



Mesozoic fossils and the phylogeny of Tipulomorpha (Insecta: Diptera)

Elena D. Lukashevich & Guilherme C. Ribeiro


To cite this article: Elena D. Lukashevich & Guilherme C. Ribeiro (2019) Mesozoic fossils and the phylogeny of Tipulomorpha (Insecta: Diptera), *Journal of Systematic Palaeontology*, 17:8, 635-652, DOI: [10.1080/14772019.2018.1448899](https://doi.org/10.1080/14772019.2018.1448899)

To link to this article: <https://doi.org/10.1080/14772019.2018.1448899>



 View supplementary material 

 Published online: 06 Apr 2018.

 Submit your article to this journal 

 Article views: 110

 View Crossmark data 

 Citing articles: 2 View citing articles 



Mesozoic fossils and the phylogeny of Tipulomorpha (Insecta: Diptera)

Elena D. Lukashevich^{a*} and Guilherme C. Ribeiro^b

^aBorissiak Paleontological Institute RAS, 123 Profsoyuznaya Str., 117997 Moscow, Russia; ^bUniversidade Federal do ABC, Centro de Ciências Naturais e Humanas, Av. dos Estados, 5001. Bairro Bangu, 09210-580, Santo André, SP, Brazil

(Received 19 October 2017; accepted 14 February 2018)

Tipulomorpha are known back to the Triassic but are very rare in the fossil record of that period. The oldest tipuloid genus, *Archilimonia* Krzemiński & Krzemińska, 2003, is redescribed based on the type and a new species from the Middle Triassic (early Anisian, 242–247 Ma) of the northern Vosges Mountains, NE France. Male terminalia of Triassic Tipulomorpha are described for the first time: a terminal gonostylus divided into a fleshy setose clasper and a lobe in *Archilimonia grauvogeliana* sp. nov. The systematic position of *Archilimonia* is investigated based on morphological characters of both extant and extinct taxa of Tipulomorpha and other infraorders. Our cladistic analysis is congruent with the family-level relationships recovered by the most recent phylogenetic studies of Tipulomorpha, and the position of some extinct taxa is discussed. The divided gonostylus is considered a synapomorphy of Tipuloidea except Pediciidae, so in our analyses we place *Archilimonia* between Pediciidae and other Tipuloidea (Limoniidae + (Tipulidae + Cylindrotomidae), with two other Triassic tipuloid genera (*Mabelysia* and *Metarchilimonia*). The family Tipulidae including the Mesozoic genus *Tipunia* is monophyletic, so Tipulidae has existed since the Late Jurassic.

<http://zoobank.org/urn:lsid:zoobank.org:pub:4C0BA500-A928-4C83-ABE1-8B42BB01A803>

Keywords: crane fly; male terminalia; Middle Triassic; new species; wing venation

Introduction

Tipuliformia was proposed by Hennig (1954), and subsequently referred to as Tipulomorpha (Hennig 1968, 1973), to include the winter crane flies (Trichoceridae) and Tipuloidea (families Limoniidae, Tipulidae and Cylindrotomidae). The systematic position of Tipulomorpha within Diptera and its familial composition are contentious issues (reviewed by Ribeiro 2008). Despite gaps in our understanding of the evolutionary patterns of the Tipulomorpha, the following conclusions can be drawn from the most recent studies (Ribeiro 2008; Petersen *et al.* 2010; Zhang *et al.* 2016; Kang *et al.* 2017): Trichoceridae is probably the sister group of the Tipuloidea; Pediciidae is likely the sister group of the other Tipuloidea families; Limoniidae is a paraphyletic taxon, with some of its members more closely related to the Tipulidae-Cylindrotomidae clade; and Tipulidae and Cylindrotomidae are monophyletic sister groups.

Tipulomorpha are known back to the Triassic but are very rare in the fossil record of that period. The oldest described members of Diptera are known from the Middle Triassic of the northern Vosges Mountains, northeastern France (Krzemiński *et al.* 1994), in the Anisian (242–247 Ma) Grès à Voltzia Formation of the Upper Buntsandstein

(Gall 1971, p. 184; Aristov *et al.* 2011; Durand 2013). Several thousand insects and other fossils from the Grès à Voltzia were collected by Louis Grauvogel (Grauvogel 1947a, b). His private collection was carefully kept by his daughter Lea Grauvogel-Stamm and is now housed in the Staatliches Museum für Naturkunde, Stuttgart, Germany. Louis Grauvogel not only found impressions, but also identified them to order level: some of his finds labelled as Diptera were subsequently described (Krzemiński *et al.* 1994; Krzemiński & Krzemińska 2003; Lukashevich *et al.* 2010).

Within Tipulomorpha, a single species has been so far described from the Grès à Voltzia: *Archilimonia vogesiana* Krzemiński & Krzemińska, 2003. The species is hitherto known only from a single specimen. *Archilimonia vogesiana* was included in the monotypic family Archilimoniidae, considered basal to all other Tipuloidea (Krzemiński & Krzemińska 2003). Later, Blagoderov *et al.* (2007) provided a comprehensive phylogenetic analysis of Diptera including many extinct Mesozoic genera such as *Vladiptera* Shcherbakov in Shcherbakov *et al.* (1995), *Dilemmala* Shcherbakov in Shcherbakov *et al.* (1995), *Psychotipa* Shcherbakov in Shcherbakov *et al.* (1995) and *Mabelysia* Shcherbakov in Shcherbakov *et al.* (1995).

*Corresponding author. Email: elukashevich@hotmail.com

These genera were included in Tipulomorpha by Shcherbakov *et al.* (1995), and this was followed by Blagoderov *et al.* (2007) based on their cladistic study. *Archilimonia* was placed in Limoniidae in its own subfamily, and considered the sister of *Metarchilimonia* Blagoderov & Grimaldi in Blagoderov *et al.* (2007), a genus containing two species from the Late Triassic of North America (late Carnian of Virginia, 228–235 Ma).

One of the significant features of the Vosges Lagerstätte is the completely articulated preservation of some of the flies. The only other known case of such preservation in the Triassic is from the late Carnian of Virginia. Most other Triassic flies are only known as isolated wings (reviewed by Lara & Lukashevich 2013). Therefore, description and illustration of body characters of Vosges true flies are possible; however, photographs were never published in earlier papers. This deficiency is partly corrected here with photographs of the holotype of *Archilimonia vogesiana* as well as photographs and illustrations of a new species found by one of us (EDL) in the collection of Louis Grauvogel and described herein. With knowledge of the detailed morphology of the new species of *Archilimonia*, the systematic position of the genus is investigated in a comparative framework including both extant and extinct taxa (Triassic as well as some Jurassic and Cretaceous genera). A discussion of the early patterns of diversification and minimum ages of the main Tipulomorpha clades, based on the systematic position of fossils, is provided.

Material and methods

Material

Triassic insects are known from 13 localities in the northern Vosges Mountains (Sinitshenkova *et al.* 2005). Diptera occur in four localities. The holotype of *Archilimonia vogesiana* was found by Louis Grauvogel in Bust (Bas Rhin, France) and the additional specimen belonging to a new species was found by him in Arzviller (Moselle, France), in lens 118b together with *c.* 80 other dipteran impressions. The distance between the two localities is 12 km. Both specimens were housed in the private collection of L. Grauvogel, Strasbourg, France for many years, but since April 2017 they have been kept in the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS). They were photographed using a Leica MZ9.5 stereomicroscope with Leica DFC420 digital camera, and photos were edited using Adobe Photoshop CS 9.0 software.

Terminology

The infraorder concept generally follows the classification of Hennig (1968, 1973). The terminology applied to the wing veins follows the interpretation of Wootton & Ennos

(1989) adopted by Shcherbakov *et al.* (1995) and recently with minor changes adopted as the standard for use throughout the *Manual of Afrotropical Diptera* (Cumming & Wood 2017). Terminology applied to the gonostylar branches of the male genitalia follows Ribeiro (2006).

Phylogenetic analysis

The phylogeny was estimated using the morphology of 47 exemplar taxa of Diptera, representing 25 Mesozoic species belonging to 15 genera and 22 extant species in 21 genera of Diptera, and three species in three genera of Mecoptera. Our ingroup taxa included extinct and extant Tipulomorpha. As outgroups, we used living representatives of Mecoptera, Pachyneuridae, Cramptonomyiidae, Tanyderidae and several Triassic Psychodomorpha (Grauvogeliidae, Nadipteridae). A complete list of the taxa used in the phylogenetic analysis is provided in the Supplementary material.

The main purpose of our analysis was to test the possible relationships of *Archilimonia* with other extinct taxa. In addition, we wanted to test the systematic position of the fossils in the framework provided by the recent taxa and the effect of characters of fossils in our understanding of the evolution of the main features used to define family-level relationships.

Our data matrix was based on the matrix of Ribeiro (2008), which included 104 taxa and 88 characters of the male imago. Our new matrix, however, is quite distinct, as we reinterpreted several of the wing venation characters of Ribeiro (2008) and included more wing characters (28 of the total 39 characters are based on wing venation), which are essential for interpreting Mesozoic fossil Diptera since most of the fossil taxa are wholly or largely defined by venation. We also excluded from the matrix of Ribeiro (2008) characters that were mostly pertinent to genus-level relationships, but included additional characters pertinent at family and superfamily levels. In addition, we focused our taxonomic sampling on taxa with characters more relevant for the fossil taxa and family-level analysis. Extinct Mesozoic taxa, which were not part of the study of Ribeiro (2008), were added and composed half of the included taxa. We studied fossil specimens of *Archilimonia*, *Leptotarsus* Guérin-Méneville, 1831 and all species that are housed in the Borissiak Paleontological Institute of RAS. Information on several fossil taxa from North America and Germany was scored from the literature (mostly original descriptions).

Non-observed and non-applicable characters were treated as missing data. The characters used in the phylogenetic analysis and data matrix are provided in the Supplementary material. The characters were polarized *a posteriori* through rooting, following the outgroup method (Nixon & Carpenter 1993). The parsimony analysis was performed with TNT software (version 1.5; Goloboff &

Catalano 2016). Different sets of analyses were performed, as detailed below.

Parsimony with equal weights (EW). One analysis with all characters receiving equal weights was performed using the New Technology Search option of TNT, using simultaneously all the available tree search algorithms (TBR, Sect. Search, Ratchet, Drift and Tree fusing). In this analysis, 5000 replications were run, keeping the maximum possible number of trees in memory (10,999 was the maximum number of trees that could be retained in the computer that we used. With no target score defined, the best score was hit 5000 times). Other search settings were kept as default.

Parsimony with implied weighting (IW). We also performed several analyses with implied weighting (Goloboff 1993, 2014; Goloboff *et al.* 2008). In differentially weighted inferences, the topologies supported by the more congruent characters are preferred at the expense of those supported by the more homoplastic characters. The strength by which the more homoplastic characters are downweighted is controlled by changing the value of the weighting constant K . Lower values of K downweight more homoplastic characters more severely than relatively higher values do. In differentially weighted inferences, the preferred trees are those with the highest fitness (and not necessarily those with the lowest number of steps). As a first exploration of the data matrix with IW, we evaluated the results as provided by K values of very different levels of magnitude. In this set of analyses, we used three values of K ($K = 5, 15$ and 105). These analyses were performed using heuristic searches (Traditional Search) with tree bisection reconnection (TBR) branch swapping, random stepwise addition sequence and 10,000 replicates holding up to 100 trees per replication, keeping the maximum possible number of trees in memory (10,999 trees).

As discussed in detail in the Results and Discussion sections, we found that the trees with $K = 5$ had much higher fitness compared with $K = 15$ and $K = 105$. In a second round of exploration of the data with IW, we performed one additional set of analyses, now varying the values of K between 3 and 10. The idea behind this set of analyses was to explore further the effect of K values of similar magnitude. Again, these analyses were performed using heuristic searches (Traditional Search) with TBR branch swapping, random stepwise addition sequence and 10,000 replicates holding up to 100 trees per replication, keeping the maximum possible number of trees in memory (10,999 trees).

As stated by Goloboff (2014), the use of implied weights may be problematical in palaeontological studies when some characters have many missing data. Characters with many missing entries may receive artificially high implied weights because those characters will (on average) display less homoplasy than characters for which

all the entries have been scored. In the new version of the TNT software (Goloboff & Catalano 2016), one can alleviate this problem with extended implied weighting (EIW). To test the effect of downweighting characters with missing data, we performed EIW using the same range of K values as the previous analysis (from 3 to 10). We set the parameters of the EIW analyses as provided in TNT by default (downweighting character with 50% of the homoplasy of the observed entries; not letting weighting strength exceed 5 times characters with no missing entries). As in the IW, these analyses were performed using heuristic searches (Traditional Search) with TBR branch swapping, random stepwise addition sequence and 10,000 replicates holding up to 100 trees per replication, keeping the maximum possible number of trees in memory (10,999 trees).

As discussed and justified later in this paper, we found that our preferred tree come from the analyses with K ranging from 3 to 10, which produced similar results. Symmetric resampling (pooled from $K = 5$), presented as group frequency difference (GC), was conducted using 1000 pseudoreplicates with a removal probability of 33%, collapsing clades with values below 1.

Systematic palaeontology

Family **Limoniidae** Rondani, 1856

Subfamily **Archilimoniinae** Krzemiński & Krzemińska, 2003

Genus **Archilimonia** Krzemiński & Krzemińska, 2003

Type species. *Archilimonia vogesiana* Krzemiński & Krzemińska, 2003 (Figs 1, 3A).

Included species. *A. vogesiana* and *A. grauvogeliana* sp. nov.

Diagnosis. Sc rather short, reaching wing margin just beyond wing midlength; Rs stem nearly aligned with R_{4+5} and R_4 ; d cell large; four medial veins, $m-m$ between M_2 and M_3 ; $m-cu$ just before or at fork M_{3+4} and before midlength of d cell; CuA apex nearer to Sc apex than to R_1 apex level.

Description. Small tipuloids (body length 3.4–3.8 mm; wing length 2.5–3.0 mm) with relatively wide and short wings subequal to abdomen length. Antenna with oval flagellomeres.

Wing. Sc rather short, reaching wing margin just beyond wing midlength; crossvein *sc-r* terminal, distal to Rs origin; R kink distinct; Rs origin between CuP apex and A_1 apex level, Rs forking into R_{2+3} and short R_{4+5} just before Sc apex, Rs stem nearly aligned with R_{4+5} and R_4 ; R_2 joining R_1 and perpendicular to longitudinal wing

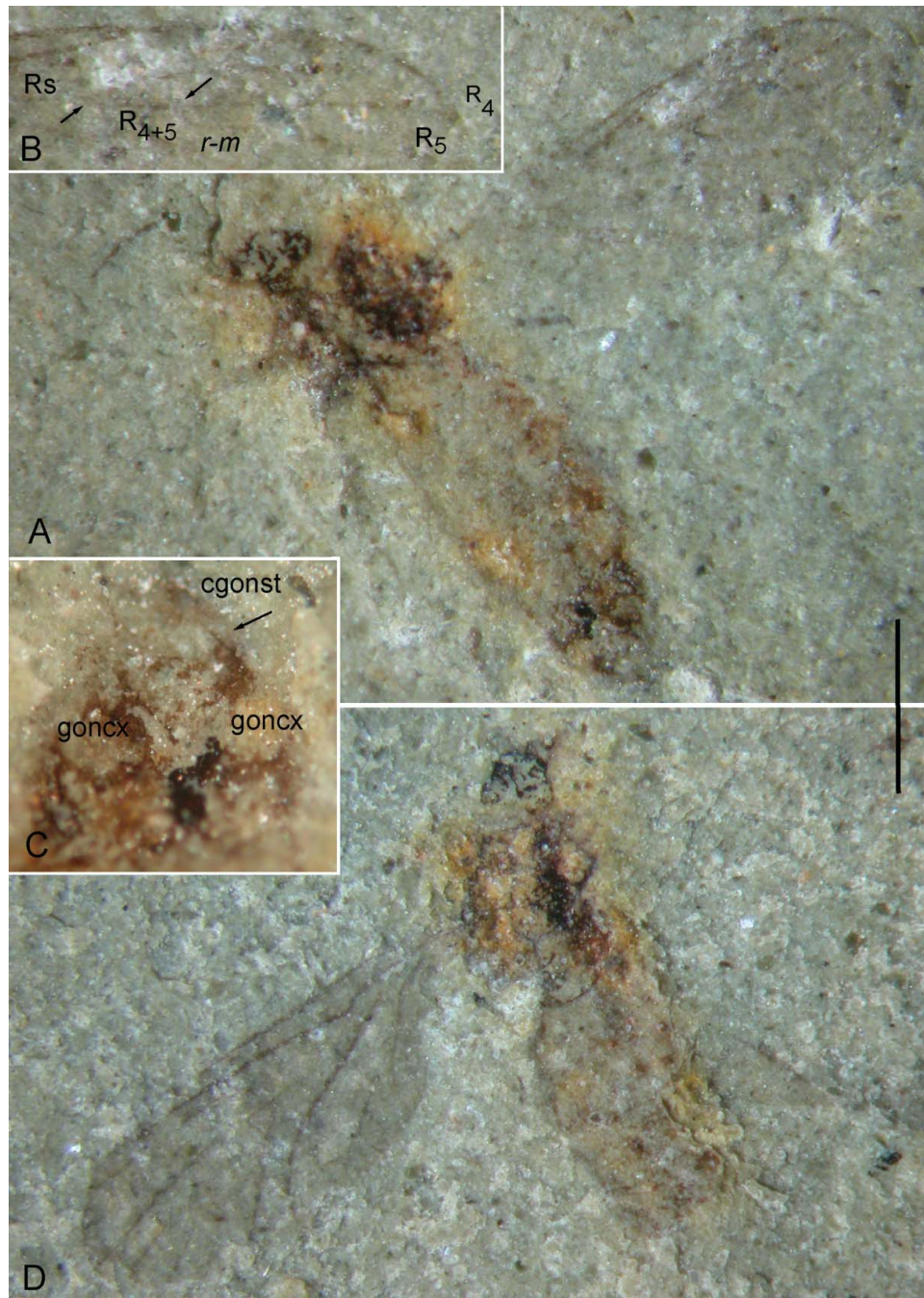


Figure 1. *Archilimonia vogesiana* Krzemiński & Krzemińska, 2003, holotype, SMNS, No. 9052. **A–C**, positive impression; **A**, habitus; **B**, distal part of wing; **C**, male genitalia. **D**, negative impression, habitus. Scale bar: 1 mm (A, D). Abbreviations: cgonst, clasper of gonostylus; goncx, gonocoxite.

axis; *r-m* between R₅ base and M₁₊₂ (*r-m* from R₄₊₅ cannot be excluded in *A. vogesiana*); M forking rather symmetrical, near wing midlength, slightly basad to Rs bifurcation; four medial veins present; M₄ leaves M₃₊₄ in middle of *d* cell; *d* cell large, *m-m* at level with R₂, between M₂ and M₃; *m-cu* just before or at fork M₃₊₄ and before midlength of *d* cell; CuA distally curved backwards; CuA apex nearer to Sc apex than to R₁ apex level; CuP not strongly diverging from CuA, with CuP apex at

wing midlength; A₁ rather long. Rs origin at 0.34–0.38, M forking at 0.48–0.50, CuA terminating at 0.62–0.64 of wing length.

Abdomen. Not long, male terminalia large.

Remarks. In the original description of *Archilimonia vogesiana* (Krzemiński & Krzemińska 2003, p. 167) the holotype was considered ‘a poor preserved female’ due to interpretation of dark spot in abdomen as three

spermathecae (Fig. 1A, C). The terminalia of the holotype is indeed very poorly preserved; however, basal parts are visible and clearly widely separated, so we suppose that it is a male (the dark spot may be a part of the heavily sclerotized median extension of tergite IX). In the original description of *A. vogesiana* the position of *r-m* most probably between the middle of R_{4+5} and 1/4 of *d* cell upper margin was mentioned. After discovery of an additional specimen and re-examination of the holotype we consider the position of *r-m* to be between R_5 and 1/3 *d* cell upper margin in both specimens; however, *r-m* is poorly visible in both cases (Figs 1, 3A).

Archilimonia grauvogeliana sp. nov.
(Figs 2, 3B, C)

Diagnosis. R_2 joining R_1 near wing margin, R_s stem nearly aligned with extremely short R_{4+5} and R_4 . Gonocoxite simple, cone shaped. Gonostylus terminal, divided into subequal lobe and clasper, clasper of gonostylus setose, fleshy; lobe of gonostylus not bifurcated.

Etymology. The species is named in honour of Lea Grauvogel-Stamm, the investigator and heiress of the palaeontological collection of Louis Grauvogel from the Vosges Mountains.

Material. Holotype: SMNS, No. 6180/6181, male. Arzviller (lens 118b), Vosges Mountains, France; Grès à Voltzia (Upper Buntsandstein), Anisian.

Description.

Wing. R_2 joining R_1 near wing margin, R_s stem nearly aligned with extremely short R_{4+5} and R_4 , R_5 7.5 times longer than R_{4+5} stem, dM_{1+2} 2.5 times longer than bM_{1+2} . R_s origin at 0.38, M forking at 0.48, CuA terminating at 0.62 of wing length.

Male terminalia. Hind margin of tergite IX with a short narrow median extension. Gonocoxite simple, cone shaped, elongated (longer than high), covered with strong setae. Gonostylus terminal, divided into subequal lobe and clasper, both with blunt apex, clasper of gonostylus setose, weakly sclerotized, fleshy, with apical well-developed, branch-like bifurcation, both apexes with longer and denser setae, distal portion and posterior margin of clasper smooth; lobe of gonostylus not bifurcated.

Measurements. Body length 3.4 mm, wing length 2.5 mm, width 0.9 mm.

Remarks. This new species is superficially more similar to *Metarchilimonia* than *A. vogesiana* due to the pattern of R_s branching with very short R_{4+5} and R_2 joining R_1 near wing margin. However, R_s forking before Sc apex and a long *d* cell (due to *m-m* connecting M_3 with M_2 , not M_{1+2} stem), longer than M_{3+4} fork, as well as CuA apex

position differentiate *Archilimonia* from *Metarchilimonia*. In the original diagnosis of *Metarchilimonia* (Blagoderov *et al.* 2007) few discriminating features were given (e.g. ' R_2 meets R_1 ' is typical of all Triassic and most Jurassic limoniids known to date) and no one character useful for comparison with *Archilimonia* was mentioned.

Results

Phylogeny

In this section we provide a synthesis of the results obtained from the different analyses performed, as well as the justifications for our preferred set of analyses. However, only the results of the preferred set of analyses are discussed in detail. A synthesis of the results is presented in Table 1.

Parsimony with equal weights (EW). The parsimony analysis with EW yielded 2414 most parsimonious trees of 222 steps [consistency index (CI) = 0.297; retention index (RI) = 0.659]. The strict consensus tree is almost unresolved (Fig. 4A). This analysis was unable to provide us with a background of family-level relationships that could be used for discussing the position of the fossils. Nevertheless, a few aspects are worth discussing.

The order Diptera appears monophyletic, and the Triassic genus *Mabelysia* is the sister group of the rest of the Diptera. The families Trichoceridae, Cylindrotomidae and Tipulidae (including their extinct representatives) are recovered as monophyletic. The families Limoniidae and Pediciidae are recovered as paraphyletic. Notably, the genus *Archilimonia* is monophyletic in this analysis, as well as the genus *Metarchilimonia*.

Parsimony with implied weighting (IW) (K 5 to 105).

The main purpose of this set of analyses was to compare the difference between results obtained with K values of different magnitudes (5, 15, and 105). The fitness of the trees decreases considerably as the value of K increases (Table 1) but it is interesting to compare the resultant topologies. With $K = 105$ (Fig. 4D), the monophyly of the Tipulomorpha (as accepted in this paper, i.e. including Trichoceridae) is not recovered. Under both $K = 5$ (Fig. 4B) and $K = 15$ (Fig. 4C), the relationships within the Tipuloidea at the family level are the same. However, the basal position of *Archilimonia* in the tree with $K = 15$ (and also in the tree with $K = 105$) implies a non-homologous development of the bifid clasper of the gonostylus, as found in *Archilimonia* and Tipuloidea.

Parsimony with implied weighting (IW) (K 3 to 10).

This set of analyses yielded topologies highly congruent to each other. For K values ranging from 3 to 5, three most parsimonious trees were found. The analyses with K ranging from 6 to 10 resulted in four most parsimonious

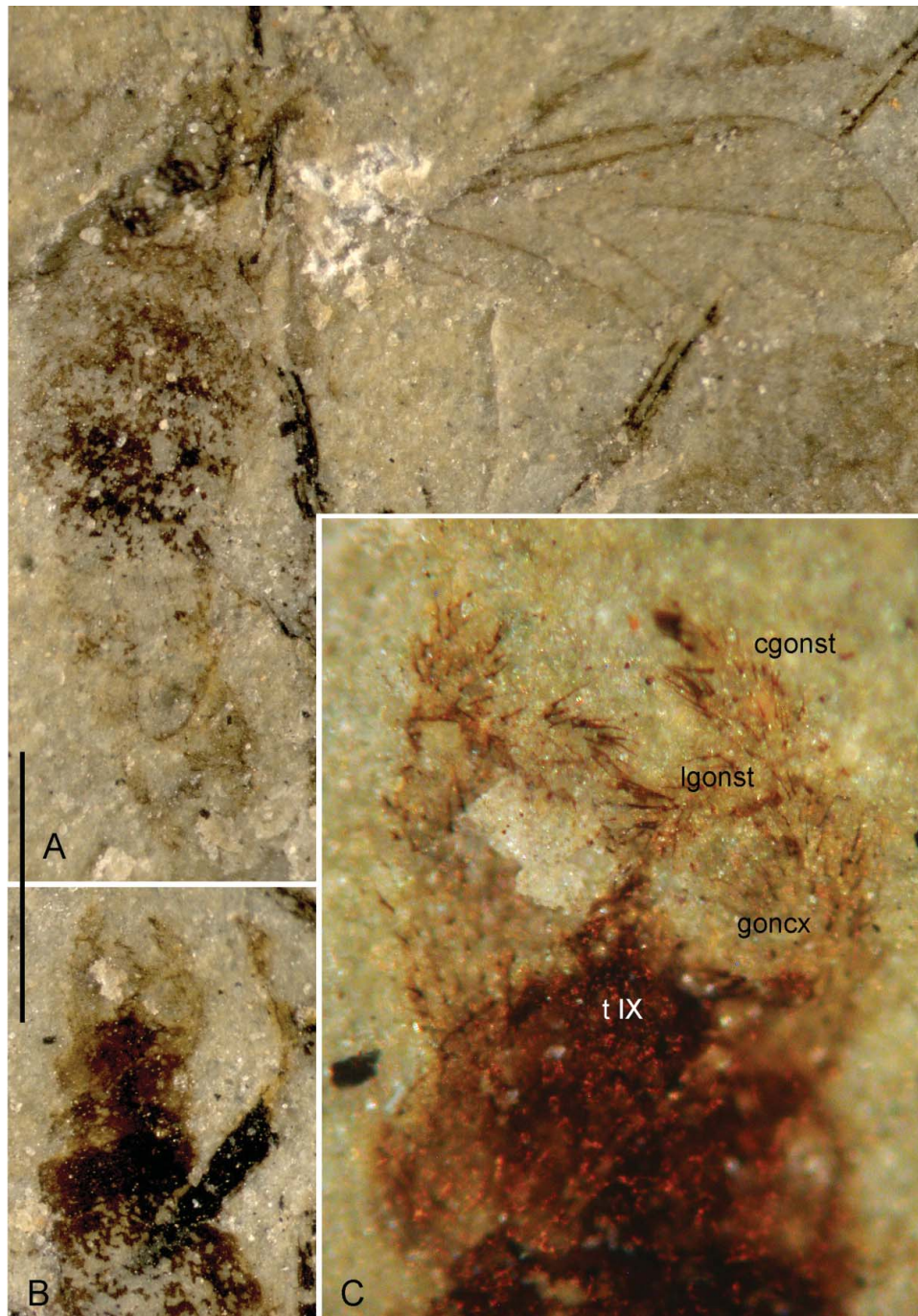


Figure 2. *Archilimonia grauvogeliana* sp. nov., holotype, SMNS, No. 6180 (6181). **A**, positive impression, habitus. **B**, **C**, negative impression; **B**, apex of abdomen; **C**, male genitalia. Scale bar: 1 mm (A, B). Abbreviations: cgonst, clasper of gonostylus; lgonst, lobe of gonostylus; goncx, gonocoxite; t IX, tergite IX.

trees (Table 1). All analyses, however, produced the same strict consensus tree (Fig. 5). This set of analyses yielded the trees with the highest fitness and provided the most internally congruent results (the same consensus tree is found with K values ranging from 3 to 10). Therefore, it is our preferred result. However, before discussing it in

detail, we must examine the set of analyses with extended implied weighting.

Parsimony with extended implied weighting (EIW) (K 3 to 10). The use of EIW had virtually no effect on the results of the IW analyses. For all values of K used, this

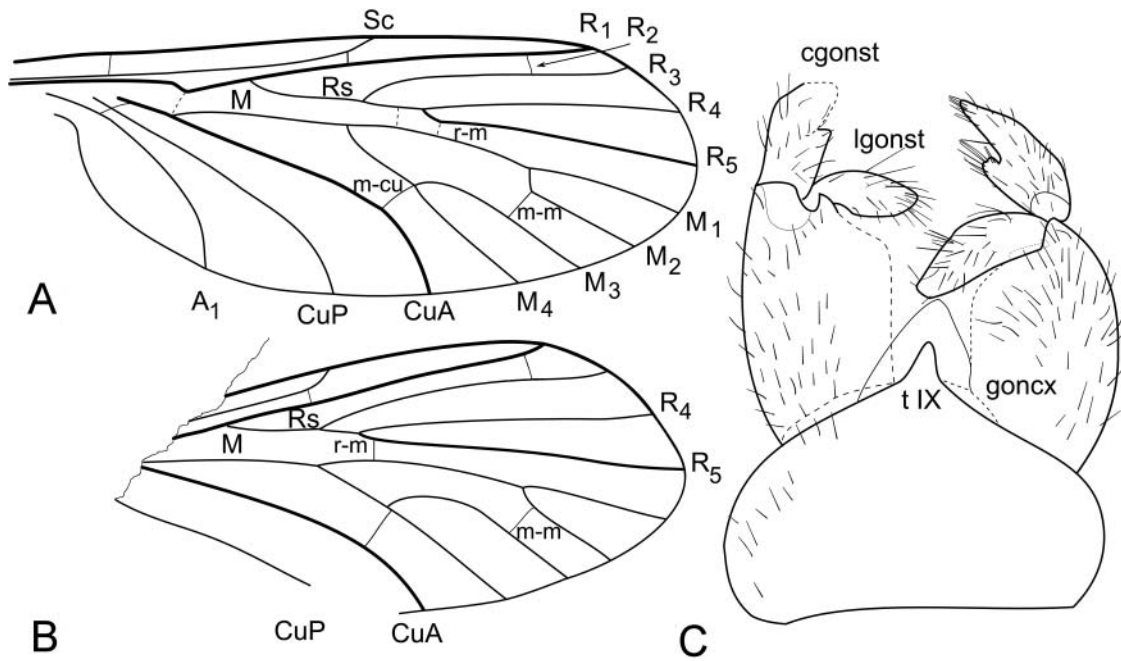


Figure 3. **A**, *Archilimonia vogesiana* Krzemiński & Krzemińska, 2003, holotype, SMNS, No. 9052, wing. **B, C**, *Archilimonia grauvo-geliana*, sp. nov., holotype, SMNS, No. 6180 (6181); **B**, wing; **C**, male genitalia. Abbreviations: cgonst, clasper of gonostylus; lgonst, lobe of gonostylus; goncx, gonocoxite; tIX, tergite IX.

set of analyses provided trees with slightly smaller fitness (Table 1). For *K* values ranging from 3 to 5, the results are identical to those from the IW analyses. For *K* ranging from 6 to 10, a single and totally resolved most parsimonious tree is found. This unique tree, however, has the same topology as one of the three trees obtained in the IW analyses.

Discussion of the preferred results. As already anticipated in several parts of this paper, our preferred results are those obtained under IW with values of *K* ranging from 3 to 10, which will be discussed in detail here. Our reasons for preferring this set of analyses are twofold: on the one hand, it produced the trees with highest fitness; more importantly, however, under this range of *K* the

topologies are more congruent with each other and with the framework of Tipuloidea phylogeny as provided by previous studies.

As stated by Goloboff *et al.* (2008), it is crucial to interpret the results of the analysis with implied weighting conservatively and to take into account the effect of changes in the analytical parameters, as in a sensitivity analysis. The method rarely produces many most parsimonious trees due to its fine-grained precision, and only those clades that resist alterations to the analytical parameters (in our case, different values of the weighting constant, *K*) should be considered. The same well-resolved consensus tree is produced by all the analyses we performed (Fig. 5), and in principle, such stability can be viewed as a sign of robustness in the depicted relationships.

Table 1. Tree statistics.

Implied weighting (IW)										
<i>K</i> value	<i>K</i> = 3	<i>K</i> = 4	<i>K</i> = 5	<i>K</i> = 6	<i>K</i> = 7	<i>K</i> = 8	<i>K</i> = 9	<i>K</i> = 10	<i>K</i> = 15	<i>K</i> = 105
Fitness	15.27	13.64	12.38	11.36	10.51	9.80	9.18	8.64	6.71	1.36
No. of trees	3 ^a	3 ^a	3 ^a	4 ^a	4 ^a	4 ^a	4 ^a	4 ^a	3	1
Length (steps)	231	229	229	227	227	227	227	227	224	222
Extended implied weighting (EIW)										
<i>K</i> value	<i>K</i> = 3	<i>K</i> = 4	<i>K</i> = 5	<i>K</i> = 6	<i>K</i> = 7	<i>K</i> = 8	<i>K</i> = 9	<i>K</i> = 10	–	–
Fitness	15.00	13.40	12.17	11.17	10.35	9.64	9.04	8.15	–	–
No. of trees	3 ^a	3 ^a	3 ^a	1	1	1	1	1	–	–
Length (steps)	231	229	229	227	226	226	226	226	–	–

^aSame consensus tree in both implied weighting (IW) and extended implied weighting (EIW) (see Figs 4B, 5).



Figure 4. A, strict consensus of 2414 most parsimonious trees obtained in the analysis with equal weights (CI = 0.297; RI = 0.659). B, strict consensus of the three most parsimonious trees obtained in the analysis with implied weighting ($K = 5$). C, strict consensus of the three most parsimonious trees obtained in the analysis with implied weighting ($K = 15$). D, single most parsimonious tree obtained in the analysis with implied weighting ($K = 105$).

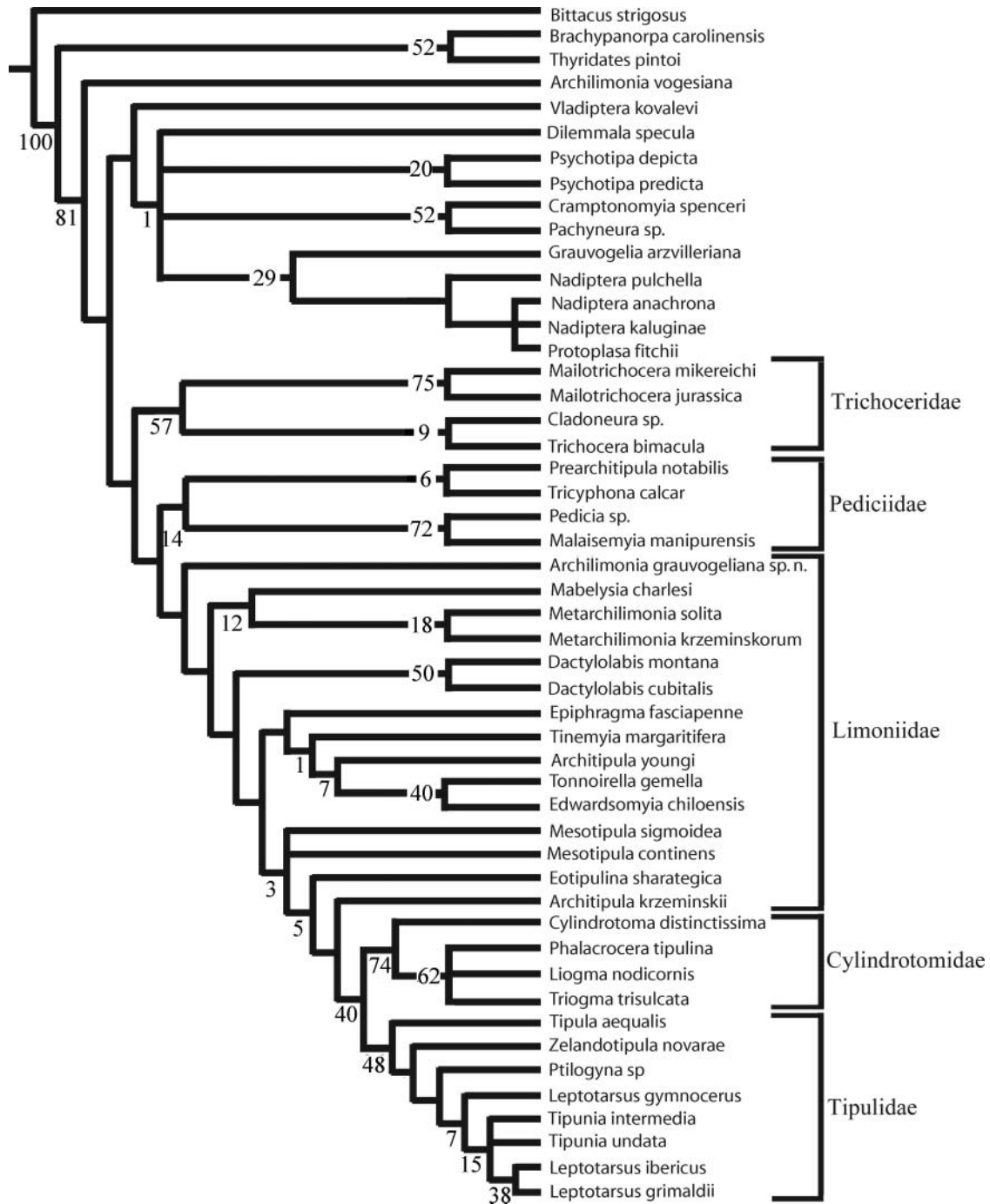


Figure 5. Consensus tree recovered by the various implied weighting (IW) analyses with different values of K (from 3 to 10). This same consensus tree is also found in extended implied weighting (EIW) analyses with K ranging from 3 to 5. Numbers below nodes are support values expressed as frequency differences obtained from symmetric resampling (pooled from analysis with $K = 5$; only for nodes with support values above 1).

Our phylogenetic analysis is congruent with the family-level relationships recovered by the most recent phylogenetic studies of the Tipulomorpha (Ribeiro 2008; Petersen *et al.* 2010; Zhang *et al.* 2016), and the position of the fossil taxa can be discussed now in this framework. However, considering that our taxonomic sampling at the genus

level is much reduced relative to the actual diversity of crane flies, we take a conservative interpretation even further and focus our discussion on the family-level clades, and on the characters pertinent in this context. The most relevant aspects of our study, as we see it, are represented in the phylogenetic tree in Fig. 6.

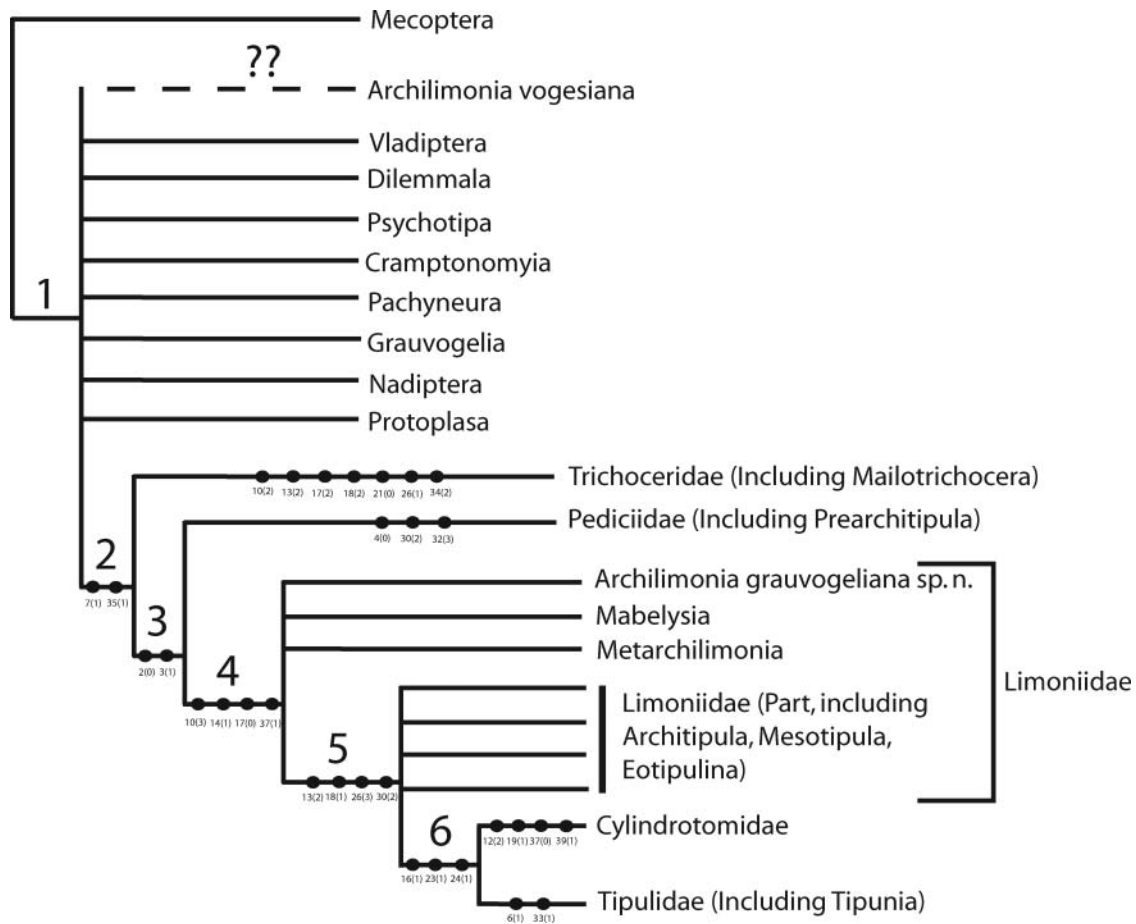


Figure 6. Conservative hypothesis of family-level relationships within Tipulomorpha including extinct members. The main features defining each of the numbered clades are discussed in the text.

In the discussion that follows, we focus on the less homoplastic characters in each node, which are indeed those more relevant for the phylogenetic picture we show considering the tree-building algorithm we used.

Tipulomorpha

Monophyly of Tipulomorpha is supported by two characters: the V-shaped mesonotal suture present (Ch. 7:1) and vein A_2 very short and submarginal (not longer than one-third of vein A_1) (Ch. 35:1).

Our results corroborate the sister-group relationship between Trichoceridae and Tipuloidea as was traditionally supposed (e.g. Hennig 1968; Starý 1992; Shcherbakov *et al.* 1995). The suggestion of Krivosheina (1988) and Wood & Borkent (1989) to include Trichoceridae in the infraorder Psychodomorpha (*sensu* Wood & Borkent 1989) was supported in some recent analyses of phylogenetic relationships of the entire order (Yeates *et al.* 2007; Lambkin *et al.* 2013). However, the close relationship between Tipuloidea and Trichoceridae is also defended by authors who did not consider the position of

Tipulomorpha *sensu* Hennig as the sister group of all the other Diptera (Hackman & Väisänen 1982; Oosterbroek & Courtney 1995; Bertone *et al.* 2008; Wiegmann *et al.* 2011; Zhang *et al.* 2016). It is worth adding that our analysis was based on adult characters, whereas Psychodomorpha *sensu* Wood & Borkent was based on larval characters. Moreover, Trichoceridae was the only family from that proposed infraorder included in our matrix, so our results (close relationships of Trichoceridae and Tipuloidea) were predictable.

Trichoceridae

A comprehensive phylogenetic tree of the family including all 13 extinct and extant genera and 12 characters was proposed recently (Krzemińska *et al.* 2009). So, for our purpose the only fossil we chose is the oldest extinct genus *Mailotrilocera* Kalugina in Kalugina & Kovalev (1985), known from as far back as the Early Jurassic. Monophyly of Trichoceridae is supported by several characters, including: vein R_4 is captured by R_{2+3} , forming a R_{2+3+4} element (Ch. 13:2); vein R_{1+2} is quite long

(Ch. 17:2), more than $3 \times$ the length of R_2 (within the Tipuloidea, a similar condition has appeared independently in the genus *Dactylolabis* Osten-Sacken, 1860); and vein A_1 is shortened but reaching the wing margin (Ch. 34:2).

In Mecoptera Rs is divided into R_{2+3} and R_{4+5} with four main radial branches reaching the wing margin. The same plesiomorphic pattern is known in recent Diptera only in two non-tipulomorph families, Tanyderidae and Psychodidae. However, in the Mesozoic such a pattern was much more widespread (Shcherbakov *et al.* 1995; Krzemiński & Krzemińska 2003): in these cases usually the R_{4+5} stem is short to extremely short, Rs stem, R_{4+5} and R_4 are aligned, so R_5 can swing basad, proximal to Rs furcation, forming a short R_{2+3+4} element. This modification is obvious in taxa with a free longitudinal R_2 such as Triassic Psychotipinae (Shcherbakov *et al.* 1995: two species of *Psychotipa* with two different patterns from the same locality) and living Tanyderidae. In Tanyderidae Rs is usually divided into R_{2+3} and R_{4+5} ; however, *Radino-derus* Handlirsch, 1909 and most specimens of *Tanyderus* Philippi, 1865 possess a short R_{2+3+4} stem (Alexander 1928; Williams 1933). In *Tanyderus pictus* Philippi, 1865, Rs can be forked either into an extremely short R_{2+3+4} and R_5 or into R_{2+3} and extremely short R_{4+5} (Lukashevich & Shcherbakov 2016). It is worth mentioning that in all described Mesozoic Tanyderidae Rs forks into R_{2+3} and R_{4+5} and such a pattern is here considered plesiomorphic for the family.

The capture of vein R_4 by R_{2+3} , as well as the fusion of R_2 with R_1 , was proposed for Pediciidae and Limoniidae by Alexander (1927, p. 44):

The upper branch of the anterior fork of the primitive sector has swung cephalad and became fused backward from the margin with vein R_1 ; in all but a few generalized members ...the dichotomous nature of the posterior fork of the sector has been lost by the capture of the anterior branch (R_4) by the stem of the upper fork (R_{2+3}), leaving R_5 along as the posterior branch of the radial field.

Analogous shifts of branching patterns can also be observed in the medial veins of some species of the Limoniidae genus *Aphrophila* Edwards, 1923 (unpublished data of G. C. Ribeiro).

As already mentioned, the capture of R_4 by R_{2+3} is not exclusive to Trichoceridae but occurred also in Clade 5 (Fig. 6) and in the Triassic *Psychotipa depicta* Shcherbakov in Shcherbakov *et al.* (1995). The vein R_{2+3+4} was suggested as a synapomorphy of Trichoceridae and Tipuloidea (Krzemińska *et al.* 2009). However, basal members of the Tipuloidea, such as some Pediciidae (Jurassic *Praearchitipula* Kalugina in Kalugina & Kovalev, 1985, recent *Tricyphona* Zetterstedt, 1838, several *Pedicia* Latreille, 1809 and *Dicranota* Zetterstedt, 1838) and Triassic *Archilimonia*, *Mabelysia* and *Metarchilimonia*, retain the plesiomorphic branching pattern of Rs. In the Jurassic species *Mesotipula*

sigmoidea Lukashevich, 2009, Rs also divides into R_{2+3} and R_{4+5} , but there is no distinct R_{4+5} stem due to R_{2+3} and R_{4+5} branching off from a single point (as well as in one specimen of *Metarchilimonia krzeminskorum* Blagoderov & Grimaldi in Blagoderov *et al.*, 2007).

Tipuloidea

Monophyly of Tipuloidea is corroborated in our study by the absence of ocelli (Ch. 2:0) and the postgenae meeting medially, not separated by a membranous area (Ch. 3:1).

While the absence of ocelli in Tipuloidea may constitute a unique novelty with no subsequent homoplasy within the group, the evolution of the posterior margin of the head is more problematic (see Ribeiro 2008, p. 661). The closing of the medial margins of the postgenae may have occurred at the base of the Tipuloidea clade, but in this case reversals would have to be assumed for members of the subfamilies Chioneinae and Limoniinae. Alternatively, there must be groups within Tipuloidea in which the plesiomorphic condition is kept, but the phylogenetic meaning of this is still obscure. Only a wider study with a larger taxonomic sampling could provide a proper test of alternative scenarios.

Some of the other evidence of the monophyly of Tipuloidea is based on characters of immature stages, not used in the present analysis. Larvae hemicephalic (head capsule can be retracted into the body) and metapneustic (functional spiracles on the last abdominal segment only), with divided hypostoma as well as pupal leg sheaths side by side, together with several other characters are listed as the synapomorphies of Tipuloidea by Oosterbroek & Theowald (1991). However, Oosterbroek & Courtney (1995) did not confirm any of seven synapomorphies which were suggested in the previous paper. In the most recent analyses including characters of immatures (Petersen *et al.* 2010), five characters were used but these authors did not discuss any immature or adult synapomorphies supporting their trees. Neugart *et al.* (2009) confirmed divided hypostoma as a unambiguous apomorphy of Tipuloidea, whereas a moderately retracted head is likely part of the groundplan of the superfamily and the more advanced condition is a potential synapomorphy of Tipuloidea excluding Pediciidae.

Pediciidae

Pediciidae, raised to full family rank by Starý (1992), is likely the sister group of all other Tipuloidea. This result is consistent with the findings of Ribeiro (2008), Petersen *et al.* (2010) and Zhang *et al.* (2016). This group has likely preserved the highest number of plesiomorphies in Tipuloidea. Oosterbroek & Theowald (1991) found several weak larval synapomorphies for the group (Pediciinae in

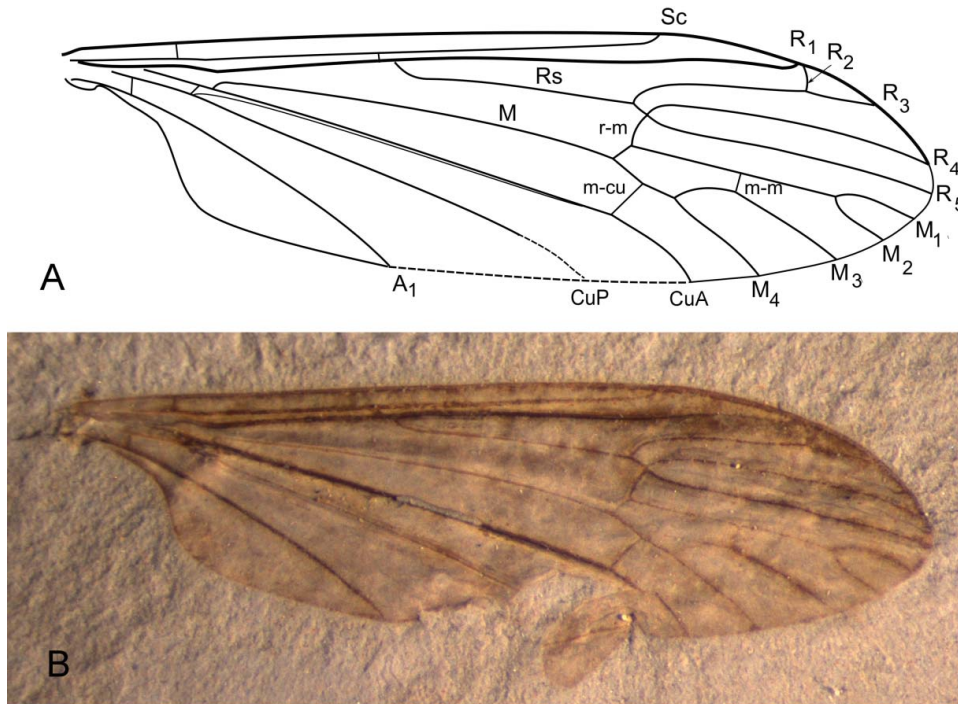


Figure 7. *Praearchitipula notabilis* Kalugina in Kalugina & Kovalev, 1985 (Pediiciidae), PIN, No. 1255/219, holotype; **A**, line drawing of wing; **B**, photograph of wing.

their system). Neugart *et al.* (2009) found a single unequivocal synapomorphy for the family: the elongated sickle-shaped distal part of the larval mandible. We could not find any other apomorphy in wing venation except for M forking in the distal half of the wing, which is present already in the Jurassic members of the family. According to our analysis, the fork of the medial vein originally is at the level of mid length of wing (Ch.30:1). Mecoptera and some Triassic genera of the families under discussion (*Vladiptera*, *Dilemmala*, *Psychotipa*, *Mailotrichocera*, *Archilimonia*, *Mabelysia* and *Metarchilimonia*) exhibit the plesiomorphic condition of this character. A shift of the M fork to a position distal to the mid length of the wing (Ch.30:2) has occurred 3 times according to our analysis. It is a synapomorphy of Pediciidae, but a similar condition has occurred independently in other Tipuloidea except *Archilimonia*, *Mabelysia* and *Metarchilimonia* (Clade 5 in Fig. 6), and in recent Trichoceridae. In our analysis, the presence of setose eyes is a synapomorphy of the family Pediciidae (Ch. 4:0), but we acknowledge that this may be an artifact of our taxon sampling, as several outgroup taxa we used including Mecoptera and Pachyneuridae (*Pachyneura* Zetterstedt, 1838) and Cramptonomyidae (*Cramptonomyia* Alexander, 1931) have bare eyes. Oosterbroek & Theowald (1991, p. 218) considered the setose eyes of the adult pediciids as “without doubt a symplesiomorphic character. Therefore, it might be expected to find the Pediciinae at the most basal position.”

We agree with this possibility but we do not have information on this character for any fossils included in our analysis. All extant Tanyderidae possess setose eyes. In extinct species such setae have been described only in *Dacochile microsoma* Poinar & Brown 2004 from mid-Cretaceous Burmese amber (Poinar & Brown 2006), but the lack of eye setae in other descriptions may probably be explained by their minute size and state of fossil preservation. Within Trichoceridae eyes are setose in recent members of *Cladoneura* Scudder, 1894 (= *Diazosma* Bergroth, 1913), but bare in *Trichocera* Meigen, 1803.

We found R_2 to be free in *Praearchitipula notabilis* Kalugina in Kalugina & Kovalev, 1985 (Fig. 7), a condition that was overlooked in the original description (Kalugina & Kovalev 1985). Alexander (1927) figured the wings of three species of *Tricyphona* (*T. protea* Alexander, 1918, *T. formosana* Alexander, 1920 and *T. novaezelandiae* Alexander, 1922) as three steps in the cephalization of R_2 , and considered *T. protea* the first stage due to R_2 being still long and nearly longitudinal. Most of the Jurassic Pediciidae (Lukashevich 2009; Gao *et al.* 2015) demonstrate the second stage, with oblique short R_2 , connecting with R_1 just near the wing margin. However, *P. notabilis* possess oblique short free R_2 . This condition of the character is most likely abnormal (R_2 is a crossvein in all other species from the same locality and from other localities), but even such an aberration corroborates the interpretation of Alexander (1927).

Archilimonia*, *Metarchilimonia* and *Mabelysia

Mabelysia and *Metarchilimonia* were described as members of the subfamily Architipulinae in Limoniidae (Shcherbakov *et al.* 1995; Blagoderov *et al.* 2007). *Archilimonia* was described as a member of the monotypic family Archilimoniidae, considered basal to all other Tipuloidea (Krzemiński & Krzemińska 2003), but later Archilimoniidae was demoted to a subfamily of Limoniidae (Blagoderov *et al.* 2007). In our analysis, *A. grauvogeliana* sp. nov., *Mabelysia* and *Metarchilimonia* are also included in Tipuloidea, although characters that support the monophyly of Tipulomorpha (the V-shaped mesonotal suture and very short submarginal vein A_2) and Tipuloidea (absence of ocelli and the postgenae meeting medially) cannot be seen in the Triassic genera under discussion (except for the V-shaped suture in *Metarchilimonia*) as in most fossils. Moreover, even vein A_1 is not visible in *A. grauvogeliana* sp. nov. due to the poor state of preservation. This presents some issues for including these genera in Tipulomorpha, and only additional findings may prove or disprove that the characters really occur in these Triassic genera. However, our resultant tree is a synthesis of several characters and in our conservative interpretation, we place these taxa in a polytomy between Pediciidae and Limoniidae + (Tipulidae + Cylindrotomidae).

The characters of wing venation uniting these three genera (Rs divided into R_{2+3} and R_{4+5} , extremely short R_{4+5} , and M forking in the wing midlength) are symplesiomorphic features, which are very rare in extant taxa of Tipuloidea. Three synapomorphic character states support the placement of *Archilimonia grauvogeliana* sp. nov., *Metarchilimonia* and *Mabelysia* in the Tipuloidea (except Pediciidae): position of *sc-r* closer to the apex of Sc (Ch. 10:3); short vein R_{1+2} (less than $2 \times$ the length of R_2 ; Ch. 17:0); and male gonostylus divided into clasper and lobe, known only for *A. grauvogeliana* sp. nov. (Ch. 37:1).

The divided male gonostylus of *A. grauvogeliana* sp. nov. provides strong evidence for the systematic position of the species within Tipuloidea without Pediciidae, but not as basal as all other Tipuloidea. A divided male gonostylus is considered a synapomorphy of Tipuloidea except Pediciidae (Clade 4 in Fig. 6). The loss of one of the gonostylar branches has occurred independently in higher nodes within Tipuloidea (in representatives of families Limoniidae and Cylindrotomidae), but the original transformation of a single, undivided gonostylus (as found in Trichoceridae and Pediciidae) into a divided one is most probably a unique development (Ribeiro 2006, 2008). In *A. grauvogeliana* sp. nov. the gonostylus is terminal with a fleshy clasper. In the Limoniidae, the clasper of the gonostylus is usually well sclerotized. The condition found in *A. grauvogeliana* sp. nov. is similar to that of some extant Limoniidae genera with fleshy claspers, such as *Dactylolabis* and *Metalimnophila* Alexander, 1922 (Ribeiro 2008,

figs 98, 128). Starý (1992) considered the strong sclerotized clasper of the gonostylus (some authors use term outer gonostylus for this clasper) to be a synapomorphy of Limoniidae except *Dactylolabis*. However, as stated above, a fleshy clasper is not exclusive to *Dactylolabis* within Limoniidae. Nevertheless, the finding of a fleshy clasper in the gonostylus of *A. grauvogeliana* sp. nov. suggests that a well sclerotized clasper may indeed be apomorphic, and that the Limoniidae genera with a fleshy clasper may be relatively basal groups within Tipuloidea. Some extant genera of Limoniidae are known back to the Cretaceous (see Lukashevich 2009), but members of *Dactylolabis* are known only to the Eocene and described mainly from Baltic amber (Podenas 2003; Krzemiński *et al.* 2010).

Shcherbakov *et al.* (1995) estimated some wing proportions for Triassic members of the infraorder Tipulomorpha: Rs origin at 0.32–0.41, M forking at 0.48–0.54, CuA terminating at 0.64–0.78 of wing length. Proportions for both species of *Metarchilimonia*, described subsequently, support these conclusions. The *Archilimonia* wing venation is similar, with only CuA slightly shorter in *A. grauvogeliana* sp. nov. Lukashevich & Shcherbakov (1999) demonstrated that no single proportion is sufficient to separate nematocerous infraorders; however, infraordinal clusters do not overlap in multidimensional character space. In other Triassic Limoniidae (i.e. *Architipula*, *Mabelysia*, *Metarchilimonia*), CuA is usually longer and as a result the CuA apex is closer to R_1 than to Sc apex level (perpendicular to the long wing axis). In *Archilimonia*, as well as in Triassic *Vladiptera* and *Psychotipa*, CuA is shorter so the CuA apex is closer to Sc. We consider this short CuA as one more plesiomorphy of *Archilimonia*, which prevents us from uniting the genus with any Triassic members of the family (with *Metarchilimonia* alone or with *Metarchilimonia* + *Mabelysia*), in spite of the similar pattern of radial sectors.

Monophyly of the genus *Archilimonia* was not recovered in our preferred set of analyses (although it was recovered in other set of analyses, such as the analysis with EW, in IW with $K = 15$ and IW with $K = 105$; Fig. 4A, C, D). This requires further explanation, especially considering our decision to keep both *A. vogesiana* and our new species in the same genus. This conservative taxonomic decision is based on the striking similarities in the wing venation of the two species, which differs from that of all other fossil and living genera (Rs forking into R_{2+3} and R_{4+5} with a distinct short R_{4+5} stem; M forking in the midlength and large discal cell combined with A_1 vein no less than half of CuA, reaching the wing margin in type species). We were unable to find synapomorphic characters of wing venation shared by *Archilimonia* species. Since the key apomorphic feature allowing the placement of the genus (divided male gonostylus) is available

for the new species only, the genus inevitably appears as paraphyletic in the analysis, with *A. vogesiana* (with very poor preserved terminalia) placed near the base of Diptera (Figs 5, 6). As an experiment, we analysed a hypothetical matrix in which we coded a divided male gonostylus for *A. vogesiana*. The result is that both species are placed in Tipuloidea as sister groups (in the same position where the new species is placed in the real tree). We speculate here that a divided gonostylus may in fact occur in *A. vogesiana* as well as in *Mabelysia* and *Metarchilimonia*, which only the finding of additional specimens may prove or disprove. We are confident that the monophyly of the genus *Archilimonia* cannot be properly tested, considering the scarcity of data available, and our decision to include the two species in *Archilimonia* is the only reasonable one.

Limoniidae

Starý (1992) considered Limoniidae a monophyletic taxon, but the paraphyly of the family has been demonstrated by all other phylogenetic analyses (Oosterbroek & Theowald 1991; Ribeiro 2008; Neugart *et al.* 2009; Petersen *et al.* 2010; Zhang *et al.* 2016), and again by this study.

A clade including the bulk of Limoniidae genera plus the families Cylindrotomidae and Tipulidae (but excluding *Archilimonia*, *Mabelysia* and *Metarchilimonia*) was found (Clade 5 in Fig. 6). In this clade (but also independently occurring in Trichoceridae and *Psychotipa depicta*), vein R_4 is captured by R_{2+3} forming a R_{2+3+4} element (Ch.13: 2). Also, the fork of vein M is positioned distal to the midlength of wing (Ch.30: 2). According to our analysis, the similar condition found in Trichoceridae (*Cladoneura* and *Trichocera* but not Jurassic *Mailotrachocera*) and in Pediciidae has occurred independently.

It is beyond the scope of this study to discuss the problem of the delimitation of the subfamilies of Limoniidae. Our taxonomic sampling was not designed to investigate this particular problem. As demonstrated by previous analyses (Oosterbroek & Theowald 1991; Ribeiro 2008; Petersen *et al.* 2010), Limnophilinae is paraphyletic, and the large subfamily Chioneinae may not be monophyletic either. Arguing about subfamilial ranks of the extinct Limoniidae does not constitute, considering our current level of knowledge, a fruitful discussion. The diagnosis of the extinct Mesozoic family Architipulidae (Handlirsch 1906–1908), which was demoted to subfamily level by Kalugina (Kalugina & Kovalev 1985), is insufficient. In spite of numerous described Architipulinae, a revision of the subfamily including crucial body characters has yet to be undertaken, as well as any description of the genitalia. In fact, all Triassic and Jurassic Limoniidae with four medial veins are considered Architipulinae. Taxa with three medial veins are considered Eotipulinae. Spurs are

absent in both subfamilies according to their diagnoses. However, species and genera with spurs have been recorded within Architipulinae, which seems to be a wastebasket taxon with endless diversity (Lukashevich 2009). Therefore, it is not unexpected that two species of *Architipula* Handlirsch, 1906 are widely separated on our tree. The status of Architipulinae and Eotipulinae is quite dubious, and these subfamilies may in fact constitute junior synonyms of Limnophilinae and Chioneinae, respectively, as suggested earlier (Kalugina & Kovalev 1985; Savchenko 1986).

Cylindrotomidae and Tipulidae

The sister-group relationship between Cylindrotomidae and Tipulidae has been demonstrated by all phylogenetic analyses so far conducted (Oosterbroek & Theowald 1991; Starý 1992; Ribeiro 2008; Petersen *et al.* 2010; Zhang *et al.* 2016). However, opinions on what would constitute larval apomorphies for the group are contradictory: Oosterbroek & Theowald (1991) suggested some, but no unambiguous apomorphies were later confirmed (Neugart *et al.* 2009). According to our study, wing vein synapomorphies support the sister-group relationship.

In its most plesiomorphic condition, R_2 and R_3 are free veins reaching the wing margin. In Tipulomorpha, R_2 is a short, erect vein, which becomes attached to R_1 , and has been sometimes considered a crossvein (e.g. Savchenko 1986; Ribeiro 2008). As was explained earlier, we endorse the interpretation of Alexander (1927) that R_2 became a transverse vein attached to R_1 . For coding convenience, we refer to the result of this configuration as the R_{1+2+3} complex. In Pediciidae and Limoniidae, this complex is directed to the distal margin of the wing. In the Cylindrotomidae-Tipulidae clade, this complex is directed to the costal margin of the wing (Ch. 16:1). Due to additional losses and reductions (e.g. loss of the tip of R_{1+2} and R_3) in derived members of each family, such a configuration may not be so clear. However, considering the overall shape and relationships among the veins, it is easy to point to the missing elements and the homology of the veins involved is clear.

The monophyly of Cylindrotomidae is supported by the loss of vein R_3 (Ch. 19:1) and the trifold aedeagus (Ch. 39:1). Due to our sampling that included only members of the subfamily Cylindrotominae, the loss of one of the gonostylar branches (Ch. 37:0) appears to be a synapomorphy of the clade. However, members of the subfamily Stibadocerinae (*Stibadocera* Enderlein, 1912 and *Stibadocercella* Brunetti, 1918) possess a bifid gonostylus. The loss of one of the gonostylar branches occurred independently in Cylindrotominae and Stibadocerinae (in the South American monotypic genus *Stibadocerina* Alexander, 1929; Ribeiro 2009).

Two synapomorphies support the monophyly of the family Tipulidae: terminal segment of palpus longer than

the preceding two together (Ch. 6:1), and vein *m-cu* long and more inclined relative to the wing axis (Ch. 33:1). The long last palpomere is typical of Tipulidae but not universal; therefore, this conclusion may be an artefact of our taxon sampling. The long and inclined vein *m-cu*, however, is likely to be a true synapomorphy of the family, and the key for understanding the systematic position of a controversial Mesozoic genus, *Tipunia* Krzemiński & Ansoerge, 1995, treated in more detail below.

Tipunia

Krzemiński & Ansoerge (1995) described the genus *Tipunia* from the lower Tithonian (*Hybonotum* zone) Solnhofen lithographic limestone (Late Jurassic of Germany). When describing *Tipunia intermedia* Krzemiński & Ansoerge, 1995, the authors mentioned that some of its wing characters (e.g. *r-r* almost parallel to costal wing margin and very broad *cu* cell) are typical features of Tipulidae. But the authors also mentioned that some other features (e.g. vein *Sc* terminating on the wing margin and relatively long *R*₃) are typical features of Limoniidae, so the genus was tentatively placed in Limoniidae due to lack of information on the body morphology. Two additional species were later described from the Late Jurassic of Mongolia based on isolated wings only, and one additional species from the Early Cretaceous of Great Britain was transferred into the genus (Lukashevich 2009).

Ribeiro & Lukashevich (2014) drew attention to the fact that many of the limoniid-like features of *Tipunia* are plesiomorphic also present in basal Tipulidae, such as *Leptotarsus* (known back to the Early Cretaceous). In addition, they hypothesized that the tipulid-like shape of the medial veins of *Tipunia*, which includes a long vein *m-cu*, may well be a synapomorphy of Tipulidae. This hypothesis was tested in the current paper and corroborated. All analyses performed by us (EW, IW and EIW) confirm a monophyletic Tipulidae including the genus *Tipunia*, which known back to the Late Jurassic, so Tipulidae has existed since the Late Jurassic, as was suspected earlier (de Jong 2014).

Discussion

Minimum ages of main Tipulomorpha clades

As mentioned earlier, the oldest Diptera (as well as the oldest Tipuloidea discussed herein) are known from the Grès à Voltzia, the age of which is early Middle Triassic (early Anisian, Upper Buntsandstein, *c.* 245 Ma). The order was already diverse at this time: all four nematocercous infraorders (*sensu* Hennig 1968) as well as Brachycera are known by this time (Krzemiński & Krzemińska 2003; Lukashevich *et al.* 2010). Molecular-based estimates of the timing of origin of Diptera and its early radiation point to a Permian origin for the clade, with rapid

diversification in the Triassic (Wiegmann *et al.* 2011; Cranston *et al.* 2012). However, there is no fossil evidence for a Permian origin of Diptera, which have not yet been found in any Permian deposits, despite numerous long-term studies of insect taxonomic diversity around the Permian–Triassic boundary, e.g. fossil insects of the Middle and Upper Permian of European Russia with special attention to Mecoptera (Aristov *et al.* 2013).

The attribution of *Archilimonia* to Tipuloidea indicates that Tipuloidea have existed at least since the Middle Triassic. The oldest members of Trichoceridae and Pediciidae are known from the Jurassic, but based on our phylogeny the origin of the families must have occurred earlier, in the Triassic at least.

We have confirmed that *Tipunia*, known back to the Late Jurassic, is a true member of Tipulidae. In this case, the minimum age of Tipulidae and of its sister group, Cylandrotomidae, must also extend back to the Late Jurassic. Cylandrotomidae fossils are known in the Cenozoic (Evenhuis 2014). However, the geographical distribution of the small and likely monophyletic subfamily Stibado-cerinae can be interpreted in terms of ancient Mesozoic biogeographical patterns (Ribeiro & Eterovic 2011).

Acknowledgements

EDL is deeply indebted to Lea Grauvogel-Stamm for the opportunity to work with material collected by her father Louis Grauvogel, and for hospitality during a visit to Strasbourg. The late Francine Marchal-Papier assisted in work with the Vosges collection. We also thank Dmitry Shcherbakov (Moscow) for preparing photographs and for informal support, Ekaterina Sidorchuk (Moscow) for help in mastering InkScape, and Vladimir Blagoderov (Edinburgh) for improving the English. We offer our sincere gratitude to the anonymous reviewers for their very useful comments on the earlier version of the manuscript. The research of EDL was partly supported by the Russian Foundation for Basic Research, project no. 16–04–01498. The research of GCR was funded by the FAPESP (São Paulo Research Foundation), project no. 010/00557–7.

Funding

Fundação de Amparo à Pesquisa do Estado de São Paulo [project no. 010/00557–7.]; Russian Foundation for Basic Research [project no. 16–04–01498].

Supplemental data

Supplemental material for this article can be accessed online at: <https://doi.org/10.1080/14772019.2018.1448899>.

References

- Alexander, C. P.** 1918. A new interpretation of the wing-venation of the pediciine crane-flies (Tipulidae, Diptera). *Entomological News*, **29**, 201–205.
- Alexander, C. P.** 1920. New or little-known crane-flies from Formosa (Tipulidae, Diptera). *Annals of the Entomological Society of America*, **13**, 249–270.
- Alexander, C. P.** 1922. New or little-known Tipulidae (Diptera). X. Australasian species. *Annals and Magazine of Natural History*, **9**, 505–524.
- Alexander, C. P.** 1927. The interpretation of the radial field of the wing in the nematocerous Diptera, with special reference to the Tipulidae. *Proceedings of the Linnean Society of New South Wales*, **52**, 42–72.
- Alexander, C. P.** 1928. The Tanyderidae of Australia (Diptera). *Proceedings of the Linnean Society of New South Wales*, **54**, 367–374.
- Alexander, C. P.** 1929. *Diptera of Patagonia and South Chile. Part I. Crane-flies (Tipulidae, Trichoceridae, Tanyderidae)*. British Museum (Natural History), London, 240 pp.
- Alexander, C.P.** 1931. A new genus and species of bibionid Diptera. *Bulletin of the Brooklyn Entomological Society*, **26**, 7–11.
- Aristov, D. S., Grauvogel-Stamm, L. & Marchal-Papier, F.** 2011. New grylloblattid insects (Insecta: Grylloblattida) from the Grès à Voltzia of the Vosges (Middle Triassic of France). *Paleontological Journal*, **45**, 159–166.
- Aristov, D. S., Bashkuev, A. S., Golubev, V. K., Gorochoy, A. V., Karasev, E. V., Kopylov, D. S., Ponomarenko, A. G., Rasnitsyn, A. P., Rasnitsyn, D. A., Sinitshenkova, N. D., Sukatsheva, I. D. & Vassilenko, D. V.** 2013. Fossil insects of the Middle and Upper Permian of European Russia. *Paleontological Journal*, **47**, 641–832.
- Bergroth, E.** 1913. A new genus of Tipulidae from Turkestan, with notes on other forms. *Annals and Magazine of Natural History*, **11**, 575–584.
- Bertone, M. A., Courtney, G. W. & Wiegmann, B. M.** 2008. Phylogenetics and temporal diversification of the earliest true flies (Insecta: Diptera) based on multiple nuclear genes. *Systematic Entomology*, **33**, 668–687.
- Blagoderov, V. A., Grimaldi, D. A. & Fraser N. C.** 2007. How time flies for flies: diverse Diptera from the Triassic of Virginia and early radiation of the order. *American Museum Novitates*, **3572**, 1–39.
- Brunetti, E.** 1918. Revision of the oriental Tipulidae with descriptions of new species, Part 2. *Records of the Indian Museum*, **15**, 255–344.
- Cranston, P. S., Hardy, N. B. & Morse, G. E.** 2012. A dated molecular phylogeny for the Chironomidae (Diptera). *Systematic Entomology*, **37**, 172–188.
- Cumming, J. M. & Wood, D. M.** 2017. Adult morphology and terminology. Pp. 89–133 in A. H. Kirk-Spriggs & B. J. Sinclair (eds) *Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. Suricata 4*. South African National Biodiversity Institute, Pretoria.
- Durand, M.** 2013. Der Buntsandstein in Nordost-Frankreich. *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften*, **69**, 635–646.
- Edwards, F. W.** 1923. A preliminary revision of the crane-flies of New Zealand (Anisopodidae, Tanyderidae, Tipulidae). *Transactions of the New Zealand Institute*, **54**, 265–352.
- Enderlein, G.** 1912. Studien über die Tipuliden, Limoniiden, Cylindrotomiden und Ptychopteriden. *Zoologische Jahrbucher, Abteilung für Systematik, Geographie und Biologie der Tiere*, **32**, 1–88.
- Evenhuis, N. L.** 2014. Family Cylindrotomidae. In *Catalog of the fossil flies of the world (Insecta: Diptera) (Version 2.0)*. Updated at: <http://hbs.bishopmuseum.org/fossilcat>, accessed 10 October 2017.
- Gall, J. C.** 1971. Faunes et paysage du Grès à Voltzia du Nord des Vosges. Essai paléocécologique sur le Buntsandstein supérieur. *Mémoires du Service de la Carte géologique d'Alsace et de Lorraine*, **34**, 1–318.
- Gao, J., Shin, C., Kopeć, K., Krzemiński, W. & Ren, D.** 2015. New species and revisions of Pediciidae (Diptera) from the Middle Jurassic of northeastern China and Russia. *Zootaxa*, **3963**, 240–249.
- Goloboff, P. A.** 1993. Estimating character weights during tree search. *Cladistics*, **9**, 83–91.
- Goloboff, P. A.** 2014. Extended implied weighting. *Cladistics*, **30**, 260–272.
- Goloboff, P. A. & Catalano, S. A.** 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, **32**, 221–238.
- Goloboff, P. A., Carpenter, J., Arias, S. & Miranda, D.** 2008. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, **24**, 758–773.
- Grauvogel, L.** 1947a. Contribution à l'étude du Grès à Voltzia. *Compte Rendu Sommaire de la Société Géologique de France (ser. 5)*, **17**, 35–37.
- Grauvogel, L.** 1947b. Note préliminaire sur la faune du Grès à Voltzia. *Compte Rendu Sommaire de la Société Géologique de France (ser. 5)*, **17**, 91–92.
- Guérin-Méneville, F. E.** 1831. Insectes. Pp. 20–21 in L. I. Duperrey (ed.) *Voyage autour du monde, execute par ordre du Roi, sur la corvette de sa majeste La Coquille etc. Histoire naturelle, zoologie*. Atlas, Bertrand, Paris.
- Hackman, W. & Väisänen, R.** 1982. Different classification systems in the Diptera. *Annales Zoologici Fennici*, **19**, 209–219.
- Handlirsch, A.** 1906–1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen. Vol. 1–3*. Engelmann, Leipzig, 1430 pp.
- Handlirsch, A.** 1909. Zur Phylogenie und Flügelmorphologie der Ptychopteriden (Dipteren). *Annalen des k. k. Naturhistorischen Hofmuseums in Wien*, **23**, 263–272.
- Hennig, W.** 1954. Flügelgeäder und System der Dipteren unter Berücksichtigung der aus dem Mesozoicum beschriebenen Fossilien. *Beiträge zur Entomologie*, **4**, 254–388.
- Hennig, W.** 1968. Kritische Bemerkungen über den Bau der Flügelwurzel bei den Dipteren und die Frage nach der Monophylie der Nematocera. *Stuttgarter Beiträge zur Naturkunde*, **193**, 1–23.
- Hennig, W.** 1973. Diptera (Zweiflügler). *Handbuch der Zoologie*, **4(2)**, 2/31, 1–337.
- Jong, H. de.** 2014. When did the Tipulidae lift off? P. 76 in N. Dorchin, M. Kotrba, X. Mengual & F. Menze (eds.) *8th International Congress of Dipterology, 10–15.8.2014. Abstract volume*. Potsdam.
- Kalugina, N. S. & Kovalev, V. G.** 1985. *Dvukrylye nasekomye Yury Sibiri [Jurassic Diptera of Siberia]*. Nauka, Moscow, 198 pp. [In Russian].
- Kang, Z., Zhang, X., Ding, S., Tang, C., Wang, Y., de Jong, H., Cameron, S. L., Wang, M. & Yang, D.** 2017. Transcriptomes of three species of Tipuloidea (Diptera, Tipulomorpha) and implications for phylogeny of Tipulomorpha. *PLoS ONE* **12(3)**, e0173207.
- Krivoshina, N. P.** 1988. Approach to solutions of questions of classification of the Diptera. *Entomologicheskoe Obozrenie*, **67**, 378–390.

- Krzemiński, W. & Ansoerge, J. 1995. New Upper Jurassic Diptera (Limoniidae, Eoptychopteridae) from the Solnhofen Lithographic Limestone (Bavaria, Germany). *Stuttgarter Beiträge zur Naturkunde*, **B 221**, 1–7.
- Krzemiński, W. & Krzemińska, E. 2003. Triassic Diptera: descriptions, revisions and phylogenetic relations. *Acta Zoologica Cracoviensia*, **46**, 153–184.
- Krzemiński, W., Kania, I. & Krzemińska, E. 2010. A new species of *Dactylolabis* (*Eobothrophorus*) from Baltic amber (Diptera: Limoniidae). *Acta Geologica Sinica*, **84**, 768–771. [English edition].
- Krzemińska, E., Krzemiński, W. & Dahl, C. 2009. *Monograph of fossil Trichoceridae (Diptera): over 180 million years of evolution*. Institute of Systematics and Evolutions of Animals, Polish Academy of Sciences, Kraków, 171 pp.
- Krzemiński, W., Krzemińska, E. & Papier, F. 1994. *Grauvogelia arzvilleriana* sp. n. – the oldest Diptera species (Lower/Middle Triassic of France). *Acta Zoologica Cracoviensia*, **37**, 95–99.
- Lambkin, C., Sinclair, B., Pape, T., Courtney, G. W., Skevington, J. H., Meier, R., Yeates, D. K., Blagoderov, V. & Wiegmann, B. 2013. The phylogenetic relationships among infraorders and superfamilies of Diptera based on morphological evidence. *Systematic Entomology*, **38**, 164–179.
- Lara, M. B. & Lukashovich, E. D. 2013. The first Triassic dipteran (Insecta) from South America, with review of Hennigmatidae. *Zootaxa*, **3710**, 81–92.
- Latreille, P. A. 1809. *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata. Tomus quartus et ultimas*. Amand Koenig, Paris and Strasbourg, 399 pp.
- Lukashovich E. D. 2009. Limoniidae (Diptera) in the Upper Jurassic of Shar Teg, Mongolia. *Zoosymposia*, **3**, 131–154.
- Lukashovich, E. D., Przhiboro, A. A., Marchal-Papier, F. & Grauvogel-Stamm, L. 2010. The oldest occurrence of immature Diptera (Insecta), Middle Triassic, France. *Annales de la Société entomologique de France (n.s.)*, **46**, 4–22.
- Lukashovich, E. D. & Shcherbakov, D. E. 1999. A new Triassic family of Diptera from Australia. Pp. 81–90 in P. Vrsansky (ed.) *Proceedings of the first palaeoentomological conference Moscow 1998*. AMBA Projects Publication, Bratislava.
- Lukashovich, E. D. & Shcherbakov D. E. 2016. On morphology of *Tanyderus pictus* (Diptera: Tanyderidae) pupa and adult from Chile. *Russian Entomological Journal*, **25**, 79–95.
- Meigen, J. W. 1803. Versuch einer neuen Gattungs-Eintheilung der europäischen zweiflügligen Insekten. *Magazin für Insektenkunde*, **2**, 259–281.
- Neugart, C., Schneeberg, K. & Beutel, R. G. 2009. The morphology of the larval head of Tipulidae (Diptera, Insecta) – the dipteran groundplan and evolutionary trends. *Zoologischer Anzeiger*, **248**, 213–235.
- Nixon, K. C. & Carpenter, J. M. 1993. On outgroups. *Cladistics*, **9**, 413–426.
- Oosterbroek, P. & Courtney, G. W. 1995. Phylogeny of the nematocerous families of Diptera (Insecta). *Zoological Journal of the Linnean Society*, **115**, 267–311.
- Oosterbroek, P. & Theowald, B. 1991. Phylogeny of the Tipuloidea based on characters of larvae and pupae (Diptera, Nematocera) with an index to the literature except Tipulidae. *Tijdschrift voor Entomologie*, **134**, 211–267.
- Osten-Sacken, C. R. 1860. New genera and species of North American Tipulidae with short palpi, with an attempt at a new classification of the tribe. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1859**, 197–256.
- Petersen, M. J., Bertone, M. A., Wiegmann, B. M. & Courtney, G. W. 2010. Phylogenetic synthesis of morphological and molecular data reveals new insights into the higher-level classification of Tipuloidea (Diptera). *Systematic Entomology*, **35**, 526–545.
- Philippi, R. A. 1865. Aufzählung der chilenischen Dipteren. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien*, **15**, 597–782.
- Podenas, S. 2003. *Dactylolabis* crane flies (Diptera: Limoniidae) in Baltic amber (Eocene). *Proceedings of the Academy of Natural Sciences of Philadelphia*, **153**, 49–65.
- Poinar, G. O., Jr. & Brown, A. E. 2004. A new genus of primitive crane flies (Diptera: Tanyderidae) in Cretaceous Burmese amber, with a summary of fossil tanyderids. *Proceedings of Entomological Society of Washington*, **106**, 339–345.
- Poinar, G. Jr & Brown, A. 2006. The enigmatic *Dacochile microsoma* Poinar & Brown: Tanyderidae or Bruchomyiinae? *Zootaxa*, **1162**, 19–31.
- Ribeiro, G. C. 2006. Homology of the gonostylus parts in crane flies, with emphasis on the families Tipulidae and Limoniidae (Diptera, Tipulomorpha). *Zootaxa*, **1110**, 47–57.
- Ribeiro, G. C. 2008. Phylogeny of the Limnophilinae (Limoniidae) and early evolution of the Tipulomorpha (Diptera). *Invertebrate Systematics*, **22**, 627–694.
- Ribeiro, G. C. 2009. The Neotropical genus *Stibadocerina* Alexander and its phylogenetic relationship to other Stibadocerinae genera: further evidence on an ancestral trans-Pacific Biota. *Systematic Entomology*, **34**, 324–333.
- Ribeiro, G. C. & Eterovic, A. 2011. Neat and clear: 700 species of crane flies (Diptera: Tipulomorpha) link southern South America and Australasia. *Systematic Entomology*, **36**, 754–767.
- Ribeiro, G. C. & Lukashovich, E. D. 2014. New *Leptotarsus* from the Early Cretaceous of Brazil and Spain: the oldest members of the family Tipulidae (Diptera). *Zootaxa*, **375**, 347–363.
- Rondani C. 1856. *Dipterologiae Italicae Prodromus. Genera Italica ordinis dipterorum ordinatim disposita et distincta et in familias et stirpes aggregata*, Stocchi, Parma, 228 pp.
- Savchenko, E. N. 1986. [Limoniid flies.] *Fauna Ukraini*, **14** (2). Naukova Dumka, Kiev, 340 pp. [In Russian].
- Scudder, S. H. 1894. Tertiary Tipulidae, with special reference to those of Florissant, Colorado. *Proceedings of the American Philosophical Society*, **32**, 163–245.
- Shcherbakov, D. E., Lukashovich, E. D. & Blagoderov, V. A. 1995. Triassic Diptera and initial radiation of the order. *International Journal of Dipterological Research*, **6**, 75–115.
- Sinitshenkova, N. D., Marchal-Papier, F., Grauvogel-Stamm, L. & Gall J.-C. 2005. The Ephemeroidea (Insecta) from the Grès à Voltzia (early Middle Triassic) of the Vosges (NE France). *Paläontologische Zeitschrift*, **79**, 377–397.
- Starý, J. 1992. Phylogeny and classification of Tipulomorpha, with special emphasis on the family Limoniidae. *Acta Zoologica Cracoviensia*, **35**, 11–36.
- Wiegmann, B. M., Trautwein, M. D., Winkler, I. S., Barr, N. B., Kim, J.-W., Lambkin, C., Bertone, M. A., Cassel, B. K., Bayless, K. M., Heimberg, A. M., Wheeler, B. M. and 16 others. 2011. Episodic radiation in the fly tree of life. *Proceedings of the Natural Academy of Sciences*, **108**, 5690–5695.
- Williams, I. W. 1933. The external morphology of the primitive tanyderid dipteran *Protoplasma fitchii* O.S., with notes on the other Tanyderidae. *Journal of the New York Entomological Society*, **41**, 1–35.
- Wood, D. M. & Borkent, A. 1989. Phylogeny and classification of the Nematocera. *Manual of Nearctic Diptera, Vol. 3. Research Branch, Agriculture Canada, Monograph*, **32**, 1333–1370.

- Wootton, R. J. & Ennos, A. R.** 1989. The implications of function on the origin and homologies of the dipterous wing. *Systematic Entomology*, **14**, 507–520.
- Yeates, D. K., Wiegmann, B. M., Courtney, G. W., Meier, R., Lambkin, C. & Pape, T.** 2007. Phylogeny and systematics of Diptera: two decades of progress and prospects. *Zootaxa*, **1668**, 565–590.
- Zetterstedt, J. W.** 1838. Sectio tertia. Diptera. Pp. 477–868 in J. W. Zetterstedt (ed.) *Insecta Lapponica*. Voss, Lipsia (= Leipzig).
- Zhang, X., Kang, Z., Mao, M., Li, X., Cameron, S. L., de Jong, H., Wang, M. & Yang, D.** 2016. Comparative Mt genomics of the Tipuloidea (Diptera: Nematocera: Tipulomorpha) and its implications for the phylogeny of the Tipulomorpha. *PLoS ONE* **11**(6), e0158167.