁ fused into M₃₊₄; distal portion curved posteriorly; CuP straight; PCu nearly straight; A1 arcuate; cua-cup elongate, nearly straight and connecting to base of CuA; one ir crossvein and two rp-m crossveins present. Basal cell about quarter of tegmen length; cells C1', C2, and C2' subrectangular; cell C5 about as wide as long, longer than other apical cells. Costal space and clavus coarsely punctate; rows of punctures around veins, attenuating towards tegmen apex; medial surface of tegmen with fine granular texture; space between costal margin and Pc arranged with singly row of small punctures; costal margin with row of raised setae bases. Colouration mostly brown, distinct mottling along costal margin; apical and subapical cells in medial area light; alternating light and dark spots along CuP; costal space and clavus light brown.

Discussion

The extinct cicadomorphan family Archijassidae, which ranges from the Middle Triassic to the mid-Cretaceous, is considered an early representative of Membracoidea (Shcherbakov 2012a; Chen *et al.* 2020; Lambkin 2020a; Fu & Huang 2022a). Most fossils attributed to Archijassidae have been described from isolated wings, resulting in the group being primarily defined based on tegminal characters. However, Archijassidae remains poorly defined, particularly in relation to other extinct cicadomorphan lineages. Becker & Migdisova (1962) loosely defined Archijassidae by the presence of ‘a wide costal space, crossveins within and between R and M, and a closed medial cell’. These characters are broad and insufficient to distinguish Archijassidae from another early cicadomorphan family, Hylicellidae which may have led Shcherbakov (1992) to propose treating Archijassidae as a subfamily of Hylicellidae. The current definition

of Archijassidae was proposed by Ansoerge (1996), who affirmed its family status. This definition distinguishes Archijassidae from Hylcellidae based on the apparent absence of bScP and a well-developed arculus (a wide apex of the basal cell, composed of the base of CuA or stem M+CuA). Shcherbakov (2012a) expanded the diagnosis of Ansoerge (1996) by incorporating additional tegmen characters: ‘CP present; bScP reduced; 6–8 full-sized apical cells; 1–3 subapical cells (one or two *rm*, sometimes *ir* absent)’.

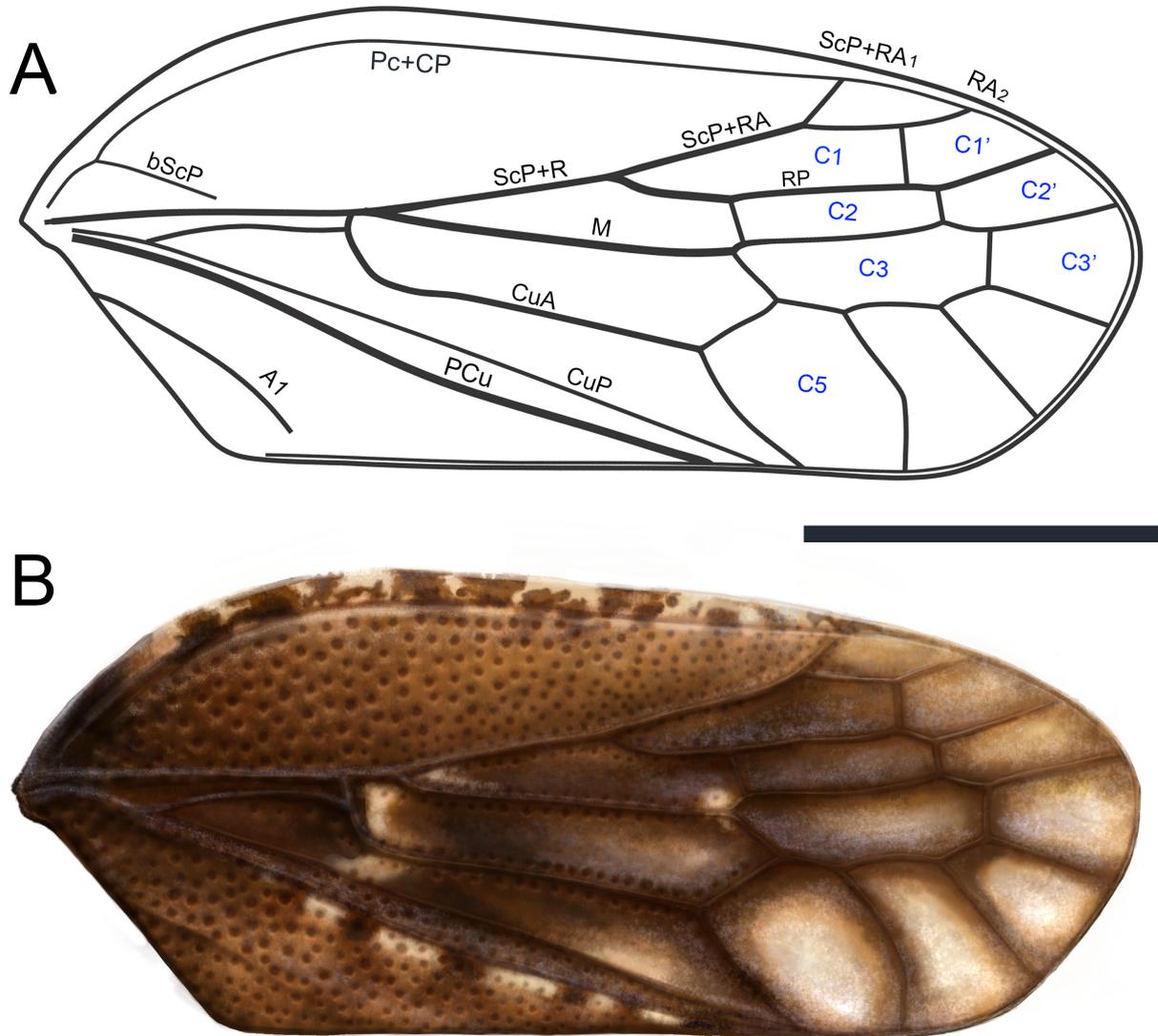


Figure 2. The line drawing and reconstruction of *Triasalus chromatus* gen. et sp. nov., holotype NIGP206018a. **A**, Line drawing. **B**, Reconstructed tegminal punctation and colour pattern.

Archijassidae and Hylcellidae are commonly interpreted to display two shortened veins at the base of the subcostal cell, however the number and identity of veins differ between authors. The more prominent ‘first’ vein is situated closer to the costal margin and appears to fork from Pc or originate at its base. The ‘second’ vein is highly reduced, either fusing with or running close to the common stem R+M+CuA, briefly separating from it along a part of the basal cell. In taxa where both veins are interpreted to be present the ‘first’ vein is consistently labeled as CP and the second bScP (e.g., Shcherbakov 2012a, Lambkin 2020a). The major difference in the identification of these veins arises when only the ‘first’ vein is depicted. In Archijassidae, this vein is conventionally labeled as CP (e.g., Shcherbakov 2012a, Lambkin 2020a, Chen *et al.* 2020, 2024), whereas in Hylcellidae, it is labeled as bScP (e.g., Shcherbakov 2012b, Lambkin 2020b, Chen *et al.* 2022, Fu & Huang 2023). Therefore, we propose that this ‘first’ vein should consistently be identified as bScP in both groups, owing to its identical point of origin (forks from Pc+CP and its general morphology), which is a ‘basally reduced version’ of the bScP found in other extinct groups of Cicadomorpha.

For instance, in Sinoalidae Wang & Szewo 2012, the basal part of ScP (bScP) is well developed, emerges from a common stem with 'Pc+CP' and ends into R+M+CuA rather distally (Wang *et al.* 2012: fig. 8E). The 'second' vein is likely a misinterpretation of the wide common stem R+M+CuA and does not represent a separate structure. The use of such reduced characters for diagnosing fossil taxa is problematic, as they are inconspicuous and may easily be overlooked, misinterpreted, or obscured by taphonomy. Given the potential homology of 'bScP' in Hylicellidae and 'CP' in Archijassidae, this character cannot be considered diagnostic for Archijassidae. Furthermore, the shape of the 'arculus' is unreliable for the diagnosis due to its variability. Some Archijassidae members, such as *Mesojassus* Tillyard, 1916 and *Eocicadellium* Fu & Huang, 2022a, possess a reduced 'arculus' similar to that of Hylicellidae. Conversely, some taxa assigned to Hylicellidae have a wide 'arculus' comparable to that of Archijassidae, as seen in *Conjucella* Shcherbakov, 2012b, *Crosbella* Evans, 1956, *Cycloscyrtina* Martynov, 1926, *Mesocixiodes* Tillyard, 1922, *Sinohylicella* Fu, Nel & Boderau, 2024, and *Vietocyrtella* Shcherbakov, 1988.

Furthermore, the extension to the definition of Archijassidae provided by Shcherbakov (2012a) applies equally to the type species of Hylicellidae and Archijassidae (*Hylicella colorata* Evans, 1956 and *Archijassus heeri* (Geinitz, 1880) Handlirsch, 1906). These species share multiple morphological similarities, including a basally broad costal space, R single forked, M with 3–4 branches, single ir crossvein, 2–3 subapical cells, and an enclosed cell in the medial area. The differences observed in *H. colorata* relative to *A. heeri* fall within the variation seen in Archijassidae, notably the common stem M+CuA (present in *Mesojassus*), RA with three branches (present in *Mesojassus*), the proximally narrowing basal cell (present in *Mesojassus* and *Eocicadellium*), and anastomosis of M and CuA₁ (present in *Eocicadellium*, *Kisa fasciata* Shcherbakov, 2012a, and *Karajassus* Martynov, 1926).

The similarity between Hylicellidae and Archijassidae, along with the intraspecific variability in venation patterns, has resulted in a complex taxonomic history for certain genera. Considerable efforts have been made to synonymize taxa and reassign them to either Hylicellidae or Archijassidae by various authors leaving some genera such as *Cixiella* Becker & Migdisova, 1962 and *Mesocicada* Becker & Migdisova, 1962 with uncertain affinities (Ansoerge 1996, Lambkin 2020a, Chen *et al.* 2024). The present specimen remains unassigned within Cicadomorpha due to the apparent variability of the 'arculus' shape and absence of a second reduced vein in both Hylicellidae and Archijassidae, which complicates the definition of Archijassidae and blurs the distinction from Hylicellidae. This issue is further compounded by the lack of well-defined synapomorphies for Hylicellidae (see discussion in Fu *et al.* 2024, in press). The similarity in venation patterns in early cicadomorphans is unsurprising, as these lineages may not have acquired their respective synapomorphies at this point in time due to the proximity of their divergence events, necessitating further studies to ascertain the affinities of Archijassidae.

Triasalus **gen. nov.** can be distinguished from most of Hylicellidae due to their proliferated RA terminals, except for *Cinemala* Shcherbakov, 2012b and *Conjucella*, which have a single RA fork, and *Hylicella* with two forks. *Triasalus* **gen. nov.** can be further separated from these genera by having two branches of RA and cell C1 width subequal to that of cell C2 (three RA branches and C1 twice as wide as C2 in *Hylicella*), two rp-m crossveins and fork of R apicad of the tegmen midline (two rp-m crossveins and fork of R in the basal tegmen half in *Cinemala*), CuA₁ simple (forked in *Conjucella*), branches of RA and RP relatively straight (jagged in *Conjucella* and *Cinemala*), C5 width subequal to its length (about half of the length in *Hylicella* and *Cinemala*) (Shcherbakov 2012b, Lambkin 2020b).

When compared to Archijassidae, *Triasalus* is most similar to *Archijassus* Handlirsch, 1906, *Ardela* Ansoerge, 1996, *Karamayojassus* Chen *et al.*, 2024, *Mesojassus*, and *Mesoledra* Evans, 1956, as well as the contentious *Cixiella* and *Mesocicada*, due to their shared basally convex costal space. However, the new genus differs from these genera by the width of cell C5 being greater than about half its length and the anastomosis of M with CuA₁ (crossvein m-cua present in others). It can be further differentiated by a simply forked RA and a simple RP, which is otherwise typical of Archijassidae (except for *Mesojassus*, which has a 3–4 branched RA and veins M and CuA reemerging together from R+M+CuA and separating distally), two crossveins rp-m (single in *Archijassus*, *Cixiella*, and *Karamayojassus*), punctuation limited to the costal space and clavus (fully covering tegmen in *Ardela* and *Karamayojassus*), and stem M bifurcating apicad of the CuA fork (basad in *Mesoledra*).

Shcherbakov (2012a) divided Archijassidae into three subfamilies, Archijassinae, Karajassinae, and Dellasharinae, based on a combination of characters, including costal space width, length of bScP, branching pattern of the veins leaving the basal cell, number of subapical and apical cells, and the presence of M+CuA anastomosis. This taxonomic framework was later accepted by some authors (Chen *et al.* 2020, 2024; Lambkin 2020a; Fu *et al.* 2024). The least variable of these characters being the shape of the costal margin and anastomosis of M+CuA. Each subfamily was characterized by a different combination of the two characters. The connection between CuA and M may vary within species of Archijassidae, as illustrated by aberrant specimens *Kisa fasciata*, and it also varies between genera of the subfamily Karajassidae (Shcherbakov 2012a). Additionally, the position of m-cua crossvein is relatively stable

within species, showing little variation in the specimens of *Archijassus heeri* and *Mesoledra pachyneura* Evans, 1956 presented by Ansoerge (1996), but differs between genera. It is important to note that the length of bScP in Archijassidae depends on the width of the costal space, as this vein consistently terminates near the center of the basal cell. Its length is primarily determined by the curvature of the costal margin, reducing its taxonomic value as a standalone character. *Triasalus* **gen. nov.** displays a wide costal space and a distal anastomosis of M with CuA, which prevents its placement in any of the subfamilies of Archijassidae as defined by Shcherbakov (2012a). Furthermore, the branching pattern of the main veins around the basal cell appears inconsistent at the subfamily level but remains stable within species and genera. The subfamily Archijassinae was partially defined by R+M fork coinciding with the apex of the basal cell (Shcherbakov 2012a). However, this character is also observed in Karajassinae, and some members of Archijassinae also exhibit a stem ScP+R+M (Becker & Migdosova 1962, Shcherbakov 2012a, Chen *et al.* 2024). Moreover, the common stem of M+CuA is present in genera across all three subfamilies such as *Cicadellium* Westwood, 1854 (Karajassinae), *Dellashara* Shcherbakov 2012a (Dellasharinae), and *Mesojassus* (Archijassinae). In other cases, the length of the common stem R+M may be slightly variable, as exemplified by *Kisa fasciata*, where some specimens have a distinctive short stem, while in others it is almost absent (Shcherbakov 2012a; Fu *et al.* 2024). The current subdivision of Archijassidae into subfamilies, as proposed by Shcherbakov (2012a), is problematic due to the plasticity of the defining characters within these groups, illustrating the necessity of future studies on body characters in untangling the relationships within this group. On the other hand, the relative stability of these characters within described genera and species supports their importance for diagnosis at lower taxonomic ranks.

Acknowledgements

We thank two anonymous reviewers for their valuable comments on an earlier version of this paper. This work was supported by the National Natural Science Foundation of China (Grant Nos. 42288201, 41925008, and 41688103), the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (Grant No. XDB0850000), the Natural Science Foundation of Jiangsu Province (Grant No. BK20241705), the LMUexcellent Postdoc Support Fund, and the Alexander von Humboldt-Stiftung.

References

- Ansoerge J., 1996. Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Palaontologische Abhandlungen* 2: 1–132.
- Bartlett C. R., Deitz L. L., Dmitriev D. A., Sanborn A. F., Soulier-Perkins A. & Wallace M. S. 2018. The diversity of the true hoppers (Hemiptera: Auchenorrhyncha), pp. 501–590. *In: Insect biodiversity: science and society. Vol. 2.* (R. G. Footitt and P. H. Adler, editors). Chichester, UK, Wiley Blackwell, 1024 pp.
<https://doi.org/10.1002/9781118945582.ch19>
- Becker-Migdisova, E. E., 1962. Nekotorye novye poluzhestkokrylye i senoedy. [Some new Hemiptera and Psocoptera]. *Paelontologicheskii Zhurnal* 1962: 89–104.
- Bourgoin T., Wang R. R., Asche M., Hoch H., Soulier-Perkins A., Stroiński A., Yap S., & Szvedo J. 2015. From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology* 134: 63–77.
<https://doi.org/10.1007/s00435-014-0243-6>
- Chen J., Wang B., Zheng Y., Jiang H., Jiang T., Wang X. L. & Zhang H. C. 2020. The youngest record of the leafhopper family Archijassidae in Kachin amber from the lowermost Upper Cretaceous of northern Myanmar (Cicadomorpha, Cicadelloidea). *Cretaceous Research* 106: 104252.
<https://doi.org/10.1016/j.cretres.2019.104252>
- Chen J., Zhang Q. Q., Jiang H., Li Y. L., Zheng Y., Yu S., Wang X. L. & Zhang H. C. 2022. Geometric morphometric analysis for the systematic elucidation of new Hylcellidae from the Jurassic of China (Hemiptera: Cicadomorpha). *Journal of Paleontology* 96(5): 1119–1131.
<https://doi.org/10.1017/jpa.2022.20>
- Chen J., Zhang Q. Q., Jiang H., Li Y. L., Yu S., Zheng Y. & Zhang H. C. 2024. First discovery of the leafhopper family Archijassidae

in the Jurassic of China (Hemiptera, Cicadomorpha). *Historical Biology* 36(4): 728–733.

<https://doi.org/10.1080/08912963.2023.2183855>

- Evans J. W. 1946.** A natural classification of leaf-hoppers (Jassoidea, Homoptera) Part 1. External morphology and systematic position. *Transactions of the Royal Entomological Society of London* 96(3): 47–60.
<https://doi.org/10.1111/j.1365-2311.1946.tb00442.x>
- Evans J. W. 1956.** Palaeozoic and Mesozoic Hemiptera. *Australian Journal of Zoology* 4(2): 165–258.
<https://doi.org/10.1071/ZO9560165>
- Fu Y. Z., Azar D. & Huang D. Y. 2021.** The first Dymorphoptilidae from the Middle Triassic of China (Hemiptera: Cicadomorpha). *Historical Biology* 33(12): 3506–3512.
<https://doi.org/10.1080/08912963.2021.1874374>
- Fu Y. Z. & Huang D. Y. 2022a.** The first Archijassidae from the Middle Triassic of China (Hemiptera, Cicadomorpha, Membracoidea). *Palaeoentomology* 5(6): 599–605.
<https://doi.org/10.11646/palaeoentomology.5.6.9>
- Fu Y. Z. & Huang D. Y. 2022b.** The first maguviopseids (Hemiptera, Cicadomorpha, Prosboloidea) from the Triassic of China. *Palaeoentomology* 5(1): 76–80.
<https://doi.org/10.11646/palaeoentomology.5.1.9>
- Fu Y. Z., Gao J. & Huang D. Y. 2022.** Revision of the genus *Sinogranulus* (Hemiptera, Granulidae) with description of a new species from the Middle Triassic of China. *Palaeoentomology* 5(1): 81–89.
<https://doi.org/10.11646/palaeoentomology.5.1.10>
- Fu Y. Z. & Huang D. Y. 2023.** New Triassic Hylicellidae from northern China (Hemiptera, Cicadomorpha). *Zootaxa* 5396(1): 10–15.
<https://doi.org/10.11646/zootaxa.5396.1.4>
- Fu Y. Z., Nel A. & Boderau M. 2024b.** A new early representative genus of Hylicellidae from the Triassic of China (Hemiptera, Cicadomorpha). *Journal of Insect Biodiversity* 60: 9–15.
<https://doi.org/10.12976/jib/2024.60.1.4>
- Fu Y. Z., Xu M. M., Gao J. & Huang D. Y. 2024a.** The Archijassidae from the Jurassic of China (Hemiptera, Cicadomorpha, Membracoidea) and its palaeoecological significance. *Historical Biology* 36(10): 2233–2238.
<https://doi.org/10.1080/08912963.2023.2250109>
- Handlirsch B. A. 1906–1908.** *Die fossilen Insekten und die Phylogenie der Rezenten Formen. Ein Handbuch für Paläontologen und Zoologen.* Engelmann, Leipzig, 1430 pp.
- Hong Y. C. 1980.** Granulidae, a new family of Homoptera from the Middle Triassic of Tongchuan, Shanxi Province. *Acta Zootaxonomica Sinica* 5(1): 63–70.
- Hong Y. C. 1984.** Curvicutitidae fam. nov. (Lepidoptera, Insecta) from Middle Triassic of Shaanxi. *Acta Palaeontologica Sinica* 23(6): 782–785.
- Lambkin K. J. 2020a.** Revision of *Mesojassus* Tillyard, 1916, from the Late Triassic of Queensland (Hemiptera: Cicadomorpha: Membracoidea: Archijassidae). *Zootaxa* 4718(3): 413–422.
<https://doi.org/10.11646/zootaxa.4718.3.9>
- Lambkin K. J. 2020b.** Revision of the Hylicellidae of the Late Triassic of Queensland (Hemiptera: Cicadomorpha: Hylicelloidea). *Zootaxa* 4790(3): 525–539.
<https://doi.org/10.11646/zootaxa.4790.3.7>
- Martynov A. V. E. 1926.** Jurassic fossil insects from Turkestan. 6. Homoptera and Psocoptera. *Известия Российской академии наук. Серия математическая*, 20:13–14, 1349–1366.
- Nel A., Prokop J., Nel P., Grandcolas P., Huang D. Y., Roques P., Guilbert E., Dostál O. & Szwedo J. 2012.** Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of morphology* 273(5): 480–506.
<https://doi.org/10.1002/jmor.11036>
- Shcherbakov D. E. 1988.** New cicadas (Cicadina) from the later Mesozoic of Transbaikalia. *Paleontological Journal* 22(4): 52–63.
- Shcherbakov D. E. 1992.** The earliest leafhoppers (Hemiptera: Karajassidae n. fam.) from the Jurassic of Karatau. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1: 39–51.
<https://doi.org/10.1127/njgpm/1992/1992/39>
- Shcherbakov D. E. 1996.** Origin and evolution of the Auchenorrhyncha as shown by the fossil record, pp. 31–45. *In: Studies on hemipteran phylogeny* (C. W. Schaefer, editor), Entomological Society of America, Lanham, Iii: 244 pp.
- Shcherbakov D. E. 2011.** New and little-known families of Hemiptera Cicadomorpha from the Triassic of Central Asia—early analogs of treehoppers and planthoppers. *Zootaxa* 2836: 1–26.
<https://doi.org/10.11646/zootaxa.2836.1.1>
- Shcherbakov D. E. 2012a.** More on Mesozoic Membracoidea (Homoptera). *Russian Entomological Journal* 21(1): 15–22.

- Shcherbakov D. E. 2012b.** A new subfamily of Mesozoic Hylcellidae (Homoptera: Cicadomorpha). *Russian Entomological Journal* 21(4): 441–444.
- Tillyard R. J. 1922.** Mesozoic Insects of Queensland. No. 9 Orthoptera, and additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. *The Proceedings of the Linnean Society of New South Wales* 47: 447–470.
- Wang B., Szvedo J. & Zhang H. C. 2012.** New Jurassic Cercopoidea from China and their evolutionary significance (Insecta: Hemiptera). *Palaeontology*, 55(6): 1223–1243.
<https://doi.org/10.1111/j.1475-4983.2012.01185.x>
- Westwood J. O. 1854.** Contributions to fossil entomology. *Quarterly Journal of the Geological Society of London* 10: 378–396.
- Zhang Q. Q., Chen J. & Zhang H. C. 2021.** New Granulidae (Hemiptera: Scytinopteroidea) from the Middle Triassic Tongchuan Formation of NW China. *Historical Biology* 34(1): 152–157.
<https://doi.org/10.1080/08912963.2021.1903892>
- Zhang Q. Q., Zheng D. R., Teng X. & Zhang H. C. 2022a.** New Scytinopteridae (Hemiptera: Scytinopteroidea) from the middle Triassic Tongchuan Entomofauna of NW China. *Historical Biology* 34(11): 2259–2264.
<https://doi.org/10.1080/08912963.2021.2010194>
- Zhang Q. Q., Zheng D. R., Wang B. & Zhang H. C. 2022b.** Review of Triassic insects in China. *Geological Society, London, Special Publications* 521: 45–60.
<https://doi.org/10.1144/SP521-2021-121>