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Jurocercopis grandis Wang & Zhang, 2009 from the Jiyuan Basin and Daohugou beds of northern China and its morphological revision (Hemiptera, Cicadomorpha, Cercopoidea)

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Abstract

Jurocercopis grandis Wang & Zhang, 2009 is confined to the Middle-Upper Jurassic Daohugou beds, Inner Mongolia, NE China. The main diagnostic characters of *Jurocercopis* were based only on tegmen, but lacked some crucial information such as basal cell, vein Pc+CP and A1. A very diverse palaeoentomofauna has been discovered lately from the Yangshuzhuang Formation of Jiyuan, Henan Province, northern China, from which we identify *J. grandis*. Herein, *Jurocercopis* is emended and provided with detailed morphological characters on the basis of nine specimens from the Jiyuan and Daohugou beds. The new discovery expands the geographic distribution of *Jurocercopis* to the Jiyuan Basin, northern China, and indicates a stratigraphic correlation between the Yangshuzhuang Formation at Jiyuan and the Haifanggou Formation of the Daohugou beds. These two units host the early assemblage of Yanliao biota, further proving that the Yanliao biota is widely distributed in northern China.

Keywords: Procercopidae, *Jurocercopis*, Jurassic, Jiyuan, Yanliao biota, biogeographic distribution

Introduction

The known Mesozoic froghoppers are attributed to three extinct families (*i.e.*, Procercopidae Handlirsch, 1906, Cercopionidae Hamilton, 1990, and Sinoalidae Wang & Szewo, 2012). Procercopidae is widely accepted as the ancient group of Cercopoidea and a transitional unit to recent lineages, known from Eurasia in the Early Jurassic to mid-Cretaceous (Shcherbakov & Popov, 2002; Wang *et al.*, 2012; Fu *et al.*, 2019; Chen *et al.*, 2020).

The systematic position, early evolution, palaeoecology and palaeodiversity of Procercopidae are poorly known due to a fragmentary fossil record

and confusing taxonomic history (Chen *et al.*, 2020). Procercopidae was originally established by Handlirsch (1906) to accommodate *Procercopis* Handlirsch, 1906 from the Lower Jurassic of Germany. Subsequently, *Liassocercopsis* Ansoerge, 1996, *Procercopina* Martynov, 1937 and additional species of *Procercopis* were successively attributed to this extinct family on the basis of isolated tegmina or hind wings from the Lower Jurassic of Germany and Central Asia (Martynov, 1937; Bode, 1953; Becker-Migdisova, 1962; Ansoerge, 1996). Many complete specimens of procercopids have been described over the past three decades, mainly from the latest Middle Jurassic to the earliest Late Jurassic Daohugou biota (*i.e.*, early assemblage of Yanliao biota) and coeval strata, and the Early Cretaceous Jehol biota of Yanliao region, NE China (Hong, 1982, 1983, 1984; Ren, 1995; Ren *et al.*, 1998; Wang & Zhang, 2009; Hu *et al.*, 2014; D Chen *et al.*, 2015a; J Chen *et al.*, 2015b, c; Fu *et al.*, 2018; Chen *et al.*, 2020). Additionally, 2 genera and 2 species have been recently described from the mid-Cretaceous amber of North Myanmar (*i.e.*, *Paranthoscytina xiai* Fu, Cai & Huang, 2019 and *Burmocercopis lingpogensis* Fu, Cai & Huang, 2019), representing the youngest record of this family (Fu *et al.*, 2019).

To date, Jurassic procercopids include 27 species assigned to 6 genera: *Liassocercopsis*, *Procercopina*, and *Procercopis* are currently reported from the Lower Jurassic in Germany, Kyrgyzstan and NE China; *Anthoscytina* Hong, 1983 is the largest genus within Procercopidae, described from the whole Jurassic of Russia and NE China; and two remarkable genera, *Jurocercopis* Wang & Zhang, 2009 and *Titanocercopis* Chen, Zhang & Wang, 2015c are confined to the Middle-Upper Jurassic Daohugou beds, NE China, the body size of which are much larger than other procercopids. Herein the morphological details of *Jurocercopis grandis* are supplemented based on several

isolated tegmen from the new locality near Anyao, Henan Province, North China, and new well-preserved specimens from the type locality of *J. grandis* at Daohugou, Inner Mongolia, NE China (Fig. 1).

Material and methods

Five specimens studied (NIGP172198–NIGP172202) consist of nearly complete forewings or wing fragments, collected from the green-greyish mudstone of the top most layers of the Yangshuzhuang Formation, near the Anyao Village, Chengliu Township, Jiyuan City, Henan Province, North China (locality map see Huang *et al.*, 2018a: fig 1C). Four individuals (NIGP172194–NIGP172197) are persevered in the greyish fine laminated tuffaceous shale, three of which are collected from the ‘Layer 1’, median section of the Daohugou beds at Xiayingzi locality, which exposes strata below the ‘conchostracan layers’; only one specimen (NIGP172196) is collected from the ‘Layer 2’, middle-upper section of the Daohugou beds at Xiaobaishan locality, which exposes strata with abundant conchostracan named *Triglypta haifanggouensis* Liao *et al.*, 2017 (detailed fossil layers of the Daohugou beds see Fu & Huang, 2019: fig 1). Both localities at Daohugou Village, Ningcheng County, Inner Mongolia, NE China (locality map see Jiang & Huang, 2017: fig 1). The geological age of the deposition of ‘Layer 1’ and ‘Layer 2’ are supposed to be close to the Middle-Upper Jurassic boundary (163.5 Ma) (Huang, 2019; Zhang *et al.*, 2019). Some specimens were carefully prepared with a sharp knife under a stereo microscope. Observations were made using an Olympus SZX7 microscope; photographs were taken using a digital camera attached to a Zeiss Discovery V16 microscope, and some were moistened with 70%

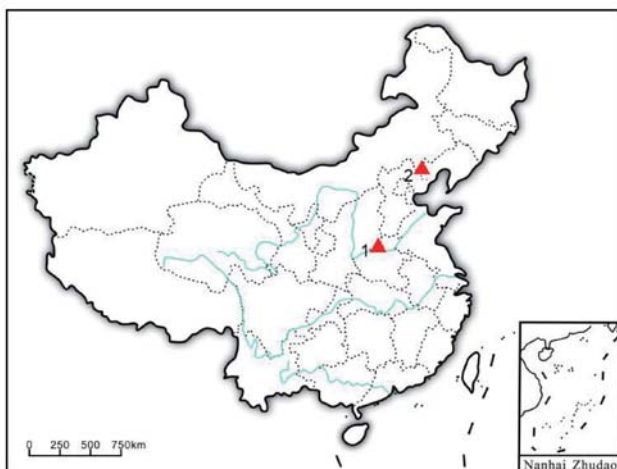


FIGURE 1. Distribution of *Jurocercopsis grandis*: 1, fossil locality near Anyao Village, Jiyuan City, Henan Province; 2, type locality at Daohugou Village, Chifeng City, Inner Mongolia.

ethanol to show fine details; stacked using Helicon Focus 6 software; all images were optimized and grouped into plates using Adobe Photoshop CS6 Extended; line drawings were drafted with Adobe Illustrator CC 2018 graphic software. The material studied here is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Wing venation terminology and cell nomenclature follows Nel *et al.* (2012) and Bourgoïn *et al.* (2015). All measurements are in millimeters.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Cicadomorpha Evans, 1946

Superfamily Cercopoidea Leach, 1815

Family Procercopidae Handlirsch, 1906

Genus *Jurocercopsis* Wang & Zhang, 2009

Type species. *Jurocercopsis grandis* Wang & Zhang, 2009; by original designation.

Diagnostic characters (revised after Wang & Zhang, 2009). Differs from other genera by a combination of the following characters: body large, length 21–24 mm (less than 15 mm in other genera except for 30 mm in *Titanocercopsis*); head small, rounded (head produced anteriorly in *Paranthoscytina* and *Burmocercopsis*); pronotum broad, with disc wrinkled, 1.9× as wide as head (pronotum 1.2–1.5× as wide as head in *Anthoscytina*, *Stellularis*, *Paranthoscytina* and *Burmocercopsis*); basal cell short, with length about 1/7 of tegmen length (basal cell length about 1/4–1/5 of tegmen length in other genera); RA and MP multi-branched (more complex wing venation compared to most procercopids except for *Cretocercopsis* and *Titanocercopsis*); MP forked distinctly distad of CuA forking (MP forked basad of CuA forking in *Titanocercopsis*, *Paranthoscytina* and *Burmocercopsis*); cross vein imp absent (imp present in *Procercopina*, *Titanocercopsis* and *Paranthoscytina*); and hind wing with MP 2-branched (MP unbranched in *Stellularis*, *Sinocercopsis* and *Burmocercopsis*, and MP₃₊₄ fused with MP₁₊₂ apically in *Cretocercopsis*).

Jurocercopsis grandis Wang & Zhang, 2009

(Figs 2–6)

Material. A total of nine individuals are included in the present study: six isolated forewings (NIGP172197–NIGP172202), and three well-preserved laterally compressed adults including two males (NIGP172194, NIGP172195) and one female (NIGP172196).

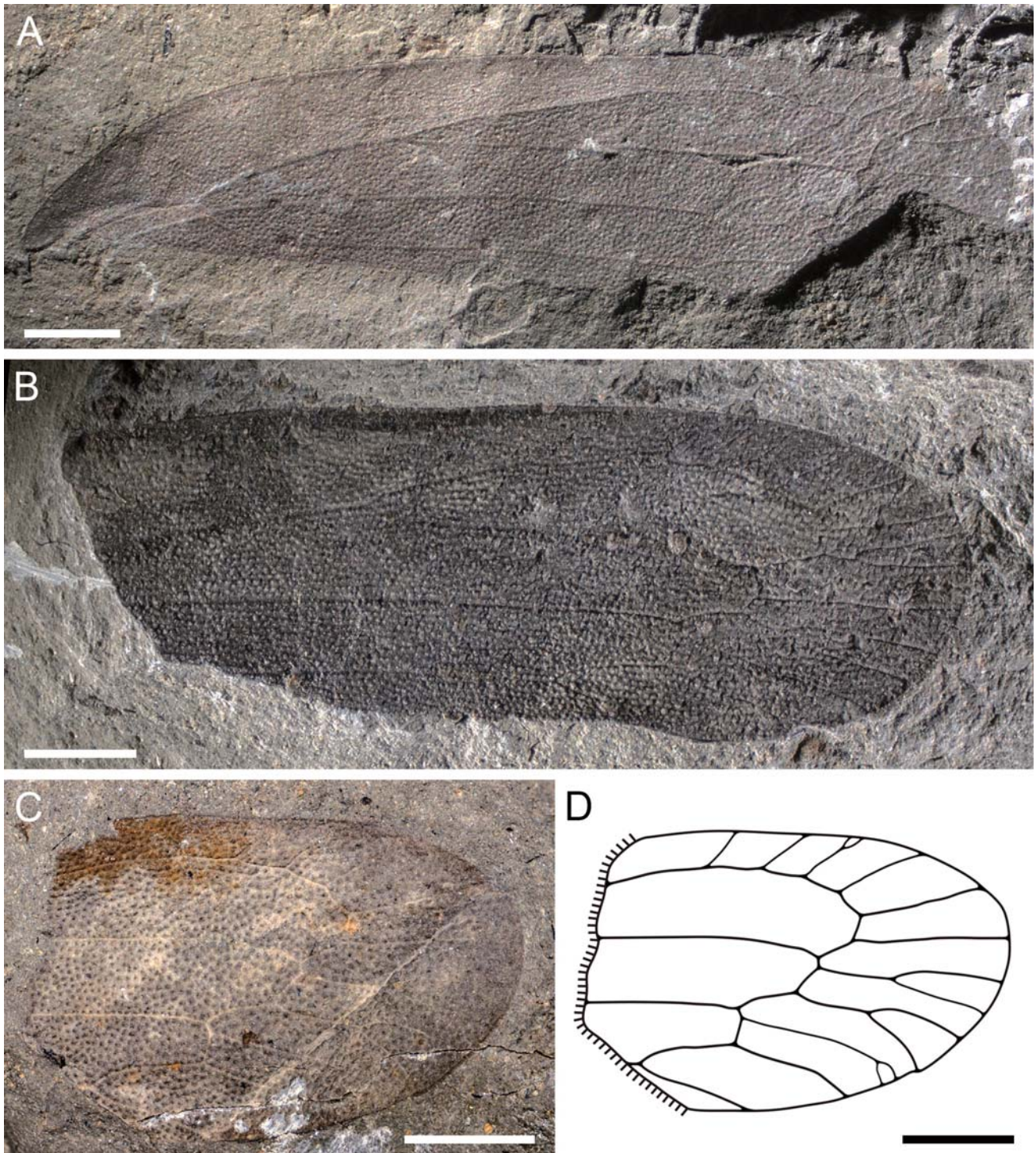


FIGURE 2. Forewings of *Jurocercopsis grandis* from the Jiyuan Basin, Henan Province, northern China. **A**, Specimen NIGP172198. **B**, Specimen NIGP172199. **C**, Specimen NIGP172200. **D**, Line drawing of NIGP172200. (Scale bars = 2 mm).

Locality and horizon. The Yangshuzhuang Formation near Anyao Village, Chengliu Township, Jiyuan City, Henan Province, northern China; and the Haifanggou Formation at Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, NE China; the Middle-Upper Jurassic.

Diagnosis. As for the genus with the following additions: antenna length 1.93 mm exceeding protibia

and tegmen length (ratio of antennae/protibia length = 0.64:1; ratio of antennae/tegmen length = 0.08:1); tegmen length 20–25 mm, with length/width ratio 3.0–3.6 (due to preservation), Pc+CP extending beyond of termination of RA₁; RA with 6–8 terminal branches, RP single or 2-branched, MP with 4–6 terminal branches.

Supplemental description. Male (NIGP172194 and NIGP172195), body length 21.1–23.8 mm (Figs 4A, B).

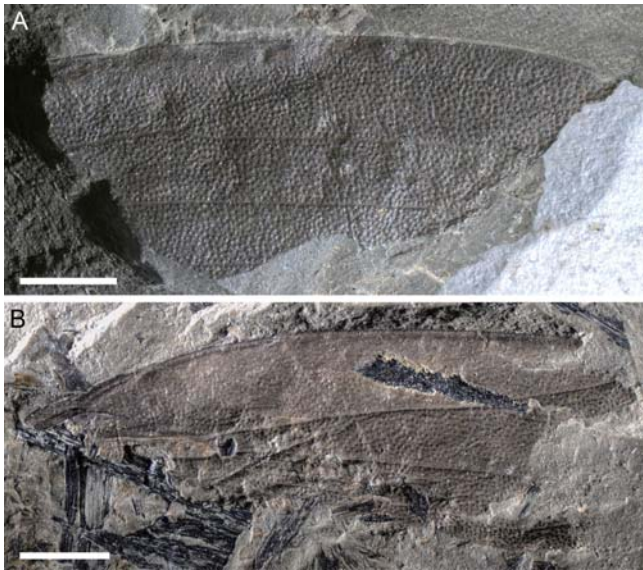


FIGURE 3. Fragmental forewings of *Jurocercopsis grandis* from the Jiyuan Basin. **A**, Specimen NIGP172201. **B**, Specimen NIGP172202. (Scale bars = 2 mm).

Female (NIGP172196), body length 22.5 mm (Fig. 4C). Body and wings with tiny granular punctures.

Head. Head small in dorsal view, rounded apically, anterior margin smoothly angled (Fig. 5A, B). Compound eyes large, ovoid, not distinctly bulging. Three ocelli on crown, between compound eyes; median ocellus globular, slightly smaller; two lateral ocelli located on vertex, oblong (Fig. 5A). Antenna with scape and pedicel stout, only preserved in NIGP172195 and NIGP172196, length 1.93 mm (Fig. 5C, D); scape large, slightly thicker than pedicel; pedicel length 0.42 mm and width 0.20 mm, almost 1.5× as long as scape, becoming progressively wider; flagellum with 7 segments (Fig. 5C), flagellomeres I–III thick and short, I–VII becoming progressively thinner. Postclypeus large, with distinct medial carina, length 3.59 mm, widest at middle (Fig. 5A, B). Anteclypeus length 1.56 mm. Rostrum obscure.

Thorax. Pronotum greatly extended, irregular hexagonal, with disc wrinkled (Fig. 5A, B); length 3.21 mm and width 6.09 mm, ratio 0.53; widest at its lateral angles, nearly 1.8× as wide as head; anterior margin nearly straight, posterior margin shallowly concaved, slightly shorter than anterior margin. Mesonotum slightly wider than head, mesoscutellum triangular. Legs covered with dense setae (Fig. 5E, F, G); prothoracic leg with protibia nearly 2.2× as long as protarsus (Fig. 5F); mesothoracic leg unobservable; metathoracic leg with metatibia widened apically, armed with two rows of apical teeth (no more than 8 for one row), spine unobservable or absent; metatarsus with basi- and midtarsomere distinct widened apically, apical teeth obscure, but subapical long

setae visible (Fig. 5G). Claw well developed, hooked, unspecialized; arolium large, slightly longer than claw, widely lobate with deep middle incision (Fig. 5E, G).

Tegmen (Figs 2, 3, 5H, 6). Length 21.6–24.8 mm width 6.3–7.6 mm, ratio 3.0–3.6; surface with punctures from base to apex; costal margin distinctly arcuate at base then less curved; anteroapical angle wide, placed apicad of posteroapical angle; apex of tegmen widely rounded; posteroapical angle wide; tornus short, arcuate; vein ScP arched in middle, slightly fused with stem R+MP+CuA at over 2/3 of basal cell length; Pc+CP extending just beyond terminal RA₁; basal cell with length about 1/7 of tegmen length, narrow, almost 6.1× as long as wide, in apical portion acute; stem ScP+R leaving basal cell basad of leave of stem MP; stem CuA with a short stalk closing basal cell, separating merely apicad of stem ScP+R leave; basal cross vein cua-cup connected to stem MP+CuA at its separation from basal cell; stem ScP+R forked at basal 0.34–0.38 of tegmen length; RA with 8 terminal branches; RP with 1–2 terminal branches; stem MP long, forked distad of stem CuA forking; claval vein Pcu simple, slightly arcuate; A1 weak, slightly concave at mid-point; cross veins ir, rp-mp₁₊₂ and mp₄-cua apicad of apex of clavus, ir apicad of rp-mp₁₊₂, and mp₄-cua more basad.

Discussion

Jurassic *Jurocercopsis*, *Titanocercopsis*, and the Cretaceous *Cretocercopsis* Ren, 1995 were considered as basal representatives within Procercopidae in Chen *et al.* (2020). *Cretocercopsis* distinctly differs from *Jurocercopsis* and *Titanocercopsis* in having a tegmen with costal margin at Pc+CP terminal obviously concave, RP multi-branched, and hind wing with MP₃₊₄ fused with MP₁₊₂ apically (Chen *et al.*, 2020). *Jurocercopsis* shares several crucial features with *Titanocercopsis* from the Daohugou beds, as large body, extended Pc+CP and multi-branched RA and MP on tegmen. However, *Jurocercopsis* can be easily discriminated from the latter by the following characters: 1) basal cell short, with length about 0.15 of tegmen length (basal cell with length about 0.22 of tegmen length in *Titanocercopsis*); 2) MP of tegmen forked distad of CuA forking (MP forked basad of or at same level of CuA forking in *Titanocercopsis*); 3) cross vein imp absent (imp present in *Titanocercopsis*); 4) cell C3 open and cell C3' absent (C3 closed and C3' present in *Titanocercopsis*).

Intraspecific variation of venation has been previously recorded in Procercopidae such as *Procercopina*, *Anthoscytina* and *Titanocercopsis* involved the number of terminal longitudinal veins and the position of cross



FIGURE 4. Photographs of *Jurocercopis grandis* from the Daohugou beds showing the general habitus. **A**, Lateral view of specimen NIGP172194. **B**, Lateral view of specimen NIGP172195. **C**, Lateral view of specimen NIGP172196, moistened with 70% ethanol. (Scale bars = 5 mm).

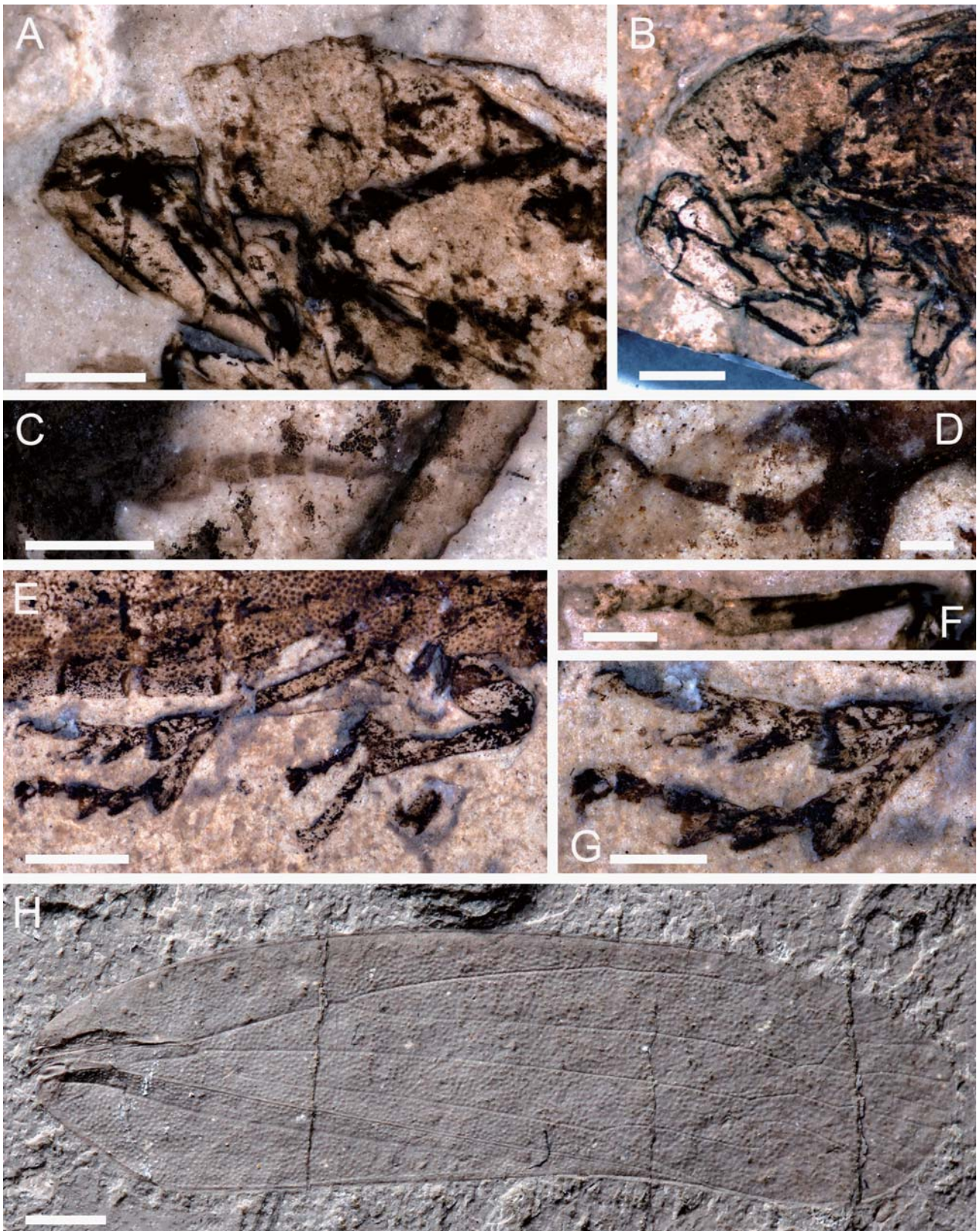


FIGURE 5. *Jurocercopsis grandis* from the Daohugou beds showing the morphological details. **A**, Head, pronotum and mesonotum (NIGP172195). **B**, Head and pronotum (NIGP172196). **C**, Enlargement of **A**, showing details of antenna. **D**, Enlargement of **B**, showing details of antenna. **E**, Overview of legs (NIGP172194). **F**, Protibial and protarsus (NIGP172195). **G**, Enlargement of **E**, showing details of metatarsus and part of metatibia. **H**, Forewing (NIGP172197). **A–G** moistened with 70% ethanol. (Scale bars = 2 mm in **A**, **B**, **E**, **H**; 1 mm in **F**, **G**; 0.5 mm in **C** and **D**).

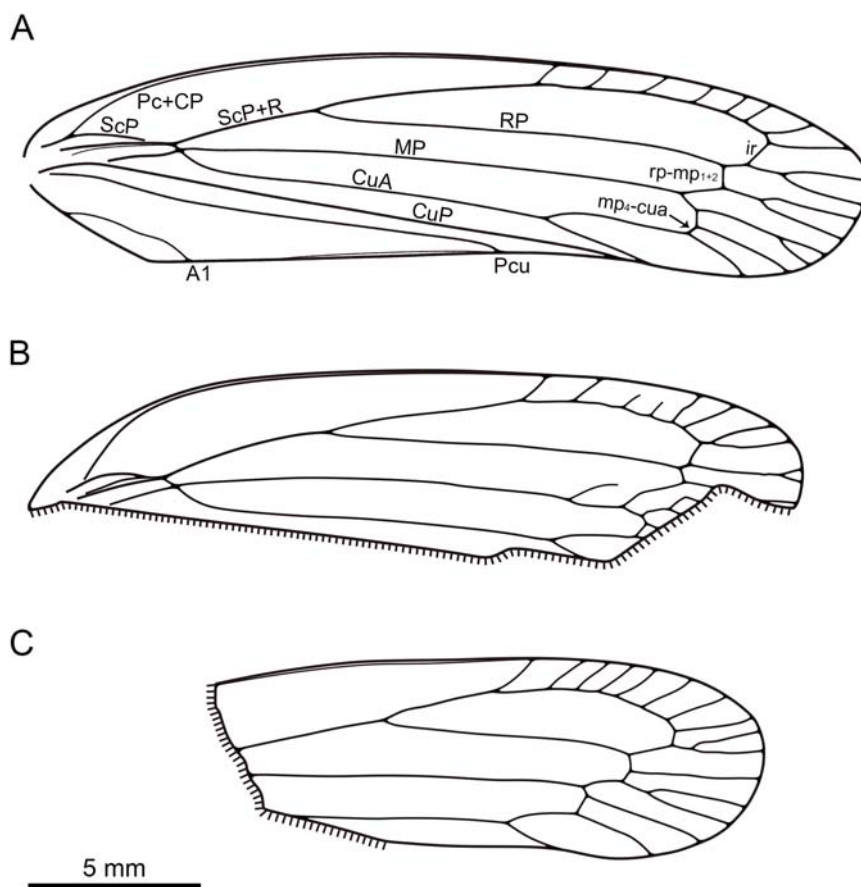


FIGURE 6. Line drawings of forewings of *Jurocercopis grandis*. **A**, Complete forewing (NIGP172197) from the Daohugou beds. **B**, NIGP172198, from the Jiyuan Basin. **C**, NIGP172199, from the Jiyuan Basin. (Scale bars = 5 mm).

veins (Ansorge, 1996; Ren *et al.*, 1998; Chen *et al.*, 2015c). The tegminal venation of *Jurocercopis* among these nine specimens and the holotype of *Jurocercopis grandis* in Wang & Zhang (2009) also apparently varied in the number of terminal branches as follow: 1) vein RA with 7 terminal branches in the holotype of *J. grandis* in Wang & Zhang (2009), while with 8 terminal branches in NIGP172197–NIGP172199; 2) RP unbranched in NIGP172200, while with 2 terminal branches in the holotype and NIGP172197–NIGP172199; 3) MP with 4 terminal branches in NIGP172199, while with 5 terminal branches in NIGP172197 and 6 terminal branches in the holotype and NIGP172200 (Figs 2, 3, 5H, 6; the holotype of *J. grandis* see Wang & Zhang, 2009: fig 1). The length/width ratio of tegmen is highly variable among several specimens probably because of the deformation of sedimentary rocks. Considering their almost identical tegmen venation and size, it is reasonable to assign these specimens to the same species *i.e.*, *Jurocercopis grandis*.

The fossil insects from the Yangshuzhuang Formation of northern China are poorly-known (Deng *et al.*, 2003). Recently, a very diverse and rich palaeoentomofauna have been found from the Yangshuzhuang Formation in

the Jiyuan Basin, and a selenothemistid damselfly named *Jurathemis incompletus* Huang & Nel, 2018 has been formally described (Huang *et al.*, 2018b). In the present study, five specimens (incomplete forewings) collected from the Yangshuzhuang Formation can be placed in *Jurocercopis* based on a series of apomorphic characters of tegmen, including tegmen length near 22 mm, basal cell short, Pc+CP extending beyond of termination of RA₁, RA multi-branched (more than 7 terminal branches), RP with 1–2 terminal branches, MP forked distad of CuA forking, with 4–6 terminal branches, and cross vein imp absent.

Jurocercopis grandis reported herein represents the second fossil insect formally described from the Yangshuzhuang Formation, widening the biogeographic distribution of *Jurocercopis* in the Middle to Late Jurassic, and indicates that the Yangshuzhuang Formation in the Jiyuan Basin, northern China correlates to the Haifanggou Formation of the Daohugou beds in Yanliao region. It also contributes to our understanding of the geological age of the Yangshuzhuang Formation, which can be assigned to the Middle Jurassic and its top layers would be reach to the beginning of the Late Jurassic. The Yanliao biota is the

crucial terrestrial biota in the Jurassic of China, providing a significant window to the understanding of terrestrial life evolution during the Middle and Late Jurassic (Huang *et al.*, 2018a; Huang, 2019). The new find further proves that Yanliao biota is widely distributed in northern China.

Acknowledgements

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