Palaeoentomology 008 (5): 512–519
https://www.mapress.com/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.8.5.8
http://zoobank.org/urn:lsid:zoobank.org:pub:FF687B1A-4E21-4013-A851-96E4A34F6C5A

Two new Jurassic species of Tipuloidea (Insecta: Diptera) from Daohugou Village, China

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Abstract

Two new species of Tipuloidea, *Tipunia ningchengensis* **sp. nov.** and *Praearchitipula procera* **sp. nov.** are described and illustrated from the Middle Jurassic Jiulongshan Formation at Daohugou Village, Inner Mongolia, China. The new species *T. ningchengensis* **sp. nov.** is not only the first Chinese record of genus *Tipunia*, but also the first record of Tipulidae in the Middle Jurassic. Thereby, it not only enriches the diversity and distribution area of *Tipunia*, but also extends the first appearance of Tipulidae back to the Middle Jurassic. The new pediciid species *P. procera* **sp. nov.** found without hairy eyes, confirms once again that the Mesozoic genus *Praearchitipula* has no pubescence of the eyes, different than the extant genera of Pediciidae. These two new species further enhance the biodiversity of Jurassic insects in the Daohugou area, and the suitable and diverse ecological environment of this region harbored so rich and diverse insect groups.

Keywords: Tipuloidea, Tipulidae, Pediciidae, Middle Jurassic, Daohugou

Introduction

Pediciidae and Tipulidae are ancient families of nematoceran Diptera, and are both belonging to the superfamily Tipuloidea of infraorder Tipulomorpha. They are important for understanding the early evolution of the Diptera. The earliest fossil record of Pediciidae is Middle Jurassic (Kalugina & Kovalev, 1985; Gao *et al*., 2015), and Tipulidae first occurred at the same time according the new fossil material in this paper. So far, only one genus with nine known species of Pediciidae, and two genera with 37 species of Tipulidae have been reported in the Mesozoic (Kopeć *et al*., 2020, 2023; Santos *et al*., 2023).

The Mesozoic genus *Tipunia* Krzemiński & Ansorge, 1995, with its type species *T. intermedia*, was originally assigned to Architipulinae within Limoniidae (Krzemiński & Ansorge, 1995), but was subsequently transferred to Tipulidae (Lukashevich & Ribeiro, 2018). Until now, only six fossil species were reported in this genus: the type species from the Upper Jurassic of Solnhofen in Germany (Krzemiński & Ansorge, 1995), *T. undata* and *T. jorgi* from the Upper Jurassic of Shar Teg in Mongolia (Lukashevich, 2009), *T. completa* from the Late Jurassic of Karatau in Kazakhstan (Kopeć *et al*., 2023), *T. austeni* from the Lower Cretaceous of Clockhouse Brickworks in UK (Jarzembowski, 1991) and *T. kania* from the Lower Cretaceous of Dorset in UK (Kopeć *et al*., 2023). *Tipunia* is now the oldest genus of Tipulidae, and possesses some typical morphological characters of Limoniidae, much the same as some extant primitive Tipulidae, such as morphology of the antennae and palpi, Sc extending to the wing margin and not merging with the cross-vein sc-r, and a long Rs (Ribeiro & Lukashevich, 2014; Lukashevich & Ribeiro, 2018; Kopeć *et al*., 2023).

Another Mesozoic genus *Praearchitipula* Kalugina, 1985, was also originally assigned to Architipulinae within Limoniidae (Kalugina & Kovalev, 1985), and later transferred to Pediciidae (Krzemiński & Evenhuis, 2000). This genus includes nine described species until now: *P. notabilis* and *P. trinervis* from the Middle Jurassic of Kubekovo in Russia (Kalugina & Kovalev, 1985); *P. abnormis*, *P. apprima* and *P. mirabilis* from the Middle Jurassic of Daohugou in China (Hao & Ren, 2009; Gao *et al*., 2015); *P. ryszardi* from the Upper Jurassic to Lower Cretaceous of Teete in Russia (Kopeć *et al*., 2020); *P. kaluginae*, *P. podenasi* and *P. ribeiroi* from the Lower Cretaceous of Khasurty in Russia (Lukashevich, 2020).

In this paper, we describe two new species, *Tipunia ningchengensis* **sp. nov.** and *Praearchitipula procera*

 Submitted: 19 Jun. 2025; accepted by D.-Y. Huang: 13 Oct. 2025: 31 Oct. 2025

sp. nov. based on two well-preserved fossil specimens found in the Middle Jurassic, Jiulongshan Formation of Daohugou Village, Inner Mongolia, China. Numerous and diverse fossil insects were found in this locality (Han *et al*., 2019), but only three species of *Praearchitipula* and none of *Tipunia* had been reported. These two new species described here further enrich the diversity of insects in Daohugou. Moreover, *Tipunia ningchengensis* **sp. nov.** shows that *Tipunia* first occurred in China, and not only enriches the diversity and distribution area of *Tipunia*, but also extends the first appearance of Tipulidae back to the Middle Jurassic.

Material and methods

The materials studied herein were found in the Middle Jurassic Jiulongshan Formation (Bathonian-Callovian, about 165 Ma) at Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China; and types of the new species are housed in Paleontological Museum of Liaoning (PMOL), Shenyang Normal University, Shenyang, China.

The new materials were examined under a Leica MZ12.5 stereomicroscope. Photographs of the whole fossil specimen were taken with a Sony ILCE–7RM2 camera and specific features of the fossil specimen were taken with an Olympus DSX1000 digital microscope. Line drawings were prepared by CorelDRAW 2018, and figures were prepared with Adobe Photoshop 2024. Nomenclature and abbreviations of wing venation used in this paper follow Krzemińska *et al*. (2009) and Kopeć *et al*. (2023), while those for genitalia adhere to Cumming & Wood (2017).

Systematic palaeontology

Order Diptera Linnaeus, 1758
Infraorder Tipulomorpha Rohdendorf, 1961
Family Tipulidae Latreille, 1802
Subfamily Tipulinae Latreille, 1802

Genus *Tipunia* Krzemiński & Ansorge, 1995

Type species. *Tipunia intermedia* Krzemiński & Ansorge, 1995.

Included species. The type species and *T. austeni* Jarzembowski, 1991; *T. undata* Lukashevich, 2009; *T. jorgi* Lukashevich, 2009; *T. completa* Kopeć, Soszyńska, Coram & Krzemiński, 2023; and *T. kania* Kopeć, Soszyńska, Coram & Krzemiński, 2023.

Key to species of *Tipunia*

This key is modified from that of Kopeć *et al*., 2023.

1. stem R_{2+3+4} short, about ½ of R_3; A_2 long, terminating wing margin significantly distal of the origination of Rs..... .....*T. jorgi*
- stem R_{2+3+4} relatively long, slightly shorter than R_3; A_2 relatively short, terminating wing margin basal of the origination of Rs 2
2. d-cell short, strongly widened at the tip (wider or equal to its length) 3
- d-cell less widened (at least half as long as its greatest width)..... 5
3. R_3 obviously longer than the stem R_{2+3+4} ....*T. intermedialis*
- R_3 nearly equal to the stem R_{2+3+4} 4
4. only one pterostigma, mM_{1+2} 2 times as long as dM_{1+2} .... *T. kania*
- three pterostigmas, mM_{1+2} slightly longer than dM_{1+2} ....*T. austeni*
5. R_2 equal to R_{2+3}, straight M_4 and the distal of M_3 .... *T. undata*
- R_2 obviously longer than R_{2+3}, curving M_4 and the distal of M_3 6
6. cross-vein sc-r far from the tip of Sc, Rs 3 times as long as R_{2+3+4}, R_{2+3+4} subequal to ⅓ length of R_4, and obviously shorter than R_3 .....*T. ningchengensis* **sp. nov.**
- cross-vein sc-r closer to the tip of Sc, Rs 2 times as long as R_{2+3+4}, R_{2+3+4} equal to ½ length of R_4, and equal to R_3..... .....*T. completa*

Tipunia ningchengensis sp. nov.

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(Figs 1, 2)

Material. Holotype No. PMOL-AI00856AB, female.

Etymology. The specific name refers to Ningcheng County, where the new species is found in Ningcheng County, Chifeng City, Inner Mongolia, China.

Diagnosis. Cross-vein sc-r located far from the tip of Sc, opposite to the bifurcation of Rs; d-cell about 2 times as long as wide, the distal part of the d-cell wider than its base; R_3 3 times as long as R_2 (r-r); Rs 3 times as long as R_{2+3+4}, R_{2+3+4} subequal to ⅓ length of R_4, and obviously shorter than R_3.

Locality and horizon. Daohugou Village, Chifeng City, Inner Mongolia, China; Middle Jurassic, Jiulongshan Formation.

Description. Female (Fig. 2A), body 15.3 mm long, head 2.1 mm long (including rostrum), thorax 3.7 mm long, and wing length 13.6 mm, width 3.9 mm.

Head (Figs 1A, 2B). Compound eye separated, large and oval; rostrum long, about half of the total length of head, covered with dense setae, outline blurred; palpus poor preserved and covered with sparse setae. Antennae long, about 1.6 mm, scape cylindrical, densely covered with setae, strong and long, at least 3 times longer than pedicel, pedicel very short, flagellomeres long, cylindrical,

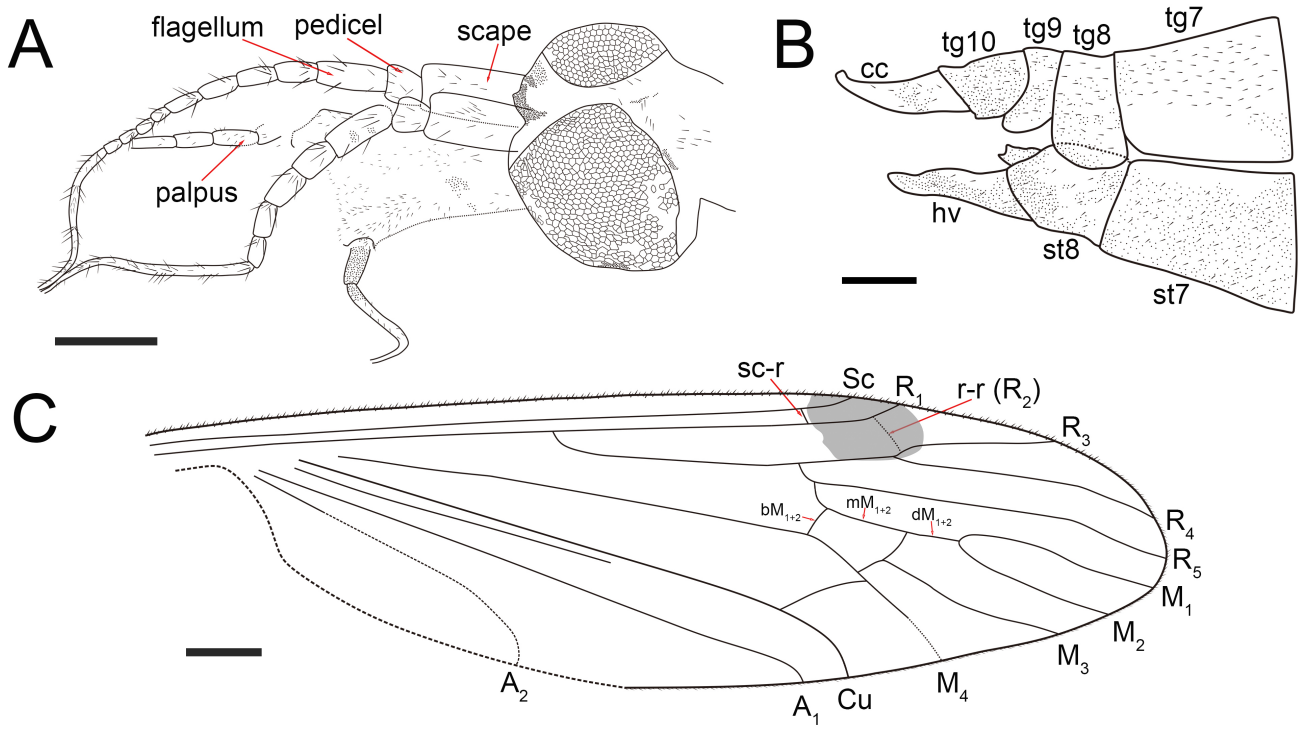

FIGURE 1. *Tipunia ningchengensis* **sp. nov.**, holotype, PMOL-AI00856. **A**, Head. **B**, Female terminalia. **C**, Wing venation. Scale bars = 0.5 mm (**A**, **B**); 1.0 mm (**C**).

the first flagellomere longest, about 2 times as long as pedicel, 2–5 flagellomeres almost same length to each other, remaining flagellomeres gradually shortened and thinned, 2–6 flagellomeres with several verticils at base, surface of each flagellomere densely covered with short setae.

Thorax. Stout, *ca*. 3.7 mm long, pronotum well developed, V-shaped prescutal suture distinct. Legs very long and slender, with setae. Wing (Fig. 1C) transparent, only with an obvious pale pterostigma, wing margin with many short setae (Fig. 2C). Vein Sc long, reaching wing margin opposite the middle of R_{2+3+4}; cross-vein sc-r short, far from the tip of Sc, and opposite the bifurcation of Rs; R_1 ends slightly beyond the fork of R_{2+3+4}, Rs long, 3 times as long as R_{2+3+4}; r-r (R_2) 2 times as long as the length from its intersection with R_1 to R_1 tip; R_{2+3+4} subequal to ⅓ length of R_4, and distinctly shorter than R_3; R_5 long and curved slightly posteriorly. M with four branches, M_1 clearly wavy, almost 2.5 times as long as mM_{1+2} (the upper edge of d-cell); M_2 slightly curved anteriorly, M_3 long and wavy, and M_4 is the shortest among the four branches of M, slightly arcuate posteriorly. d-cell relatively short, about 2 times as long as wide. Cross-vein m-cu long, slightly arcuate, and connecting M_4 and Cu. Cu and A_1 relatively long and straight, only curved at the apex, Cu entering wing margin against the tip of Sc, and A_1 ending wing margin against the bifurcation of Rs. A_2 relatively short, clearly arched.

Abdomen. Elongate, *ca*. 11.3 mm long, tapering posteriorly, covered with dense setae. Female genitalia (Figs 1B, 2D, E), tergite 8 shortened, about ⅓ length of tergite 7, and at least 2 times as long as tergite 9, tergite 9 narrowest, tergite 10 is distinctly longer than tergite 9; cercus shorter than the combined length of tergites 8–10, and slightly curved upward at the distal. Sternite 8 elongate, attaching with hypovalve in the distal, hypovalve shorter than cercus, spermatheca three, irregularly oval. (Fig. 2D).

Remarks. This new species corresponds to the generic characters of *Tipunia* Krzemiński & Ansorge, 1995, and is mostly similar to known species from Late Jurassic of Karatau, Kazakhstan, *T. completa*, but differs from the latter by the cross-vein sc-r far from the tip of Sc, opposite the fork of Rs, Rs 3 times as long as R_{2+3+4}, R_3 is 3 times as long as R_2 (r-r), R_{2+3+4} subequal to one-third length of R_4, and obviously shorter than R_3.

Family Pediciidae Osten-Sacken, 1860
Subfamily Pediciinae Osten-Sacken, 1860

Genus *Praearchitipula* Kalugina, 1985

Type species. *Praearchitipula notabilis* Kalugina, 1985, Middle Jurassic, Kubekovo, Russia.

Included species. The type species and *P. abnormis* (Hao & Ren, 2009); *P. apprima* Gao, Shih, Kopeć, Krzemiński & Ren, 2015; *P. kaluginae* Lukashevich,

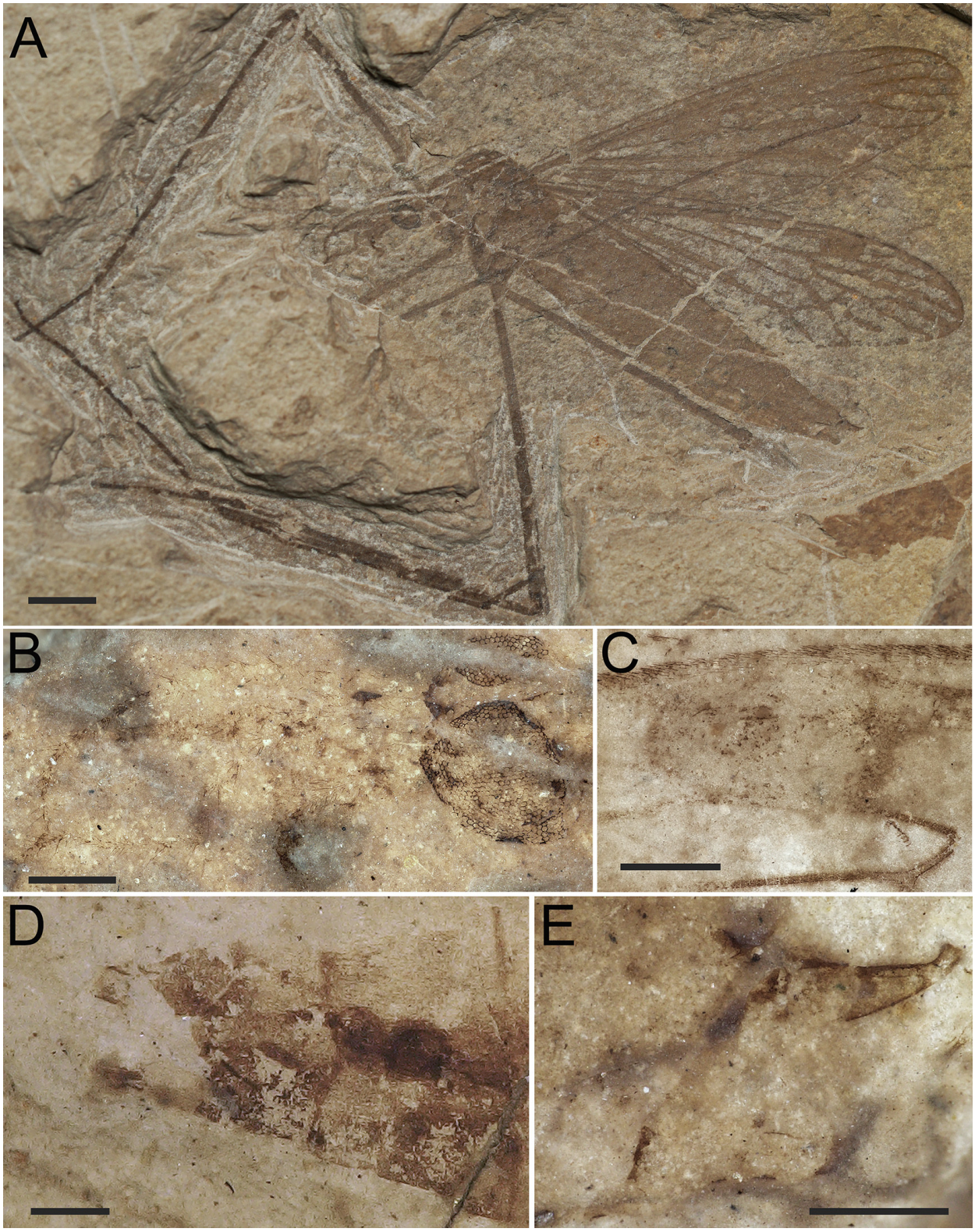

FIGURE 2. *Tipunia ningchengensis* **sp. nov.**, holotype. **A**, Habitus, PMOL-AI00856B. **B**, Head, PMOL-AI00856B. **C**, Pterostigma, PMOL-AI00856A. **D**, Female terminalia, PMOL-AI00856A. **E**, Female terminalia, PMOL-AI00856B. Scale bars = 2.0 mm (**A**); 0.5 mm (**B**–**E**).

2020; *P. mirabilis* Gao, Shih, Kopeć, Krzemiński & Ren, 2015; *P. podenasi* Lukashevich, 2020; *P. ribeiroi* Lukashevich, 2020; *P. ryszardi* Kopeć, Skibińska & Soszyńska, 2020; and *P. trinervis* Kalugina, 1985.

Key to species of *Praearchitipula*

1. R_{4+5} absence, R_{4+5} departed from Rs at the R_{4+5} bifurcation .... *P. podenasi*

- R_{4+5} present, R_{4+5} departed from Rs proximal of R_{4+5} bifurcation..... 2
2. r-m connected R_{4+5} stem and M_{1+2} 3
- r-m connected R_{4+5} bifurcation or R_5, and M_{1+2} 5
3. d-cell narrow and long, nearly 4 times as long as wide..... .....*P. ryszardi*
- d-cell relatively short and wide, at most 2 times as long as wide 4
4. bM_{3+4} obviously shorter than dM_{3+4}, R_2 opposite M_{1+2} bifurcation..... *P. kaluginae*
- bM_{3+4} obviously longer than dM_{3+4}, R_2 opposite distal of M_{1+2} bifurcation ..... *P. apprima*
5. r-m connected R_{4+5} bifurcation and M_{1+2} 6
- r-m connected R_5 and M_{1+2} 8
6. R_2 connected wing margin and R_3, dM_{1+2} longer than M_1, wing small (6.0 mm long) .....*P. notabilis*
- R_2 connected R_1 and R_3, dM_{1+2} shorter than M_1, wing large (>10.0 mm long)..... 7
7. d-cell elongate, about 3 times as long as wide, A_1 extending to wing margin distal of the bifurcation of R_{4+5}, wing relatively small (11.2 mm).....*P. procera* **sp. nov.**
- d-cell relatively short and wide, about 2 times as long as wide, A_1 extending to wing margin basal of the bifurcation of Rs, wing large (17.2-17.6 mm) .....*P. ribeiroi*
8. d-cell relatively short and wide, slightly longer than wide.... .....*P. abnormis*
- d-cell relatively narrow and long, 2 times as long as wide.... 9
9. sc-r located at a very short distance distal of the origin of Rs, and m-cu just proximal of the bifurcation of M_{3+4}, wing large (8.0 mm long) ..... *P. mirabilis*
- sc-r located a short distance basal of the origin of Rs, and m-cu located at the middle of mM_{3+4}, wing small (4.7 mm long)..... *P. trinervis*

***Praearchitipula procera* sp. nov.**

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(Fig. 3)

Material. Holotype No. PMOL-AI15440AB, female. The right wing of this specimen is relatively well-deserved, but the outer margin is missing.

Etymology. The specific name is derived from the Latin word "procerus", referring to the slender and tall shape.

Diagnosis. Cross-vein sc-r located at some distance (slightly longer than m-cu) from the origin of Rs; cross-vein r-m connected the bifurcation of R_{4+5} and M_{1+2}; M_1 about 1.4 times as long as dM_{1+2}; d-cell narrow and elongate, about 3 times as long as its width; m-cu located basal ⅓ length of lower margin of d-cell; A_1 long, ends beyond the fork of R_{4+5}.

Locality and horizon. Daohugou Village, Chifeng City, Inner Mongolia, China; Middle Jurassic, Jiulongshan Formation.

Description. Large female (Fig. 2A), body 12.2 mm long, head 1.4 mm long (including rostrum), thorax 1.8 mm long, and wing length 11.2 mm, width 2.9 mm, and abdomen 12.2 mm long.

Head (Fig. 2D, F). Rostrum relatively short, distinctly shorter than head. Eyes wide separated, ommatidia clearly visible, without setae between ommatidia near to border of eye. Antennae 14-segmented bearing sparse setae, scape strong, cylindrical, twice as long as pedicel, pedicel short, subequal to the first flagellum, and 1–11 flagellomeres cylindrical, covered with 1–2 long setae, and last flagellomere short, with several setae apically.

Thorax. Pronotum well developed, V-shaped prescutal suture distinct; legs not preserved. Wing (Fig. 2G) transparent, only with a light pterostigma. Sc long, extending to wing margin after the bifurcation of R_{4+5}; sc-r short, located at some distance (slightly longer than m-cu) from the origin of Rs; R_1 long, connected with wing margin before the midpoint of R_3, and clearly curved anteriorly at its tip; Rs subequal to R_{2+3} in length, r-r (R_2) close to R_1 tip, R_3 shorter than the half of R_{2+3}; R_{4+5} short, subequal to m-cu, and subequal to about ⅙ length of R_{2+3}, R_4 and R_5 long, and R_5 about 1.5 times as long as Rs; r-m slightly shorter than R_{4+5}, and connecting the bifurcation of R_{4+5} and M_{1+2}. M_1 about 1.4 times as long as dM_{1+2}, M_2 slightly shorter than M_1, M_3 1.5 times as long as M_4; d-cell elongate, about 3 times as long as its wide; m-cu longer than r-m, and located basal ⅓ length of lower margin of d-cell. Cu long, and relatively straight, only slightly arcuate beyond the intersection of m-cu and Cu. A_1 long, and entering wing margin against the Sc tip; A_2 extending to wing margin against the sc-r. Halter preserved faintly, stem narrow, knob enlarged.

Abdomen. Elongate, covered with sparse setae. Female genitalia (Fig. 3B, C, E): Tergite 8 at least twice as long as tergite 9 in lateral view, tergite 9 narrowest, and tergite 10 is subequal long to tergites 8, cercus longer than the combined length of tergites 8–10, and slightly curved upward (Fig. 3B, C, E). Sternite 8 elongated, attaching to hypovalve, hypovalve straight, clearly shorter than cercus, narrowing apically.

Remarks. The new species has the typical venation character of *Praearchitipula* Kalugina, 1985, and is mostly similar to another species from Middle Jurassic of Daohugou, China, *Praearchitipula abnormis* (Hao & Ren, 2009), but differs from the latter by d-cell is longer (the length-to-width ratio is larger), sc-r is closer to the fork of Rs, and the distal of Cu is less curved.

Discussion

Tipunia represents the earliest-diverging and extinct lineage within Tipulidae, yet its paleontological significance remains constrained by an extremely limited fossil record. Herein, we describe *Tipunia ningchengensis* **sp. nov.**, a well-preserved impression fossil representing

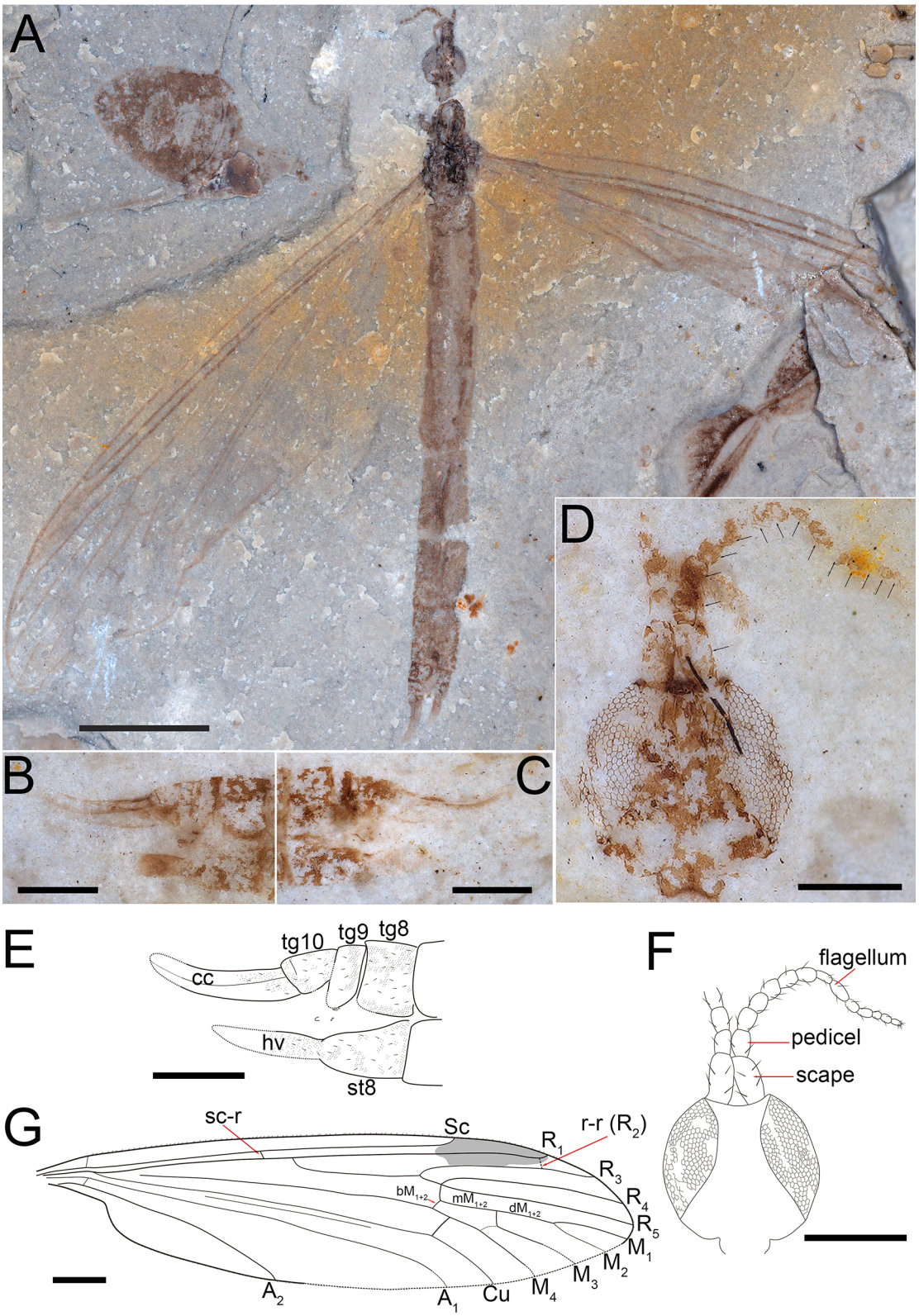

FIGURE 3. *Praearchitipula procera* **sp. nov.**, holotype. **A**, Habitus, PMOL-AI15440A. **B**, Female terminalia, PMOL-AI15440A. **C**, Female terminalia, PMOL-AI15440B. **D**, Head, PMOL-AI15440B. **E**, Illustration of female terminalia. **F**, Illustration of head. **G**, Illustration of wing venation. Scale bars = 2.0 mm (**A**); 0.5 mm (**B**–**F**); 1.0 mm (**G**).

the earliest definitive member of Tipulidae. This new species can be assigned to *Tipunia* mainly based on the following character: 1) long Sc terminates obviously distal to Rs bifurcation; 2) pterostigma present, dark; 3) Rs long, forks into R_{2+3+4} stem and R_5, R_5 terminates at wing apex; 4) d-cell shorter than fork M_{1+2}, distal part of

d-cell conspicuously widened; 5) m-cu long, and almost parallel to wing margin, connecting M_4 and Cu; 6) A_1 close and subparallel to Cu, wing membrane along Cu and A_1 wrinkled. Also, this new species not only represents first occurred of *Tipunia* in China, but also shows the first appearance of Tipulidae extending back to the Middle Jurassic. So far, seven species have been formally described including the new species herein. These species exhibit a broad Eurasian distribution spanning from the Middle Jurassic to the Early Cretaceous. It provides more information on the early evolution and radiation of Tipulomorpha.

Another new species *Praearchitipula procera* **sp. nov.** is the fourth species of Pediciidae recorded from Daohugou. These species exhibit diverse morphological characters of this family, such as antenna, venation, female terminalia and so on. Additionally, the very distinct compound eyes were preserved in this new species, but the setae on eyes were absent, reconfirming that the Mesozoic genus *Praearchitipula* has no pubescence of the eyes, which is different than the extant genera of Pediciidae. Its assignment to the family Pediciidae is supported by the structure of the radial sector, particularly the presence of the vein R_{4+5} (Kopeć *et al*., 2020).

The discovery of two new species of Tipuloidea enhances the biodiversity of Jurassic insects in the Daohugou area, such a high level of insect diversity is attributed to the suitable and diverse ecological environment of this region. For example, Tipulidae usually occupies moist riparian zones (Jong *et al*., 2008), while Pediciidae has been shown to inhabit low deciduous vegetation near forested streams and lakes (Özgül & Koç, 2016). The palaeoclimatic analysis of Daohugou area of the Middle Jurassic Yanliao Biota reveals that the climate of this region was warm and humid, with a mean annual temperature of 15–20°C, mean annual precipitation at 1500–2000 mm, and altitude of 1000–1500 m, and harbored the silvan, edaphic, hydrophytic, and alpine insect communities (Chen *et al*., 2025).

Acknowledgements

We sincerely appreciate anonymous reviewer and the Editors for corrections and suggestions in improving this manuscript. We are grateful to Qi Feng and Chenxin Zhou in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University for their assistance. This research was supported by the Natural Science Foundation of China (No. 31672332), and the Research and Innovation Practice Project for Postgraduate Students at Shenyang Normal University (No. YJSCX20250046).

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