

The genera *Architipula* Handlirsch, 1906 and *Grimmenia* Krzemiński and Zessin, 1990 (Diptera: Limoniidae) from the Lower Jurassic of England

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ABSTRACT

A new diagnosis and systematic clarification of the genus *Architipula* Handlirsch, 1906 (Diptera, Limoniidae) are presented. *Architipula seebachiana* Handlirsch, 1906 and *A. seebachi* (Geinitz, 1884) are synonymised. *Liassotipula* Tillyard, 1933 from the Lower Jurassic (Toarcian) of England is here considered to be a junior synonym of *Architipula*. The subgenus *Architipula* (*Grimmenia* Krzemiński and Zessin, 1990) is raised to the rank of genus *Grimmenia* and a new species, *Grimmenia tillyardi* n. sp., is described from the Toarcian of England.

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INTRODUCTION

Currently, Limoniidae (limoniid crane flies) are one of the largest families of Diptera (true flies), with approximately 11,000 described extant species (Oosterbroek, 2016). The earliest fossils of the family are well represented from the Triassic (Krzemiński, 1992a, 1992b; Shcherbakov et al.,

1995; Krzemiński and Evenhuis, 2000; Krzemiński and Krzemińska, 2003; Blagoderov et al., 2007), and they are particularly abundant in the Jurassic (Handlirsch, 1906, 1939; Bode, 1953; Rohdendorf, 1962; Kalugina and Kovalev, 1985; Krzemiński and Kovalev, 1988; Krzemiński and Zessin, 1990; Krzemiński and Krzemińska, 2003; Lukashevich, 2009; Gao et al., 2015b; Oberprieler et al., 2015).

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Handlirsch (1906, 1939) described a number of species from the Lower Jurassic of Dobbertin, Germany, which were classified as a separate family, the Architipulidae. However, Kalugina, 1985 (in Kalugina and Kovalev, 1985) determined that the wing venation of Architipulidae is very similar to that of Limoniidae and assigned them to this family in the rank of a subfamily, Architipulinae. The genus *Architipula* is the biggest in this subfamily. There are approximately 50 described species, but most of them need to be revised. The oldest representative of the genus is *A. youngi* Krzemiński from the Norian (Upper Triassic) of North America (Krzemiński, 1992a), but the great majority of species derive from the Jurassic Period (Handlirsch, 1906, 1939; Tillyard, 1933; Bode, 1953; Rohdendorf, 1962; Kalugina, 1985 [in Kalugina and Kovalev, 1985]; Krzemiński and Kovalev, 1988; Krzemiński and Zessin, 1990; Krzemiński, 1992a, 1992b; Evenhuis, 1994; Krzemiński and Evenhuis, 2000; Krzemiński and Krzemińska, 2003; Blagoderov et al., 2007; Lukashovich, 2009).

Information about the Limoniidae from the Lower Jurassic of England can be found in Brodie (1845) and Tillyard (1933). Study of their original fossil material and specimens of Architipulinae from the Lower Jurassic of Germany described by Handlirsch (1906) and Krzemiński and Zessin (1990) revealed that the genus *Liassotipula* Tillyard, 1933 should be synonymised with the genus *Architipula* Handlirsch, 1906.

This article aims to give an overview of limoniid material from the Toarcian (Lower Jurassic) of England, which comprises eight wings, six of which belong to the genus *Architipula*, the other two to *Grimmenia* Krzemiński and Zessin, 1990. Additional Lower Jurassic limoniid material has recently been recovered from older Sinemurian deposits by one of the authors (RAC) and will be described separately.

MATERIAL AND METHODS

The English Toarcian material was collected in the early nineteenth century by P.B. Brodie and T.J. Slatter from Alderton Hill and Dumbleton, Gloucestershire. It was acquired by the Natural History Museum, London, in 1888 and is housed in the Palaeontological Collection, Department of Earth Sciences. Examined type material from the Toarcian of Germany is housed in the collection Ernst-Moritz-Arndt-Universität Greifswald, Germany.

The specimens were studied with the use of a Leica MZF LII stereomicroscope under reflected and transmitted light. Photographs were made with

a Leica DFC 295 camera attached to the microscope. Wetting the surfaces with 98% ethyl alcohol improved image contrast. All line drawings were made from the photographs and digitally processed. Line drawings were prepared with GIMP graphic software (www.gimp.org/). The terminology of wing venation followed Krzemiński and Krzemińska (2003) and Krzemińska et al. (2009).

SYSTEMATIC PALAEOLOGY

Order DIPTERA Linnaeus, 1758

Infraorder TIPULOMORPHA Rohdendorf, 1961

Family LIMONIIDAE Speiser, 1909

Synonymy. Architipulidae Handlirsch, 1906 (synonymised by Kalugina In: Kalugina and Kovalev, 1985, p. 50); Eoasilidae Bode, 1953 (synonymised by Krzemiński and Kovalev, 1988, p. 55-56).

Subfamily ARCHITIPULINAE Handlirsch, 1906

Type genus. *Architipula* Handlirsch, 1906.

Genus ARCHITIPULA Handlirsch, 1906

Synonymy. *Liassotipula* Tillyard, 1933 (new synonymy); *Eoasilidea* Bode, 1953 (synonymised by Krzemiński and Kovalev, 1988, p. 55-56); *Protipula* Handlirsch, 1906 (synonymised by Evenhuis, 1994, p. 62); *Paratipula* Bode, 1953 (synonymised by Evenhuis, 1994, p. 62).

Type species. *Architipula seebachiana* Handlirsch, 1906 (= *Architipula seebachi* [Geinitz, 1884]), Toarcian (Lower Jurassic), Dobbertin in Mecklenburg, Germany.

Included species. Of the approximately 50 named species, the following, from the Lower Jurassic of Germany, can be confidently assigned to the genus *Architipula*: *A. arcuifera* Bode, 1905; *A. bodeisimilis* Bode, 1953; *A. formosa* Bode, 1953; *A. fragmentosa* (Bode, 1953); *A. maior* Handlirsch, 1939; *A. stigmatica* Handlirsch, 1906; and *A. latipennis* Handlirsch, 1906. Re-examination of the holotypes of other named species is required to establish membership of *Architipula* since their generic affiliation cannot be determined on the basis of existing descriptions and drawings. *Architipula youngi* Krzemiński from the Norian (Upper Triassic) of North America is the oldest representative of the genus (Krzemiński, 1992a).

Revised diagnosis. Vein Sc ends after fork of vein Rs into R_{2+3+4} and R_5 ; Rs long, subequal to or a little shorter than veins R_{2+3} and R_3 combined; d-cell characteristically deeply indented in basal part (Figures 1-2), upper part of d-cell 1.5-2x longer than its lower part (from the forking of Mb to cross-vein m-cu); cross-vein m-m between M_{1+2} and M_3

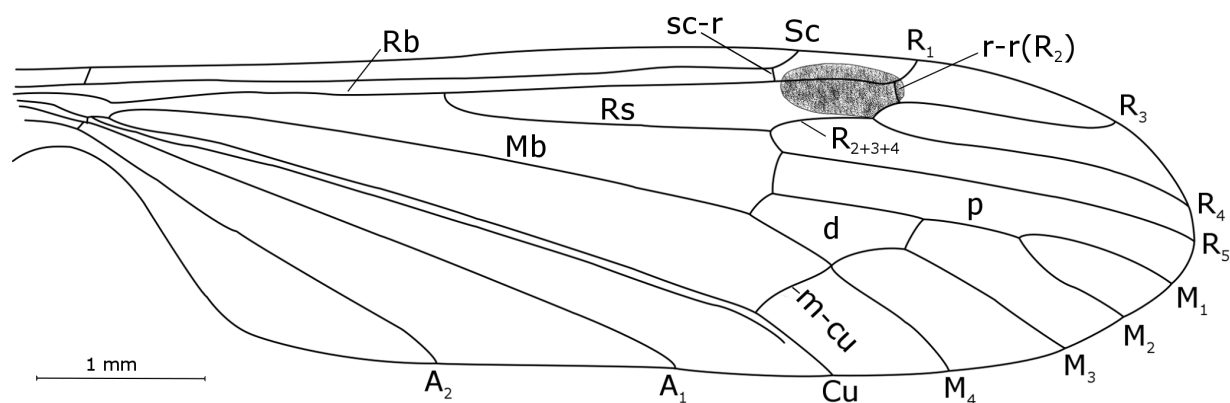


FIGURE 1. Wing venation of *Architipula seebachi* (Geinitz, 1884). SGWG 122/82, holotype of *A. seebachiana* Handlirsch, 1906.

distinctly inclined, its bottom part shifted towards the wing's base (unlike in most Limoniidae); vein M_3 usually distinctly sinuous; cross-vein m-cu situated close to origin of the fork of M_{3+4} into M_3 and M_4 ; A_2 usually short and straight.

Architipula seebachi (Geinitz, 1884)
Figures 1, 2

Synonymy. *Phryganidium (Hydropsyche) seebachi* Geinitz, 1884; *Architipula seebachiana* Handlirsch, 1906 (new synonymy).

Material examined. SGWG 119/6, holotype of *Architipula seebachi* (Geinitz, 1884) and SGWG 122/82, holotype of *Architipula seebachiana* Handlirsch, 1906. Both from Toarcian (Lower Jurassic) of Dobbertin (Germany) and deposited in the collection Ernst-Moritz-Arndt-Universität Greifswald.

Redescription. Vein Sc ends before mid-point of vein R_{2+3+4} ; Rs long, subequal to veins $R_{2+3+4}+R_{2+3}$ and R_3 combined; R_4 three times longer than

R_{2+3+4} ; stigma large and distinct; d-cell characteristically deeply indented in basal part, upper part of d-cell 1.5- 2 times longer than its lower part (from the forking of Mb to cross-vein m-cu); d-cell about 0.14 the length of the wing; cross-vein m-m between M_{1+2} and M_3 distinctly inclined, its bottom part shifted towards the wing base; vein M_3 usually distinctly sinuous; M_1 equal in length to d-cell; cross-vein m-cu situated in the fork of M_{3+4} into M_3 and M_4 ; A_2 usually short and straight.

Remarks. Originally considered to be the type species of the genus, *Architipula seebachiana* Handlirsch, 1906 is synonymous with *Architipula seebachi* (Geinitz, 1884), which was described as *Phryganidium (Hydropsyche) seebachi* Geinitz, 1884 and incorrectly assigned to the order Trichoptera, before being transferred to *Architipula* by Handlirsch in 1906. Both specimens came from the same Toarcian locality of Dobbertin in Germany, and their wings are almost indistinguishable in vein

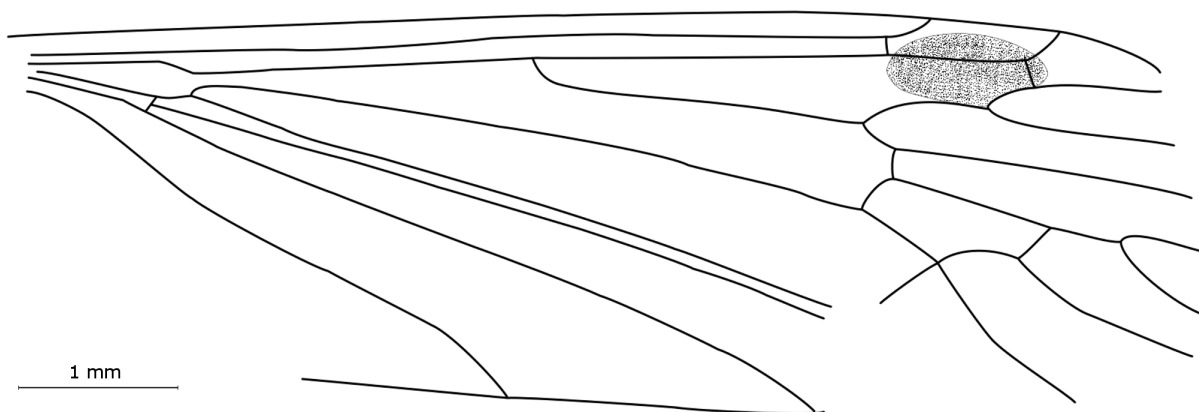


FIGURE 2. Wing venation of *Architipula seebachi* (Geinitz, 1884). SGWG 119/6, holotype.

lengths and proportions. Observable morphological differences, such as the degree of curvature of M_4 and the slightly longer Sc vein in *A. seebachi*, we consider to be accounted for by intraspecific variation.

Architipula anglicana (Tillyard, 1933) — comb. nov.
Figure 3

Revised diagnosis. Wing 7.5–10.0 mm long; Sc ending opposite mid-length of R_{2+3+4} ; R_4 about three times as long as R_{2+3+4} ; and slightly longer than R_3 ; M_1 about three times longer than petiolus; upper part of d-cell approximately twice as long as lower; M_3 markedly undulate.

Redescription. Sc terminates opposite mid-length of R_{2+3+4} ; cross-vein sc-r situated twice its length before tip of Sc; R_1 ends opposite one third length of R_{2+3} and R_3 combined; r-r (R_2) situated almost twice its length before tip of R_1 ; Rs very long, almost equal to R_4 ; R_4 3.5 times as long as R_{2+3+4} and slightly longer than R_3 ; d-cell large (about 0.17 the length of the wing), elongate along the upper edge (top of cross-vein m-m shifted away from wing base); M_1 about three times longer than petiolus and slightly longer than the d-cell; M_3 prominently undulate and almost 3.5 times longer than the basal part of d-cell; mc-u in holotype just before bifurcation of M_{3+4} into M_3 and M_4 , in the remaining specimens located at the fork M_{3+4} ; A_2 relatively long and almost straight, terminally slightly curved to wing margin.

Material examined. Holotype: In. 11298, Alderton Hill from Brodie collection. Other material: I. 11272 also from Alderton Hill; I. 11313, I. 11365, and I. 11398 from Dumbleton, Upper Lias (Lower Jurassic: Toarcian). All specimens are housed in the Natural History Museum, London.

Remarks. Examination of the holotype In. 11298 and additional specimens of *Architipula anglicana* allowed us to rectify mistakes in the drawing of the holotype by Tillyard (1933, p. 76), which led to his creation of a new genus; for example, in the position of cross-vein m-cu, the addition of cross-veins in the radial sector and the length of Sc. The venation of *A. anglicana* is, in fact, very similar to that of *A. seebachi*, notably in the length of vein Sc and the construction of the d-cell, cross-vein m-m situated between M_{1+2} and M_3 , strongly oblique, its upper part towards the distal part of the wing; M_3 distinctly wavy. It clearly differs in the ratio of the length of the d-cell to the length of the wing, the proportion of M_1 to its petiolus and the location of cross-vein m-cu (Figures 1-3). These differences justify separation at the species, but not genus level, and we have therefore synonymised *Liassotipula* with *Architipula*.

Genus *Grimmenia* Krzemiński and Zessin, 1990 — stat. n.

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Type species. *Architipula* (*Grimmenia*) *prima* Krzemiński and Zessin, 1990; Lower Jurassic (Toarcian) of Germany.

Revised diagnosis. Sc ending before or opposite the fork of Rs; cross-vein sc-r at the end of Sc; Rs long; four medial veins present; d cell long and its lower part not incised like in the genus *Architipula*; cross-vein m-cu in or near the fork of M_{3+4} .

Included species. In addition to the type species and new species described below, *Grimmenia secunda* Krzemiński and Zessin (1990), from the Lower Jurassic (Toarcian) of Grimmen, Germany.

Grimmenia tillyardi n. sp.

Figure 4

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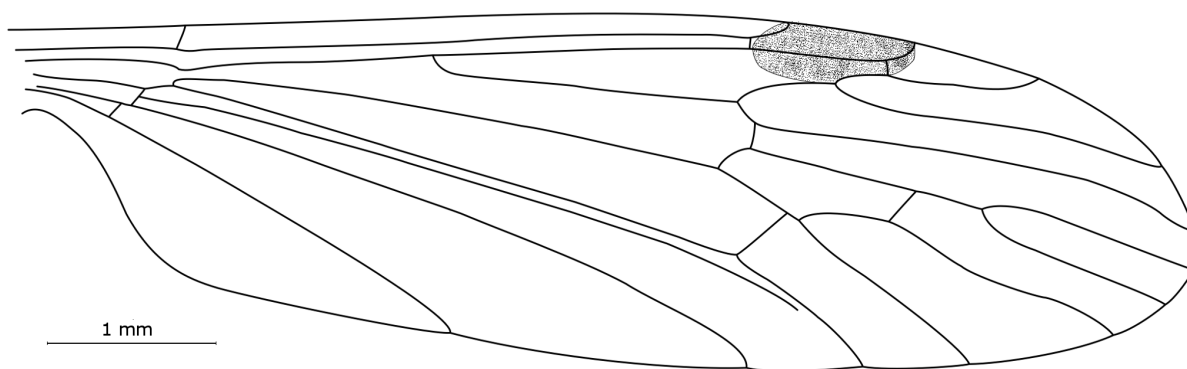


FIGURE 3. Wing venation of *Architipula anglicana* (Tillyard, 1933). In. 11298, holotype.

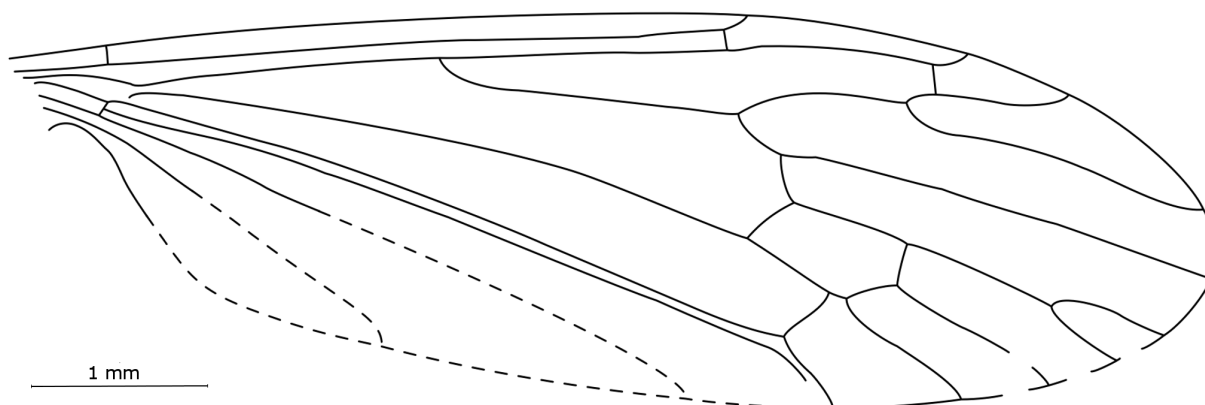


FIGURE 4. Wing venation of *Grimmenia tillyardi* new species. I. 3328, holotype.

Etymology. The species name is dedicated to Robin John Tillyard, the palaeoentomologist who described the first Limoniidae from the Jurassic of England.

Holotype. I. 3328 from Alderton Hill (Gloucester), Upper Lias (Lower Jurassic: Toarcian), housed in the Natural History Museum, London.

Diagnosis. Sc terminates opposite fork of Rs into R_{2+3+4} and R_5 ; R_{2+3+4} long, distinctly longer than in other known species of the genus, equal to R_{2+3} and R_3 combined; Rs almost twice as long as R_{2+3+4} ; d-cell short and wide, which clearly differentiates this species from all congeners.

Description. Wing length 3.8 mm; Sc ends opposite bifurcation of Rs into R_{2+3+4} and R_5 ; cross-vein sc-r situated its own length before tip of Sc; R_1 ends opposite one third length of R_{2+3} and R_3 combined; R_{2+3+4} very long, as long as R_{2+3} and R_3 combined; Rs almost twice as long as R_{2+3+4} ; R_4 equal in length to Rs and twice as long as R_{2+3+4} ; d-cell 0.125 the length of the wing; almost rectangular, its upper part almost the same length as its basal part; top part of cross-vein m-m inclined towards the wing base; M_1 shorter than petiolus; m-cu situated towards distal end of d-cell, just before fork of M_{3+4} into M_3 and M_4 .

Remarks. *Grimmenia tillyardi* n. sp. is very similar to *G. prima* from the Toarcian of Grimmen, Germany (Krzemiński and Zessin, 1990). However, it clearly differs from this species in its longer vein R_{2+3+4} ; the shape of the d-cell, which is short and wide, and longer veins M_1 and M_2 .

DISCUSSION

The limoniid fauna from the Toarcian of England has a very strong resemblance to that

from Germany. In both faunas, species of the genus *Architipula* are the most commonly found as fossils. Handlirsch (1906, 1939) believed that Jurassic Diptera with wing venation similar to the family Limoniidae belonged to a separate family, Architipulidae; as did Tillyard (1933), Bode (1953) and Rohdendorf (1962). Kalugina (1985, in Kalugina and Kovalev 1985) instead included Architipulidae in the family Limoniidae as a subfamily. However, so far the subfamily has not been clearly defined, because Kalugina did not re-examine the material described by Handlirsch (1906, 1939) or Bode (1953). Her decision was based on the published drawings and rare material from Asia. Bode's drawings, in particular, are very inaccurate and not suitable for comparative studies.

In addition to the revision of material of *Architipula* and *Grimmenia* herein, work on clarifying the systematics of the Architipulinae is in progress. It is known that genera from other subfamilies (Limnophilinae) and families (Tipulidae and Pediciidae) have been incorrectly assigned to the subfamily. For example, *Praearchitipula abnormis* (Hao and Ren, 2009) has recently been transferred from Architipulinae to family Pediciidae (Gao et al., 2015a).

Continued re-examination of deposited specimens, in particular holotypes, is required, as well as collection of new material. Most of the Early Jurassic species have been described only from isolated wings. Discovery of more complete specimens would permit determination of other characters important for clarification of taxonomic relationships, such as the structure of the male genitalia and presence or absence of tibial spurs.

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