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A new sinoalid assemblage from the topmost Late Jurassic Daohugou Bed indicating the evolution and ecological significance of *Juroala* Chen & Wang, 2019 (Hemiptera: Cercopoidea) during more than one million years

YANZHE FU [1,2] & DIYING HUANG [2,3]

[1] *State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Paleoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China*
[2] *University of Science and Technology of China, Hefei 230026, China*
[3] *Corresponding author. E-mail: dyhuang@nigpas.ac.cn*

Abstract

Herein, two recently described nominal genera of Sinoalidae, *Juroala* Chen & Wang, 2019a, with a single species, and *Parasinoala* Fu & Huang, 2019a with three species from the Middle to Upper Jurassic Daohugou Bed, are revised. *Parasinoala* is considered a junior synonym of *Juroala* **syn. nov.**, and *Parasinoala minuta* is transferred to *Juroala* **comb. nov.**; and because of also transferring *P. daohugouensis* to *Juroala*, it is preoccupied and is given the new replacement name *Juroala daidaleos* **nom. nov.**. A new fossil horizon yielding very rich sinoalid assemblage was recently discovered at the topmost Daohugou Bed with many specimens of *Juroala* collected. On the basis of these well-preserved new materials, the morphological details of three described species of *Juroala* are revised and intraspecific variation is discussed. The new fossil horizon has a geological age distinctly younger than other described sinoalid assemblages. All the three species of *Juroala* present extremely limited morphological changes but slightly larger sizes than the previously described specimens. The new fossil horizon is rich in sinoalids, unlike other layers from the Daohugou Bed that are dominated by the procercopids, suggesting a possible different high altitude adaptability of Jurassic cercopoids.

Keywords: Sinoalidae, Jurassic, Daohugou, Yanliao biota, Yanshan Movement

Introduction

The hemipteran superfamily Cercopoidea Leach, 1815 includes five extant families (*i.e.*, Cercopidae, Aphrophoridae, Clastopteridae, Machaerotidae, and Epipygidae) and three extinct families (*i.e.*, Procercopidae, Cercopionidae, and Sinoalidae) that are collectively called spittlebugs or froghoppers (Hamilton, 2001; Dietrich, 2002; Shcherbakov & Popov, 2002, Cryan & Svenson, 2010; Wang *et al*., 2012; Paladini *et al*., 2018). The extinct family Procercopidae Handlirsch, 1906, is widely accepted as belonging to the stem group of the superfamily, and known from the Early Jurassic to the Early Cretaceous of Eurasia and Australia (Evans, 1956; Hamilton, 1992); Cercopionidae Hamilton, 1990, are exclusively recorded in the Lower Cretaceous Crato Formation of Brazil; and Sinoalidae Wang & Szwedo, 2012, originally established from the Middle to Upper Jurassic Daohugou Bed, have a mixture of plesiomorphic character states, could be closely related to Procercopidae, and share some synapomorphies with Hylicelloidea (Wang *et al*., 2012). Recently, the number of species in this group has risen rapidly over the past three years. To date, nine genera with 13 species have been attributed to Sinoalidae from the Middle to Upper Jurassic Jiulongshan (= Longmen) and Haifanggou Formations of northeastern China (Chen *et al*. 2019a; Fu & Huang, 2019a, b). In addition, five monotypic genera have been described from mid-Cretaceous Burmese amber, providing some detailed morphological features that have never been previously observed in sinoalids (Chen *et al*., 2018, 2019b, 2019c, 2019d; Fu & Huang, 2019b).

Fu & Huang (2019a) and Chen *et al*. (2019a) described the same genus of Sinoalidae from the Middle to Upper Jurassic Daohugou Bed, published in *Alcheringa* and *Journal of Systematic Palaeontology*, respectively. The *Journal of Systematic Palaeontology* paper was registered in ZooBank on 24 March 2019 and the online version came out on 11 April 2019. The *Alcheringa* paper states that it was published online on 8 January 2019 but the ZooBank registration numbers in the article were not registered until 15 April 2019. Thus, the online version of *Journal of Systematic Palaeontology* paper (*i.e.* Chen *et al*. 2019a) has priority. *Parasinoala* Fu & Huang, 2019a

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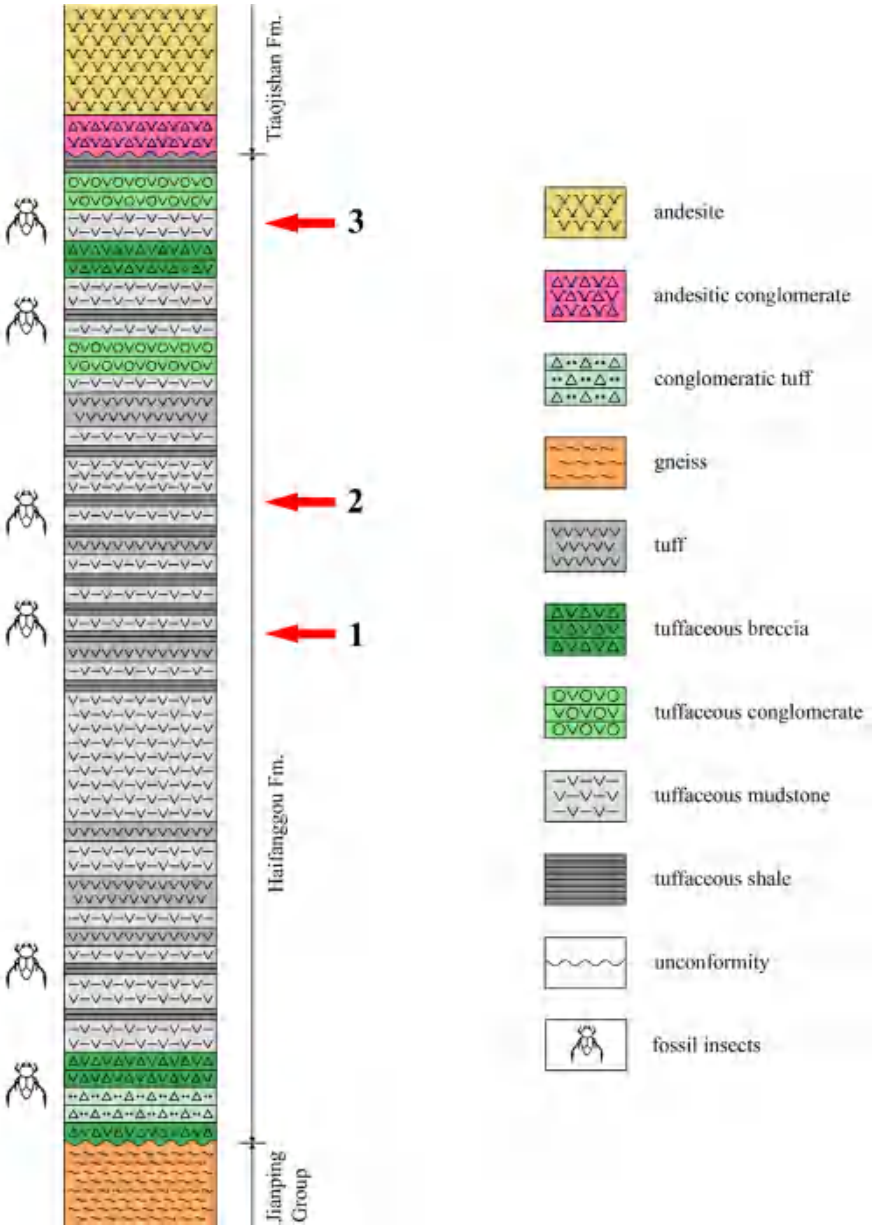

FIGURE 1. Stratigraphic column for the Haifanggou Formation near Daohugou Village, with three red arrows indicating fossil layers.

is thus here considered a junior synonym of *Juroala* Chen & Wang, 2019a, **syn. nov.**.

Chen *et al*. (2019a) erected *Juroala* with single species, *Juroala daohugouensis* on the basis of 42 specimens with body length from 12–18 mm and the colour pattern on tegmen with obvious differences that could represent different species. Fu & Huang (2019a) erected *Parasinoala* on the basis of 15 specimens with three species (*i.e.*, *Parasinoala daohugouensis*, *P. magnus* and *P. minuta*). Among them, *P. magnus* is here considered a junior synonym of *J. daohugouensis*, **n. syn.**, and *P. daohugouensis* and *P. minuta* represent the other two species and are transferred here to *Juroala* **comb. nov.** Because the type species of *Juroala* is *J. daohugouensis*, which is same name as the type species of *Parasinoala*, *P. daohugouensis,* the latter is here given the new replacement name of *Juraloa daidaleos*, **nom. nov.** With these taxonomic and nomenclatural changes, *Juroala* now comprises three species, *J. daohugouensis* Chen & Wang, 2019, *J. daidaleos* Fu & Huang, 2019, and *J. minuta* (Fu & Huang, 2019).

Herein the morphological details of these three species of *Juroala* are revised based on a dozen new well-preserved specimens. The new material was collected from the topmost layer of the Daohugou Bed that is obviously younger than other described material of *Juroala* (Fig. 1). Therefore, the intraspecific variation of these three species is also discussed.

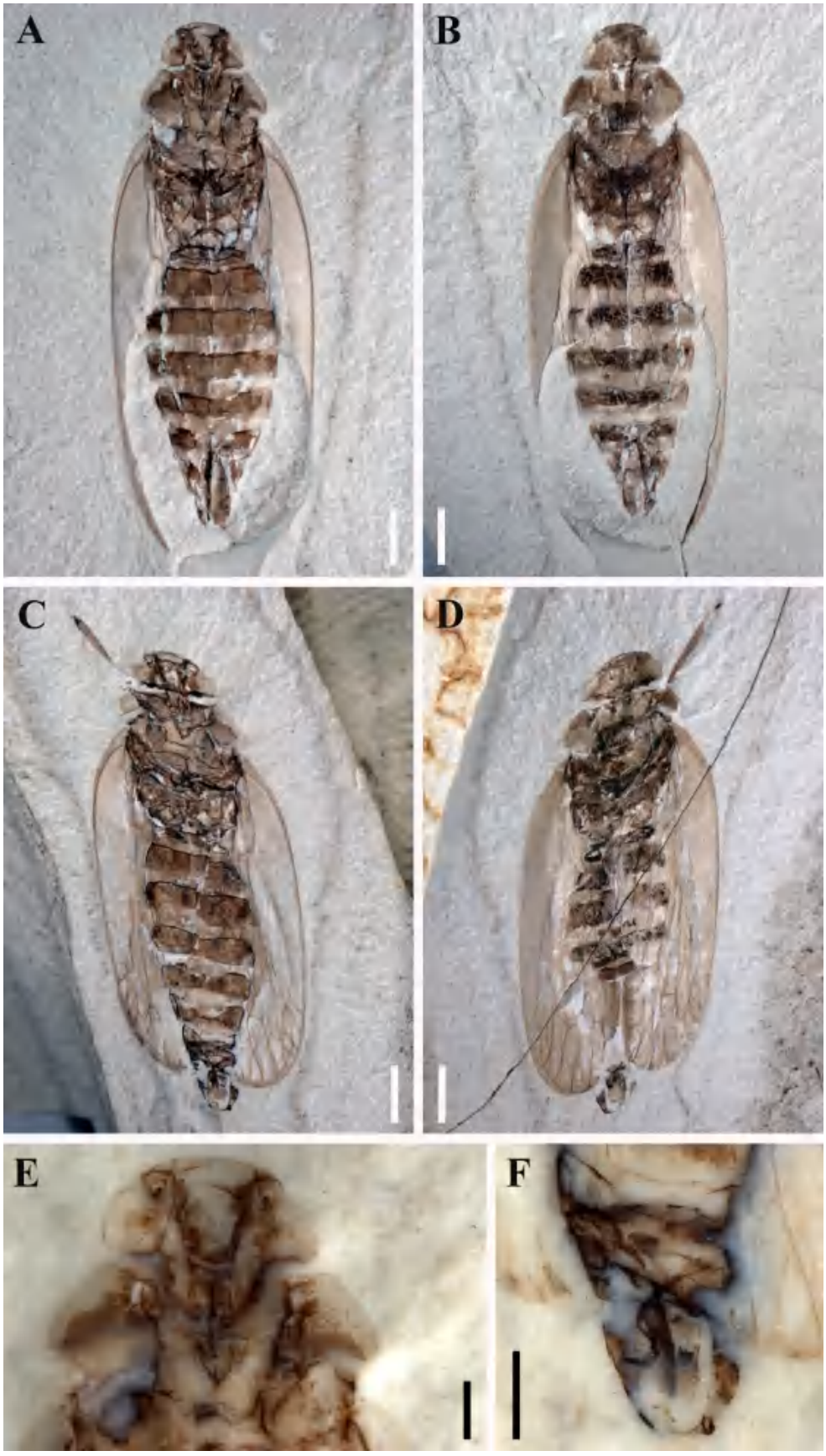

FIGURE 2. *Juroala daohugouensis*. **A**, A nearly complete specimen in dorsal view, part (NIGP170037a). **B**, Counterpart (NIGP170037b). **C**, A nearly complete specimen in dorsal view, part (NIGP170038a). **D**, (NIGP170038b). **E**, Enlargement of **A**, showing details of head and pronotum. **F**, Enlargement of **C**, showing details of genitals. **E**, **F** moistened with 70% ethanol. (Scale bar = 2 mm in **A**–**D**; 1 mm in **E**, **F**).

Material and methods

Twelve well-preserved specimens of *Juroala* (NIGP169400, NIGP169401, NIGP170028–NIGP170037), all complete with parts and counterparts, comprising: three males and six females of *Juroala daidaleos*, one male and one female of *Juroala daohugouensis*, and one male of *Juroala minuta*. All specimens are dorso-ventrally compressed as in typical preservation of sinoalids. They display fine detail of features including antennae, tegmina ornaments, metatibia spines, and terminals. They are preserved in whitish finely laminated tuffaceous shale. All these fossils were collected from the same bedding plane that comes from the topmost of Daohugou Bed, at Nanliang locality, Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, northeastern China (detailed locality map see Huang, 2015).

Some specimens were carefully prepared using a sharp knife. 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% ethanol to show fine details (*e.g.*, metatibia and antenna); confocal images were made using Helicon Focus 6 software. 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 largely follows Bourgoin *et al*. (2015) as well as that based on forewing-venation patterns among Fulgoromorpha (Nel *et al*., 2012). The following standards were used for measurements: body length measured from the apex of the vertex to the apex of the abdomen; body width measured at the widest part of the abdomen. All measurements are presented in millimeters (Table 1).

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Cicadomorpha Evans, 1946
Superfamily Cercopidea Leach, 1815
Family Sinoalidae Wang & Szwedo, 2012
Genus *Juroala* Chen & Wang, 2019a

Juroala Chen & Wang, 2019a. Type species. *Juroala daohugouensis* Chen & Wang, 2019a; by original designation.

Parasinoala Fu & Huang, 2019a. Type species: *Parasinoala daohugouensis* Fu & Huang, 2019a, by original designation, **syn. nov.**

We consider *Parasinoala* and *Juroala* congeneric by virtue of identical body structure and wing venation, including head semicircular in dorsal view, pronotum with anterior margin straight, metatibia with two rows of lateral spines (four at most in each row), tegmen with vein Pc+CP short, ending not beyond tip of basal cell, RA with 1–4 branches, RP single, MP with 3–4 branches, and MP of hind wing with two branches.

TABLE 1. Measurements of *Juroala daohugouensis*, *Juroala daidaleos* and *Juroala minuta*. M = male; F = female. Measurements are in millimeters.

***Juroala daohugouensis* (M)**	170036					
body length	15.9					
body width	3.8					
***Juroala daohugouensis* (F)**	170037					
body length	17.1					
body width	4.8					
***Juroala daidaleos* (M)**	170028	170029				
body length	10.3	10.7				
body width	2.7	3.0				
***Juroala daidaleos* (F)**	170030	170031	170032	170033	170034	169400
body length	12.3	12.7	12.4	13.0	12.7	12.3
body width	3.7	4.5	4.0	3.70	3.7	4.1
***Juroala minuta* (M)**	170035					
body length	7.9					
body width	2.0					

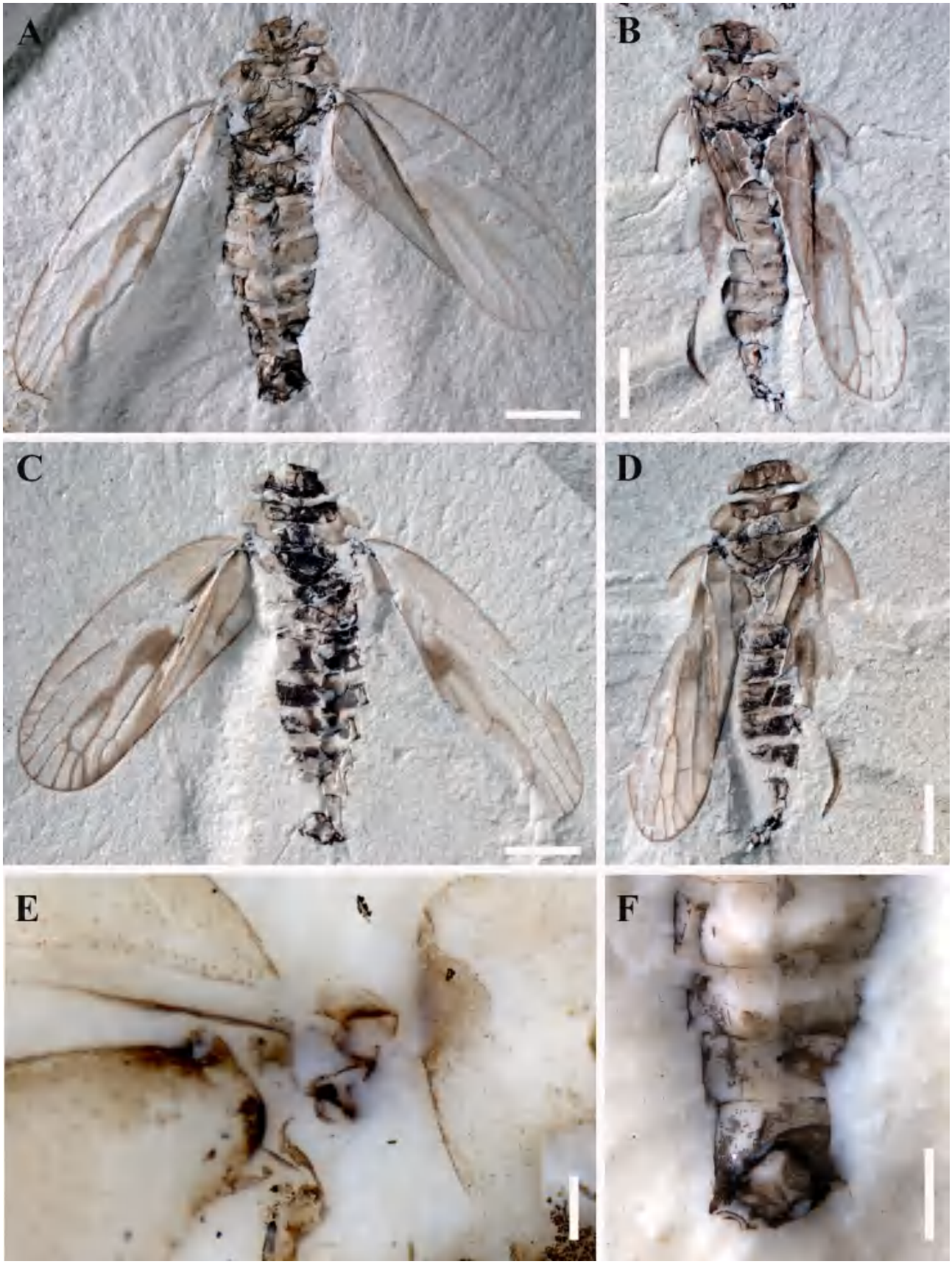

FIGURE 3. *Juroala daidaleos*, males, from the upmost Daohugou Bed. A nearly complete specimen in dorsal view, part (NIGP170028a). **B**, Counterpart (NIGP170028b). **C**, An incomplete specimen in dorsal view, part (NIGP170029a). **D**, Counterpart (NIGP170029b). **E**, Enlargement of **B**, showing details of base of tegmen. **F**, Enlargement of **A**, showing details of genitals. **E**, **F** moistened with 70% ethanol. (Scale bar = 2 mm in **A**–**D**; 1 mm in **F**; 0.2 mm in **E**).

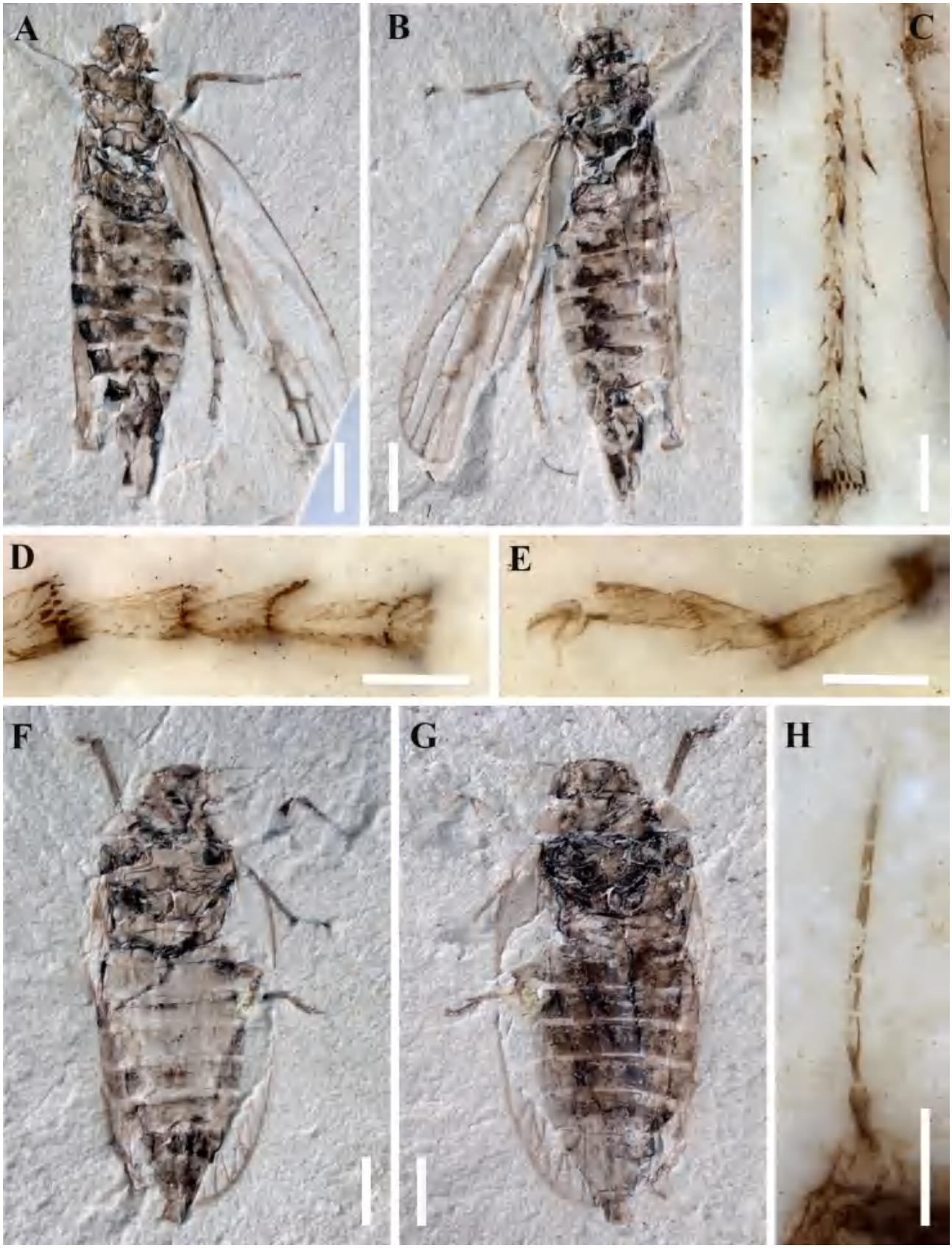

FIGURE 4. *Juroala daidaleos*, females, from the upmost Daohugou Bed showing the general habitus and morphological details. **A**, An incomplete complete specimen in dorsal view, part (NIGP170030a). **B**, Counterpart (NIGP170030b). **C**, Enlargement of **A**, showing details of metatibia. **D**, Enlargement of **A**, showing details of metatarsus. **E**, Enlargement of **F**, showing details of metatarsus. **F**, A nearly complete specimen in dorsal view, part (NIGP170031a). **G**, Part (NIGP170031b). **H**, Enlargement of **F**, showing details of antenna. **C**, **D**, **E**, **H** moistened with 70% ethanol. (Scale bar = 2 mm in **A**, **B**, **F**, **G**; 0.5 mm in **C**–**E**, **H**).

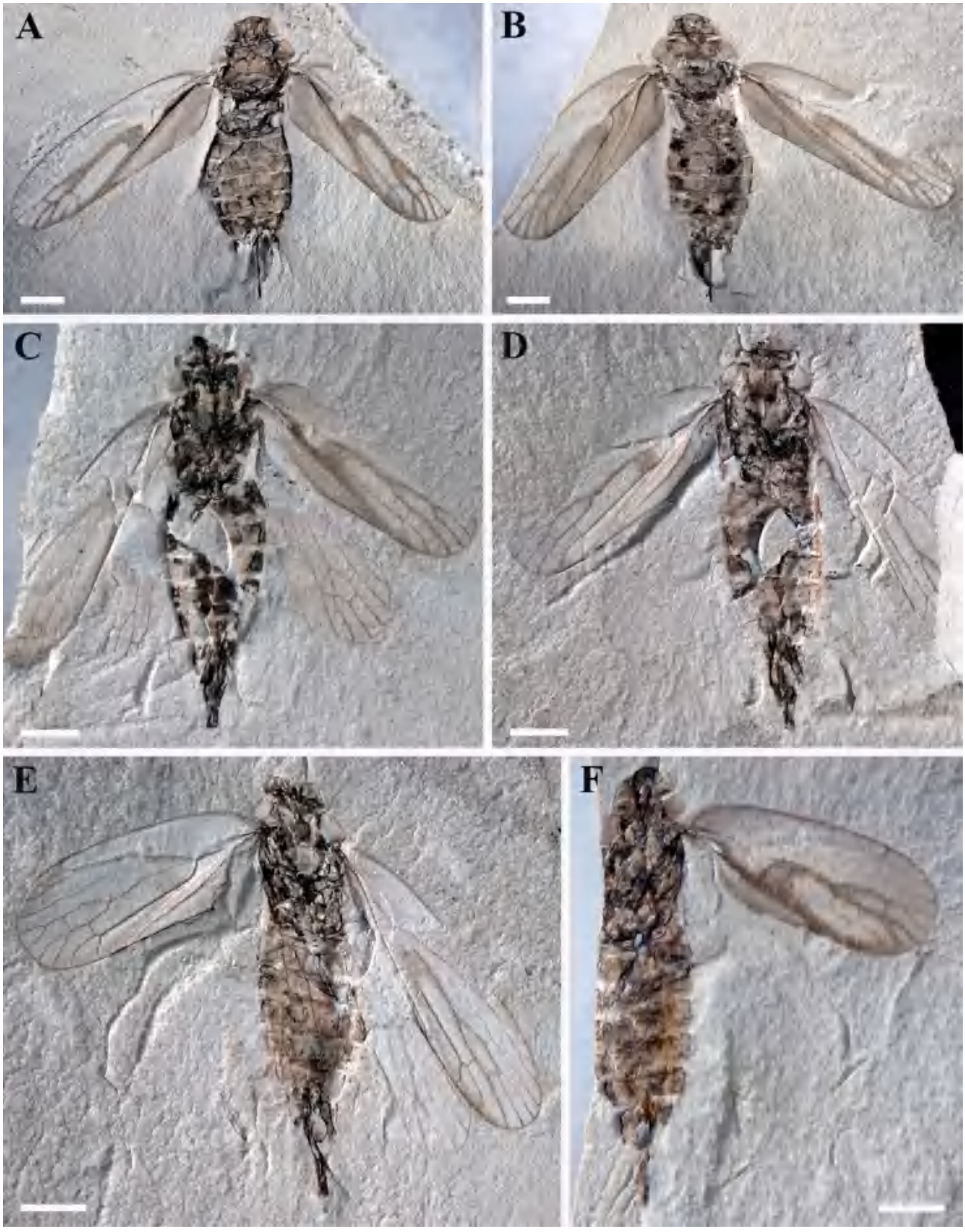

FIGURE 5. *Juroala daidaleos*, females, from the upmost Daohugou Bed showing the general habitus and color band on forewing. **A**, A nearly complete specimen in dorsal view, part (NIGP170032a), showing the well-preserved color band on the forewing. **B**, Counterpart (NIGP170032b). **C**, A nearly complete specimen in dorsal view showing the hind wing, part (NIGP170033a). **D**, Counterpart (NIGP170033b). **E**, A complete specimen in dorsal view, part (NIGP170034a). **F**, (NIGP170034b), an incomplete specimen showing the color band. (Scale bars = 2 mm).

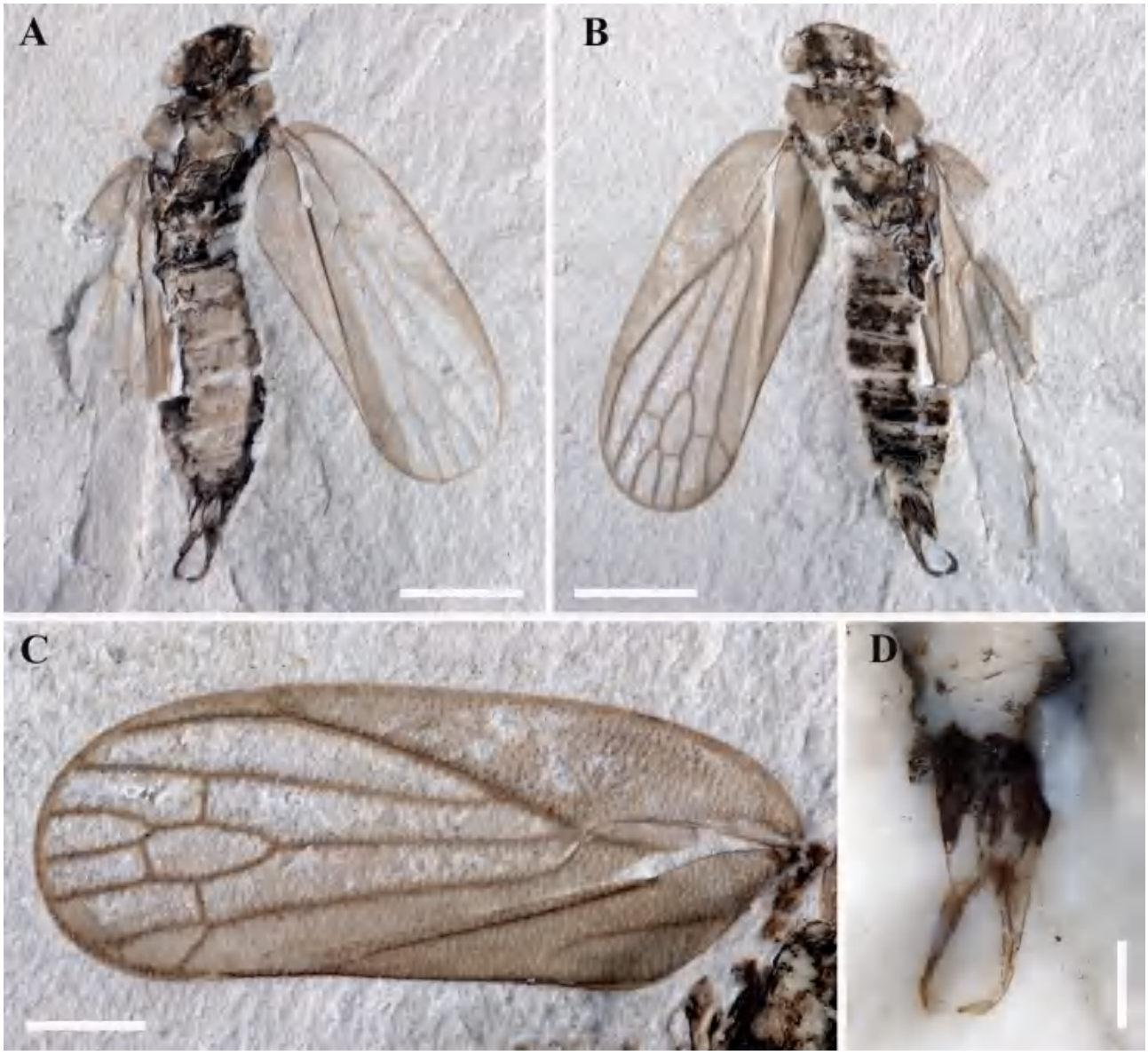

FIGURE 6. *Juroala minuta*. **A**, A nearly complete specimen in dorsal view, part (NIGP170030a). **B**, Counterpart (NIGP170030b). **C**, Enlargement of **B**, showing details of right tegmen. **D**, Enlargement of **A**, showing details of genitals. **D** moistened with 70% ethanol. (Scale bar = 2 mm in **A**, **B**; 1 mm in **C**; 0.5 mm in **D**).

***Juroala daohugouensis* Chen & Wang, 2019a**
(Fig. 2)

Juroala daohugouensis Chen & Wang, 2019a.
Parasinoala magnus Fu & Huang, 2019a, **syn. nov.**

Revised diagnosis (after Chen & Wang, 2019a and Fu & Huang, 2019a)**.** Body length 15.2–18.1 mm; tegmen with small dark bands on the median section; Pc+CP short, ending at costal margin not beyond tip of basal cell, ScP+RA relatively short; RA with 2–4 branches; crossvein ir present; MP with 4 branches; hind wing, MP branching basal of CuA branching; crossvein rp-mp basal of mp-cup.

Supplemental description. Male (NIGP170036), body length 15.9 mm, body width 3.8 mm (Figs 2C, D). Female (NIGP170037), body length 17.1 mm, body width 4.8 mm (Figs 2A, B).

Head (Fig. 2E) rounded apically, compound eyes large, circular in ventral view, with compound eyes about 1.5 times narrower than pronotum, width with compound eyes nearly 3.0 mm in dorsal view; antenna inserted in deep cavities between the eyes; postclypeus broad, with transverse grooves, anteclypeus with a median longitudinal carina. Abdomen tapered, segment II broadest and segments II to VII becoming progressively narrower;, segment IX rather elongate; pygofer short and wide; genital plates long, lunate in ventral view. (Fig. 2F).

Remarks. Two described species, *Parasinoala*

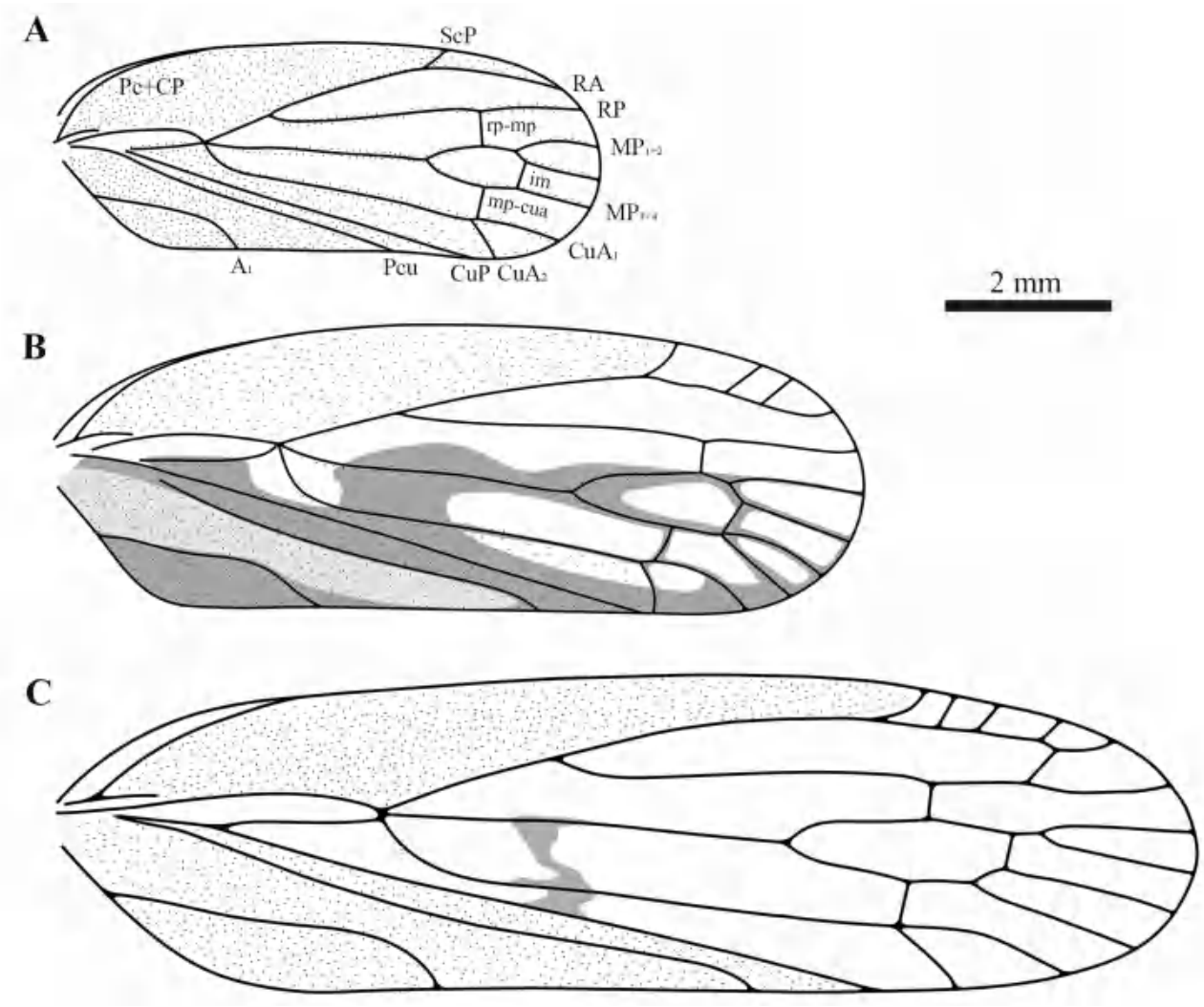

FIGURE 7. Line drawings of forewing of *Juroala*. **A**. *Juroala minuta*. **B**. *Juroala daidaleos*. **C**. *Juroala daohugouensis* (Scale bar = 2 mm).

magnus Fu & Huang, 2019a and *Juroala daohugouensis* Chen & Wang, 2019a were discovered in the same horizon at the same locality (Middle–Upper Jurassic Daohugou Bed). We consider them the same species by virtue of similarity in size, tegmen with small dark patterns on the median section, and RA of tegmen with maximum of 4 branches. Therefore *P. magnus* is here considered a junior synonym of *J. daohugouensis*, **syn. nov.**

***Juroala daidaleos* Fu & Huang, 2019a**
(Figs 3–5)

Parasinoala daohugouensis Fu & Huang, 2019a (preocc. by Chen & Wang, 2019a)**.**

Juroala daidaleos Fu & Huang, 2019a, **nom. nov.** for *Parasinoala daohugouensis* Fu & Huang, 2019a.

Etymology. The specific epithet derives from the Greek, daidaleos, meaning, "dappled", and is a generalized reference to the patterning of the tegmina.

Revised diagnosis (from Fu & Huang, 2019a)**.** Body length 10.3–13.0 mm; flagellum with seven elongate segments; tegmen with distinct colour pattern on the lower median section; ScP+RA branching into ScP and RA after MP branching; RA with 2–3 branches; crossvein ir absent; MP with 3–4 branches; hind wing with MP branching basal of CuA branching; cross vein rp-mp at the same level as mp-cup.

Supplemental description. Male (NIGP170028 and NIGP170029), body length 10.3–10.7 mm, body width 2.7–3.0 mm (Fig. 3). Female (NIGP170030–NIGP170034, NIGP169400 and NIGP169401), body length 12.3–13.0 mm, body width 3.8–4.5 mm (Figs 4, 5).

Head rounded apically, with compound eyes 1.4–1.6 times narrower than pronotum, width with compound eyes about 2.3 mm in dorsal view; antenna about 1.77 mm long

(Fig. 4H), only persevered in NIGP170031, scape large, pedicel as long as but much thinner than scape, becoming progressively wider from base to end; flagellum with seven elongate segments, flagellomeres I–VI becoming progressively thinner. Tegmen (Fig. 7B) armed with dark color bands stained on the lower median section, along MP, anterior of CuA, Pcu, CuP and A_1, with lighter color bands between Pcu and A_1; costal area, claval punctate and longitudinal veins covered with piliferous granules; RA with 2–3 branches, crossvein ir absent; crossvein mp-cup connecting MP_{3+4} and CuA_1 or branch point of CuA. Hind wing with crossvein im present. Legs covered with densely dispersed setae, especially metatibia; metatibia (Fig. 4C) with tiny spines and two rows of seven piliferous strong spines in total (three and four in number for each row), two rows of apical teeth (four and nine visible in number for each row); metatarsus (Figs 4D, E) nearly 1.7 mm long, basi- and midtarsomere widened apically, armed with one row of apical teeth with long setae at apex; tarsal claws robust; arolium large.

Remarks. The tegminal venation of these nine specimens has intraspecific variation and even intra-individual variation in several characters evidenced by: 1) RA with two branches in NIGP170029 and the right tegmen of NIGP170034, but with three branches in the left tegmen of NIGP170034 and other specimens; 2) MP with three branches in NIGP170030, the right tegmen of NIGP170033, and the left tegmen of NIGP170034, but with four branches in the left tegmen of NIGP170033, the right tegmen of NIGP170034 and other specimens; 3) the position of crossvein mp-cua is variable, mp-cua connecting MP_{3+4} and CuA_1 in NIGP170028 and NIGP170034, but connecting MP_{3+4} and branch point of CuA in other specimens, thus are not appropriate for species-level diagnosis.

***Juroala minuta* (Fu & Huang, 2019a)**
(Fig. 6)

Parasinoala minuta Fu & Huang, 2019a.
Juroala minuta (Fu & Huang, 2019a), **comb. nov.**

Revised diagnosis (from Fu & Huang, 2019a)**.** Body small, length 7.5–8.3 mm; tegmen without colour patterns; ScP+RA branching into ScP and RP basal of MP branching; RA with single branch; crossvein ir absent; MP with 3 branches; hind wing with MP branching at the same level as CuA branching; crossvein rp-mp at the same level as mp-cup.

Supplemental description. Male (NIGP170035), body length 7.9 mm, body width 2.0 mm (Figs 6A, B); tegmen about 6.4 mm long and 2.5 mm wide, with length/width ratio 2.6.

Head rounded apically, compound eyes large, with compound eyes almost 1.2 times narrower than pronotum, width with compound eyes about 2.1 mm in dorsal view. Tegmen (Figs 6C, 7A) with costal area, claval and longitudinal veins covered with piliferous granules; vein RA simple, crossvein ir absent; ScP+RA relatively long, almost 2.5 times longer than ScP+R; crossvein mp-cup slightly after CuA branching and connecting with CuA_1. Genitalia well-preserved (Fig. 6D), pygofer short and wide, anal segments and anal style short and small, genital styles very long, quite curved distally in ventral view.

Discussion

To date, there are six sinoalid genera with nine species from the Daohugou Bed. They include *Sinoala parallelivena* Wang & Szwedo, 2012, *Jiania crebra* Wang & Szwedo, 2012, *J. gracila* Wang & Szwedo, 2012, *Luanpingia daohugouensis* Fu *et al*., 2018, *Shufania hani* Chen *et al*., 2017, *Stictocercopis wuhuaensis* Fu & Huang, 2018, *Juroala daohugouensis* Chen & Wang, 2019a, *J. daidaleos* Fu & Huang, 2019a, and *J. minuta* (Fu & Huang, 2019a). The monotypic genus *Chengdecercopis* from the Jiulongshan Formation of Xiaofanzhangzi, originally assigned to Procercopidae (Hong, 1983), closely resembles *Juroala* in having similar wing venation, and should be transferred to Sinoalidae.

All specimens in the present paper were collected from three fossil layers of the Daohugou Bed (Fig. 1): Layer 1 belongs to the middle section of the Daohugou Bed, which exposes strata below the conchostracan layers with the geological age of the deposit close to the Middle to Upper Jurassic boundary (163.5 Ma; Zhang *et al*., 2019), characterized by abundant anostracans (Huang, 2016; Huang *et al*., 2018). Layer 2 belongs to the middle and upper section of the Daohugou Bed, which exposes strata with abundant conchostracan named *Triglypta haifanggouensis* (Liao *et al*., 2017); it is supposed to be an earliest Late Jurassic period (Huang, 2019). Layer 3 belongs to the topmost section of the Daohugou Bed, characterized by presence of cladocerans (Huang, 2016; Huang *et al*., 2018), which represents a geological age distinctly younger than Layer 2 and Layer 1.

Juroala comprises three species collected from the Daohugou Bed. All specimens of *J. daidaleos* and *J. minuta* were found below the conchostracan layers and are associated with abundant anostracans (Fig. 1). *Juroala daohugouensis* displayed a wider distribution in both the conchostracan and anostracans layers (Fu & Huang, 2019a). The present new fossil layer that yielded rich sinoalids, was discovered at the topmost of Daohugou Bed, associated with many cladocerans (Huang, 2016; Huang *et al*., 2018).

These new specimens of *Juroala,* combined with the previously described specimens, share a set of consistent characters, such as nearly identical wing venation and body structure, especially the colour patterns on the tegmen. Therefore, they could be assumed to be the same species. However, these specimens from the new layer show that there are some variations in the morphology with previously described specimens in Fu & Huang (2019a): 1) body sizes of all three species are a little larger than the previously described specimens. For instance, the body length of female of *J. daidaleos* is about 12.3–13.0 mm in contrast to 11.4–11.9 mm in the previously described specimens; body length of female of *J. daohugouensis* about 17.1 mm in contrast to 15.3–16.1 mm in the previously described specimens; 2) most of specimens of *J. daidaleos*, vein RA of tegmen with three branches (except for NIGP170029 and NIGP170034) in contrast to RA with only two branches in the previously described species; 3) crossvein im of tegmen is present in *J. daidaleos* in contrast to im absent in the previously described specimens; 4) tegmen colored with dark bands stained on the lower median section, along MP, Pcu, CuP and A_1 in the previously described specimens of *J. daidaleos* in contrast to tegmen armed with lighter color bands between Pcu and A_1 in new specimens.

The Daohugou biota has yielded abundant cercopoids insects, represented by Procercopidae and Sinoalidae, viz., six genera with nine species of sinoalids and three genera with six species of procercopids reported to date (Fu *et al*., 2018; Fu & Huang, 2019a). In fact, the population of sinoalids is reduced and their distribution is limited in the Daohugou Bed despite their relative diversity. Nevertheless, procercopids are abundant and widely spread in the Daohugou Bed. For example, *Anthoscytina longa* is the representative species of the Yanliao biota.

In the analyses of the occurrence of cercopoids in three significant layers of the Daohugou Bed, Layer 1 is very rich in procercopids and most of sinoalids but the latter are still relatively rare. Layer 2 is dominated by procercopids such as *Anthoscytina longa* and also other species *A. brevineura*, *A. elegans* and *A. daidaleos* (Chen *et al*., 2015; Fu *et al*., 2018). Only two specimens of *J. daohugouensis* of sinoalids were collected from the Layer 2 (Fu & Huang, 2019a). Layer 3 (new layer) contents rich sinoalids, such as *Juroala*, and procercopids are absent. Such different distributions of cercopoids suggest an ecological competition between procercopids and sinoalids. The northern North China Plate (*e.g.* Daohugou region) was uplifted during the Yanshan Movement Phase A1 (168–161 Ma) that gradually formed mountains range over 2000 meters (Huang, 2019). The Daohugou deposit records the gradual uplifting process of the deposit from the Layers 1–3 in this paper (Fig. 1). The gradual rise of sinoalids suggests that this group is possibly more adaptable to the mountain-plateau environment, although the procercopids is widely distributed in all layers of the Daohugou Bed from the bottom to top.

The new fossil horizon discovered in this paper is very close to the topmost of the Daohugou Bed. Shortly afterwards, a strong tectonic deformation and a large-scale volcanic activity occurred, resulting in a serious collapse of the ecosystems of Daohugou area, with biota migrating to the surrounding areas.

Conclusion

The detailed layers of fossil insects from the Daohugou Bed have always been poorly-known. Therefore the palaeoecosystems were misunderstood by the presence of mixed fossils. Herein, we tentatively analyzed the morphological and ecological evolution on cercopoids based on the verified fossil layer record. New material of *Juroala* shows that there is a slightly variable tendency over the age of the Middle to Upper Daohugou Bed. The Daohugou fossil layers record the gradual uplifting process of the deposit from the Layers 1–3. The gradual raised population of sinoalids suggests that this group was possibly more adaptable to the mountain-plateau environment than the procercopids. The decline of procercopids is also probably resulting from the competitive displacement with sinoalids.

Acknowledgements

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