

Triassic Diptera: descriptions, revisions and phylogenetic relations

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Abstract. Triassic Diptera are reviewed and their systematic classification and phylogenetic importance are discussed. Four new species of Diptera are described from the Lower/Middle Triassic of France: *Louisa nova*, n. gen. et sp. (Grauvogeliidae), *Tanus triassicus*, n. gen. et sp. (Nadpteridae), *Archilimonia vogesiana*, n. gen. et sp. (Archilimoniidae, n. fam.), *Vymrhypus blagoderovi* n. sp. (Protorhyphidae) and *Gallia alsatica* n. gen. et sp. (Rhagionidae), which – together with *Grauvogelia arzvilleriana* earlier described from the same deposits – represent the oldest Diptera known. The following changes in taxonomy are introduced: family Vladipteridae with species: *Vladiptera kova-levi* and *Dilemmala specula* SHCHERBAKOV 1995 is transferred to Mecoptera. The subfamilies: Psychotipinae and Kuperwoodinae are raised to a family rank. Subfamily Gnomuscinae is considered a doubtful Diptera and transferred, with some reservation, to the Trichoceromorpha at the family rank. Family Alinkidae is transferred from infraorder Tabanomorpha to Xylophagomorpha. Two new infraorders are established: Hennigmatomorpha and Tillyardomorpha. Phylogenetic trees of all five suborders of Diptera are presented (i. e., of the Diarchineura, Neoneura, Polyneura, Anisoneura and Brachycera). Representatives of all these suborders are known from the Triassic, and, with exception of the Neoneura, were present already in the Lower/Middle Triassic of France, i. e., the oldest deposits bearing the Diptera.

Key words: new species, new genus, new family, Diptera, fossil, Triassic, France, phylogeny.

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I. INTRODUCTION

The hitherto oldest Diptera were discovered in the Vosges Mts (France, Alsace) by Louis GRAUVOGEL and Jean-Claude GALL and are dated at the turn of Lower to Middle Triassic (Voltzia-Buntsandstein, c. 240 Ma; GALL & GRAUVOGEL 1966). The collection comprises several thousand of fossil insects of various orders. Among the Diptera there are larvae, pupae, adults and their separate wings. Till now one species, *Grauvogelia arzvilleriana* KRZEMIŃSKI, KRZEMIŃSKA & PAPIER (1994) of a new family Grauvogeliidae was described. In the present paper remaining four species of this collection. They represent main four lineages of the Diptera: Diarchineura, Polyneura, Anisoneura and Brachycera.

Up to 90' the Triassic Diptera were very scarce; since then however they became more numerous and now representatives of 16 families are known (listed in the Appendix). The first species described, *Crosaphis anomala* EVANS 1971 from the Upper Triassic of Australia, was classified erroneously to the Homoptera; later identified as a dipteran species of Crosaphididae (Anisopodomorpha) by KOVALEV (1983a). Upper Triassic Diptera from North America were recorded by OLSEN et al. (1978) and later described by KRZEMIŃSKI (1992). There were three species representing Limoniidae (Tipulomorpha), one species of Proqramptomomyiidae (Anisopodomorpha), one species of Alinkidae (Tabanomorpha, now Xylophagomorpha) and one specimen incerta sedis of the Eoptychopteridae (Ptychopteromorpha). Other findings of Triassic Diptera from Ferganskaya Valley (Kyrgyzstan) were recorded by KOVALEV (1983b) and described later by SHCHERBAKOV et al. (1995) together with other Triassic Diptera from Central Asia. Thirteen species of five families (Vladipteridae, Limoniidae, Nadipteridae, Hennigmatidae and Protorhyphidae) were distinguished by these authors. However, classification of some to the Diptera is doubtful and their position is revised herein.

From the Upper Triassic of Australia BLAGODEROV (1999) described two new species of Proqramptomomyiidae and Paraxymyiidae and LUKASHEVICH & SHCHERBAKOV (1999) described a new family Tillyardipteridae basing on one species. From the Upper Triassic of England the oldest species of the extant family Chironomidae is known (KRZEMIŃSKI & JARZEMBOWSKI 1999) and a representative of a new fossil family Rhaetanidae (KRZEMIŃSKI & KRZEMIŃSKA 2002).

The Diptera described by ROHDENDORF (1961, 1962) from Issyk-Kul (Kyrgyzstan, Asia) and dated at the Triassic were later estimated at the Lower Jurassic (GENKINA 1966). All insects described from the Permian by TILLYARD (1929), RIEK (1977) and WILLMANN (1989) belong to the Mecoptera. A vast majority of information on fossil Diptera described before 1994 is comprised in the catalogue by EVENHUIS (1994).

The aim of this work is the description the Diptera from Lower/Middle Triassic of France, and their placement in right taxonomic and phylogenetic context. To enable this, a revision of some Triassic and Jurassic materials was necessary (see the Systematic Part). Also discussed are the basic apomorphies of dipteran wing, which lay at the stem of the order.

A c k n o w l e d g e m e n t s. We are grateful to J.-P. GALL and L. GRAUVOGEL-STAMM (Institut de Géologie de l'Université Louis Pasteur, Strasbourg) for a loan of Diptera described herein. We thank also D. SHCHERBAKOV and other Colleagues from the Laboratory of Fossil Insects, Paleontological Institute RAS in Moscow for making the specimens discussed herein available to us, for their warm (as always) welcome and long, inspiring discussions, which, however, have not changed our respective views on the taxonomy and phylogeny of the Diptera.

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II. MATERIAL AND METHODS

The collection of GRAUVOGEL et GALL from the Vosges Mts (France, Alsace) comprises following Diptera: 54 specimens of *Grauvogelia arzvilleriana*, at least two larvae of Diptera, several pupae and also five adults which are the subject of the present study. Three of them have body partially preserved, and two are known only from separate wings. Their condition is generally poor and some of features described below are visible only after a very careful examining in polarized light. All specimens are covered with a diluted Arabic gum which prevents their wetting with water or alcohol.

Nomenclature and homology of wing veins

We follow here the nomenclature of BYERS (1989), i. e., with four medial veins, one cubital and two anal veins, a system usually applied in the Tipulomorpha. This system is both the simplest one and most probably homologous with that of higher Mecoptera (Fig. 1). Although hypothetic groundplans of Diptera venation (MCALPINE 1981: Fig. 2.67, after HENNIG 1973: Fig. 111) present a basal cubital vein forked in two veins (CuA1 and CuA2), such pattern does not occur in any Mecoptera with dipteroidal venation, nor in most primitive Diptera (fossil and Recent representatives

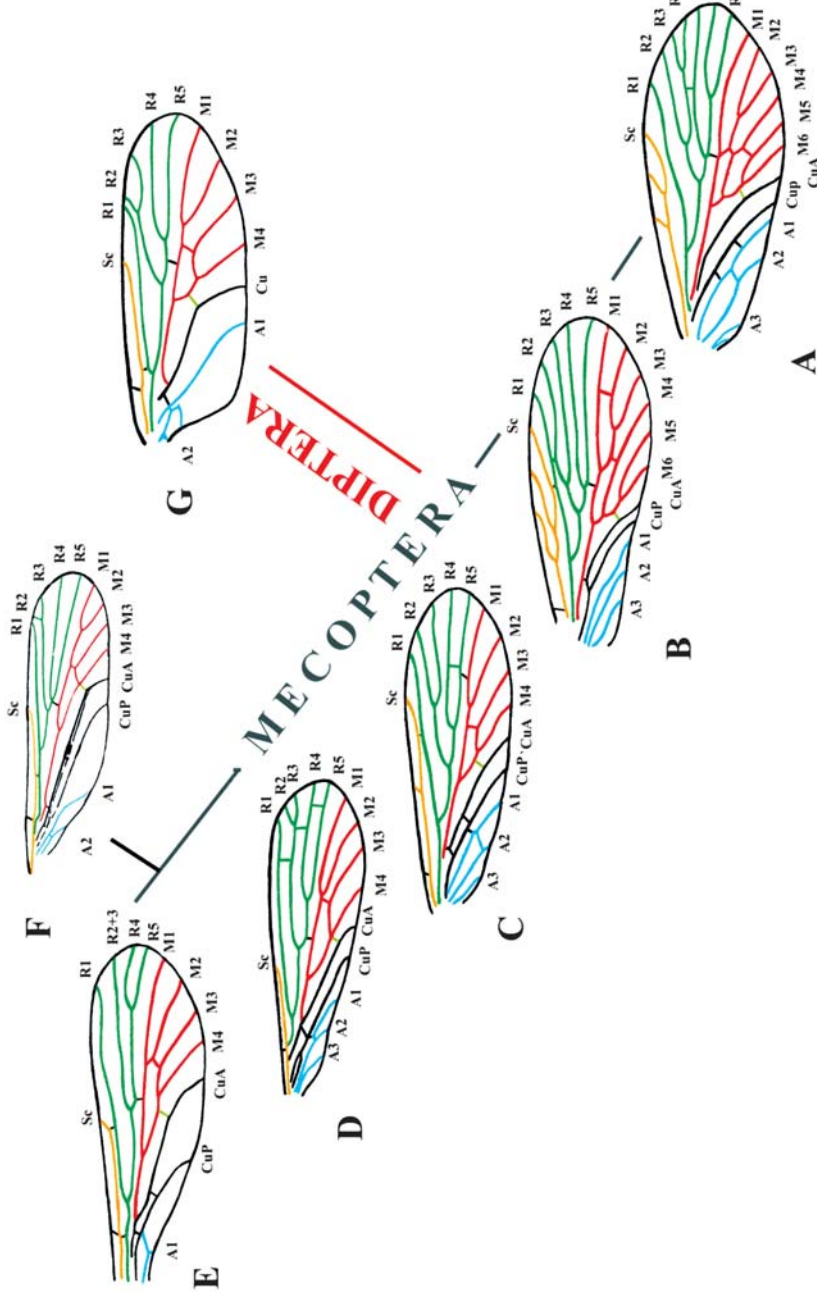


Fig. 1. Phylogenetic relations within the Mecoptera with dipteroidal venation (A-F) and the origin of Diptera at the beginning of Triassic. Colour of veins: yellow – subcostal field; green – radial; red – medial; black – cubital; blue – anal. Cross-vein m-cu highlighted in light green to show its constant position. A. *Oochorista gunderseni* MARTYNOV 1933 (Permochoiritidae; Upper Permian, Asia); B. *Petromantis sar-balensis* MARTYNOVA 1961 (Permochoiritidae; Upper Permian, Asia); C. *Prochoristella megaioprepia* RIEK 1952 (Permochoiritidae; Upper Permian, Australia); D. *Robinjohnia tillyardi* MARTYNOVA 1948 (Robinjohnidae; Upper Permian, Australia); E. *Permotipula patricia* TILLYARD 1929 (Permotipulidae; Upper Permian, Australia); F. *Vladiptera kovalevi* SHCHERBAKOV 1995 (Vladipteridae; Upper Triassic, Asia); G. *Grauvogelia arzvilleriana* KRZEMINSKI, KRZEMINSKA & PAPIER 1994; (Grauvogeliidae; Lower/Middle Triassic, France). A, B, D after NOVOKSHONOV 1997; C, E after WILLMANN 1989; F after SHCHERBAKOV 1995.

of both groups included). In these groups we find invariably one basal medial vein Mb forked into two branches, which in Mecoptera fork dichotomically into numerous medial veins. In the Diptera these are reduced to four ones, M1 - M4 in a sequence of reductions which can be traced easily in the Permian Mecoptera with dipteroidal venation (Fig. 1). Also invariably, in both groups the cross-vein m-cu connects the medial vein with the cubital one (Fig. 1). This position and role of cross-vein m-cu has been misinterpreted in the groundplan of Diptera by MCALPINE (1981: Fig. 2.67) where this cross-vein is considered a basal section of CuA1, while a basal section of M4 plays the role of m-cu.

III. SYSTEMATIC PART

ORDER: MECOPTERA

Family: **Vladipteridae** SHCHERBAKOV 1995

The family was described within the Diptera, from the Upper Triassic of Kazakhstan (Central Asia) by SHCHERBAKOV (in: SHCHERBAKOV et al. 1995) and originally comprised two subfamilies: Vladipterinae and Psychotipinae.

Vladipterinae comprise two monotypic genera described on species: *Vladiptera kovalevi* SHCHERBAKOV and *Dilemmala specula* SHCHERBAKOV. My (WK) repeated, meticulous reexamination of these holotypes resulted in stating that *Vladiptera kovalevi* does not belong to Diptera and should be classified to the Mecoptera with dipteroidal venation, similar to that in *Robinjohnia tillyardi* RIEK (Fig. 1D) or *Permotipula patricia* TILLYARD (Fig. 1E), or *Permila borealis* (MARTYNOVA). *V. kovalevi* (Fig. 1F) has two cubital and two anal veins (CuA, CuP, A1 and A2, according to SHCHERBAKOV et al. 1995), as, ex., in *Robinjohnia* and *Permila*. Till now this pattern is known only in the Mecoptera, some Lepidoptera and some Trichoptera, and never was found in the Diptera.

The cubital and anal fields of this single wing are so poorly preserved that we do not know whether it belongs to the four- or two-winged specimen; the venation, according to our present knowledge, speaks for a four-winged insect, probably of the Mecoptera. However, if an undoubtedly two-winged specimen with that venation is found in future, the four veins in cubito-anal field would deserve a distinguished position among the Diptera, at least of a separate suborder, a sister group of all remaining Diptera.

The second species of this subfamily, *Dilemmala specula*, lacks the cubito-anal field. Thus its classification to the Diptera is also insufficiently based. Summarizing, the Vladipteridae (without Psychotipinae) belong in our opinion to the Triassic Mecoptera with dipteroidal venation, a group flourishing in the Permian.

Diagnosis and description are given by SHCHERBAKOV et al. (1995: 86). Family comprises two species of two genera: *Vladiptera kovalevi* and *Dilemmala specula*.

The Psychotipinae, with one genus and two species, *Psychotipa predicta* SHCHERBAKOV 1995 and *P. depicta* SHCHERBAKOV 1995, were originally described as a subfamily of Vladipteridae. They have three veins in cubito-anal field and undoubtedly belong the Diptera. The long A2 vein places them safely within the Polyneura, infraorder Tipulomorpha, as a separate family Psychotipidae, comb. nov. (see Appendix and Fig. 7). Differences in wing venation between its two species indicate that in the Triassic this group was more numerous and diversified.

ORDER: DIPTERA

The oldest finds of Diptera come from the end of Lower Triassic. Already these scarce findings evidence earlier radiation of this group into different lineages, as will be presented later. Therefore it seems plausible that Diptera had branched off the main stem of the Mecoptera about the turn of Permian to the Triassic. It is very probable that Diptera originated from Permochoresitidae (Fig. 1), very common during the Permian, or from other mecopteran lineage close to this family. Permian Mecoptera exhibited a strong tendency to a). reduction of venation in fore wings, and b). reduction of hind wings size (and function).

These tendencies can be observed in the Permian and Triassic Mecoptera (Polycentropodidae, Permochoristidae, Robinjohniidae, Permotipulidae and Laurentipteridae; Fig. 1), and also are present in Recent Mecoptera. For instance, Nannochoristidae show reduced wing venation, while Boreidae and Apteropanorpidae have wings strongly reduced. WOOD & BORKENT (1989) had even supposed that Nannochoristidae could be a sister group to the Diptera + Siphonaptera. However, this idea lacks the evidence, because according to NOVOKSHONOV (1997) the oldest Nannochoristidae are not known before the Lower Jurassic, and the Siphonaptera stay closer to the Mecoptera than the Diptera.

The phylogenetic tree (Fig. 1) presents relations between Mecoptera and Diptera. A tendency to reduction of wing venation in Mecoptera can be observed. The same parallel tendency in Diptera is well known.

Wing venation in Recent Diptera is easily distinguishable from that of the Mecoptera by numerous apomorphies. However, wings of the oldest Diptera do not differ so much from some mecopteran wings; hence the difficulties in classifying single fossil wings (see the section on Vladipteridae). Four main synapomorphies of wings of the Diptera are known:

1. Hind wing reduced to a haltere
2. One cubital vein present
3. Anal veins reduced to anal loop
4. Anal lobe present.

Transformation of the mecopteran hind wing into a dipteran haltere is the primordial apomorphy of the Diptera. Sometimes only a finding of a body with wings allows to discern oldest Triassic and Diptera from the Mecoptera, because wing venation of separate wings in both orders happens to be too similar to ensure safe classification to the order. Examples of such errors are known (TILLYARD 1929, 1937; RIEK 1977; JELL & DUNCAN 1986; WILLMANN 1989); separate wings were originally classified to the Diptera by these authors, and only later findings of more complete specimens allowed to verify their position and to transfer them to the Mecoptera. Most probably, this will be also the case of the Vladipteridae.

According to the present state of knowledge, the fore wing of Mecoptera with dipteroidal venation can be very similar to the dipteran one. Only two differences seem to exist: Diptera have only one cubital vein, probably CuA (in result of complete reduction of the second, probably CuP), and the presence of the anal loop in place of mecopteran A2 and A3.

Anal loop (or: anal ring in KRZEMIŃSKI & EVENHUIS 2000) is a poorly recognizable structure present at base of anal field in many Recent Diptera: Tanyderidae, Ptychopteridae, Anisopodidae, Cramptonomyiidae, and almost all Lower Brachycera. Only a find of *Grauvogelia arzwilleriana*, the hitherto oldest Diptera (Lower/Middle Triassic of France; KRZEMIŃSKI et al. 1994), allowed to recognize its previous, ancestral shape and propose its possible homology with second and third anal vein of the Mecoptera. A grauvogeliid anal loop is the fully developed vein with scarce bristles (Fig 1G). A similar anal loop is also known in some Lepidoptera and Trichoptera (KRZEMIŃSKI et al. 1994; KRZEMIŃSKI & EVENHUIS 2000). The anal loop, well developed in *G. arzwilleriana*, underwent a stepwise reduction in some lineages, and vanished completely in others (ex. higher Brachycera); while in other (Polyneura), quite contrarily, it have been expanded into a long anal vein. All these modifications of anal venation can be led from the anal loop of this oldest fly (Figs 3, 8).

Broad anal lobe distinguishes the dipteran wing from the mecopteran one. Physically and functionally, it partially fulfills the role of a hind wing of Mecoptera. Hence isolated mecopteran wings can be usually recognized by the lack of anal lobe; the wing base is narrowed in petiole-like way, or even excised to make place for a smaller hind wing (as in *Laurentiptera gallica* LAURENTIAUX et GRAUVOGEL (in LAURENTIAUX 1953); illustrated in KRZEMIŃSKI & KRZEMIŃSKA 1996 and in KRZEMIŃSKI & EVENHUIS 2000: Fig 10). Also the connection of wing with the body is generally more narrow in Diptera, allowing better maneuverability of the wing. In some advanced Recent

Diptera the anal lobe is absent (Psychodidae, Vermileonidae), but most Diptera have it. Exception are some separate wings of unrecognized origin, as Vladipteridae or Gnomuscidae (discussed later).

The order Diptera is divided into five distinct lineages defined as the suborders: Diarchineura, Neoneura, Polyneura, Anisoneura and Brachycera (Fig. 2).

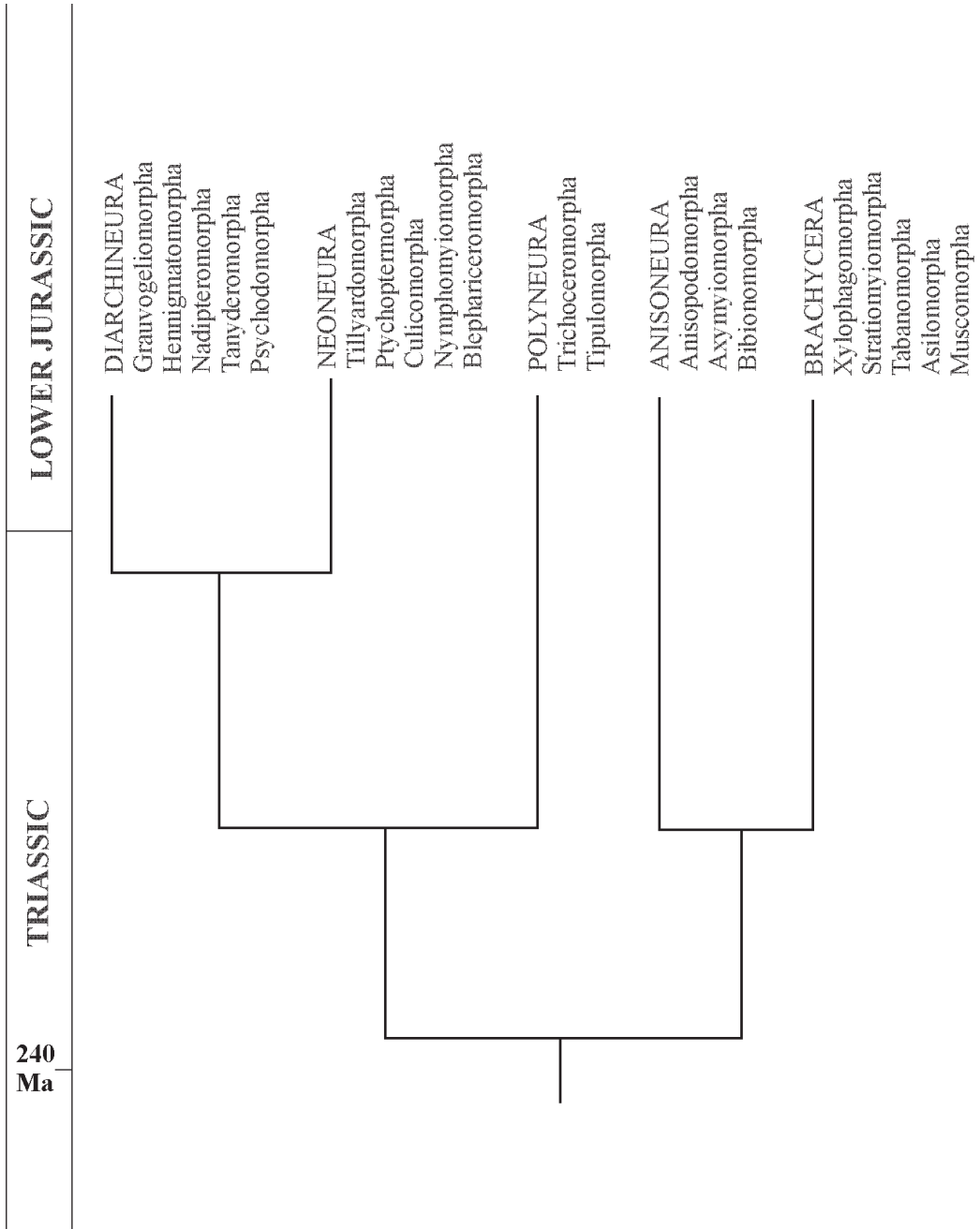


Fig. 2. General phylogenetic system of the Diptera. Triassic Diptera evidence rapid radiation of the order and show distinct division into five main evolutionary lineages: Diarchineura, Neoneura, Polyneura, Anisoneura and Brachycera (after KRZEMIŃSKI & EVENHUIS 2000). Relations within particular lineages are presented separately (Figs 3, 6, 7, 10, 12, 13).

SUBORDER: DIARCHINEURA KRZEMIŃSKI, 1992

D i a g n o s i s o f s u b o r d e r. (First diagnosis was given by KRZEMIŃSKI, 1992; new fossil Diptera described since that time require updating of diagnosis as follows). Five radial veins terminate in wing margin; cross-vein r-r absent; four medial veins present; second anal vein shaped as anal loop of various shape and size.

R e d e s c r i p t i o n. Sc usually reaching beyond mid wing (shorter in some Recent Tanyderidae and Psychodidae); sc-r at base of Sc (Grauvogeliidae, Nadipteridae), in mid of Sc (Hennigmatidae) or at end (Tanyderidae, Psychodidae); five radial and four medial veins terminating in wing margin (only in some fossil and Recent Psychodidae the radial and medial veins are partially reduced, but this reduction can be always recognized as obvious apomorphy). Discal cell variable, usually rather large, and/or conspicuously elongated (Hennigmatidae, Nadipteridae, Tanyderidae, some fossil Psychodidae); only in Psychodidae open by atrophy of cross-vein m-m between M2 and M3; in majority of Diarchineura d cell is petiolate, i.e., a free section of M1+2 is present beyond d cell (petiole absent only in Tanyderidae and Psychodidae). Cross-vein m-cu usually in distal portion of M3+4 (i.e., at base of d cell), sometimes in fork of this vein or beyond it (then directly attached to M4); only in Grauvogeliomorpha in mid of M3+4. Between Cu and A1 pseudovein usually present (no trace of it only in Grauvogeliidae). Second anal vein forming characteristic loop, probably homologous to and arisen from two anal veins (A2 and A3) of Mecoptera, connected by cross vein (Fig. 1G).

Family Grauvogeliidae from the Lower/Middle Triassic of France is the oldest and most characteristic member of this suborder.

Diarchineura are represented by four extinct families: Grauvogeliidae (Lower/Middle Triassic), Kuperwoodidae (Upper Triassic), Hennigmatidae (Lower Jurassic to Lower Cretaceous), Nadipteridae (Lower/Middle Triassic to Lower Jurassic), and by two Recent families: Tanyderidae (known since Lower Jurassic) and Psychodidae (known since Middle Jurassic). These families represent five infraorders: Grauvogeliomorpha, Hennigmatomorpha, Nadipteromorpha, Tanyderomorpha and Psychodomorpha. Fig. 3 presents their relationships within the Diarchineura, illustrated by wing venation of main representatives.

Infraorder: Grauvogeliomorpha KRZEMIŃSKI, KRZEMIŃSKA & PAPIER, 1994

The infraorder separates Grauvogeliidae KRZEMIŃSKI, KRZEMIŃSKA & PAPIER, 1994.

Family: Grauvogellidae

The family was till now represented by one monotypic genus and species, *Grauvogelia arzville-riana* KRZEMIŃSKI, KRZEMIŃSKA & PAPIER 1994 from the Lower/Middle Triassic of France. Among the same material a specimen of the same family, but representing a second genus and species was found.

D i a g n o s i s of the family remains unchanged.

Genus: *Louisa* gen. nov.

D i a g n o s i s. Arculus present; r-m just behind fork of Rs into R2+3 and R4+5 and in mid of upper margin of d cell; m-cu in fork of M3+4.

Type species: *Louisa nova*, sp. n., Lower/Middle Triassic of France.

E t y m o l o g y. The new genus name is dedicated to the collector and owner of the collection, Louis GRAUVOGEL. Gender: feminine.

D e s c r i p t i o n of the genus is covered by that of its only species.

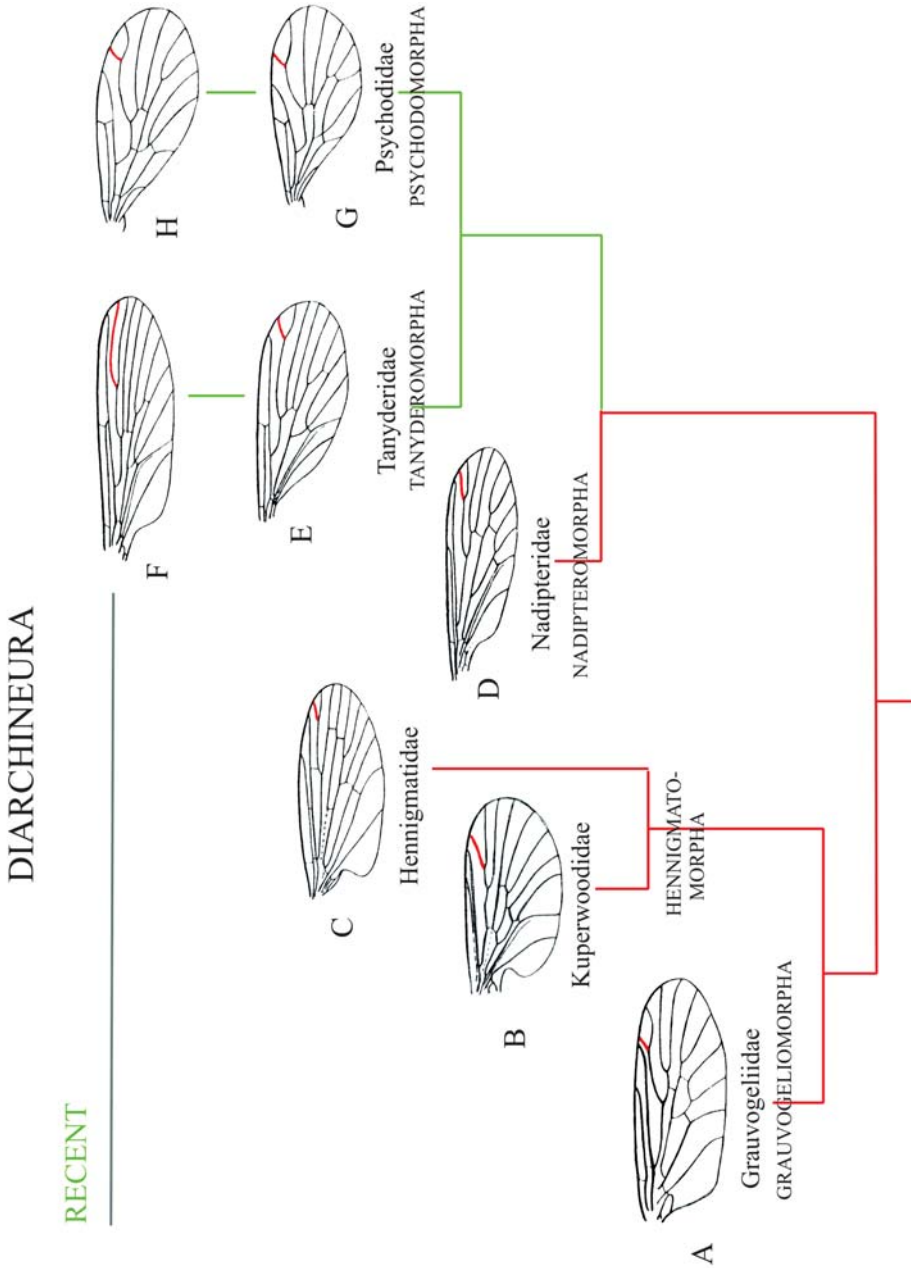


Fig. 3. Phylogenetic relations within the suborder Diarchineura. A. *Grauvogelia arzwilleriana* KRZEMIŃSKI, KRZEMIŃSKA & PAPIER 1994 (Grauvogeliidae; Lower/Middle Triassic, France); B. *Kuperwoodia benefica* LUKASHEVICH 1995 (Kuperwoodiidae; Middle/Upper Triassic, Kyrgyzstan); C. *Metatrichopteridium cladistorum* (SHCHERBAKOV) 1995 (Hennigmatidae; Lower Cretaceous, Mongolia); D. *Tanis triassicus* n. sp. (Nadipteridae; Lower/Middle Triassic of France); E. *Nannotanyderus krzeminski* ANSORGE 1994 (Tanyderidae; Lower Jurassic, Germany); F. *Macrochile spectrum* LOEW 1850 (Tanyderidae; Upper Eocene); G. *Tanypsycha connexa* ANSORGE 1994 (Psychodidae; Lower Jurassic, Germany); H. *Liasopsychodina pommerana* ANSORGE 1994 (Psychodidae; Lower Jurassic, Germany). (Source: B, C: SHCHERBAKOV 1995; E, G, H: ANSORGE 1994).

Louisa nova, sp. n.

Fig. 4.

D i a g n o s i s is the same as diagnosis of the genus.

M a t e r i a l examined. Holotype No. 6507/6508 (+,-), Arzviller (locality No. 118b), Vosges Mts, France. Age: Lower/Middle Triassic. Coll. L. GRAUVOGEL and J.-P. GALL; housed in the Institut de Géologie de l'Université Louis Pasteur, Strasbourg, France.

D e s c r i p t i o n. An almost complete single wing 3.1 mm long, with a small basalmost portion lacking; specimen covered with diluted Arabic gum. Venation (Fig. 4): Sc, R1 and Cu distinctly stronger than remaining veins; Sc ending before mid of wing, mildly curved and not parallel to costal wing margin, which is convex; Rb without basal kink; arculus shaped as strong cross-vein; outlet of Rs obscure; five radial veins terminate in wing margin (R2 better visible in negative counterpart); R2+3 three times longer than R2 and R3 twice longer than R2; r-m connecting first fork of Rs and mid of d cell upper margin; fork of R4+5 poorly visible; R4 is probably 4 times longer than R4+5; four medial veins present; d cell small (1/7 of wing length) and positioned under level of Mb; petiole of d cell present, c. 1/4 of M2 length; m-cu in fork of M3+4; Cu long, curved to wing margin; A2 not retained.

R e m a r k s. A new species reminds *Grauvogelia arzvilleriana*, the most important distinguishing features being: arculus present; Rb without basal kink; r-m in fork of Rs and m-cu in fork of M3+4. Regarding the phylogenetic (RIEK 1977) importance implied by presence/absence of arculus and initial shape of Rb, we separate the specimen in a new genus.

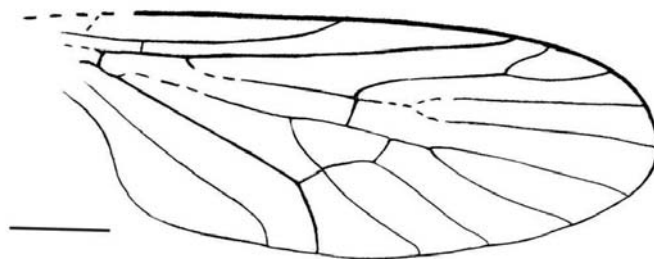


Fig. 4. *Louisa nova*, sp. n., wing (Grauvogeliidae, Lower/Middle Triassic of France). Bar 0.5 mm.

Infraorder: Hennigmatomorpha, n. comb.

D i a g n o s i s. R5 long, originating directly from Rs (and not from R4+5); Rs forking into R2+3+4 and R5.

Two families are included: Hennigmatidae from the Lower Jurassic of Germany and from Lower Cretaceous of Mongolia, and Kuperwoodidae from Middle/Upper Triassic (Ladinian – Carnian) of Kyrgyzstan (Central Asia).

Superfamily: **Hennimatoidea** SHCHERBAKOV, 1995

Family: **Hennigmatidae** SHCHERBAKOV et al., 1995

Family Hennigmatidae described from the Middle Triassic of Central Asia comprised two genera: *Hennigma* SHCHERBAKOV 1995 and *Anemeca* SHCHERBAKOV 1995, until ANSORGE (2001) proved that the genus *Hennigma* is a younger synonym of *Metatrichopteridium* HANDLIRSCH 1939, described from the Lower Jurassic of Germany and originally placed in Trichoptera.

The genus *Anemeca* with one species, *A. liya*, was described from the Upper Triassic of Kyrgyzstan (Central Asia). The shape of this single wing (SHCHERBAKOV et al. 1995: Fig. 32; KRZEMIŃSKI

& EVENHUIS 2000: Fig. 14.16) devoid of anal lobe indicates rather a four-winged insect (Mecoptera or Trichoptera), and not a representative of Diptera. In any case, differences in wing venation between *Metatrichopteridium* (= *Hennigma*) and *Anemeca* are too large to fall within one family.

In our opinion the family Hennigmatidae comprises only one genus, *Metatrichopteridium*, with two species: *M. confusum* HANDLIRSCH 1939 from the Lower Jurassic of Germany (a type species), and *M. cladistorum* (SHCHERBAKOV 1995) from the Lower Cretaceous of Mongolia. In this situation no representatives of this family are known from the Triassic.

D i a g n o s i s of family (modified herein after removing *Anemeca*). Wing (Fig. 3C) very broad, with large anal lobe; five radial and four medial veins terminate in wing margin; d cell very narrow and almost as long as half wing length; additional cross veins present in cells r1, r4 and r5.

Type species: *Metatpychopteridium confusum* HANDLIRSCH 1939 from Lower Toarcian of Dobbertin (Germany).

Family: **Kuperwoodiidae**, comb. nov.

Subfamily: Kuperwoodiinae LUKASHEVICH, 1995

Genus: ***Kuperwoodia*** LUKASHEVICH, 1995.

Fig. 3B

The subfamily Kuperwoodiinae is raised to a family level because of numerous striking differences in shape and venation of wing (compare Kuperwoodiidae and Hennigmatidae: Fig. 3B, C).

D i a g n o s i s of family remains the same as that of a former subfamily (SHCHERBAKOV et al. 1995: p. 92). The family comprises one genus and species, *Kuperwoodia benefica* LUKASHEVICH (in: SHCHERBAKOV et al. 1995) from Middle/Upper Triassic of Kyrgyzstan.

Infraorder: Nadipteromorpha KRZEMIŃSKI & EVENHUIS 2000.

D i a g n o s i s. Five radial veins, four medial and one anal vein terminate in wing margin; d cell very long and narrow; cross-vein m-cu beyond mid of M3+4 or between M4 and Cu.

One family is included, Nadipteridae, with two genera and four species known from the Middle/Upper Triassic to Lower Jurassic of Asia and Europe.

Family: **Nadipteridae** LUKASHEVICH, 1995

The family Nadipteridae is removed from Ptychopteroidea (where it was originally classified; SHCHERBAKOV et al. 1995) and separated into own infraorder. Nadipteridae (Fig. 3D), with five radial veins, represent the oldest lineage of the Diptera (Diarchineura) and have all diagnostic characters ascribed to this infraorder. Ptychopteromorpha with four radial veins belong other evolutionary lineage, the Neoneura.

D i a g n o s i s of the family is the same as that of the infraorder.

The family comprises now two genera: *Nadiptera* LUKASHEVICH, 1995 with three species: *N. kaluginae* and *N. pulchella* LUKASHEVICH 1995 from the Middle/Upper Triassic of Kyrgyzstan and *Nadiptera anachrona* LUKASHEVICH from the Lower Jurassic of Kyrgyzstan, and a new genus and species from the Lower/Middle Triassic of France.

Genus: ***Tanus***, n. gen.

D i a g n o s i s. Five radial veins terminate in wing margin; R2 very short; R2+3 long, 5 times longer than R2; r-m in midlength of R4+5 and in proximal 1/5 of d cell upper margin; d cell probably without petiole; cross-vein m-m between M2 and M3; cross-vein m-cu between M4 and Cu.

Type species: *Tanus triassicus*, n. sp., Lower/Middle Triassic of France.

E t y m o l o g y. A new genus name refers its probable direct descendants, a Recent family Tanyderidae. Gender: masculine.

D e s c r i p t i o n of new genus is covered by that of its only species.

Tanus triassicus, n. sp.

Fig. 5 A-D

D i a g n o s i s is the same as that of the new genus.

E t y m o l o g y. Species name refers to age its age, the Triassic.

M a t e r i a l. Holotype No. 5336, male, Arzwiller (locality No. 108), Vosges Mts, France. Age: Lower/Middle Triassic. Coll. L. GRAUVOGEL and J.-P. GALL; leg. GRAUVOGEL 24.08. 1924; housed in the Institut de Géologie de l'Université Louis Pasteur, Strasbourg, France.

D e s c r i p t i o n. Male specimen preserved in dorsal view. Body length 4 mm, wing length 2.8 mm. Head, antennae, one wing almost complete, only basal part of anal lobe is missing; second wing folded and poorly identifiable; one, probably mid, leg completely preserved; two other in worse condition; abdomen and genitalia well preserved.

Head round, front part with palpi invisible, covered by mineral material. Antennae (Fig. 5A) partially preserved, probably composed of 14 flagellomeres, were twice longer than head width; when bent backwards, they would reach bases of wings; scape invisible, pedicel round, with short bristles, almost twice as large as first flagellomere; all flagellomeres round, as long as broad, with short strong bristles retained on some of them.

Legs (Fig. 5B): long and thin, tibia with spurs and strong bristles, first tarsomere almost as long as the second and third ones combined; base of the fourth is swollen; this tarsomere and the last one are shaped in a way suggesting that they might have formed a clasping organ.

Wing venation (Fig. 5C): arculus invisible, probably absent; Sc well identifiable only in middle part, ending almost opposite r-m; position of sc-r not certain, probably in midlength of Sc; five radial veins terminate in wing margin; Rb and R1 stronger than other veins; Rb with distinct basal kink; R1 long and straight; Rs almost equal R2+3; R2 very short, c. 1/5 of R2+3 length; R3 longer than R2; R4+5 very short, c. 1/3 of Rs length and 1/4 of R4 length; r-m between mid of R4+5 and basal 1/5 of M1+2; d cell narrow, long; m-m poorly preserved, probably between M2 and M3 (i.e., petiole of d cell absent); proximal half of M3 poorly visible; m-cu just behind M3+4 fork, in 1/6 of M4; Cu strong; basalmost section of A1 not preserved; A2 not preserved but must have been very short, since only a small portion of wing is lacking.

Genitalia (Fig. 5D): gonocoxites slender and long, gonostyles single, bent to inside, with acute, strongly sclerotized tips. Penis probably unforked. Entire hypopygium covered with bristles.

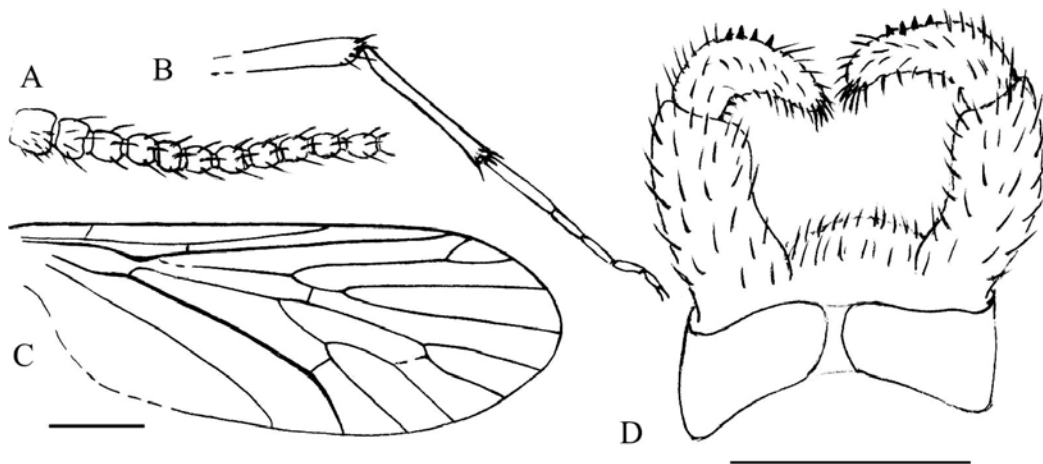


Fig. 5. *Tanus triassicus*, n. sp., Nadipteridae, Lower/Middle Triassic of France: A. antennae, B. leg; C. wing; D. genitalia. Bar 0.5 mm (C, D).

R e m a r k s. Following characters allow to place this genus among the Nadipteridae: five radial veins and long d cell with long M3+4 forming nearly half of d cell base. The new genus and species differs from other Nadipteridae by position of r-m and m-cu and lack of petiole of d cell. Most probably, it represents an ancestral line of the Tanyderidae.

Infraorder: Tanyderomorpha

Family: **Tanyderidae**

Tanyderidae are the only family of this infraorder. Till now no Triassic representatives were found; the oldest Tanyderidae come from the Lower Jurassic of Europe and Asia (ANSORGE 1994; KRZEMIŃSKI & REN 2001, ANSORGE & KRZEMIŃSKI 2002). Recent representatives were characterized by KRZEMIŃSKI & JUDD (1997).

The position of this family in various phylogenetic systems is very different (HENNIG 1973; MCALPINE et al. 1981; WOOD & BORKENT 1989; KRZEMIŃSKI 1992; ANSORGE 1994; OOSTERBROEK & COURTNEY 1995; SHCHERBAKOV et al. 1995; MICHELSEN 1996). In our opinion (unchanged since 1992) this is the most plesiomorphic family still living, a real "living fossil". Some fossil Tanyderidae show close relationship with the Psychodidae (KRZEMIŃSKI 1992; ANSORGE 1994; KRZEMIŃSKI & EVENHUIS 2000).

Infraorder: Psychodomorpha

Family: **Psychodidae**

Psychodidae are a very diversified family. The oldest species from the Lower Jurassic (ANSORGE 1994) and from the Lebanese amber of the Lower Cretaceous (AZAR et al. 1999) have discal cell closed, which is a plesiomorphic condition absent in Recent representatives.

Psychodidae have been placed deep inside phylogenetic systems of the Diptera (e.g., HENNIG 1973; WOOD & BORKENT 1989; OOSTERBROEK & COURTNEY 1995). This is one of the greatest errors performed in study on the Diptera evolution. All fossil evidences prove without any doubt close relationship between Psychodidae and Tanyderidae, especially in wing venation (ANSORGE 1994; KRZEMIŃSKI & EVENHUIS 2000). Some Jurassic and Cretaceous Psychodidae had discal cell closed and venation pattern almost identical with the Tanyderidae, while the Lower Jurassic tanyderids were small, as are the Recent Psychodidae (KRZEMIŃSKI 1992; ANSORGE 1994; AZAR et al. 1999; KRZEMIŃSKI & EVENHUIS 2000; AZAR & NEL 2002).

Despite these facts, the Psychodomorpha are generally treated as an unanchored group, a kind of dustbin for all families of unknown origin. This is evident when comparing phylogenetic trees of ROHDENDORF 1964; HENNIG 1973; OOSTERBROEK & COURTNEY 1995; SHCHERBAKOV et al. 1995.

According to our current knowledge, the infraorder can comprise only two families, Psychodidae and Phlebotomidae.

SUBORDER: NEONEURA KRZEMIŃSKI 1992

Representatives of this suborder are not known before the Upper Triassic; hence its origin, i.e., branching off the Diarchineura, took place probably about the Middle Triassic. Very few fossils document this first stage of the Neoneura and they represent four families: Rhaetaniidae (Upper Triassic of England; KRZEMIŃSKI & KRZEMIŃSKA 2002), Eoptychopteridae (Upper Triassic of North America; KRZEMIŃSKI 1992), Tillyardidae (Upper Triassic of Australia; LUKASHEVICH & SHCHERBAKOV 1999) and Chironomidae (a Recent family known since Upper Triassic of England; KRZEMIŃSKI & JARZEMBOWSKI 1999). Within this suborder five lineages (infraorders) are distinguished: Tillyardomorpha, Ptychopteromorpha, Culicomorpha, Blephariceromorpha and Nymphomyiomorpha (Fig. 6).

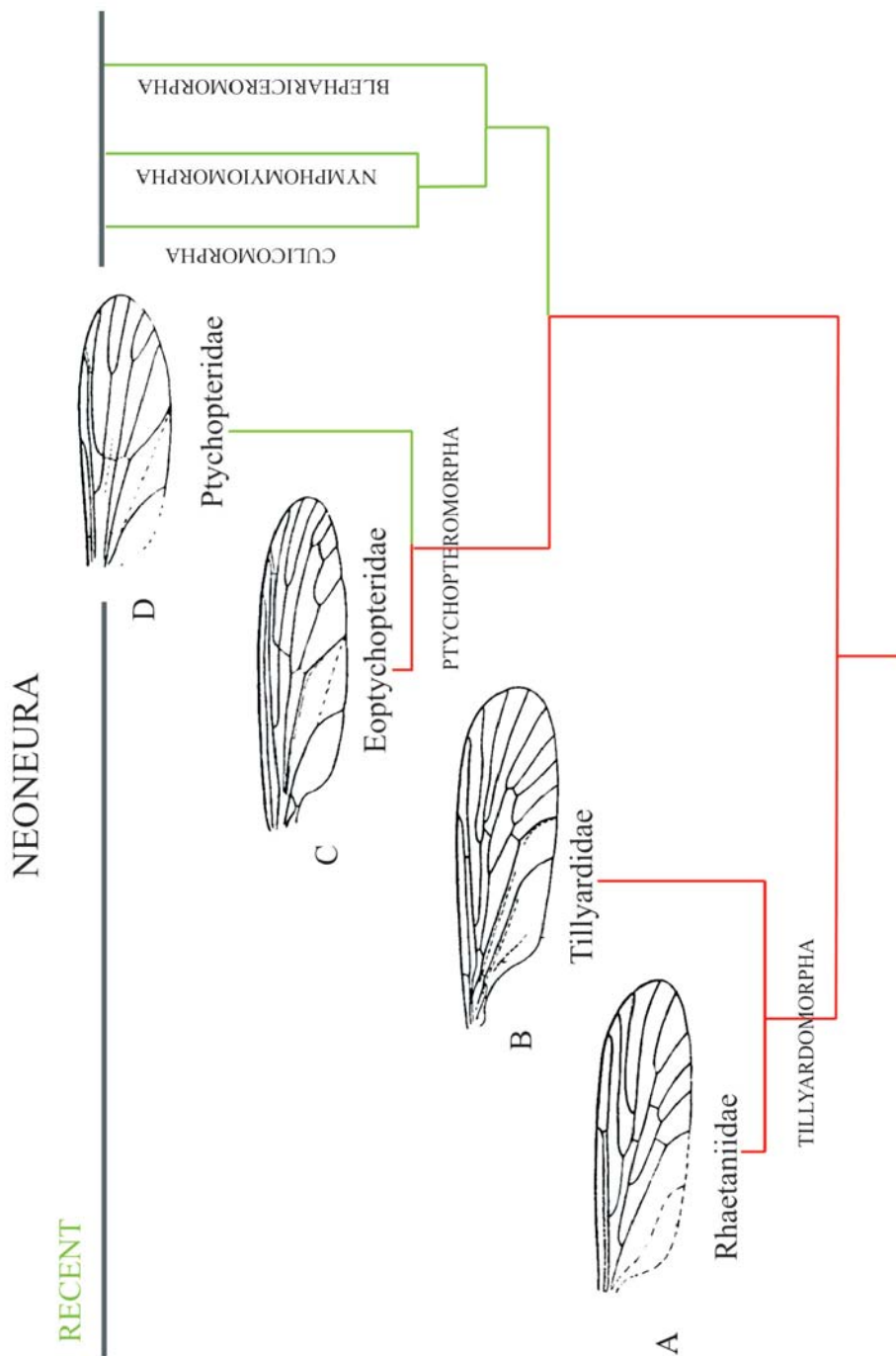


Fig. 6. Phylogenetic relations within the suborder Neoneura. A. *Rhaetania diana* KRZEMINSKI & KRZEMINSKA 2002 (Rhaetaniidae; Upper Triassic, England); B. *Tillyardiaptera prima* LUKASHEVICH & SHCHERBAKOV 1999 (Tillyardiidae; Upper Triassic, Australia); C. *Eoptychoptera eximia* (BODE) 1953 (Eoptychopteridae; Lower Jurassic, Germany); D. *Ptychoptera mesozoica* KALUGINA 1989 (Ptychopteridae; Lower Cretaceous, Asia). (Source: B. LUKASHEVICH & SHCHERBAKOV 1995; C. LUKASHEVICH 1998; D. KALUGINA 1989).

Infraorder: Tillyardomorpha, n. infraorder

D i a g n o s i s. Sc long, sc-r in terminal part of Sc; four radial and four medial veins terminate in wing margin; r-r (R2) absent; d cell long; m-cu positioned beyond mid of d cell.

Characteristic members of this infraorder are the Tillyardidae, represented by *Tillyardipectera prima* LUKASHEVICH & SHCHERBAKOV 1997 from the Upper Triassic of Australia. Also the family Rhaetaniidae with one genus and species, *Rhaetania triassica* KRZEMIŃSKI & KRZEMIŃSKA 2002, from the Upper Triassic of England, is classified here.

Fossil materials suggest the direct origin of Tillyardomorpha from the family Nadipteridae of the Diarchineura.

Infraorder: Ptychopteromorpha WOOD & BORKENT 1989

This infraorder comprises two families: extinct Eoptychopteridae and Recent Ptychopteridae. Eoptychopteridae are known since the Upper Triassic of North America; abundantly represented in the Jurassic and Lower Cretaceous of Europe and Asia (LUKASHEVICH et al. 1998). One species is known from the Lower Cretaceous of Brazil (Santana Formation; KRZEMIŃSKI and ANSORGE, in prep.) and from the Lebanese amber (Lower Cretaceous) (LUKASHEVICH & AZAR 2003, this volume). The family became extinct at the turn of Lower to Upper Cretaceous; and their direct descendants are the Recent Ptychopteridae. It is an unquestioned example of a linear transition of a fossil family into a Recent one, without branching off.

Infraorder: Culicomorpha HENNIG 1973

This is the most numerous and diverse infraorder of the Neoneura. Its oldest representative, *Aenne triassica* KRZEMIŃSKI & JARZEMBOWSKI 1999 (KRZEMIŃSKI & JARZEMBOWSKI 1999; ANSORGE 1999) represents the family Chironomidae, a family of much more apomorphic characters in the venation than the remaining Culicomorpha, as: Rhaetomyiidae, Chaoboridae or Dixidae, which are known from numerous fossils from the Lower and Middle Jurassic (KALUGINA & KOVALEV 1985). Almost certainly these families are much older and their findings among Triassic material are expected.

Culicomorpha comprise two superfamilies, Culicoidea and Chironomidea (WOOD & BORKENT 1989; BORKENT 1993; SZADZIEWSKI 1988, 1990, 1995, 1996). Fossil Culicomorpha are dealt with by LUKASHEVICH (1996a, b). Phylogeny of the Recent Culicomorpha is extensively discussed by SAETHER (2000).

Infraorder: Blephariceromorpha WOOD & BORKENT, 1989

Traditionally, this taxon includes two Recent families, Blephariceridae and Deuterophlebiidae, which probably are not closely related. The oldest Blephariceridae are known from the Late Cretaceous (KOVALEV 1987; LUKASHEVICH & SHCHERBAKOV 1997). SHCHERBAKOV et al. (1995) classify here also an Upper Jurassic family Ansorgiidae KRZEMIŃSKI & LUKASHEVICH (1993) from Kazakhstan.

Infraorder: Nymphomyiomorpha ROHDENDORF, 1964

This infraorder comprises only one family, Nymphomyiidae. According to ROHDENDORF (1964), morphology of larvae and adults distinguishes this family among all remaining Diptera and deserves this separated taxonomic position. Nymphomyiidae stay closer to the Culicomorpha than to Blephariceromorpha, although they are often included into that latter taxon.

Oldest Nymphomyiidae are known only from the Saxonian amber (Upper Eocene) (WAGNER et al. 2000).

SUBORDER: POLYNEURA BRAUER, 1863

D i a g n o s i s. A2 long (at least 10% of wing length), terminating in wing margin. Cross-vein r-r present, only in Psychotipidae terminating in wing margin as R2, and in some Limoniidae completely reduced.

R e m a r k s. A basic autapomorphy of this lineage is an elongated A2. Cross vein r-r plausibly originated from R2, which became vertical and shortened and thus had lost contact with wing margin to terminate in R1. This mode of r-r origin was a hypothesis and now is documented within the Psychotipidae: in some species R2 is not fully contacting R1, and in some it even terminates in wing margin (Fig. 7C).

Stages of A2 elongation can be easily traced in fossil material of the Trichoceridae, Limoniidae and Psychotipidae (Fig. 8). Especially the Limoniidae from the Triassic to Recent times present a model of elongation of A2. This tendency is observed also among the Recent representatives of young and apomorphic genera of the Limoniidae (e.g., *Molophilus*, *Symplecta*, *Eriocnopa*), and also in the Trichoceridae (*Diazosma*).

The suborder comprises two infraorders: Tipulomorpha and Trichoceromorpha (Fig. 7).

Infraorder: Tipulomorpha ROHDENDORF, 1961

The infraorder comprises families: Limoniidae, Cylindrotomidae, and Tipulidae (all represented by fossil and Recent species), Psychotipidae (Middle/Upper Triassic) and the oldest – Archilimoniidae n. family from the Lower/Middle Triassic of France, described below.

SHCHERBAKOV et al (1995) included in Limoniidae also a Middle Triassic subfamily Gnomuscinae, but expressed some doubts to this classification. We are not sure whether Gnomuscinae are Diptera at all; but even if so, then they should belong rather Trichoceromorpha, not Tipulomorpha (see below).

Family: Archilimoniidae n. fam.

D i a g n o s i s. Sc rather short, reaching just beyond midlength of wing; Rs forking into R2+3 and R4+5; d cell large; M4 leaves M3+4 in mid of d cell; four medial veins present; m-m between M2 and M3; m-cu in fork of M3+4.

Type genus: *Archilimonia* n. gen., Lower/Middle Triassic of France.

D e s c r i p t i o n of the family is covered by that of its only genus and species.

Genus: *Archilimonia* n. gen.

D i a g n o s i s is covered by that of the new family; description is given under its type species.

Type species: *Archilimonia vogesiana*, n. sp., Bust, Vosges Mts, France, Lower/Middle Triassic.

E t y m o l o g y. A new genus represents the oldest known ancestor of the Limoniidae. Gender: feminine.

***Archilimonia vogesiana*, n. sp.**

Fig. 9A, B

D i a g n o s i s is the same as that of the new family.

M a t e r i a l. Holotype No. 9052 (+,-), female, Bust (locality No. 215), Vosges Mts, France, Lower/Middle Jurassic. Coll. L. GRAUVOGEL and J.-P. GALL; housed in the Institut de Géologie de l'Université Louis Pasteur, Strasbourg, France.

D e s c r i p t i o n. A poorly preserved female; body length 3.8 mm, wing length 3 mm. Head small and round; palpi invisible. Antennae (Fig. 9A) with 9 basal flagellomeres identifiable,

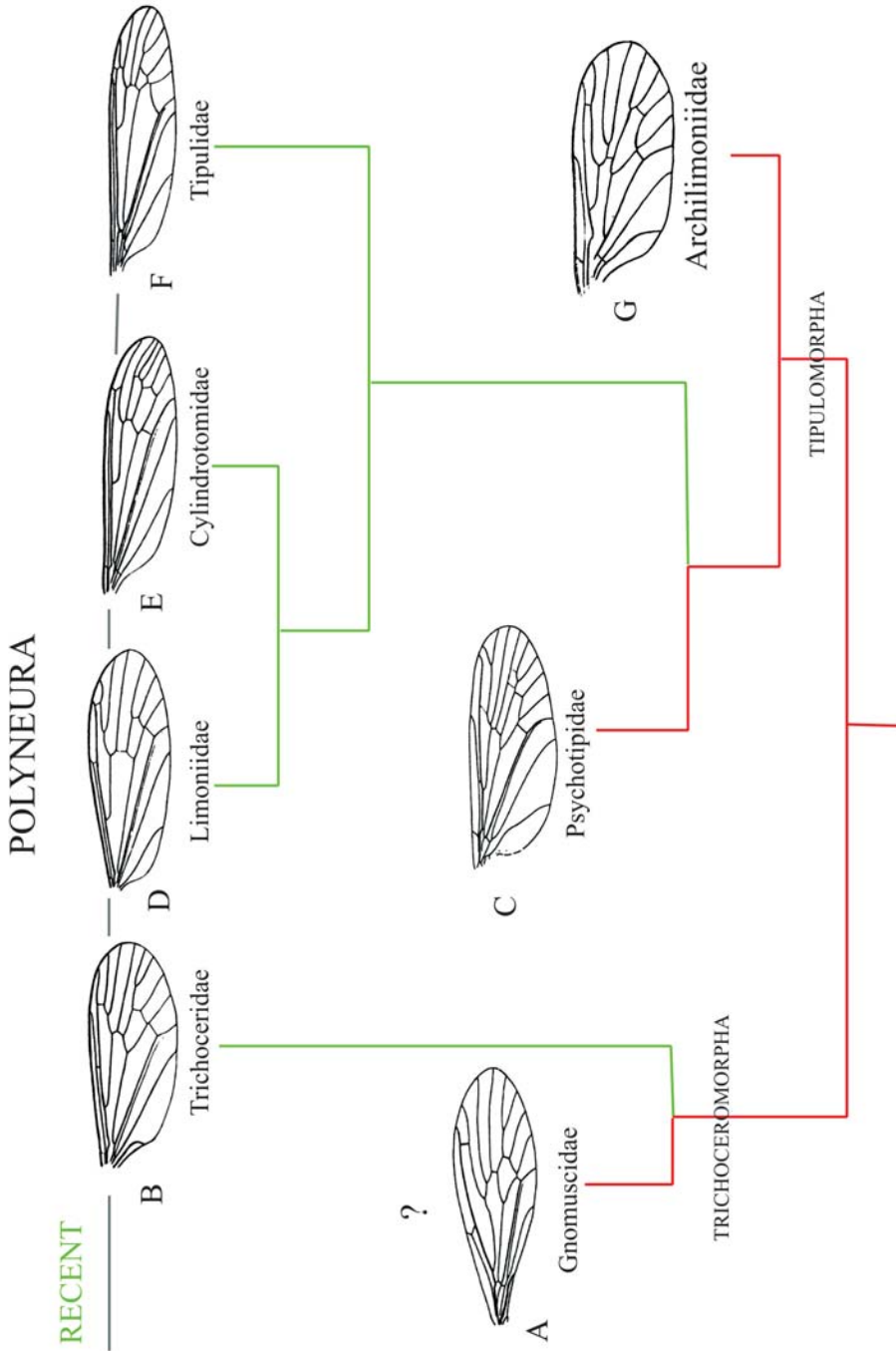


Fig. 7. Phylogenetic relations within the suborder Polyneura. A. a doubtful Diptera: *Gnomusca molecula* SHCHERBAKOV 1995 (Gnomuscidae; Middle/Upper Jurassic of Kyrgyzstan); B. representative of the oldest Trichoceridae (Lower Jurassic, Germany); C. *Psychotipa depicta* SHCHERBAKOV 1995 (Psychotipidae; Middle Triassic, Kyrgyzstan); D. *Eotipula parva* HANDLIRSCH 1906 (Limoniidae; Lower Jurassic, Germany); E. *Cyrtaromyia rayona* FREIWALD & KRZEMIŃSKI 1991 (Cylindrotomidae; Oligocene, Europe); F. *Tipula* sp. (Tipulidae, Recent); G. *Archilimonia vogesitana* n. sp. (Lower/Middle Triassic, France). Source: A, C: SHCHERBAKOV et al. 1995.

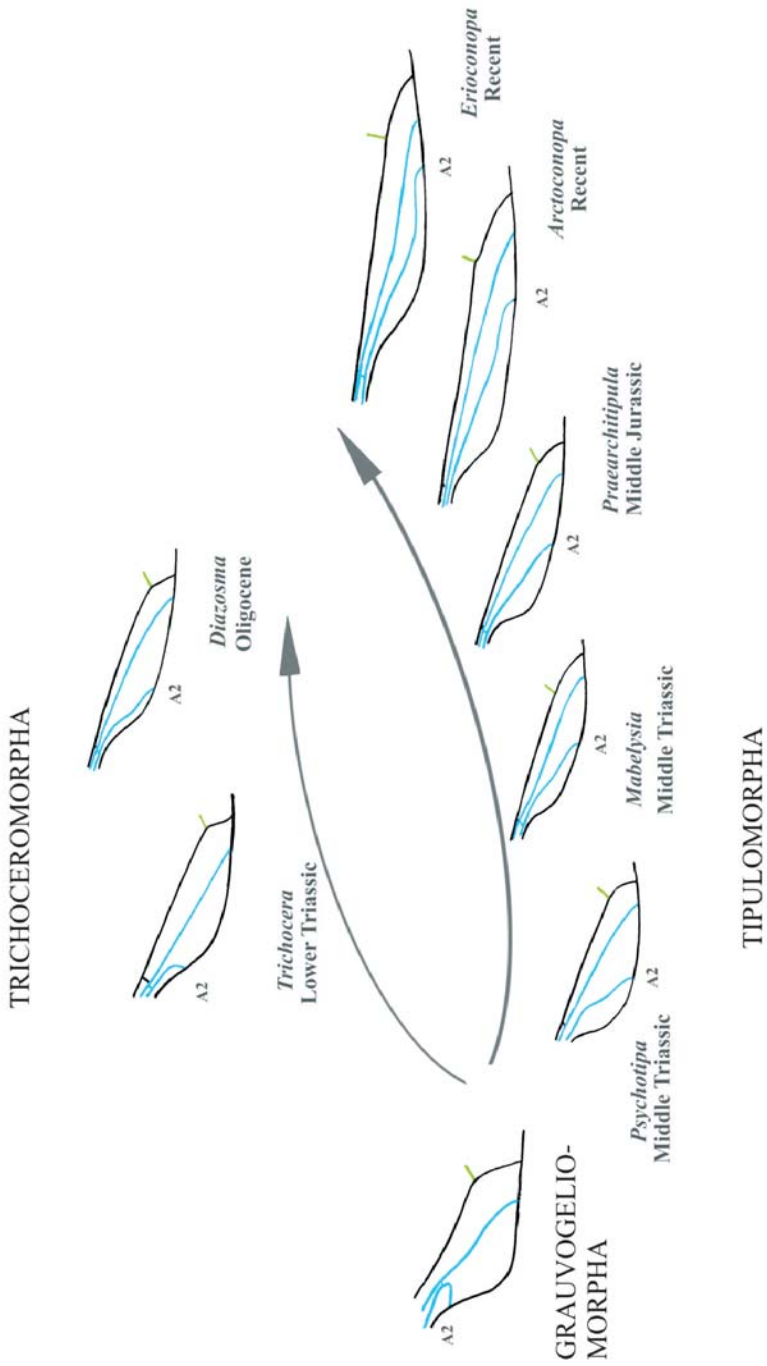


Fig. 8. Parallel elongation of the second anal vein in both infraorders of the Polyneura, illustrated by fossil and Recent species.

oval, a little longer than wide. One complete wing present. Legs and ovipositor missing; three spermathecae visible (one only in fragments).

Wing venation (Fig. 9B): R1, R5 and Cu distinctly thicker than other veins; area of d cell poorly visible. Sc mildly lowered, not parallel to costal wing margin and ending about mid of wing; sc-r probably at its two lengths before Sc tip; Rb with distinct basal kink; arculus absent; four radial veins terminate in wing margin; Rs short, c. 1/3 shorter than R2+3 and twice shorter than R4; r-r (R2) at its 3 lengths before R1 tip; r-m most probably between mid of R4+5 and 1/4 of d cell upper margin; R4+5 arched, c. as long as 1/5 of R5; d cell large, almost 1/4 of wing length and below Mb level; d cell without petiole (i.e., m-m connects M2 and M3); M3+4 fork before mid of d cell lower margin; m-cu just before fork of M3+4; A1 straight, long, very delicate; cross-vein a-a present; A2 slightly sinuous, strong.

R e m a r k. This species is classified to the Polyneura on basis of four radial veins present, r-r between R1 and R3 and long A2. Size of d cell reminds species of the Recent genus *Lechria* SKUSE (family Limoniidae); in the new species however the cross-vein m-cu is positioned close to fork of M3+4; this plesiomorphic condition is characteristic also of the subfamily Architipulinae (Limoniidae) known from the Triassic.

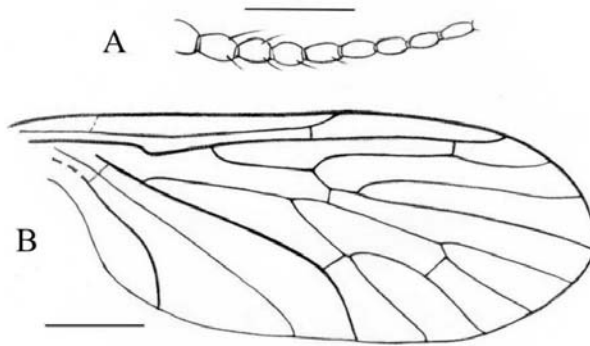


Fig. 9. *Archilimonium vogesiana*, n. sp. (Archilimoniidae, Lower/Middle Triassic of France). A. antenna (bar 0.2 mm); B. wing (bar 0.5 mm).

Family: **Psychotipidae**, comb. nov.

Psychotipinae SHCHERBAKOV: SHCHERBAKOV et al. (1995): 86-88; Figs 19, 20.

Representatives of this taxon were classified to the subfamily Psychotipinae within the Vladipteridae by SHCHERBAKOV in SHCHERBAKOV et al. (1995). A taxonomic position of this family was discussed herein.

The **d i a g n o s i s** and **d e s c r i p t i o n** of this family and its composition is not changed. Two species, *Psychotipa predicta* SHCHERBAKOV 1995 and *P. depicta* SHCHERBAKOV 1995, come from the Middle Triassic of Kyrgyzstan (Central Asia).

Infraorder: Trichoceromorpha KRZEMIŃSKI, 1992

The infraorder is separated to comprise the family Trichoceridae, known since the Lower Jurassic (data in preparation) until recently (Recent Trichoceridae are characterized in DAHL & KRZEMIŃSKA 1997).

Family: **Gnomuscidae**, comb. n.

From the Middle Triassic of Kyrgyzstan (Central Asia) SHCHERBAKOV (in SHCHERBAKOV et al. 1995) described a subfamily Gnomuscinae within the Limoniidae. It remains doubtful whether both species of the Gnomuscinae, *Gnomusca molecula* SHCHERBAKOV 1995 and *G. renyxa* SHCHERBAKOV 1995, belong to the Diptera. Again, this is the case of separate wings completely devoid of anal

lobe. Such wings, in our opinion, rather belonged four-winged insects. If the Gnomuscidae are to be included in the Diptera, their place is rather within the Trichoceromorpha, according to the diagnostic character of short anal vein. In that case the group should be given the status of a family Gnomuscidae, comb. nov.

NEODIPTERA MICHELSEN, 1996 [= SUBORDERS: ANISONEURA AND BRACHYCERA]

The first known radiation of the Diptera occurred already in the Lower Triassic, as is documented by KRZEMIŃSKI, KRZEMIŃSKA & PAPIER (1994) and discussed by KRZEMIŃSKI & EVENHUIS (2000). We assume that from the oldest Diptera – the Diarchineura, defined by four apomorphies, gave origin to younger lineages. Among the first ones were the Anisoneura and Brachycera (KRZEMIŃSKI 1998; KRZEMIŃSKI & EVENHUIS 2000). According to MICHELSEN (1996), both suborders constitute an informal group called Neodiptera. Recent representatives of both suborders share some morphologic characters of sclerites; their phylogenetic proximity is also confirmed by wing venation of fossils.

The Lower and Middle Triassic Neodiptera are defined by one synapomorphy: complete absence of R2 (or: r-r) (Fig. 10). Other characters of the lower Anisoneura (as Protorhyphidae) and Lower Brachycera (as Rhagionidae) are very similar to or identical with the Diarchineura represented by Grauvogeliidae. These plesiomorphic characters are: sc-r close to origin of Sc; r-m proximally of first fork of Rs (into R2+3 and R4+5); d cell rather small and sometimes with petiole retained (= free section of M1+2 beyond d cell); four medial veins; m-cu close to fork of M3+4 into M3 and M4 (Fig. 3). Fossil materials are scarce, but suggest a one step transition from the Diarchineura to Neodiptera. The first, Lower Triassic Neodiptera are: Protorhyphidae (of the Anisoneura) and Rhagionidae (of Brachycera). Both these lineages had early separated from each other. Judging from the fossil record, in the Triassic and Lower Jurassic they were poorly represented, (especially the Brachycera), but since the Middle Jurassic rapid radiation of both lineages is documented, resulting in enormous variety and abundance in the Cretaceous.

SUBORDER: ANISONEURA, KRZEMIŃSKI & EVENHUIS, 2000

Anisoneura, now a very diversified and rich group, were in the Triassic represented only by Anisopodomorpha. The suborder comprises three infraorders: Anisopodomorpha, Axymyiomorpha and Bibionomorpha (Fig. 10).

About the turn of the Lower to Middle Triassic the Anisoneura were represented only by the Protorhyphidae, which became extinct in the Jurassic. One and the oldest species of this family, described below, had four long radial and four medial veins, and closed d cell. The direct descendants of Protorhyphidae are the Anisopodidae, which have lost R4 and have only three radial veins, R1, R3 and R5 (or: R4+5; the mode of reduction of R4 is not known).

Infraorder: Anisopodomorpha KRZEMIŃSKI & EVENHUIS, 2000

Already four families of the Anisoneura are known from the Triassic: Protorhyphidae, Crosaphididae, Proqramptomomyiidae and Paraxymyiidae. The oldest species is *Vymrhyphus blagoderovi*, n. sp. (Protorhyphidae; Lower/Middle Triassic of France) described below. To the same genus are classified two species: *V. tuomikoskii* and *V. triassicus* BLAGODEROV 1995 from the Middle/Upper Triassic of Kyrgyzstan (Asia). The family Crosaphididae is represented by *Crosaphis anomala* EVANS from the Upper Triassic of Australia (EVANS 1971; KOVALEV 1983a); the Proqramptomomyiidae are known two species: *Yala argentata* KRZEMIŃSKI from the Upper Triassic of USA (KRZEMIŃSKI 1992) and *Austrocramptomomyia minuta* BLAGODEROV 1999 from the Upper Triassic of Australia (BLAGODEROV 1999). Triassic Paraxymyiidae are represented by *Veriplecia handlirschi* BLAGODEROV 1999 from the Upper Triassic of Australia. The relations within the Anisopodomorpha are discussed by BLAGODEROV et al. (1993) and KRZEMIŃSKI & KRZEMIŃSKA (1994).

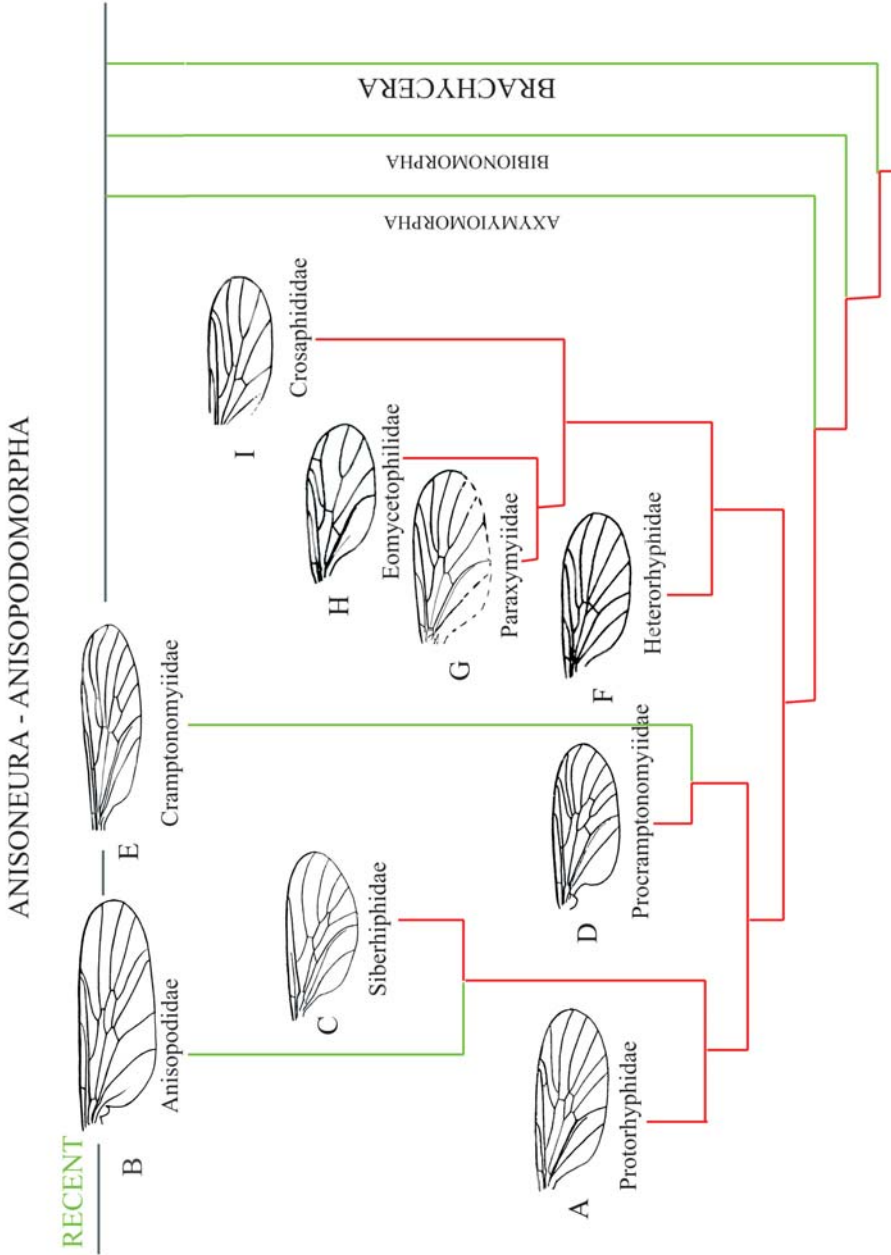


Fig. 10. Phylogenetic relations within the suborder Anisoneura, infraorder Anisopodomorpha. A. *Protorhaphus simplex* (GEINITZ) 1887 (Protorhaphidae; Lower Jurassic, Germany); B. *Oligaster sackeni* EDWARDS (Anisopodidae, Recent); C. *Siberhiphus lebedevi* KOVALEV 1990 (Siberhiphidae; Middle Jurassic, Asia); D. *Yala argentata* KRZEMIŃSKI 1992 (Procramptonomyiidae; Upper Triassic of North America); E. *Cramptonomyia spenceri* ALEXANDER (Cramptonomyiidae, Recent); F. *Heterorhaphus triangularis* ANSORGE 1996 (Heterorhaphidae; Lower Jurassic, Germany); G. *Veriplecta handlirschi* BLAGODEROV 1999 (Paraxymyiidae; Upper Triassic, Australia); H. *Eomycetophilula asymmetrica* KOVALEV 1990 (Eomycetophilidae; Upper Jurassic, Asia); I. *Crosaphis anomala* EVANS 1971 (Crosaphididae; Upper Triassic, Australia). Source: A, F, H: ANSORGE 1996; C: KOVALEV 1990; I: KOVALEV 1983.

The infraorder comprises ten families: Protorhyphidae, Siberhiphidae, Anisopodidae, Pro-cramptonomyiidae, Cramptonomyiidae, Heterorhyphidae, Paraxymyiidae, Crosaphididae, Eomy-cetophilidae and Eoditomyiidae, which belong three superfamilies: Anisopodoidea, Cramptonomyidae and Crosaphidoidea. Only Anisopodidae and Cramptonomyiidae are represented recently. Extinct families remain unknown to many dipterologists studying Recent Diptera, and is a source of too complicated, improbable hypotheses based only on Recent flies.

Family: **Protorhyphidae** HANDLIRSCH, 1906

This extinct family existed since Lower/Middle Triassic and became extinct at the turn of the Jurassic to Cretaceous. Its Triassic representatives are known from Europe, North America and Australia (listed above).

Genus: *Vymrhyphus* BLAGODEROV, 1995

Vymrhyphus blagoderovi, n. sp.

Fig. 11.

D i a g n o s i s. Cross-vein r-m between R5 and upper margin of d cell; d cell with petiole; m1 cell very broad; A2 relatively long and wavy, as in Anisopodidae, but not reaching wing margin.

E t y m o l o g y. A new species name is dedicated to an outstanding paleontologist Volodia BLAGODEROV, the author of this genus.

M a t e r i a l. Holotype No. 9077 (+,-), Arzviller (locality No. 118 L), Vosges Mts, France, Lower/Middle Triassic. Coll. L. GRAUVOGEL and J.-P. GALL; housed in the Institut de Géologie de l'Université Louis Pasteur, Strasbourg, France.

D e s c r i p t i o n. A single, almost complete wing in rather poor condition; basal and anal portions obscure; length 4.2 mm. Venation makes appearance of two wings folded together and overlapping, since veins of distal part seem to be double. This phenomenon is caused by dislocation of lower membrane in relation to the upper during fossilization. This peculiar effect, quite often observed in fossil wings over a limited area, here affects almost half of the wing.

Venation (Fig. 11): Sc rather long (better discernible in negative counterpart); sc-r invisible; Rb with distinct basal kink; four long radial veins of nearly equal length terminate in wing margin; Rs twice as long as R4+5; arculus absent; r-m just behind fork of R4+5, connecting R5 and mid of d cell upper margin; d cell below level of Mb, narrow, less than 6 times shorter than wing length; d cell with a very short petiole, equal 1/7 of M2; cross-vein m-cu in 1/3 of d cell base; Cu slightly curved beyond m-cu; A2 rather long, poorly retained, not reaching wing margin.

R e m a r k s. The wing venation is similar to that in *Vymrhyphus tuomikoskii* BLAGODEROV (in: SHCHERBAKOV et al. 1995) from the Middle Triassic of Kyrgyzstan (Asia), with following differences in venation present in a new species: R4+5 shorter in relation to Rs, position of r-m and long A2. *Vymrhyphus blagoderovi* has also distinctly broader wing, but narrower than other species of the family Protorhyphidae.

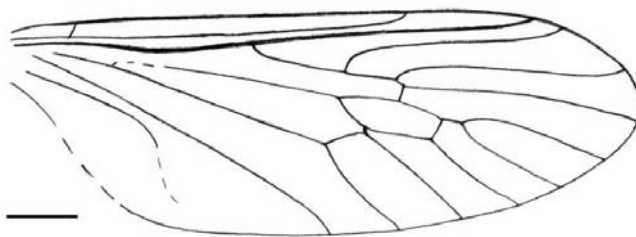
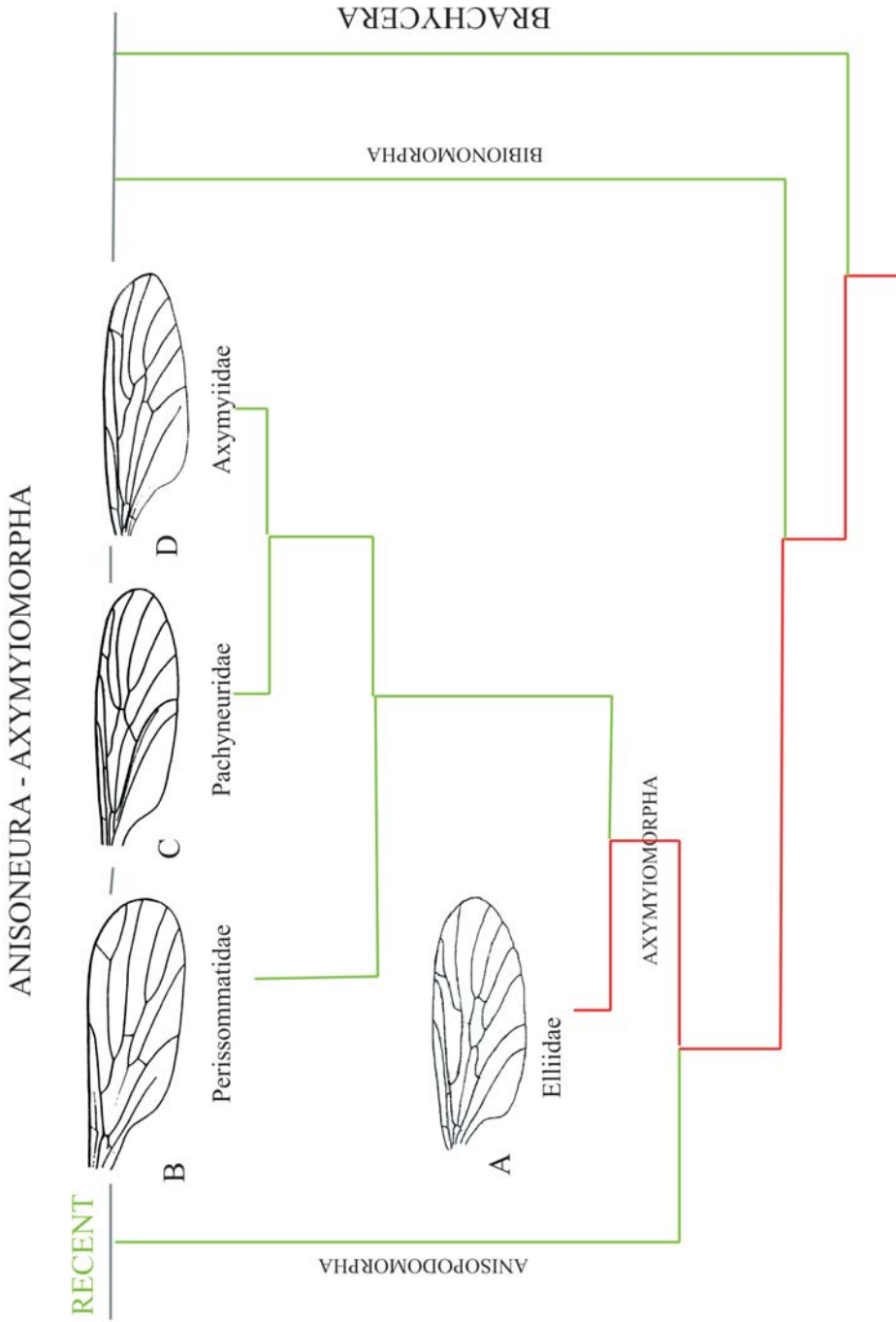


Fig. 11. *Vymrhyphus blagoderovi*, n. sp. (Protorhyphidae; Lower/Middle Triassic of France). Bar 0.5 mm.



12. Phylogenetic relations within the suborder Anisoneura, infraorder Axymyiomorpha. A. *Ellia colorissima* KRZEMIŃSKA, BLAGODEROV & KRZEMIŃSKI 1993 (Ellidae; Lower Cretaceous, Asia); B. *Palaeoperissoma collessi* KOVALEV 1985 (Perissomatidae; Middle Jurassic, Asia); C. *Pachyneura fasciata* ZETTERSTEDT (Pachyneuridae; Recent); D. *Axymyia fuscata* MCATEE 1921 (Axymyiidae; Recent). Source: B: KALUGINA & KOVALEV 1985.

Infraorder: Axymyiomorpha WOOD & BORKENT, 1989

WOOD & BORKENT (1989) created this infraorder to contain Recent families: Axymyiidae, Perissomatidae and Pachyneuridae. The oldest extinct families, Ellidae and probably Boholdoyidae, come from the Lower Jurassic. Fossil Axymyiomorpha and their phylogenetic relations are described by KRZEMIŃSKA et al. (1993), and, with some minor changes, are shown in Fig. 12.

Infraorder: Bibionomorpha HENNIG, 1973

The infraorder Bibionomorpha became more uniform and relations between its families more evident after separating the infraorders Axymyiomorpha and Anisopodomorpha. Recent families included in this infraorder are grouped in superfamilies Bibionoidea, Sciaroidea and Scatopsidoidea. Fossil families are: Protopleciidae, Pleciofungivoridae, Pleciomimidae and Mesosciophilidae. The oldest Bibionomorpha are known since the Lower Jurassic (ANSORGE 1996).

SUBORDER: BRACHYCERA MACQUART, 1834

There are no distinct differences in wing venation of Anisoneura and so called Lower Brachycera (infraorders: Stratiomyomorpha, Xylophagomorpha, Tabanomorpha and Asilomorpha). In spite of this, Brachycera are still considered a monophyletic group (YEATES & WIEGMANN 1999). This possibly concerns only the so called higher Brachycera, i. e., infraorder Muscomorpha. Generally, this system of five infraorders listed (Fig. 13) is acknowledged at present.

Brachycera did not origin from the Nematocera by a long, stepwise evolution, as was supposed until quite recently. Fossil evidences show that they arose very early, and the oldest are found together with other oldest representatives of main dipteran lineages in the Lower/Middle Triassic of France (KRZEMIŃSKI 1998; KRZEMIŃSKI & EVENHUIS 2000), described below.

Two main synapomorphies in wing venation of the Brachycera are:

- Cu and A1 terminate together in one point on wing margin, or very close to each other
- R4 and R5 are fused over a long section of R4+5.

In the most primitive Rhagionidae, Protobranchyceridae, Acroceridae, Eremochaetidae, and probably Alinkidae, these characters may be not fully expressed, but became so in all more modern Brachycera.

Triassic Brachycera are very scarce: only Rhagionidae (Tabanomorpha) and Alinkidae (Xylophagomorpha) were found till now. Since the Middle Jurassic the Brachycera became frequent, and started to dominate in the Cretaceous. The Mesozoic Brachycera are reviewed by NAGATOMI & YOUNG (1998). Numerous new fossil Brachycera were described recently (KOVALEV 1981, 1982; MOSTOVSKI 1996, 1997, 1999; MOSTOVSKI & JARZEMBOWSKI 2000 and MOSTOVSKI et al. 2000). These findings have improved our comprehension of the evolution of this group and will probably induce profound changes in the phylogenetic system of the Lower Brachycera.

Infraorder: Tabanomorpha

For a long time, the oldest representative of the Tabanomorpha, and of all Brachycera, was considered *Palaeobranchyceron liassinum* HANDLIRSCH (1920) from the Lower Jurassic of Germany. With the present description the origin of the Brachycera is pushed back to the Lower/Middle Triassic. This new species provides evidence of the early origin of Brachycera and of rapid radiation of the Diptera at the beginning of their evolution.

Tabanomorpha comprise Recent families: Rhagionidae, Pelecorhynchidae, Athericidae, Vermileonidae and Tabanidae. The extinct Protobranchyceridae, because of their close relations with Rhagionidae, were counted to the Tabanomorpha until MOSTOVSKI & JARZEMBOWSKI (2000) transferred this family to the Xylophagoidea, to the infraorder Xylophagomorpha.

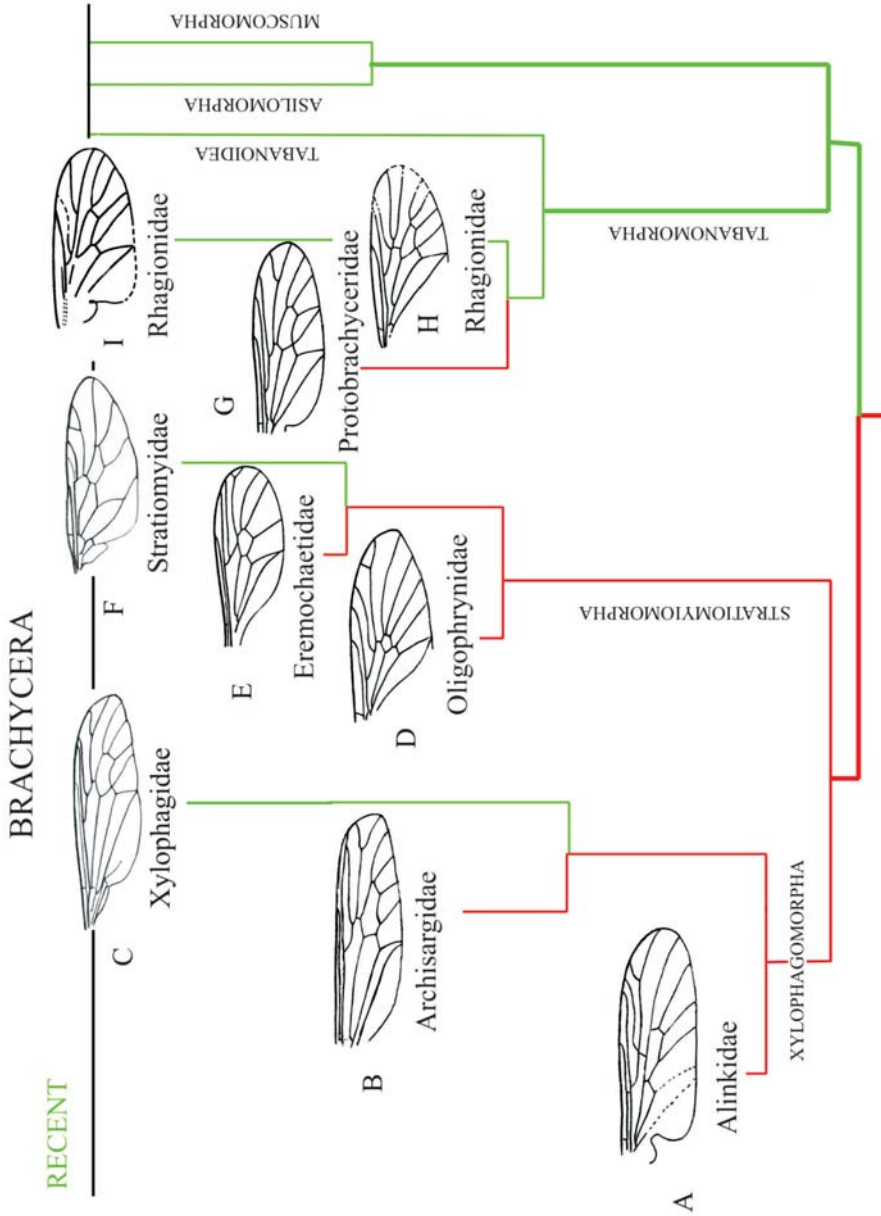


Fig. 13. Phylogenetic relations within the suborder Brachycera. A. *Alinka cara* KRZEMIŃSKI 1992 (Alinkidae; Upper Triassic, North America); B. *Calosargus (Pterosargus) tanasymus* MOSTOVSKI 1997 (Archisargidae; Upper Jurassic, Asia); C. *Xylophagus abdominalis* LOEW (Xylophagidae; Recent); D. *Oligophryne britannica* ANSORGE & KRZEMIŃSKI 1994 (Oligophrynidae; Lower Jurassic, England); E. *Eremomukha (Eremocreata) addita* MOSTOVSKI 1997 (Eremochaetidae; Lower Cretaceous, Asia); F. *Neopachygyaster maculicornis* (HINE) (Stratiomyidae; Recent); G. *Protobranchyceron liassimum* HANDLIRSCH 1920 (Protobranchyceridae; Lower Jurassic, Germany); H. *Gallia alsatica* n. sp. (Rhagionidae; Lower/Middle Triassic, France); I. *Pitolinites raypearcei* MOSTOVSKI, JARZEMBOWSKI, CORAM & ANSORGE 2000 (Rhagionidae; Lower Cretaceous, England). Source: B, E: MOSTOVSKI 1997; D: ANSORGE & KRZEMIŃSKI 1994; I: MOSTOVSKI et al. 2000).

Family: **Rhagionidae** LATREILLE, 1802Genus: *Gallia* n. gen.

D i a g n o s i s. R4+5 very short; Rs 3 times longer than R4+5, R5 7 times longer than R4+5; d cell with petiole; m-cu just behind fork of M3+4.

Type species *Gallia alsatica*, n. sp., Arzviller, France, Lower/Middle Triassic.

E t y m o l o g y. A new genus name is dedicated to an outstanding French paleontologist, Jean-Claude GALL, whom we owe access to these fascinating materials described herein. Gender: feminine.

D e s c r i p t i o n of a new genus is covered by that of its only species.

Gallia alsatica n. sp.

Fig. 14.

D i a g n o s i s is given under a new genus.

M a t e r i a l. Holotype No. 6171 (+,-), Arzviller (locality No. 118 b), Vosges Mts, France, Lower/Middle Jurassic. Coll. L. GRAUVOGEL and J.-P. GALL; housed in the Institut de Géologie de l'Université Louis Pasteur, Strasbourg, France.

D e s c r i p t i o n. A poorly preserved male of body length c. 5 mm, wing length 3 mm. Antennae not visible, probably hidden under sediment (further exposing it is risky since the specimen is covered with Arabic gum). One wing preserved without greater part of anal field; the second is heavily folded; one haltere visible; one leg almost complete, without distal part of 5th tarsomere. Genital apparatus preserved.

Venation (Fig. 14): Sc ending behind midlength of wing; sc-r if present then close to wing base (no trace of this vein is seen in further, better preserved part of subcostal field); Rb with slight basal kink; presence of arculus uncertain; four long radial veins terminate in wing margin: R1, R3, R4 and R5; R3 twice longer than Rs; R4+5 very short, c. 1/3 of Rs; r-m between 1/3 of R4+5 and 1/3 of M1+2; d cell 1/5 of wing length; d cell with very short petiole; m-cu just behind M3+4 fork; tips of Cu and A1 fused (this important brachyceran feature is clearly visible in both counterparts); remaining anal field not preserved.

Leg short and thick, densely covered with bristles. Tibia with at least one strong spur; 1st tarsomere half the length of tibia; 2nd tarsomere c. half the length of 1st (proximal segment border a little uncertain); 3rd and 4th tarsomeres are equal and a trifle shorter than 2th one; distal part of 5th tarsomere lacking.

Shape of genitalia difficult to resolve; probably male.

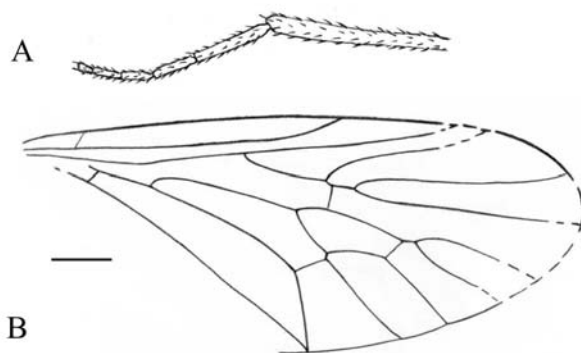


Fig. 14. *Gallia alsatica* n. sp. – the oldest Brachycera (Rhagionidae; Lower/Middle Triassic, France). A. leg; B. wing (bar 0.5 mm).

R e m a r k s. The specimen is the oldest representative of Brachycera. Although the presence of “short antennae” cannot be proved without a risk of destroying the specimen, the character of A1 and Cu fused at their tips places this specimen close to this lineage. Another very primitive features are: very short R4+5 and d cell with petiole. Generally, all characters of this specimen show similarity to primitive Rhagionidae, especially those of the Lower Cretaceous of England (MOSTOVSKI et al. 2000).

Infraorder: Xylophagomorpha

The oldest representative of this taxon is *Alinka cara* (Alinkidae) from the Upper Triassic of USA, originally classified to the Tabanomorpha (KRZEMIŃSKI 1992). The infraorder comprises Recent Xylophagidae and extinct Archisargidae and Alinkidae. Judging from their fossil representatives, in our opinion also the Acroceridae and Nemestrinidae stay closer Xylophagomorpha and Tabanomorpha than the Muscomorpha, where they are usually included.

Infraorder: Stratiomyomorpha

The oldest representatives are the Lower Jurassic Oligophrynidae described by ROHDENDORF (1962) from Karatau (central Asia) and by ANSORGE & KRZEMIŃSKI (1994) from England. The infraorder comprises also fossil family Eremochaetidae (MOSTOVSKI 1996) and Recent families: Stratiomyiidae and Xylomyidae.

Infraorder: Asilomorpha

The taxon comprises the superfamily Asiloidea (Asilidae, Apioceridae, Mydidae, Scenopinidae, Therevidae, Bombylidae and Mythicomyiidae). To this infraorder usually also the Empidoidea are included (families: Empididae and Dolichopodidae). However, we share the opinion of those authors (HENNIG 1976, CHVÁLA 1983; YEATES & WIEGMANN 1999) who consider Empidoidea a sister group of the Muscomorpha, the so called Eremoneura.

Fossil Asiloidea are known since the Middle and Upper Jurassic (USSATCHOV 1968; MOSTOVSKI 1999).

Infraorder: Muscomorpha

Diptera of this infraorder (including the Empidoidea) differ markedly from the other Brachycera (Lower Brachycera) and deserve a rank of a separate suborder. Empidoidea existed already in the Lower Jurassic (MOSTOVSKI 1999), while the majority of the Muscomorpha, the Cyclorrhapha, had originated not before the Cretaceous (GRIMALDI 1987, 1990; GRIMALDI & CUNNING 1999; MOSTOVSKI 1999; KRZEMIŃSKI & EVENHUIS 2000) and now survive peak of their radiation.

DELFINADO & HARDY (1973, 1975, 1977) proposed to separate the Cyclorrhapha in their own suborder, but probably the entire Eremoneura should be raised to this rank.

CONCLUSIONS

The Triassic began ca. 245 Ma ago and had lasted 37 Ma, and this was the most important period of evolution of the Diptera. The oldest specimens come from the Lower/Middle Triassic of France (ca. 240 Ma), but their morphological diversity indicates that the branching off the Mecoptera had happened much earlier, probably with the end of the Permian or beginning of the Triassic. These first Diptera (only five species known!) already offer a surprisingly wide spectrum of their diversity. Save the Neoneura, all other main lineages (Diarchineura, Polyneura, Anisoneura and Brachycera) are represented among these materials and give evidence of rapid, even explosive radiation of the order, at this first stage of the Diptera evolution.

The oldest species families known from the Triassic: Grauvogeliidae, Kuperwoodidae, Rhaetaniidae, Nadipteridae, Tillyardidae, Psychotipidae, Archilimoniidae n. fam., Protorhyphidae and Alinkidae had numerous plesiomorphic characters in their wing venation. On the other hand, from the Triassic come some families represented till now: Limoniidae, Rhagionidae and Chironomidae.

Among the last discoveries the most important are the Grauvogeliidae (suborder Diarchineura) with their primitive venation including a full and functioning anal loop composed of two anal veins. This venation is plausibly ancestral to all other Diptera (Figs 1 and 3).

According to expectations (KRZEMIŃSKI 1992; KRZEMIŃSKI & EVENHUIS 2000), in the Triassic and Jurassic flourished also other Diptera of this most primitive suborder, now represented only by Tanyderidae and Psychodidae, while in the Triassic still lived the Kuperwoodidae, Nadipteridae and Hennigmatidae.

The next exciting finding was the first representative of the Brachycera, *Gallia alsatica*, n. sp. Its venation is almost identical with that of primitive Rhagionidae. The idea that Brachycera “must be” much younger than the Nematocera was so persistent that a find of an Upper Triassic Brachycera in 1992 (KRZEMIŃSKI 1992) was not acceptable to some dipterists at that time. Now the even much earlier origin of Brachycera becomes an undeniable fact.

Although the Neoneura are till now absent among the first Diptera from the Lower/Middle Triassic, it was just this group that had changed most rapidly during the Triassic. While the most primitive families: Rhaetaniidae, Tillyardidae and Eoptychopteridae are characterized by large body size, the tendency to miniaturization and reduction of wing veins appeared early in suborders Culicomorpha: Chironomidae and Ceratopogonidae, and Nymphomyiomorpha.

The Polyneura were never a very diversified group, but compared Triassic, Jurassic and Recent wing venation patterns illustrate the mode of transition of a longitudinal radial vein R2 into a cross-vein r-r (Fig. 7). This process had probably been forced by elongating A2 (Fig. 8). Within this suborder a tendency to gigantism is visible, expressed in the Tipulidae, Cyndrotromidae and partially also the Limoniidae. Also one giant representative of Trichoceridae of wing size ca. 2 cm is known from the Jurassic/Cretaceous (description in preparation).

Anisoneura are already present among the first Diptera from the Lower/Middle Triassic. This group had evolved explosively during the Triassic, which is evidenced by Protorhyphidae Procrampptomomyiidae, Paraxymyiidae and Crosaphididae (Fig. 10).

In the Triassic the last representatives of the Mecoptera with true dipteroid wing venation – the Vladipteridae - had died out. This group of Mecoptera probably did not survive a strong concurrence of rapidly developing Diptera.

REFERENCES

- ANSORGE J. 1994. Tanyderidae and Psychodidae (Insecta: Diptera) from the Lower Jurassic of northeastern Germany. *Palaeontologische Zeitschrift*, **68**(1/2): 199-210.
- ANSORGE J. 1996. Insekten aus dem obern Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Palaeontologische Abhandlungen*, **2**: 1-132.
- ANSORGE J. 1999. *Aenne liasina* gen. et sp. nov. - the most primitive non biting midge (Diptera, Chironomidae) from the Lower Jurassic of Germany. *Polskie Pismo Entomologiczne* - in press.
- ANSORGE J. 2001. Lower Jurassic Hennigmoatidae (Diptera) from Germany. *Studia Dipterologica*, **8**(1): 97-102.
- ANSORGE J., KRZEMIŃSKI W. 1994. Oligophrynidae, a Lower Jurassic dipteran family (Diptera, Brachycera). *Acta zoologica cracoviensia*, **32** (2): 115-119.
- ANSORGE J., KRZEMIŃSKI W. 2002. Lower Jurassic Tanyderids (Diptera: Tanyderidae) from Germany. *Studia dipterologica*, **9**(1): 21-29.
- AZAR D., NEL A., SOLIGNAC M., PAICHELER J.-C., BOUCHET F. 1999. New genera and species of psychodid flies from the Lower Cretaceous Amber of Lebanon. *Palaeontology*, **42**(6): 1101-1136.

- AZAR D., NEL A. 2002. New Cretaceous psychodid flies from Lebanese amber and Santana Formation (Chapada do Araripe, Brazil) (Diptera). *Annales de la Société de Entomologique de France* (N.S.), **38**(3): 253-262.
- BLAGODEROV V.A. 1999. New Bibionomorpha from the Triassic of Australia and Jurassic of Central Asia with notes on Paraxymyiidae Rohdendorf (Insecta, Diptera). Proceedings of the First Palaeontological Conference Moscow 1998. AMBA Projects Internat. Bratislava. Pp. 11-15.
- BLAGODEROV V.A., KRZEMIŃSKA E., KRZEMIŃSKI W. 1993. Fossil and recent Anisopodomorpha (Diptera, Oligoneura): family Cramptonomyiidae. *Acta zoologica cracoviensia*, **35**: 573-79.
- BORKENT A. 1993. A world catalogue of fossil and extant Corethrellidae and Chaoboridae (Diptera), with a listing of references to keys, bionomic information and descriptions of each known life stage. *Entomologica scandinavica*, **24**: 1-24.
- BYERS G. W. 1989. Homologies in wing venation of primitive Diptera and Mecoptera. *Proceedings of the Entomological Society of Washington*, **91**(4): 497-501.
- CHVÁLA M. 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The families Hybotidae, Atelestidae and Microphoridae. *Fauna Entomol. Scand.*, **12**: 1-297.
- DAHL Ch., KRZEMIŃSKA E. 1997. Family: Trichoceridae. In: Contributions to a Manual of Palaearctic Diptera, vol. 2. Eds. L. PAPP and B. DARVAS. Science Herald, Budapest. Pp. 227-236.
- DELFINADO M. D., HARDY D. E. 1973: A catalog of the Diptera of the Oriental region. I. Suborder Nematocera. Honolulu. Pp. 1-618.
- DELFINADO M. D., HARDY D. E. 1975. A catalog of the Diptera of the Oriental region. II. Suborder Brachycera, through division Aschiza, suborder Cyclorrhapha. Honolulu. Pp. 1-459.
- DELFINADO M. D., HARDY D. E. 1977. A catalog of the Diptera of the Oriental region. III. Suborder Cyclorrhapha (excluding division Aschiza). Honolulu. Pp. 1-854.
- DAHL Ch., KRZEMIŃSKA E. 1997. Family: Trichoceridae. [In:] L. PAPP and B. DARVAS (Eds) - Contributions to a Manual of Palaearctic Diptera, vol. 2. Science Herald, Budapest. Pp. 227-236.
- EVANS J. W. 1971. Some Upper Triassic Hemiptera from Mount Crosby, Queensland. *Memoirs of the Queensland Museum*, **16**: 145-51.
- EVENHUIS N. L. 1994. Catalogue of the fossil flies of the world (Insecta: Diptera). Leiden (Backhuys Publishers). Pp. 600.
- GALL J.-C., GRAUVOGEL L. 1966. Faune du Buntsandstein 1. Pontes d'invertébrés du Buntsandstein supérieur. *Annales Paléontologie, Invertébrés*, **52**(2): 155-161.
- GENKINA R. Z. 1966. Fossil flora and stratigraphy of Lower Mesozoic deposits of the Issyk-Kul depression. Moscow, Pp. 1-148. (In Russian).
- GRIMALDI D. A. 1987. Amber fossil Drosophilidae (Diptera), with particular reference to the Hispaniolan taxa. *American Museum Novitates*, **2880**: 23.
- GRIMALDI D. A. 1990. Chapter 9. Diptera, [In:] GRIMALDI D. A. (ed.). - Insects from the Santana formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum Natural History*, **195**: 164-183.
- GRIMALDI D., CUMMING J. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum Natural History*, **239**: 1-124.
- HANDLIRSCH A. 1920. Palaeontologie (part) (= Lieferung 5). [In:] SCHROEDER C. W. M. (ed.). - Handbuch der Entomologie. Band III. G. Fischer, Jena. Pp. 117-208.
- HANDLIRSCH A. 1939. Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. II. Teil. *Annalen Naturhistorischen Museum Wien*, **49**: 1-240.
- HENNIG W. 1973. 31. Diptera (Zweiflügler). [In:] HELMCKE, J.-G., D. STARK & H. WERMUTH (eds.) - Handbuch der Zoologie. Eine Naturgeschichte der Stämme des Tierreichs. IV. Band: Arthropoda-2. Hälfte: Insecta. Zweite Auflage. 2. Teil: Spezielles. W. De Gruyter, Berlin. Pp. [3] + 337 p.
- HENNIG W. 1976. Das Hypopygium von Lonchoptera lutea Panzer und die phylogenetischen Verwandtschaftsbeziehungen der Cyclorrhapha (Diptera). *Stuttgarter Beiträge zur Naturkunde* (A), **283**: 1-66.
- JELL P. A., DUNCAN P. M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. [In:] P A. JELL and J. ROBERTS (Eds) - Plant and invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland Victoria. Association of Australian Palaeontologists, Sydney. Pp. 111-202.
- KALUGINA N. S. 1989. New Mesozoic psychodomorph dipteran insects from Siberia (Diptera: Eoptychopteridae, Ptychopteridae). *Paleontologicheskij Zhurnal*, **1**: 65-77. (In Russian) [English translation, 1990, in: *Paleontological Journal*, **23**(1): 62-73.].
- KALUGINA N. S., KOVALEV V. G. 1985. [Dipterous insects of Jurassic Siberia]. Paleontological Institute, Akademia Nauk, Moscow. Pp. 1-198. (In Russian).
- KOVALEV V. G. 1981. [The oldest representatives of the Diptera with short antennae from the Jurassic in Siberia]. *Paleontologicheskij Zhurnal*, **3**: 85-101. (In Russian) (English translation, 1981, in: *Paleontological Journal*, **15**(3): 85-101).

- KOVALEV V. G. 1982. Some Jurassic Diptera—rhagionids (Muscida, Rhagionidae). *Paleontologicheskii Zhurnal*, **3**: 88-100. (In Russian) (English translation, 1982, in: *Paleontological Journal*, **16**(3): 87-99).
- KOVALEV V. G. 1983a. A new subfamily of the Diptera from the Triassic deposit of Australia and its presumable descendants (Diptera, Crosaphididae fam. nov., Mycetobiidae). *Entomologicheskoe Obozrenie*, **62**(4): 800-805. (In Russian).
- KOVALEV V. G. 1983b. New data on the early stages of evolution of Diptera. [In:] Diptera (Insecta), their systematics, geographic distribution and ecology. USSR Academy of Sciences, Zoological Institute. Pp. 60-66. (In Russian).
- KOVALEV V. G. 1987. Classification of the Diptera in light of palaeontological data. [In:] W.P. NARCHUK (ed.), Insecta Diptera: systematics, morphology, ecology. Leningrad. Pp. 40-48. (In Russian).
- KRZEMIŃSKA E., BLAGODEROV V., KRZEMIŃSKI W. 1993. Elliidae, a new fossil family of the infraorder Axymiomorpha (Diptera). *Acta zoologica cracoviensia*, **35**: 581-91.
- KRZEMIŃSKI W. 1992. Triassic and Lower Jurassic stage of Diptera evolution. *Mitteilungen der schweizerischen entomologischen Gesellschaft*, **65**: 39-59.
- KRZEMIŃSKI W. 1998. Origin and the first stages of evolution of the Diptera Brachycera. 4th Internat. Congress of Dipterology. 6-13th Sept, 1998. Keble College, Oxford, UK. Abstract Volume. Pp. 113-114.
- KRZEMIŃSKI W., EVENHUIS N. 2000. Review of Diptera palaeontological records. [In:] Contributions to Manual of Palaeartic Diptera. Vol. 1. L. PAPP and B. DARVAS (Eds.) Science Herald, Budapest. Pp: 535-564.
- KRZEMIŃSKI W., JARZEMBOWSKI E. A. 1999. Aenne triassica n. sp., the oldest representative of the Chironomidae (Diptera). *Polskie Pismo Entomologiczne*, **68**: 445-449.
- KRZEMIŃSKI W., JUDD D. 1997. Family: Tanyderidae. [In:] L. PAPP and B. DARVAS (Eds.) - Contributions to a Manual of Palaeartic Diptera, vol. 2. Science Herald, Budapest. Pp. 281-290.
- KRZEMIŃSKI W., KRZEMIŃSKA E. 1994. Procramptonomyia marianna, a new species from the Upper Jurassic of Great Britain (Diptera, Anisopodomorpha, Procramptonomyiidae). *Acta zoologica cracoviensia*, **37**(2): 101-105.
- KRZEMIŃSKI W., KRZEMIŃSKA E. 1996. Revision of Laurentiptera gallica from the Lower/Middle Triassic of France (Mecoptera: Liassophilidae). *Polskie Pismo Entomologiczne*, **65**: 267-274.
- KRZEMIŃSKI W., KRZEMIŃSKA E. 2002. Rhaetaniidae, a new family of the Diptera from the Upper Triassic of Great Britain (Diptera: Nematocera). *Annales Zoologici*, **52**(2): 211-213.
- KRZEMIŃSKI W., KRZEMIŃSKA E., PAPIER F. 1994. *Grauvogelia arzvilleriana* sp. n. – the oldest Diptera species (Lower/Middle Triassic of France). *Acta zoologica cracoviensia*, **37**(2): 95-99.
- KRZEMIŃSKI W., LUKASHEVICH L. 1993. Ansoigiidae, a new family from the Upper Cretaceous of Kazakhstan (Diptera, Ptychopteromorpha). *Acta zoologica cracoviensia*, **35**: 593-96.
- KRZEMIŃSKI W., REN D. 2001. *Praemacrochile chinensis* sp. n. from the Middle Jurassic of Cina (Diptera: Tanyderidae). *Polskie Pismo Entomologiczne*, **70**: 127-129.
- LAURENTIAUX D. 1953. Classe des Insectes. Pp. 397-527 [In:] PIVETEAU J. (ed.) *Traité de Paléontologie*, 3. Masson, Paris.
- LUKASHEVICH E. D. 1996a. Mesozoic Dixidae (Insecta: Diptera) and the systematic position of the genera Dixamima Rohdendorf, 1964 and Rhaetomyia Rohdendorf, 1962). *Paleontological Journal*, **1**: 48-53. (In Russian).
- LUKASHEVICH E. D. 1996b. New Mesozoic Chaoboridae of Mongolia (Diptera: Chaoboridae). *Palaeontological Journal*, 55-60. (In Russian).
- LUKASHEVICH E. D., ANSORGE J., KRZEMIŃSKI W., KRZEMIŃSKA E. 1998. Revision of Eoptychopterinae (Diptera: Eoptychopteridae). *Polskie Pismo Entomologiczne*, **67**: 311-343.
- LUKASHEVICH E. D., AZAR D. First Eoptychopteridae (Insecta: Diptera) from the Early Cretaceous Lebanese amber. – this volume.
- LUKASHEVICH E. D., SHCHERBAKOV D. E. 1997. A first find of net-winged midges (Blephariceridae, Diptera) in the Mesozoic. *Neues Jahrbuch Geologie Palaeontologie Mh*, **11**: 639-646.
- LUKASHEVICH E. D., SHCHERBAKOV D. E. 1999. A new Triassic family of Diptera from Australia. Proceedings of the First Palaeontological Conference Moscow 1998. AMBA Projects Internat. Bratislava. Pp. 81-89.
- MCALPINE J. F. 1981. Morphology and terminology – adults. [In:] Manual of Nearctic Diptera. Vol. 1. Ottawa, Canada, Research Branch Agriculture Canada. Pp. 9-63.
- MCALPINE J. F. 1989. Phylogeny and classification of the Muscomorpha. [In:] MCALPINE J. F., M. WOOD (eds.). Manual of Nearctic Diptera. Volume 3. Research Branch, Agriculture Canada. Monograph No. 32. Ottawa. Pp. 1397-1518.
- MICHELSSEN V. 1996. Neodiptera: New insights into the adult morphology and higher level phylogeny of Diptera (Insecta). *Zoological Journal of the Linnean Society*, **117**: 71-102.
- MOSTOVSKI M. B. 1996. To the knowledge of Archisargoidea (Diptera, Bracgycera). Families Eremochaetidae and Archisargidae. *Russian Entomological Journal*, **5**(1-4): 117-124.
- MOSTOVSKI M. B. 1997. To the knowledge of fossil dipterans of superfamily Archisargoidea. *Paleontological Journal*, **1**: 72-77.

- MOSTOVSKI M. B. 1999. A brief review of brachycerous flies (Diptera, Brachycera) in the Mesozoic, with descriptions of some curious taxa. Proceedings of the First Palaeontomological Conference Moscow 1998. AMBA Projects Internat. Bratislava. Pp. 103-110.
- MOSTOVSKI M. B., JARZEMBOWSKI E. A. 2000. The First Brachycerous Flies (Diptera: Rhagionidae) from the Lower Jurassic of Gondwana. *Paleontological Journal*, **34**(3): 5367-5369.
- MOSTOVSKI M. B., JARZEMBOWSKI E. A., CORAM R. A., ANSORGE J. 2000. Curious snipe-flies (Diptera: Rhagionidae) from the Purbeck of Dorset, the Wealden of the Weald and the Lower Cretaceous of Spain and Transbaikalia. *Proceedings of the Geologists' Association*, **111**: 153-160.
- NAGATOMI A., YANG D. 1998. A review of extinct Mesozoic genera and families of Brachycera (Insecta, Diptera, Orthorrhapha). *Entomologist's monthly Magazine*, **134**: 95-192.
- NOVOKSHONOV V. G. 1997. Early evolution of scorpionflies (Insecta: Panorpoda). Nauka. 140 pp. (In Russian).
- OLSEN P. E., REMINGTON C. L., CORNET B., THOMSON K. S. 1978. Cyclic change in Late Triassic lacustrine communities. *Science*, **201**: 72-73.
- OOSTERBROEK P., COURTNEY G. 1995. Phylogeny of the nematocerus families of Diptera (Insecta). *Zoological Journal of the Linnean Society*, **115**: 267-311.
- RIEK E. F. 1977. Four-winged Diptera from the Upper Permian of Australia. *Proceedings of the Linnean Society of New South Wales*, **101**: 250-55.
- ROHDENDORF B. B. 1961. [The oldest infraorders of Diptera from the Triassic of Middle Asia]. *Paleontologicheskij Zhurnal*, **2**: 90-100. (In Russian).
- ROHDENDORF B. B. 1962. Order Diptera., p. 307-45. [In:] ROHDENDORF, B. B.(ed.) - Fundamentals of Paleontology. Volume 9. Arthropoda, Tracheata, Chelicerata. Izdatel'stvo Akademii. Nauk, Moscow. (In Russian), (English translation, 1991).
- ROHDENDORF B. B. 1964. [Historical development of dipterous insects]. *Trudy Paleontologicheskogo Instituta AN SSSR*, **100**: 1-311. (In Russian). (English translation: ROHDENDORF, 1974).
- SAETHER O. A. 2002. Phylogeny of Culicomorpha (Diptera). *Systematic Entomology*, **25**: 223-234.
- SHCHERBAKOV D. E., LUKASHEVICH E. D., BLAGODEROV V. A. 1995. Triassic Diptera and initial radiation of the order. *An International Journal of Dipterological Research*, **6**(2): 75-115.
- SZADZIEWSKI R. 1988. Biting midges (Diptera, Ceratopogonidae) from Baltic amber. *Polskie Pismo Entomologiczne*, **57**: 3-283.
- SZADZIEWSKI R. 1990. The oldest fossil biting midges (Ceratopogonidae). Abstracts of the 2nd International Congress of Dipterology. Bratislava 1990. P. 231.
- SZADZIEWSKI R., SCHLÜTER T. 1992. Biting midges (Diptera: Ceratopogonidae) from Upper Cretaceous (Cenomanian) amber of France. *Annales Société entomologique France (N.S.)*, **28**: 73-81.
- SZADZIEWSKI R. 1995. The oldest fossil Corethrellidae from Lower Cretaceous Lebanese amber. *Acta zoologica cracoviensia*, **8**(2): 177-181.
- SZADZIEWSKI R. 1996. Biting midges from Lower Cretaceous amber of Lebanon and Upper Cretaceous Siberian amber of Taimyr (Diptera, Ceratopogonidae). *Studia dipterologica*, **3**(1): 83-86.
- TILLYARD R. J. 1929. Permian Diptera from Warner's Bay, N.S.W. *Nature*, **123**: 778-79.
- TILLYARD R. J. 1937. The ancestors of Diptera. *Nature*, **139**:66-67.
- USSATCHOV D. A. 1968. [New Jurassic Asilomorpha (Diptera) in Karatau]. *Entomologicheskoe Obozrenie*, **47**: 617-28. (In Russian).
- WAGNER R., HOFFEINS C., HOFFEINS W. 2000. A fossil nymphomyiid (Diptera) from the Baltic and Bitterfeld amber. *Systematic Entomology*, **25**: 115-120.
- WILLMANN R. 1989. Rediscovered: Permotipula patricia, the oldest known fly. *Naturwissenschaften*, **76**:375-377.
- WOOD D. M., BORKENT A. 1989. Phylogeny and classification of the Nematocera. [In:] MCALPINE J. F., WOOD D. V.(Eds.). Manual on Nearctic Diptera. Vol. 3. Ottawa, Research Branch Agriculture Canada. Pp. 1333-1370.
- YEATES D. K., WIEGMANN M. B. 1999. Congruence and controversy: Toward and Higher-Level Phylogeny of Diptera. *Annual Reviews Entomology*, **44**: 397-428.

APPENDIX

Taxonomic system of the Diptera, with Triassic representatives. Those described herein are marked bold.

Suborder: DIARCHINEURA

Infraorders:

1. Grauvogeliomorpha

Grauvogeliidae:

Grauvogelia arzvilleriana KRZEMIŃSKI, KRZEMIŃSKA et PAPIER, 1994 (Lower/Middle Triassic of France)

Louisa nova, n. sp. (Lower/Middle Triassic of France)

2. Hennigmatomorpha, n. infraorder

Kuperwoodidae, comb. nov.:

Kuperwoodia benefica LUKASHEVICH 1995 (Middle/Upper Triassic of Kyrgyzstan)

3. Nadipteromorpha

Nadipteridae:

Nadiptera kaluginae LUKASHEVICH, 1995 (Upper Triassic of Kazakhstan)

Nadiptera pulchella LUKASHEVICH 1995 (Middle/Upper Triassic of Kyrgyzstan)

Tanus triassicus, n. sp., Lower/Middle Triassic of France

4. Tanyderomorpha

5. Psychodomorpha

Suborder: NEONEURA

Infraorders:

1. Tillyardomorpha, n. infraorder

Tillyardipteridae:

Tillyardiptera prima LUKASHEVICH & SHCHERBAKOV, 1998 (Upper Triassic of Australia)

Rhaetanidae:

Rhaetania diana KRZEMIŃSKI & KRZEMIŃSKA, 2002 (Upper Triassic of Great Britain)

2. Ptychopteromorpha

Eoptychopteridae HANDLIRSCH, 1906 : wing fragment (Upper Triassic of USA)

3. Culicomorpha

Chironomidae MACQUART, 1838:

Aenne triassica KRZEMIŃSKI & JARZEMBOWSKI, 1999 (Upper Triassic of Great Britain)

4. Nymphomyiomorpha

5. Blephariceromorpha

Suborder: POLYNEURA

Infraorders:

1. Tipulomorpha

Archilimoniidae, n. fam.:

Archilimonia vogesiana, n. sp., Lower/Middle Triassic of France

Psychotipidae comb. nov.:

Psychotipa predicta SHCHERBAKOV 1995 (Middle/Upper Triassic of Kyrgyzstan)

Psychotipa depicta SHCHERBAKOV 1995 (Middle/Upper Triassic of Kyrgyzstan)

Limoniidae (RONDANI, 1856):

Mabelysia charlesii SHCHERBAKOV 1995 (Middle/Upper Triassic of Kyrgyzstan)

Architipula youngi KRZEMIŃSKI 1992 (Upper Triassic of USA)

2. Trichoceromorpha

(?) Gnomuscidae comb. nov. SHCHERBAKOV 1995:

(?) *Gnomusca molecula* SHCHERBAKOV 1995 (Middle/Upper Triassic of Kyrgyzstan)

(?) *Gnomusca renyxa* SHCHERBAKOV 1995 (Middle/Upper Triassic of Kyrgyzstan)

Suborder: ANISONEURA

Infraorders:

1. Anisopodomorpha

Protorhyphidae HANDLIRSCH, 1906:

Vymrhyphus expectus, n. sp. Lower/Middle Triassic of France

Vymrhyphus tuomikoskii BLAGODEROV 1995 (Middle/Upper Triassic of Kyrgyzstan)

Vymrhyphus triassicus BLAGODEROV 1995 (Middle/Upper Triassic of Kyrgyzstan)

Procramptonomyiidae KOVALEV, 1985:

Yala argentata KRZEMIŃSKI 1992 (Upper Triassic of USA)

Austrocramptonomyia minuta BLAGODEROV 1998 (Upper Triassic of Australia)

Paraxymyiidae ROHDENDORF, 1946:

Veriplecia handlirschi BLAGODEROV, 1998 (Upper Triassic of Australia)

Crosaphididae KOVALEV, 1983:

Crosaphis anomala EVANS 1971 (Upper Triassic of Australia)

2. Axymyiomorpha

3. Bibionomorpha

Suborder: BRACHYCERA

Infraorders:

1. Tabanomorpha

Rhagionidae LATREILLE, 1802:

Gallia alsatica, n. sp. (Lower/Middle Triassic of France)

2. Xylophagomorpha

Alinkidae KRZEMIŃSKI, 1992:

Alinka cara KRZEMIŃSKI, 1992 (Upper Triassic of USA)

3. Stratiomyiomorpha

4. Asilomorpha

5. Muscomorpha