

Review of the Jurassic *Protipula* limoniid craneflies

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Protipula unites poorly understood group of species in Architipulinae. This is caused by a limited amount of available material, which makes it difficult to verify already described taxa. In this paper we re-examined the type species of *Protipula*, *Protipula crassa*, from the lower Toarcian of Dobbertin (Germany). We also described a new species, *Protipula oosterbroeki* Krzemiński, Kopeć, & Ansorge sp. nov., from the Upper Jurassic of Karatau in Kazakhstan. Furthermore, we reassessed the holotype of *Architipula areolata* from Dobbertin and subsequently transferred it to *Protipula*. New evidence suggests that the genus *Protipula*, and the subfamily Architipulinae, were more diverse and had a wider distribution in Laurasia than previously thought.

Key words: Insecta, Tipulomorpha, Toarcian, Jurassic, Dobbertin, Grimmen, Karatau.

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Introduction

Anton Handlirsch (1906–1908, 1920, 1939) published three contributions on fossil Diptera from the Lower Jurassic of Germany. In these works, he described approximately 30 species belonging to the infraorder Tipulomorpha, as well as the family Architipulidae Handlirsch, 1906, which was subsequently recognised as a subfamily of the family Limoniidae by Kalugina in Kalugina and Kovalev (1985: 50).

Currently, the subfamily Architipulinae includes the following genera: *Architipula* Handlirsch, 1906; *Cretolimonia* Kalugina, 1986; *Dipterodictya* Rohdendorf, 1961 (recently revised by Krzemiński et al. 2025); *Grimmenia* Krzemiński & Zessin 1990; *Haplotipula* Bode, 1953; *Leptotipuloides* Carpenter, 1986; *Mesotipula* Handlirsch, 1920; *Ozotipula* Bode, 1953, and *Protipula* Handlirsch, 1906. The genera *Architipula*, *Haplotipula*, *Leptotipuloides*, and *Ozotipula* require further work, while the revision of *Protipula* is provided herein.

New Mesozoic material from Laurasia shows that Architipulinae was a diverse and numerous subfamily of Limoniidae during this geological era, widespread in Laurasia, the northern part of Pangaea. Undoubtedly, the subfamily Architipulinae was a group of Diptera subjected to rapid and intense evolutionary pressure during the Mesozoic.

Nomenclatural acts.—This published work and the nomenclatural act it contains have been registered in Zoobank: urn:lsid:zoobank.org:pub:EF8C6651-4025-4960-B1B8-97BD9AF52174.

Institutional abbreviations.—GG, University of Greifswald, Germany; ISEA PAS MP, Natural History Museum of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; PIN, A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia.

Other abbreviations.—A₁, A₂, anal veins; C, costal vein; Cu, cubital vein; d, discal cell; h, humeral vein; M₁₊₂–M₄,

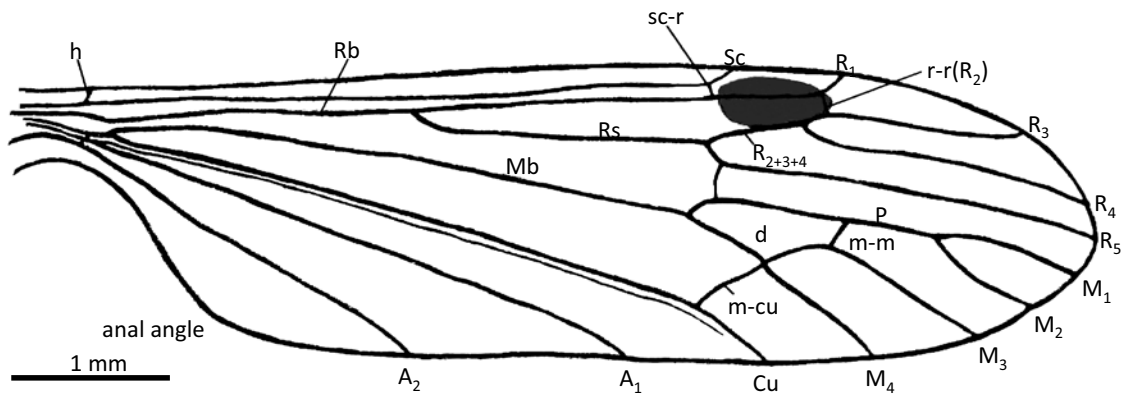


Fig. 1. Limoniid dipteran *Architipula seebachi* (Geinitz, 1884). SGWG 122/82, holotype of *Architipula seebachiana* Handlirsch, 1906 (junior synonym), lower Toarcian Grimmer Formation, Dobbertin, Germany, wing venation redrawn from Kopeć et al. (2017).

medial veins; m-cu, medial-cubital crossvein; R_1 – R_5 , radial veins; Rs, radial sector; Sc, subcostal vein; sc-r, subcostal radial crossvein.

Material and methods

The specimens were studied with a Leica MZF LII stereomicroscope under reflected light. Photographs were taken either with a Leica DFC 295 camera mounted to the microscope or a Nikon Coolpix 4500 digital camera with mounted CARL ZEISS Jena objective. Wetting the surfaces with 98% ethanol improved image contrast. In addition, the holotype of *Protipula crassa* was whitened with ammonium chloride (NH_4Cl) to improve the contrast of the wing. All line drawings were made from photographs and digitally processed. The terminology of the wing venation follows Krzemiński and Krzemińska (2003) and is illustrated in Fig. 1.

Systematic palaeontology

Order Diptera Linnaeus, 1758

Infraorder Tipulomorpha Rohdendorf, 1961

Family Limoniidae Speiser, 1909

Remarks.—The family Eoasilidae Bode, 1953, has been synonymized with Limoniidae Speiser, 1909, by Krzemiński and Kovalev (1988: 55–56).

Subfamily Architipulinae Handlirsch, 1906

Type genus: *Architipula* Handlirsch, 1906; lower Toarcian, Lower Jurassic, Grimmer Formation, Dobbertin, Germany.

Remarks.—The family Architipulidae Handlirsch, 1906, has been downranked to subfamily by Kalugina in Kalugina and Kovalev (1985).

Genus *Protipula* Handlirsch, 1906

Fig. 1.

Type species: *Protipula crassa* Handlirsch, 1906: 491; pl. 43: 11, by original designation; lower Toarcian, Lower Jurassic, Grimmer Formation, Dobbertin, Germany.

Emended diagnosis.—Small flies reaching approximately 5–7 mm wing length. Wing c. $3\times$ longer than wide. Venation: Sc ending beyond the fork of Rs into R_{2+3+4} and R_5 ; R_{2+3+4} very short, arched, reaching c. 0.25 the combined length of R_{2+3} and R_3 ; d cell small, constituting c. 0.125–0.083 of wing length; four medial veins extending to wing margin present; m-cu just before or at bifurcation of M_{3+4} into M_3 and M_4 ; anal angle proximal to origin of Mb, no pterostigma. The closest genus, *Architipula*, differs by its larger size (c. 10 mm); narrower wing ($3.6\times$ longer than wide); larger, pentagonal d cell (c. 0.143 of wing length); m-m positioned obliquely, its upper (costal) end pointing towards distal wing margin; anal angle distal to origin of Mb (compare with Fig. 1).

Remarks.—The genus was described as monotypic, comprising a single species, *Protipula crassa*. However, a revision of the species described by Handlirsch (1906, 1939) as belonging to the genus *Architipula* has shown that *Architipula areolata* Handlirsch, 1939, also belongs to the genus *Protipula*. The genus now comprises three species from the Jurassic of Germany and Kazakhstan.

Stratigraphic and geographic range.—Jurassic, Eurasia.

Protipula crassa Handlirsch, 1906

Figs. 2, 3.

1906 *Protipula crassa* Handlirsch, 1906: 491; pl. 43: 11.

Emended diagnosis.—Vein Sc ending just beyond fork of Rs into R_{2+3+4} and R_5 ; M_1 almost $1.5\times$ length of upper margin of d cell; d cell small, c. 0.125 of wing length, over $1.3\times$ longer than wide; m-cu at distal 0.75 of the d cell base (= vein M_{3+4}).

Material.—Holotype GG 122/84, probably male, Dobbertin and ISEA PAS MP LGA 1268 (JA collection), singular wing, Grimmer; Germany, lower Toarcian, Lower Jurassic, Grimmer Formation, Exaratum Subzone.

Description.—Holotype relatively well-preserved, comprising the head, abdomen and one wing 6.5 mm in length. Wing narrow; Sc ending just beyond fork of Rs into R_{2+3+4} and R_5 ; R_{2+3} slightly longer than R_{2+3+4} ; R_3 $2\times$ longer than R_{2+3} ; M_1 $1.5\times$ longer than upper margin of d cell and slightly longer than its petiole (= M_{1+2}); d cell c. $1.3\times$ longer than

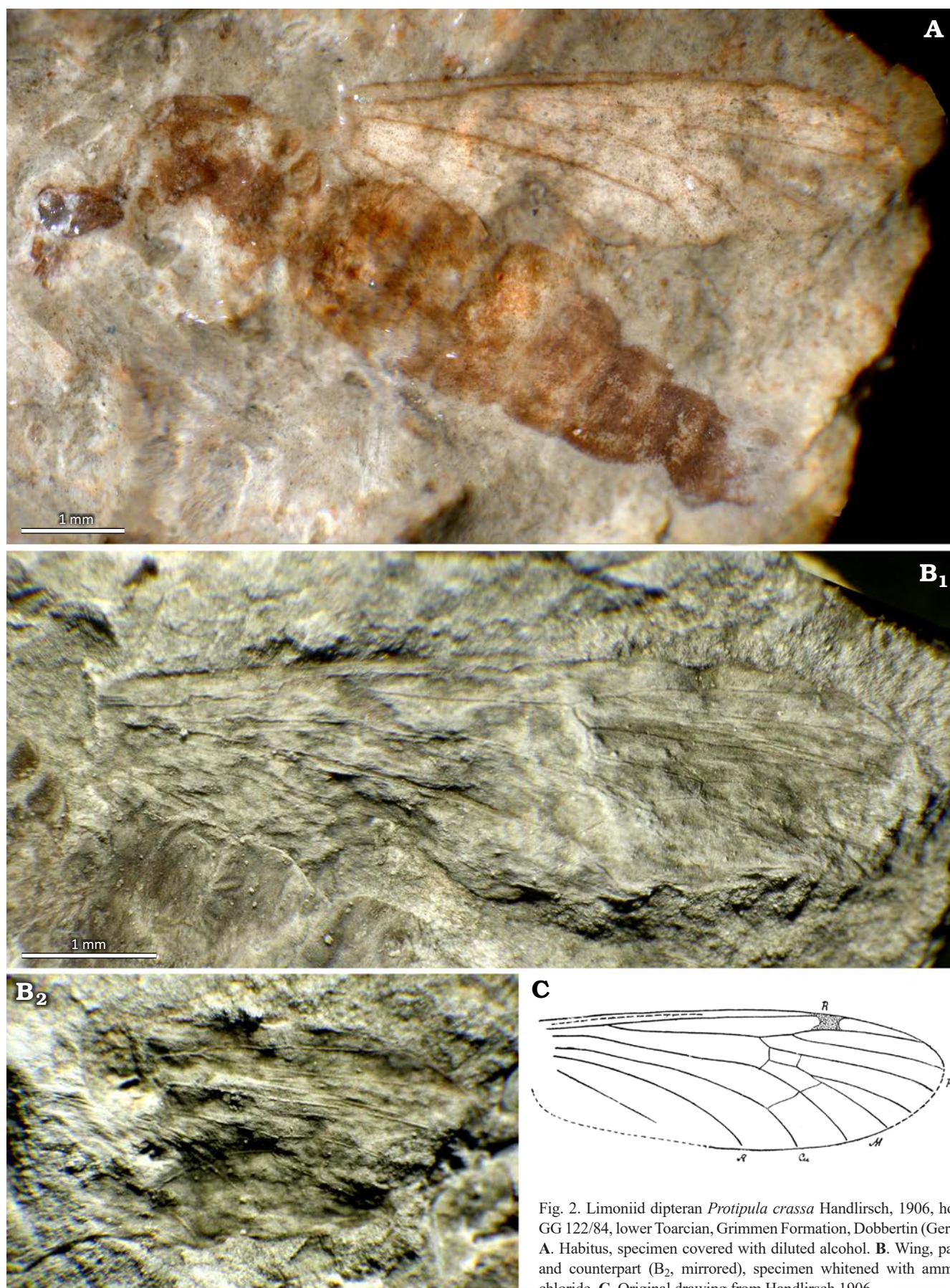


Fig. 2. Limoniid dipteran *Protipula crassa* Handlirsch, 1906, holotype GG 122/84, lower Toarcian, Grimmer Formation, Dobbartin (Germany). A. Habitus, specimen covered with diluted alcohol. B. Wing, part (B₁) and counterpart (B₂, mirrored), specimen whitened with ammonium chloride. C. Original drawing from Handlirsch 1906.

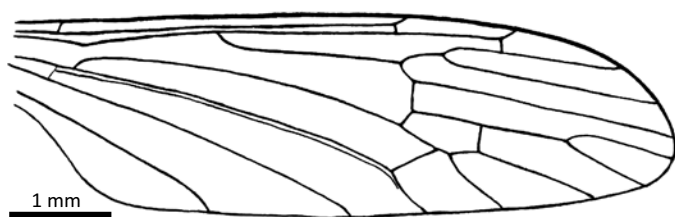


Fig. 3. Limoniid dipteran *Protipula crassa* Handlirsch, 1906, holotype GG 122/84, lower Toarcian, Grimmer Formation, Dobbertin (Germany), re-interpretation based on original drawing of wing from Handlirsch (1906).

wide; m-cu at distal 0.75 of d cell base (= vein M_{3+4}); vein A_2 straight, strongly bent at tip towards the wing margin.

Stratigraphic and geographic range.—Lower Toarcian, Lower Jurassic, Grimmer Formation, Germany.

Protipula areolata (Handlirsch, 1939) comb. nov.

Figs. 4, 5.

1939 *Architipula areolata*; Handlirsch 1939: 110, pl. 11: 203.

Emended diagnosis.—Vein Sc ending opposite midpoint of R_{2+3+4} ; M_1 1.5× longer than upper margin of d cell; d cell slightly more than 2× as long as wide, widening towards tip; m-cu at tip of d cell, at fork of M_{3+4} into M_3 and M_4 .

Material.—Holotype GG 123/113, single, complete wing imprint and ISEA PAS MP LDA 1384 (JA collection), single, complete wing imprint, both from Dobbertin, Germany,

lower Toarcian, Lower Jurassic, Grimmer Formation, Exaratum Subzone.

Description.—Holotype is a single, complete wing, 6 mm long. Wing broad; vein Sc ending opposite midpoint of R_{2+3+4} ; R_{2+3} 2× length of R_{2+3+4} ; R_3 0.33× longer than R_{2+3} ; M_1 1.5× longer than upper margin of d cell, its petiole almost 1.5× longer than vein M_1 ; d cell 1.5× longer than its width; m-cu at tip of d cell, at fork of M_{3+4} into M_3 and M_4 ; vein A_2 slightly sinuous.

Stratigraphic and geographic range.—Lower Toarcian, Lower Jurassic, Grimmer Formation, Germany.

Protipula oosterbroeki Krzemiński, Kopeć, & Ansorge sp. nov.

Figs. 6, 7.

Zoobank LSID: urn:lsid:zoobank.org:act:43A7920F-9D1C-46F3-8409-3FFA85929795.

Etymology: Dedicated to Pjotr Oosterbroek, in acknowledgement for his outstanding knowledge of Tipulomorpha and enormous work on the Catalogue of Fossil Crane Flies.

Type material: Holotype, PIN 2066/2130, fossil imprint of a single wing in sedimentary rock.

Type locality: Mikhailovka, Karatau, Kazakhstan.

Type horizon: Upper Jurassic, Karabastau Formation.

Diagnosis.—Vein Sc ending distinctly beyond fork of R_s into R_{2+3+4} and R_5 ; d cell of uniform width along entire

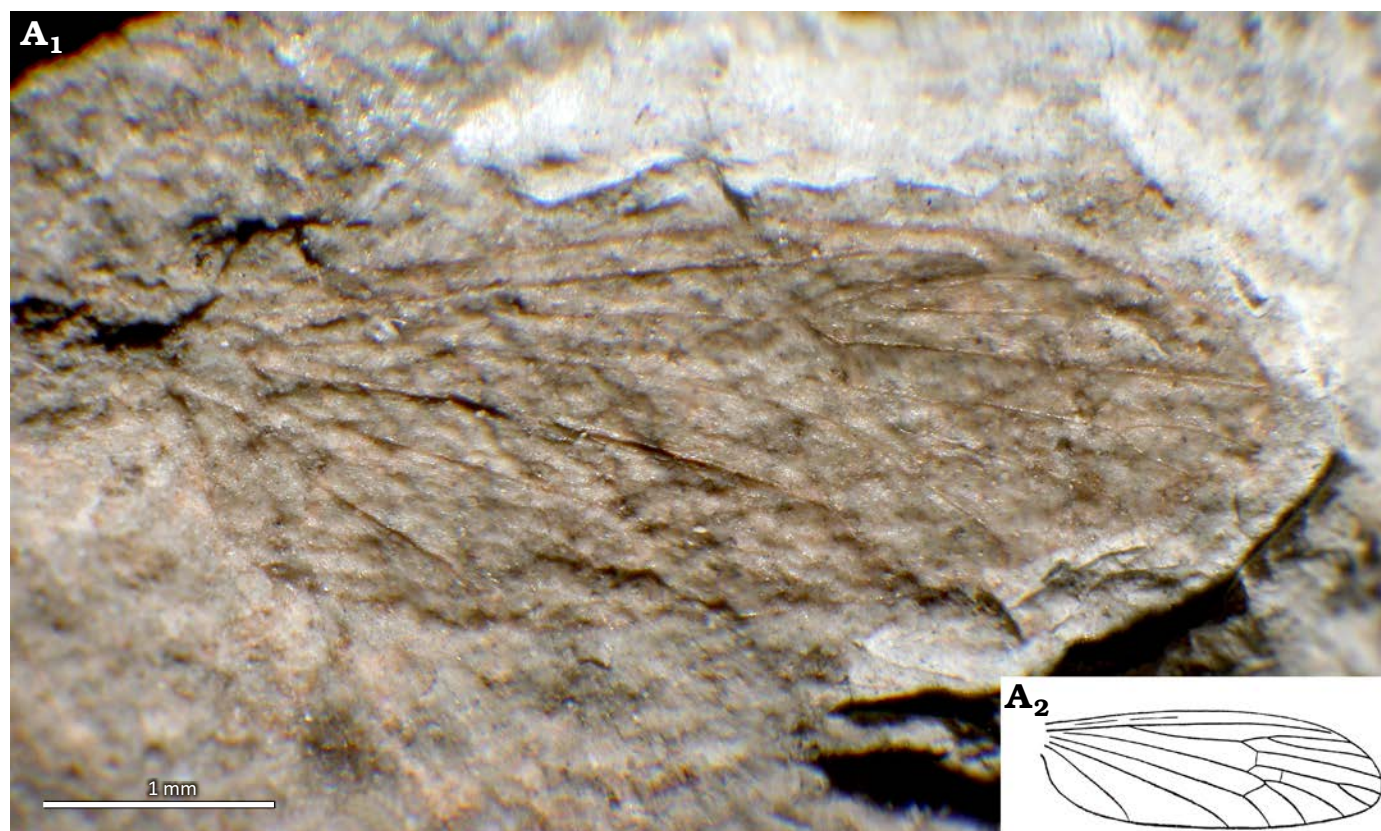


Fig. 4. Limoniid dipteran *Protipula areolata* (Handlirsch, 1939) comb. nov., holotype GG 123/113, lower Toarcian, Grimmer Formation, Dobbertin (Germany), wing. A₁, photograph; A₂, original drawing from Handlirsch (1939).

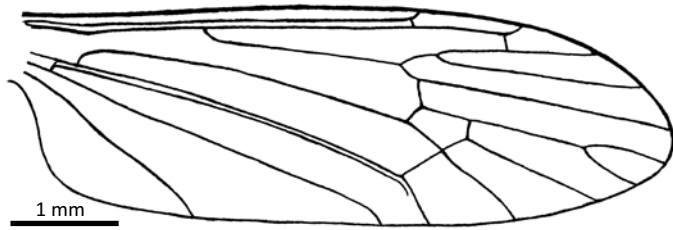


Fig. 5. Limoniid dipteran *Protipula areolata* (Handlirsch, 1939) comb. nov., holotype GG 123/ 113, lower Toarcian, Grimmen Formation, Dobbertin (Germany), re-interpretation based on original drawing of wing, from Handlirsch (1939).

length, $2\times$ long as wide; M_1 equal in length to upper margin of d cell; m-cu at distal $3/4$ of d cell base (= vein M_{3+4}).

Material.—Holotype and PIN 2239/1930; 2992/2939; all only wings.

Description.—Holotype is a single, complete wing, 6.3 mm long. Wing broad; vein Sc ending distinctly beyond fork of Rs into R_{2+3+4} and R_5 ; R_{2+3} slightly longer than R_{2+3+4} ; R_3 $1.3\times$ longer than R_{2+3} ; M_1 equal in length to upper margin of d cell, its petiole c. $0.5\times$ longer than M_1 ; d cell slightly lon-

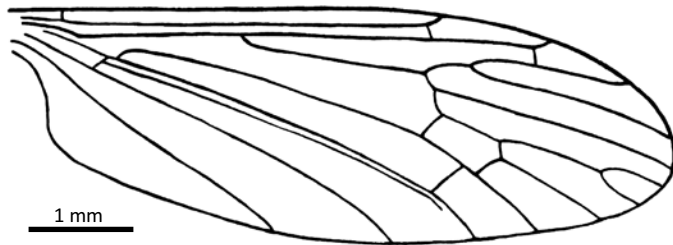


Fig. 7. Limoniid dipteran *Protipula oosterbroeki* Krzemiński, Kopeć, & Ansoerge sp. nov., holotype PIN 2066/2130, Upper Jurassic Karabastau Formation, Mikhailovka, Karatau, Kazakhstan, interpretative drawing of the wing.

ger than its width, of uniform width along its entire length; m-cu at distal 0.75 of d cell base (= vein M_{3+4}); A_2 long, almost straight.

Remarks.—From the three species of *Protipula*, *P. areolata* has smallest d cell (only 0.9 as long as wing), while in *P. crassa* and *P. oosterbroeki* Krzemiński, Kopeć, & Ansoerge sp. nov. the d cell is 0.133 – $0.116\times$ as long as wing, respectively. *Protipula oosterbroeki* is discerned from *P. crassa* by petiole of d cell twice as long as M_1 , and end of A_2 positioned distally to origin of Rs when compared to the petiole equal to M_1 , and end of A_2 in proximal position to Rs origin in *P. crassa*.

Stratigraphic and geographic range.—Upper Jurassic, Karabastau Formation, Kazakhstan.

Discussion

The revision of the genus *Protipula* presented in this paper significantly alters our current understanding of both its morphological scope and its systematic position within Architipulinae. The inclusion of the species originally described as *Architipula areolata* into *Protipula*, and the description of a new species from the Upper Jurassic of Kazakhstan, indicate that *Protipula* was more diverse and more widely distributed than previously assumed. Judging from the venation of the wings, the genus is undoubtedly most closely related to *Architipula*. Their distribution across the Pangaea during the Jurassic is illustrated in Fig. 8.

Analysis of features in the wing venation, particularly the position of the tip of vein Sc, the proportions of radial veins R_{2+3+4} and R_3 , and the shape and size of the d cell, reveal a greater morphological variation within the genus *Protipula*. In particular, the position of the m-cu crossvein and the ratio

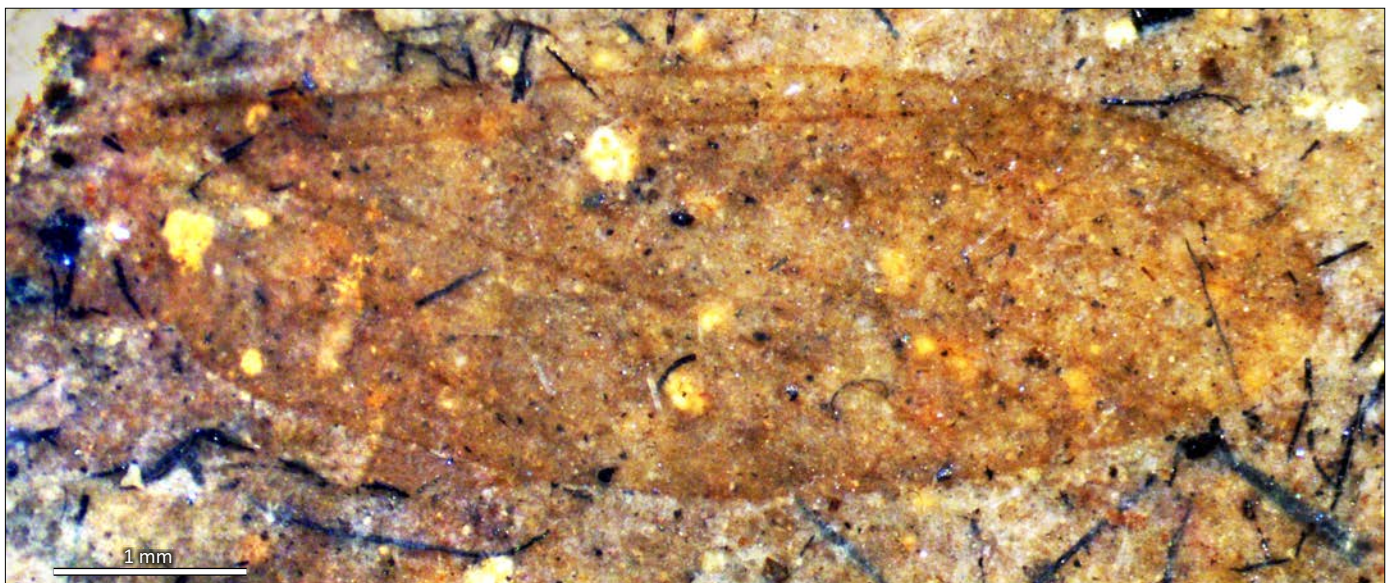


Fig. 6. Limoniid dipteran *Protipula oosterbroeki* Krzemiński, Kopeć, & Ansoerge sp. nov., holotype PIN 2066/2130, Upper Jurassic Karabastau Formation, Mikhailovka, Karatau, Kazakhstan, photograph of the wing.

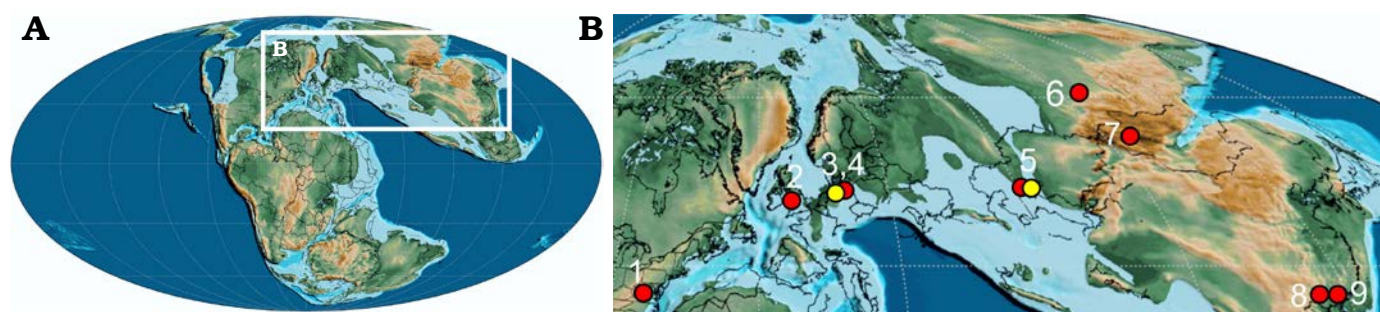


Fig. 8. Localities of *Architipula* (red circles) and *Protipula* (yellow circles) in the Jurassic (A, continents' setting; B, close-up of localities' distribution). Localities: 1 (A 1), USA, Virginia; 2 (A 1) Alderton, Great Britain; 3 (A 14), Braunschweig, Niedersachsen, Germany; 4 (A 17, P 2) Dobbartin and Grimmen, Mecklenburg-Vorpommern, Germany; 5 (A 1, P 1) Michailowka, Karatau, Kazakhstan; 6 (A 1) Kubeikovo, Krasnoyarskiy Kray, Russia; 7 (A 2) Altai Gobi, Mongolia; 8 (A 4) Inner Mongolia, China; 9 (A 1) Shandong, China. Abbreviations: A, *Architipula*; P, *Protipula* (number in brackets relate to the number of species described from a particular locality). Source of the map: [https://en.wikipedia.org/wiki/Jurassic#/media/File:Mollweide_Paleographic_Map_of_Earth,_170_Ma_\(Bajocian_Age\).png](https://en.wikipedia.org/wiki/Jurassic#/media/File:Mollweide_Paleographic_Map_of_Earth,_170_Ma_(Bajocian_Age).png).

of the length of M_1 to the upper margin of the d cell are of significant diagnostic importance. These features indicate morphological consistency within the genus, despite the apparent differences between Early Jurassic and Late Jurassic species. This may suggest a gradual evolution of the venation pattern rather than abrupt transformations.

The occurrence of *Protipula* in Europe (Lower Jurassic of Germany) and Asia (Upper Jurassic of Kazakhstan) may indicate that it had a widespread distribution within Laurasia or migrated from one area to the other. This distribution fits the general pattern of Mesozoic Limoniidae, which inhabited extensive, humid continental environments. It is significant that sites such as Dobbartin and Grimmen represent Early Jurassic prodeltaic and brackish-marine environments associated with fluvial-deltaic systems (Ansorge et al. 2026), whilst Karatau indicates a continental lacustrine environment of the Late Jurassic, the so-called “Jurassic Lake Karatau” (Kopylov and Rasnitsyn 2025). The presence of *Protipula* in such diverse environments suggests a wide range of habitat preferences within this group. The subfamily Architipulinae emerges as one of the key groups of early Tipulomorpha, characterised by high morphological diversity and a wide geographical range during the Jurassic. The presence of numerous genera (e.g., *Architipula*, *Mesotipula*, *Grimmenia*) indicates intense adaptive radiation during this period. This diversity may be interpreted as a response to the dynamic environmental changes of the Jurassic, including the development of extensive freshwater ecosystems and humid terrestrial habitats. At the same time, the observed differences in wing venation may reflect ecological differences, such as habitat preferences or flight strategies.

One interesting aspect is the possibility that the Architipulinae lineage survived beyond the Cretaceous period. As mentioned above, some modern taxa classified as Limnophilinae may represent relict lineages with archaic features, such as the distal position of the m-cu crossvein. If this hypothesis proves correct, the Architipulinae would not be an entirely extinct group, but rather a paraphyletic assemblage comprising the earliest forms of modern Limoniidae, i.e., Limnophilinae. In this context, *Protipula* could be considered

a morphological “intermediate type”, combining primitive features, such as a complete set of medial veins, with the more advanced venation patterns observed in later Limoniidae.

Further taxonomic revisions based on new specimens and a re-examination of old collections are crucial for understanding the evolution of this group and its relationship with the modern Limoniidae.

Conclusions

Hasty decisions regarding the synonymisation of previously described taxa, particularly fossil groups, may subsequently cause chaos in systematics. New fossil material is constantly being discovered and may provide new data to support the validity of problematic higher-level taxa. Re-examination of previously described material, together with access to new data, has provided strong arguments for retaining *Protipula* as a valid genus within the subfamily Architipulinae.

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Authors' contributions

WK developed the study concept and design, collected the data, supervised and carried out the interpretation and analysis of the data, wrote and revised the manuscript; KK developed the study concept and design, supervised and carried out the data analysis, interpretation and analysis of the material, and the environmental analysis, wrote and revised the manuscript and the figures; JA revised the manuscript and photographed specimens; MS translated and revised the manuscript;

EK produced the map and revised the manuscript. All authors reviewed the final manuscript.

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Data availability: All data generated or analysed during this study are included in this published article.

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