

Zeitschrift:	Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society
Herausgeber:	Schweizerische Entomologische Gesellschaft
Band:	65 (1992)
Heft:	1-2
Artikel:	Triassic and Lower Jurassic stage of Diptera evolution
Autor:	Krzeminski, Wieslaw
DOI:	https://doi.org/10.5169/seals-402471

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 27.01.2026

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

Triassic and Lower Jurassic stage of Diptera evolution

WIESLAW KRZEMINSKI

Institute of Systematics & Evolution of Animals, Polish Academy of Sciences, ul. Slawkowska 17, 31-016 Krakow, Poland

This work deals with the Upper Triassic Diptera from USA (Carolina and Virginia, Dan River group). The representatives of four families are described: Eoptychopteridae (incerta sedis specimen, infraorder Ptychopteromorpha), *Yala argentata* n.sp. (Procramptonomyiidae, infraorder Anisopodomorpha), *Alinka cara* n.sp. (Alinkidae n.fam., infraorder Tabanomorpha), *Architipula youngi* n.sp. (Limonidae, infraorder Tipulomorpha). A new phylogenetical system of Diptera is proposed, based on the Triassic and Lower Jurassic materials. The order is divided into four suborders: Diarchineura n. suborder, Neoneura n. suborder, Oligoneura and Polyneura.

Keywords: Fossils, Diptera, Evolution, Phylogeny, New Species

TRIASSIC DIPTERA FROM USA

Introduction

Although the origin and evolution of Diptera have been discussed since more than 100 years, their direct ancestors and time of appearance remain obscure. The first fossil Diptera were recorded from younger geological periods: Miocene, Oligocene and Eocene (PRESL, 1822; HEER, 1849; LOEW, 1850; SCUDDER, 1894 and others). Being very similar to the recent flies, these materials did not contribute much to our knowledge on the beginnings of Diptera evolution. The discussion on this subject started with the first Lower Jurassic Diptera, recorded by HANDLIRSCH (1906-1908, 1937-1939) from German Lias (190 Ma). Later these records became numerous from Asia (ROHDENDORF, 1961, 1964; KALUGINA & KOVALEV, 1985; KALUGINA, 1986, 1989; KOVALEV, 1986) and from Europe (BRODIE, 1845; HANDLIRSCH, 1906-8, 1937-9; TILLYARD, 1933; BODE, 1953; USATCHEV, 1968; KRZEMINSKI & KOVALEV, 1988; KRZEMINSKI & ZESSIN, 1990).

The older materials are very scarce and show characters difficult to evaluate. In most cases their classification into the Diptera is doubtful. TILLYARD (1929) described from a single wing the species *Permotipula patricia* from Australian Upper Permian (250 Ma) classified then to the Diptera. However, in 1937 he revised his previous opinion and showed that the single wing was not sufficient to state whether it was a Diptera or not, as the venation of the hind wings of the so called four-winged Paratrichoptera is very similar to that of some Diptera. The comparison of the wing venation of the Mecoptera, *Permotipula patricia* (Paratrichoptera) and the Diptera is presented in Fig. 1. The holotype of this species was redescribed by WILLMANN (1989b). However, in spite of an intriguing title: "Rediscovered: *Permotipula patricia*, the oldest known fly, the author concludes: "Permotipula patricia cannot

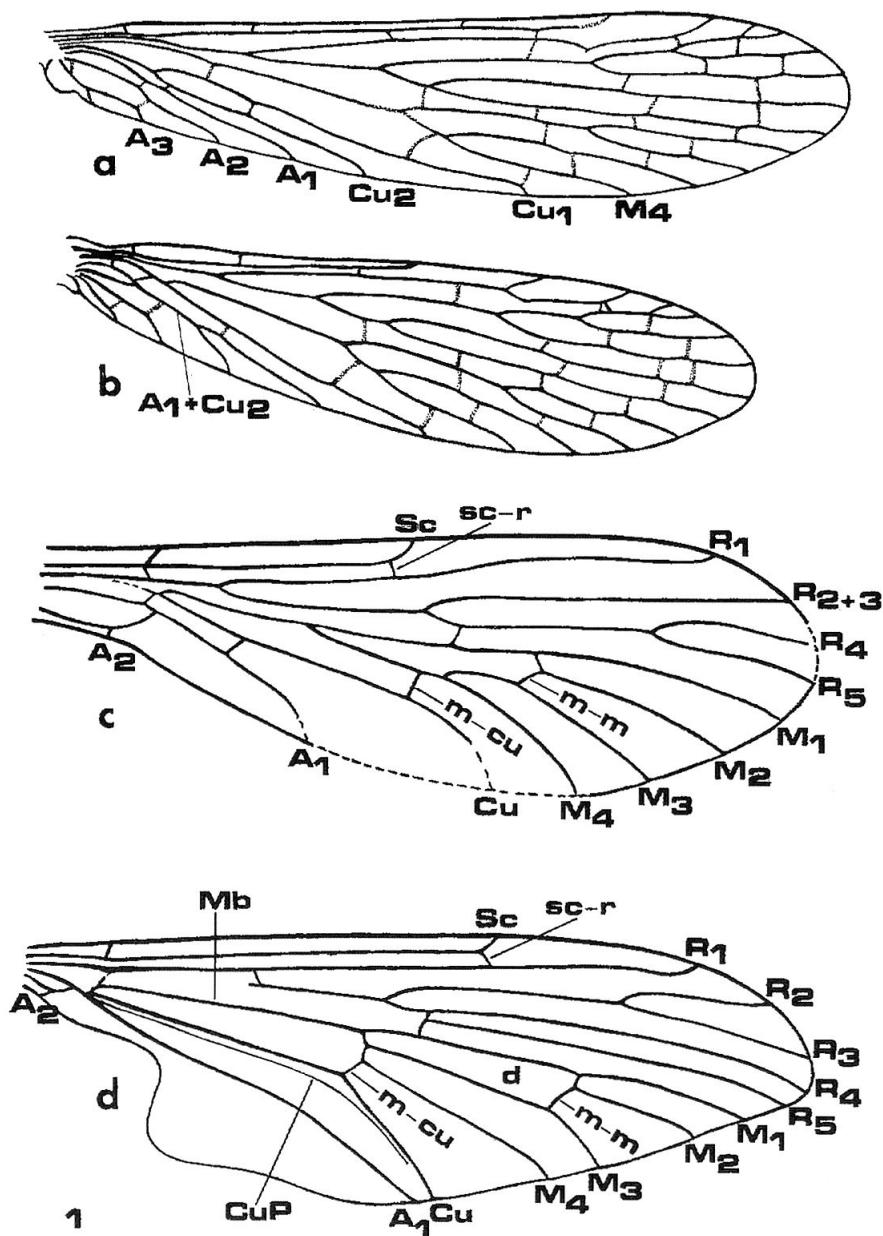


Fig. 1. Wing venation of: a.- *Panorpodes paradoxa* McLACHLAN (Mecoptera) fore wing, b.- hind wing, same species, c.- *Permotipula patricia* TILLYARD (Paratrichoptera), d.- *Tanyderus fitchii* OSTEN-SACKEN (Diptera) (a, b, c after WILLMANN, 1989a with veins names added).

be one of the direct ancestor of the recent Diptera". Also the so called four-winged Diptera described from Permian by RIEK (1977) do not give us sufficient reasons for their classification to Diptera (HENNIG, 1981).

ROHDENDORF (1961, 1964) recorded numerous species of Diptera from Issyk Kul, dated then Upper Triassic. Later their age was corrected for Lower Jurassic, probably Sinemurian (200 Ma). Despite of this mistake, for a long time they were considered to be the oldest known remnants of Diptera.

From the Upper Triassic of Australia, EVANS (1971) described a single wing classified to a new genus *Crosaphis* of the order Homoptera. The revision made by KOVALEV (1983) proved that the wing belonged to a representative of an extinct

family Crosaphididae, infraorder Anisopodomorpha (Fig.2). In the same work he published the drawings of two wings of supposed-to-be Diptera from Ferganskaya Valley (USSR, Asia) from Middle/Upper Triassic without denoting the species. Since the specimens are in a very bad condition and the drawings are not fully reliable, their taxonomic status remains unknown.

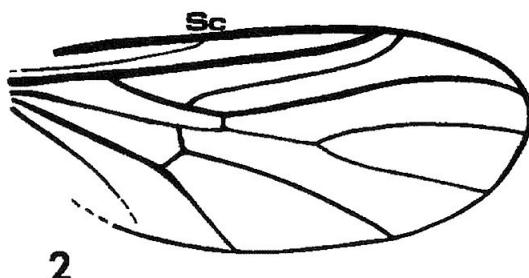


Fig. 2. *Crosaphis* sp. (Crosaphididae) - wing (after KOVALEV, 1983).

Next record on the Upper Triassic Diptera was published by OLSEN *et al.* (1978) from North America. The authors supposed that the specimens belonged to the families Tipulidae and Bibionidae. These materials were made accessible to me and are described in the present work. The specimens represent four infraorders: Tipulomorpha, Ptychopteromorpha, Anisopodomorpha and Tabanomorpha and are the oldest true Diptera known so far. They allow the more intrinsic look into the beginning of Diptera evolution.

Abbreviations

PMNH = Peabody Museum of Natural History, Yale University, New Haven, USA.

MND(I), MND(III) = McALPINE *et al.*, Manual of Nearctic Diptera, I and III band, respectively.

Materials and methods

The subject of the present work are Upper Triassic Diptera, dealt with in OLSEN *et al.* (1978). They were found in North Carolina and Virginia (Dan River group), USA. Their condition is very good owing to a very delicate sediment in which they are preserved. The collection contains 11 specimens, representing 4 families (and 4 infraorders): Limoniidae (Tipulomorpha) - 7 specimens, Procrampomyiidae (Anisopodomorpha) - 1 specimen, Eoptychopteridae (Ptychopteromorpha) - 1 specimen, Alinkidae n. fam. (Tabanomorpha) - 2 specimens and 2 specimens of uncertain status. Three last families are extinct. All drawings are based on the camera pictures of the specimens. The specimens were studied and photographed while wetted with 96° ethanol. The venation nomenclature applied is presented in Fig.12d.

Systematic part

Infraorder Ptychopteromorpha

This infraorder was created by the authors of MND(I) to separate the family Ptychopteridae. In MND(III) also the family Tanyderidae is included, although with

some restraint. In my opinion this infraorder comprises the extinct family Eoptychopteridae and the extant family Ptychopteridae, while Tanyderidae does not belong there (the reasons are given in the chapter on the new system proposed).

Superfamily Eoptychopteroidea

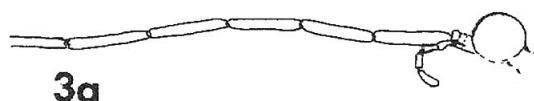
This taxon comprises the single, fossil family Eoptychopteridae from the Mesozoic. The genera included there are very different, some maybe deserve raising their status to separate families.

Family Eoptychopteridae HANDLIRSCH, 1906

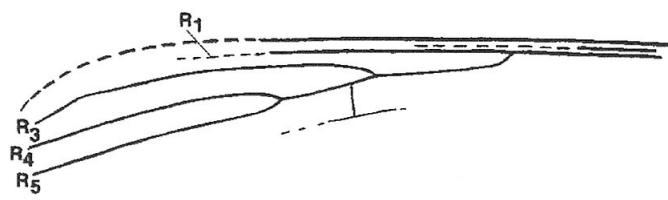
The family was described from the Lower Jurassic of Europe (German Lias), with 3 genera included by HANDLIRSCH (1906, 1937) and BODE (1953), and further 5 genera added by KALUGINA (1985, 1989) from the Jurassic and Cretaceous of Asia.

In the Upper Triassic materials from USA one specimen of this family was found. Its remnants do not allow assigning it to a genus, although they resemble the members of two genera: *Proptychoptera* HANDLIRSCH and *Crenoptychoptera* KALUGINA. The former comprises 6 species from the German Lias and 2 species from the Middle Jurassic of Asia. The latter is known from 2 species from Lower and Middle Jurassic of Asia.

Description of a specimen of uncertain status: Body length ab. 4.5 mm, wing length 5 mm. Head small; palpi as long as the head, probably 5-segmented. Antennae partially preserved (Fig.3a), at least equal half of body length; scapus short, cylindrical; pedicel small, oval; flagellomeres very long, cylindrical. Wing (Fig.3b): only radial field preserved, which is characteristic for the family (compare Fig.8b,c). Thorax and abdomen well preserved, but genital organs lacking. Sex unknown, probably male. Material examined: No. 100000, Upper Triassic, Virginia, USA. Housed in PMNH.



3a



3b

Fig. 3. Representative of Eoptychopteridae (Upper Triassic, USA): a.- head with palpus and antenna, b.- wing fragment preserved.

Infraorder Tipulomorpha

Superfamily Tipuloidea

Family Limoniidae

An extant family, comprising ca 11000 species of worldwide distribution. Fossil Limoniidae were found in all the continents beside Antarctica. The most numerous finds were recorded from Asiatic and European localities, beginning from Lower Jurassic.

Subfamily Architipulinae HANDLIRSCH, 1906

HANDLIRSCH (1906) described several species from German Lias (Lower Jurassic, Toarcian), counted to a new fossil family Architipulidae. KALUGINA (1985) lowered its status to a subfamily, since no conspicuous differences distinguishing the fossil species from the recent Limoniidae could be stated. Other representatives of this subfamily were recorded from Europe and Asia by HANDLIRSCH (1937-39), BODE (1953), ROHDENDORF (1961, 1964), TILLYARD (1933), KALUGINA (1985, 1986), KRZEMINSKI & KOVALEV (1988) and KRZEMINSKI & ZESSIN (1990).

Genus *Architipula* HANDLIRSCH, 1906

Till now ca. 30 species were recorded from European and Asiatic Jurassic and Cretaceous, but the majority of them should be revised.

Architipula youngi n.sp.

Diagnosis: small species of body length ca. 3 mm. Vein R1 very long; cross-vein r-r at the end of R1; proximal part of d cell very narrow, almost triangular.

Origin of name: the species is dedicated to Dr Chen W. YOUNG from the Carnegie Museum of Natural History, Pittsburgh, a specialist of recent Limoniidae.

Description: small head, with medium sized, oval eyes. Palpi unidentifiable; antennae partially preserved (Fig.4a), nearly twice longer than the head, probably 14-segmented; scape and pedicel invisible, flagellomeres short and thick, with single bristles not much longer than the segments. Wing (Fig.4b): 3.2 mm long, narrow. Right wing folded, left one with folded anal part. Sc rather short, not reaching fork of Rs; cross-vein sc-r faint, probably at the end of Sc; R1 very long, its distal section subsinuous; cross-vein r-r (R2) faint, at the R1 tip; Rs twice shorter than R5; four medial veins present; upper part of d cell equal petiole of M1 and M2 and somewhat shorter than M1; d cell small, its length equal 1/7 of wing length and a little shorter than M3, proximal angle of d cell almost regularly triangular; cross-vein m-cu just before M3+4 fork; A2 only partially identifiable. Legs not preserved. Only 8 segments of abdomen preserved, genital organ not preserved. Sex unknown.

Material examined: holotype No 1103 (+,-), Upper Triassic, USA, Virginia. Other materials: No. 30077; No.3; YEN 1167; No.100000 - all in very bad condition. Housed in PMNH.

Remarks: the species differs from the other representatives of the genus in the shape of d cell being more triangular and shorter antennae, composed of thick segments.

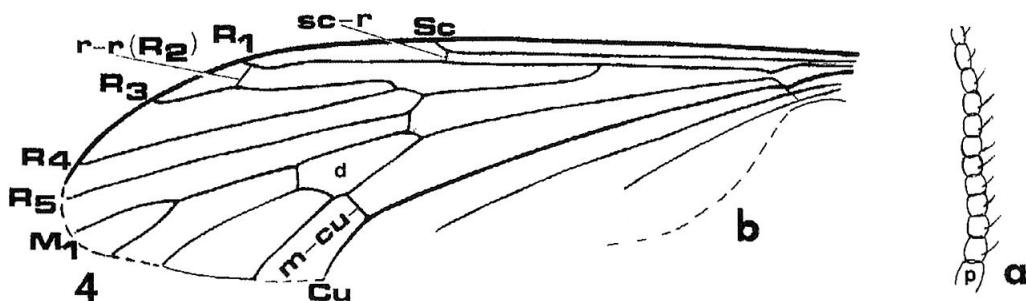


Fig. 4. *Architipula youngi* n. sp., Limoniidae (Upper Triassic, USA), holotype: a.- antenna, b.- wing.

Infraorder Anisodopomorpha

The taxon was proposed by KROVOSHEINA (1988), to enclose the families: Trichoceridae, Canthyloscelidae, Scatopsidae, Mycetobiidae and Anisopodidae. For the reasons given in the chapter Discussion the first one apparently does not belong there. In the Upper Triassic and Lower Jurassic the Anisopodomorpha were very numerous and variable. The taxon is divided into two superfamilies: Anisopodoidea and Mycetobioidea. The representatives of both are known from the Mesozoic.

Superfamily Anisopodoidea

Flies enclosed here were characterized by the d cell closed and four medial veins present (while in Mycetobioidea d cell is open and one medial vein reduced). In Lower and Middle Jurassic the superfamily was represented by 3 families: Protorhyphidae, Procramptonomyiidae and Siberhyphidae.

Family Procramptonomyiidae KOVALEV, 1985

An extinct family described by KOVALEV (1985) from Lower and Middle Jurassic of Asia with two species of the genus *Procramptonomyia*.

Genus *Yala* n. gen.

Diagnosis and description of the genus is identical with these of the type species *Yala argentata* n.sp., the only representative of the genus.

Yala argentata n.sp.

Diagnosis: three branches of Rs present; d cell closed; M4 fork almost in the middle of d cell base.

Description: wing length 3.3 mm, body length 5 mm. Head small, palpi invisible. Antennae (Fig.5a) a little longer than the head, probably 11-segmented; scapus long and thick, cylindrical; pedicel large and rounded; 1st flagellomere very thick, barrel-like, the following become gradually narrower and longer. Wing (Fig.5b) wide; Sc long, reaching beyond Rs fork; cross-vein sc-r nearly in the middle of Sc, opposite Rb fork; R1 long; cross-vein r-r (R2) absent; Rs rather short, ab. 1/3 shorter than R3, which is slightly curved to costal margin; R4+5 very short, equal 1/14 of R4; R4 and R5 long, distal 1/3 of the latter curved towards anal margin; cross-vein r-m positioned in 2/3 of M1+2 and connecting this vein to R5; M1+2 fork in 2/3 of d cell length; cross-vein m-m connecting M2 and M3; M3+4 fork

almost opposite the middle of d cell base; d cell closed; cross-vein m-cu almost in the middle of M3+4. Legs slender, probably without tibial spurs. Male genital organ (Fig. 5c) well preserved. Gonocoxites short, thick, gonostyles probably single, broad, deeply forked. I could not state with certainty whether the distinct structure between them is an aedeagus or sternite process, or proctiger.

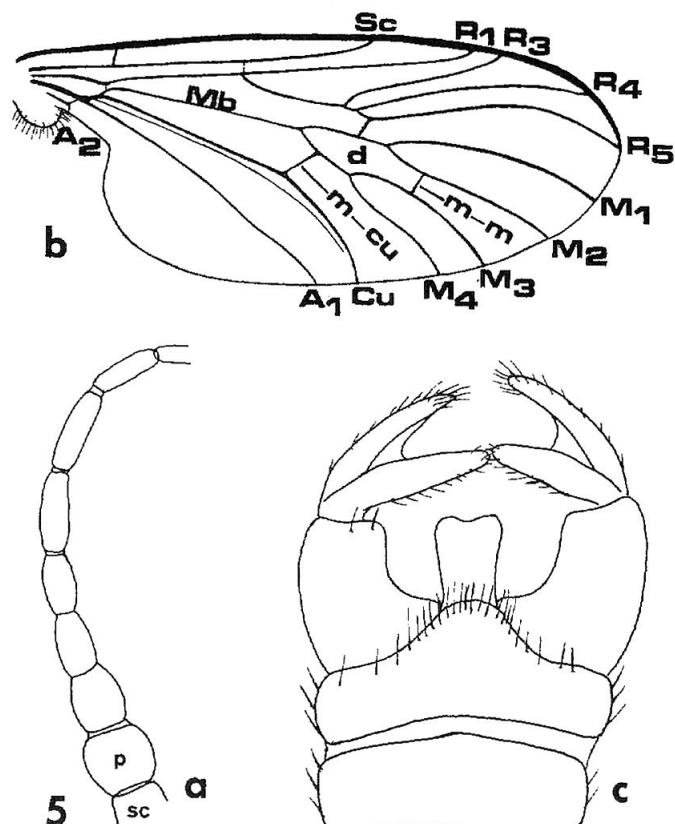


Fig. 5. *Yala argentata* n. sp., Procrampomyiidae (Upper Triassic, USA), holotype: a.- antenna (sc - scapus, p - pedicel), b.- wing, c.- hypopygium.

Material examined: holotype No. 16826 (+,-), male, Upper Triassic, Virginia, USA. Housed in PMNH.

Infraorder Tabanomorpha

Superfamily Tabanoidea

Family Alinkidae n. fam.

Genus *Alinka* n. gen.

Diagnosis of the family and genus is identical with those of the only known species, *Alinka cara* n.sp from Upper Triassic, USA.

Origin of name: the new genus name is dedicated to my daughter.

Alinka cara n.sp.

Description: wing length 2.3 mm, body length ab. 3.5 mm. Head partially preserved in male only, palpi invisible. Antennae (Fig.6a) twice longer than head, 10-segmented; scapus short, thick; pedicel large, thick, rounded; 1st flagellomere thick, longer than each of 3 following; 4 terminal ones longer and narrower, spindle-like. Wing (Fig.6b): wide, with large anal field and conspicuous stigma. Vein Sc reaching beyond Rs fork; cross-vein sc-r almost in the middle of Sc and just before Rb fork; cross-vein r-r (R2) absent; R3 long and slightly curved toward costal margin; R4+5 very long; R4 short, curved toward costal margin; cross-vein r-m between Rs fork and the middle of d cell upper part; cross-vein m-m connecting M2 and M3; M3+4 fork almost in 1/2 of d cell base; d cell large, as long as 1/4 of wing length; cross-vein m-cu just beyond Mb fork. Cu and A1 cannot be reconstructed exactly. Legs short, probably spurless. Male genital organ poorly preserved. Female genital organ presented on Fig.6c.

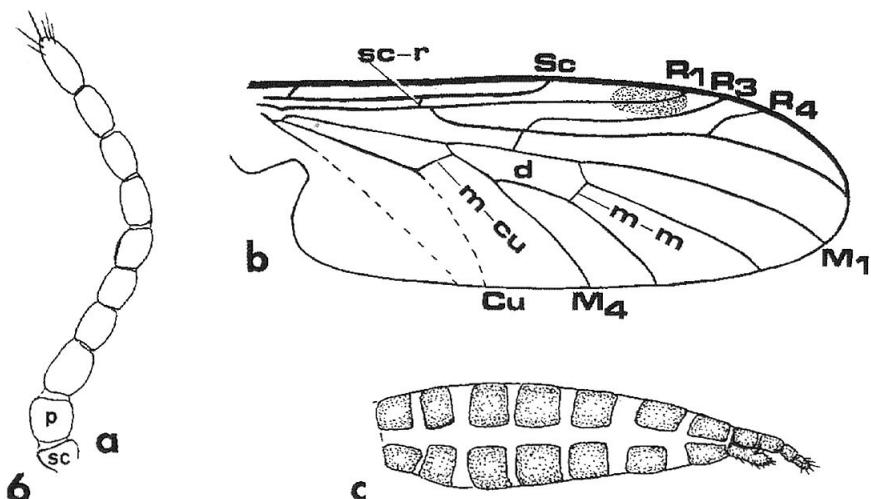


Fig. 6. *Alinka cara* n. sp., Alinkidae n. fam. (Upper Triassic, USA), holotype: a.- antenna (sc - scapus, p - pedicel), b.- wing, specimen No. 400000, c.- female abdomen.

Material examined: holotype No. 100000, male. Other materials: No. 400000, female, Upper Triassic, Virginia, USA. Housed in PMNH.

PHYLOGENETICAL SYSTEM OF DIPTERA PROPOSED

ROHDENDORF's system revised

The first comprehensive trial of including the paleontological data into the phylogenesis of Diptera was attempted by HANDLIRSCH (1906-1908, 1909). A first and till now only complete taxonomic system based on fossil and Recent Diptera was created by ROHDENDORF (1964). The author divided the order Diptera into two suborders: Archidiptera and Eudiptera. The former encloses 4 extinct families, described by him from 6 specimens, representatives of 6 species. ROHDENDORF's work was criticized by HENNIG (1968, 1981) who suspected that ROHDENDORF had misinterpreted the wing venation in some cases. This opinion was confirmed by KOVAL'EV (1987).

Together with late Dr V. KOVALEV we have restudied materials from the ROHDENDORF's collection that constituted the suborder Archidiptera and stated that they all belong to the known families of Tipulomorpha and Bibionomorpha. Thus the suborder Archidiptera does not exist. The Tipulomorpha specimens are on the way to be revised by me and will be published later. The part dealing with the Bibionomorpha was to be published by Dr. V. KOVALEV, but his sudden death made this impossible.

Nevertheless, I wanted to present the final conclusions already now, as the ROHDENDORF's system is still being discussed. *Dictyodiptera multinervis* ROHDENDORF, 1961 (Dictyodipteridae) does not belong to Diptera; *Dipterodictya tipuloides* ROHDENDORF, 1961 (Dictyodipteridae) belongs to Limoniidae; *Diplopolyneura mirabilis* ROHDENDORF, 1961 (Diplopolyneuridae) belongs to Limoniidae; *Dyspolyneura longipennis* ROHDENDORF, 1961 (Dyspolyneuridae) belongs to Protopleciidae (Bibionomorpha); *Paradictyoptera trinalis* ROHDENDORF, 1961 (Dictyodipteridae) and *Hyperpolyneura phryganoides* ROHDENDORF, 1961 (Hyperpolyneuridae) belong to the infraorder Bibionomorpha, but their bad state of preservation does not allow the classification to the families.

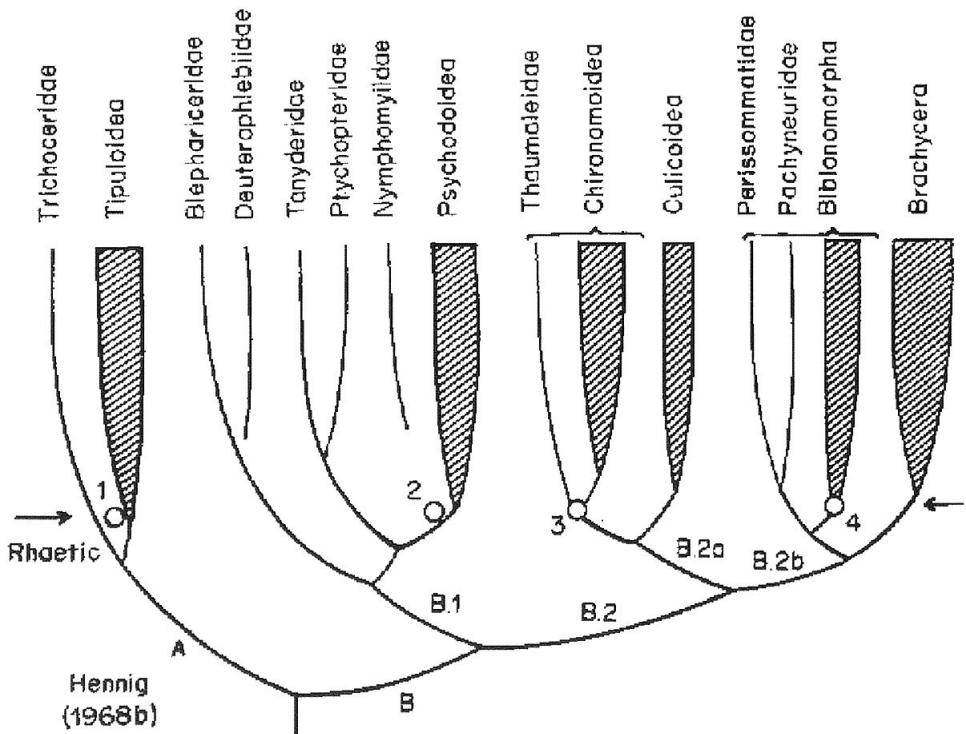


Fig. 7. Phylogenetical tree of Diptera (after HENNIG, 1968).

After a rejection of ROHDENDORF's system we are left with the systems based only on the recent materials, with the Hennigian one being most widely accepted (Fig.7), although subjected to numerous modifications by the author himself (1968,

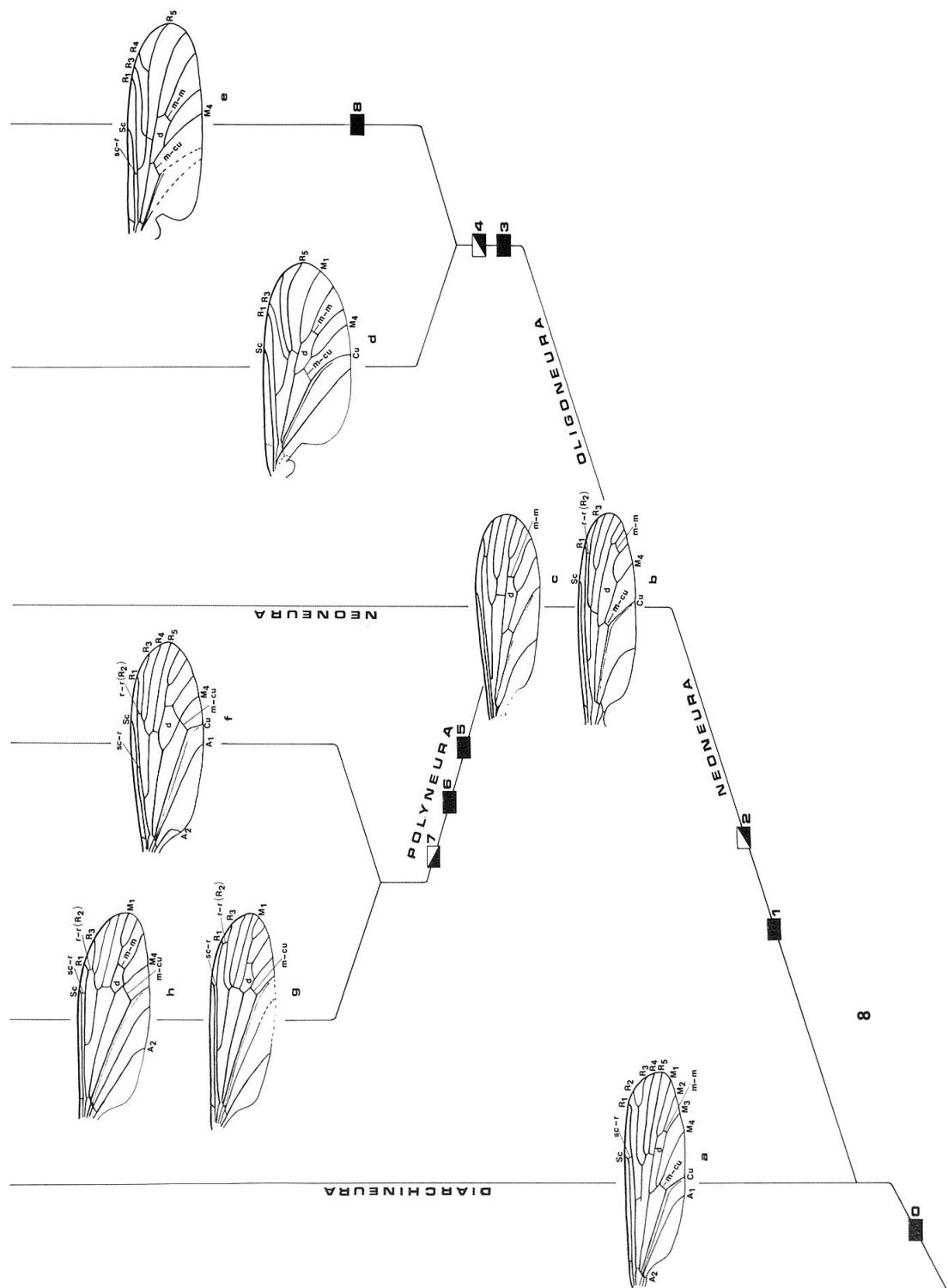


Fig. 8. Main evolutionary trends in wing venation of Triassic/Lower Jurassic Diptera. Apomorphies: 0 - basic apomorphies of Diptera (see text); 1 - long R₂ absent; 2 - sc-r absent; 3 - r-r absent; 4 - reduction of radial and medial veins; 5 - long A₂; 6 - d cell raised over Mb level; 7 - R₃+4 present; 8 - R₄+5 very long. Wings: a.- Tanyderidae (German Lias, Lower Jurassic), b.- and c.- Eoptychopteridae (b. *Proptychoptera* sp., German Lias, Lower Jurassic; c. *Eoptychopterina* sp., Siberia, USSR, Lower Jurassic), d.- Procrampomyiidae: *Yala argentata* n.sp. (Upper Triassic, USA), e.- Alinkidae n.fam.: *Alinka cara* n.sp. (Upper Triassic, USA), f.- Trichoceridae representative (Siberia, Middle Jurassic), g.- and h.- Limoniidae (g.- *Praearchitipula* sp., Siberia, USSR, Lower Jurassic, h.- *Architipula* sp., German Lias).

1981) and by other authors. The review of almost all the papers dealing with phylogenetic systems of Diptera is presented in the MND(III), plus the authors' own proposition. To their list the work of KOVALEV (1987) should be added, in which the phylogenetic tree of Diptera is presented (to the level of infraorder and superfamily), based on the Recent and some fossil taxons included. Some chosen aspects of the Diptera phylogenesis are dealt with in the work of KRIVOSHEINA (1988).

The new system proposed

A starting point of the proposed system is the wing venation of Tanyderidae (Fig.1d, 8a). That this is the most archaic group of Diptera is well documented. HENNIG (1981, p. 427) wrote: "The venation of the Tanyderidae is more primitive than that of all the other Diptera, *except in the reduction of the 2nd anal vein*: the radial sector has four branches which reach the wing margin independently; the discal cell is large and is situated at the middle of the wing; and the anal lobe is broad. *It is surprising that such a primitive venation has not been found in any of the Mesozoic fossils*" (my underlining).

Comparing the venation of Tanyderidae to *Permotipula patricia* TIL. (Fig.1c) I came to the conclusion, that this type, with short anal vein is primitive (plesiomorphic), and the long A2 (as in Tipulomorpha) is a derived apomorphy. The type of anal field venation represented by the Tanyderidae is consistent with that of *Permotipula patricia* and some other fossil insects laying between Diptera and Mecoptera.

The characters regarded by HENNIG as the most primitive (listed above) are dominating in Triassic and Lower Jurassic Diptera (KOVALEV in KALUGINA & KOVALEV, 1985; KALUGINA, 1986; KRZEMINSKI & ZESSIN, 1990). So the intuition of HENNIG has been supported by the fossil evidences.

As a consequence of the change of polarity of A2 character, the entire system of Diptera ought to be changed. Analyzing the venation of Triassic and Lower Jurassic specimens led me to the conclusion that already then the Diptera were divided into four separate evolutionary lineages, (which I propose to give a suborder status): Diarchineura n. suborder, Neoneura n. suborder, Polyneura BRAUER and Oligoneura BRAUER. They are described below.

Order Diptera

Suborder Diarchineura n. suborder

Venation (Fig.1d, 8a): cross-vein sc-r always at the end of Sc; five long radial veins terminating in wing margin; cross-vein r-r absent; four medial veins present; cross-vein m-m connecting M2 and M3; d cell, if present, always very long and always below level of Mb (i.e., M1+2 lies in the straight prolongation of Mb); cross-vein m-cu just beyond fork of Mb; A2 always very short.

From Triassic and Lower Jurassic only the family Tanyderidae (infraorder Tanyderomorpha) is known. Recently also the family Psychodidae (infraorder Psychodomorpha) belongs there.

Suborder Neoneura n. suborder

Venation (Fig.8b, c): cross-vein sc-r absent; only four long radial veins escaping in wing margin; cross-vein r-r (R2) present; in fossil representatives three or four medial veins present; cross-vein m-m connecting either M2 and M3 or M1+2

and M3; d cell always very long and below level of Mb, like in Diarchineura (in the Recent Ptychopteridae d cell is open, i.e. m-m absent); cross-vein m-cu just beyond fork of Mb; A2 very short.

From Triassic and Lower Jurassic only the extinct family Eoptychopteridae known. Recently only the family Ptychopteridae belongs here.

Suborder Oligoneura BRAUER, 1863

Venation (Fig.8d, e): cross-vein sc-r if present then generally far before end of Sc; radial veins usually reduced, rarely all four present; cross-vein r-r (R2) absent; medial veins also reduced, rarely all four present; cross-vein m-m if present then usually connecting M2 and M3; d cell if present then usually long and always below level of Mb; cross-vein m-cu usually just beyond fork of Mb; A2 absent or very short.

From Triassic and Lower Jurassic families: Rhaetomyiidae, Chaoboridae, Chironomidae, Procramp桐omyidae, Protorhyphidae, Eoplectiidae, Crosaphididae, Protopleciidae, Pleciofungivoridae, Pleciomimidae, Boholdoyidae, Protoscapsidae, Alinkidae, Vermileonidae and Rhagionidae are known. Recently all the remaining families of Diptera belong there.

Suborder Polyneura BRAUER, 1863

Venation (Fig.8f, g, h): cross-vein sc-r at end or near middle of Sc; no more than four radial veins escaping in wing margin; if all four present, then R4 and R5 separate over their entire length; cross-vein r-r (R2) usually present; three or four medial veins present; cross-vein m-m if present then always connecting M1+2 and M3 (i.e. M1 and M2 with petiole); d cell usually small and always over the level of Mb (i.e. most proximal section of M1+2 curved upwards and not forming straight prolongation of Mb); cross-vein m-cu in fossil representatives between middle of d cell base and fork of M3+4 (while in recent species usually positioned more centrally). From Triassic and Lower Jurassic only Limoniidae and Trichoceridae known. Recently also Tipulidae and Cylindrotomidae.

The new phylogenetical system of Triassic and Lower Jurassic Diptera is presented in Fig.8. It is illustrated exclusively by the wings of fossil insects of this time.

Comments

1. By the symbol “apomorphy 0” is understood the list of characters distinguishing Diptera from the Mecoptera, as: one pair of wings preserved (homologous with fore wings of Mecoptera), halteres, single long Sc, single Cu, two anal veins present and broad anal lobe. The possible relations of Mecoptera, Diptera and groups between them (Paratrichoptera and Nannochoristidae) are presented on Fig.9. However, before the revision of Paratrichoptera is done, the further discussion on the supposed sister group of the Diptera is fruitless.

2. Diarchineura represent the most primitive type of venation with five long radial veins reaching wing margin, large d cell situated below the level of Mb, cross-vein m-m connecting M2 and M3 and a very short A2.

3. The first apomorphy visible in the fossil material, that can separate all the other Diptera from Diarchineura, is the reduction of one radial vein, R2 (apomorphy 1). This way the Neoneura had branched off from the Diarchineura. It is not clear whether R2 takes a position of a cross-vein (i.e. becomes the cross vein r-r), or r-r arises independently. Within the Diptera both examples of cross-veins origin

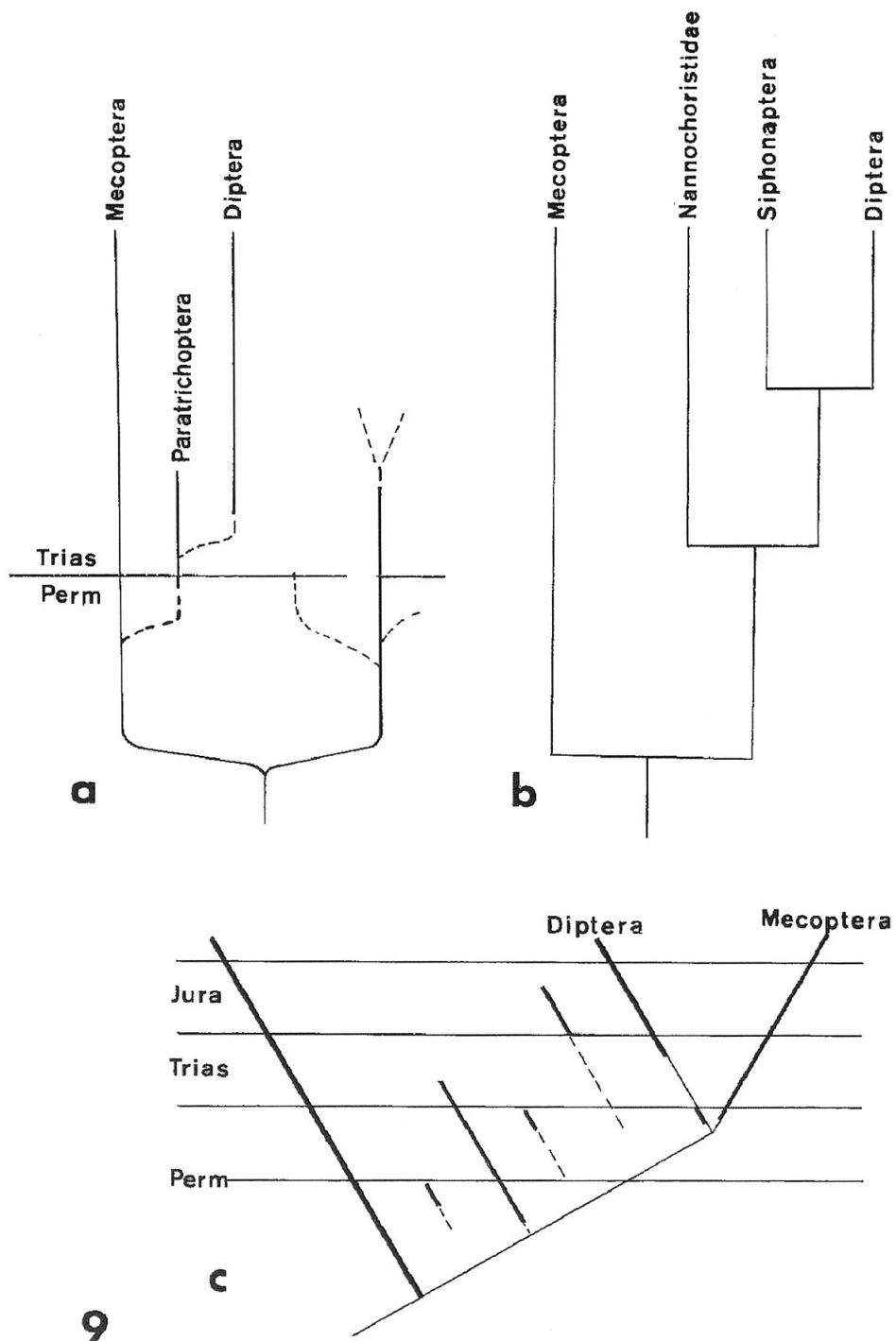


Fig. 9. Hypothetical relations between Mecoptera and Diptera: a.- after TILLYARD, 1919, b.- after MND(III), c.- after WILLMANN, 1989a.

are known (see also the discussion on homology of veins in this paper). Whatever the origin of r-r would be, the type of venation represented by the Neoneura was shared by all the subsequently arising groups from the Triassic on. The character "sc-r absent" (apomorphy 2) is shared by all the Neoneura known so far (i.e., a fossil family Eoptychopteridae and the Recent Ptychopteridae). It is marked as an

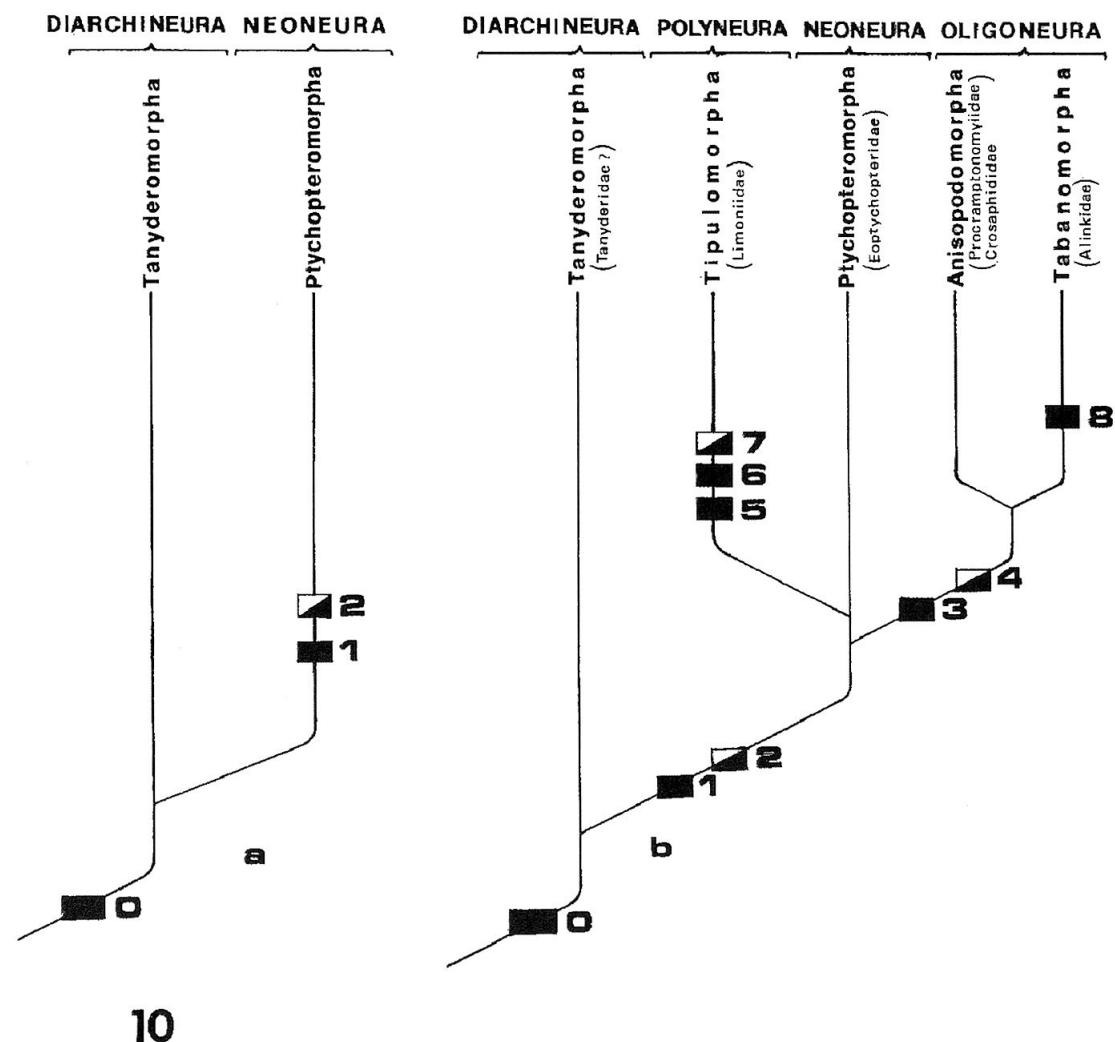


Fig. 10. Phylogenetical tree of Diptera: a.- Lower Triassic (hypothetical), b.- Upper Triassic (based on fossils).

incomplete apomorphy, because there are very rich materials of Eoptychopteridae not described yet and maybe some genera may have sc-r. If this character appears to be a strong apomorphy, then in all the Diptera (beside the Diarchineura) sc-r whenever present, would be an independently acquired character (homoplasy). This would have its consequences for the entire system of Diptera.

4. The Oligoneura, being very similar to the Neoneura, is distinguished from the remaining suborders by the cross-vein r-r absent (apomorphy 3) and the tendency to reduction of radial and medial veins (apomorphy 4). This latter is marked as an incomplete apomorphy, because in the oldest fossil Oligoneura (Protocrampomyiidae and Alinkidae) all four radial and four medial veins are present. The reduction is observed in younger families (Crosaphidiidae, Eopleciidae and others - see Fig.2). The Oligoneura became very expansive and gave rise to the majority of the Recent Diptera. Already in the Triassic they have separated into two infraorders: Anisopodomorpha and Tabanomorpha (apomorphy 8: very long R4+5).

5. The Polyneura is characterized by long A2 vein (apomorphy 5) and d cell positioned over the level of Mb (apomorphy 6). The vein R3 is reduced and fused

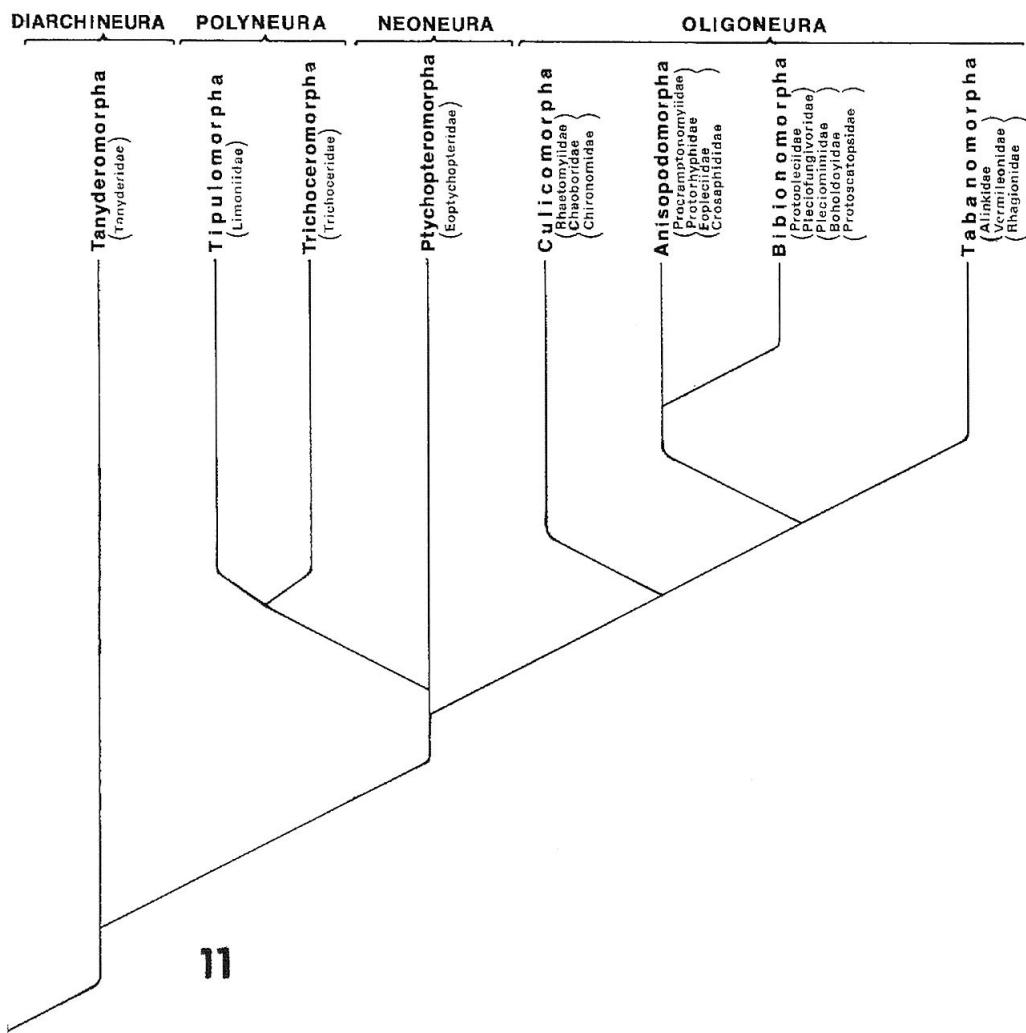


Fig. 11. Phylogenetical tree of Diptera in Lower Jurassic (based on fossils).

with R4 over a shorter or longer section in a majority of species (apomorphy 7). However, there are some fossil (*Mesotipula* HANDLIRSCH) and Recent (*Tricyphona* ZETTERSTEDT) genera more archaic, with these veins fully separated. An additional character, present in the entire Polyneura is the cross-vein m-m connecting M1+2 with M3 (=M1 and M2 with petiole). It is not marked as an apomorphy, because also two genera of Eoptychopteridae (*Ptychoptera* KALUGINA and *Eoptychoptera* KALUGINA) share it.

The Figs 10 and 11 present the phylogenetical tree of Diptera and its evolution: in the Lower Triassic (10a -hypothetical situation), in the Upper Triassic (10b) and Lower Jurassic (11). Both last trees are evidenced by the fossil representatives of the families, described so far (including the present paper).

It should be noticed that if we would confine ourselves strictly to the cladistic rules, the construction of a reliable phylogenetic tree would not be possible. Both fossil and Recent data indicate that all the main four lineages of the Diptera: Diarchineura, Neoneura, Polyneura and Oligoneura had branched off from their respective stem groups and are represented in the Recent fauna (and had not branched

with the extinction of ancestors). As a consequence the suborders: Diarchineura and Neoneura are defined - from a cladist's point of view - only by plesiomorphies. It should not be missed that these characters: venation of the Diarchineura and characters "1" and "2" of the Neoneura were once apomorphic, when these suborders were branching off. They had become automatically plesiomorphic when the next lineages had branched off.

Analysing these figures we can try to answer some questions concerning relations between different groups of Diptera.

Tanyderidae is closer to the Ptychopteromorpha than to Tipulomorpha and yet cannot be included in any of these two groups.

Brachycera is closer to the Anisopodomorpha than to Bibionomorpha: this former is more archaic what can be stated while comparing the venation of the fossil Anisopodomorpha and the fossil Bibionomorpha. Brachycera (represented by the Tabanomorpha) is the sister group of Anisopodomorpha and not of the entire Nematocera. Trichoceridae belong clearly to the Polyneura. There are no reasons for including them into Psychodomorpha (which belong to a different suborder, Diarchineura).

The place of the Culicomorpha in the Oligoneura leaves no doubts: the taxon is present on Fig.11, because the representatives of the Rhaetomyidae, Chaoboridae and Chironomidae were found in the Lower Jurassic. Dixidae were stated in the Lower Cretaceous, while the Culicidae were not found before the Paleocene (KALUGINA in KALUGINA & KOVALEV, 1985; KALUGINA, 1986). The great similarities between Tanyderomorpha, Psychodomorpha, Tipulomorpha, Trichoceromorpha, Ptychopteromorpha, Anisopodomorpha and Tabanomorpha are caused by their evolutionary proximity. These lineages had originated in the first stages of Diptera evolution, while the rapid radiation of Diptera from the Middle Jurassic to the Upper Cretaceous had obscured the clear Triassic and Lower Jurassic relations. Hence our difficulties in estimating the true importance of characters and relations, if we confine ourselves to the Recent forms.

Discussion on the homology of veins

How difficult it is to establish the homologies in wing venation within the Diptera, is best reflected in the existence of several nomenclature systems being now in use (reviewed in MND I and III). The main inconsistencies between them are listed below, with author's own opinion based on the venation of fossil specimens.

a) Subcostal vein field. - The cross-vein sc-r of the "ground plan" of MND (Fig.12b) is in Tipulomorpha considered to be the long vein Sc2. The tip of R1 is sometimes called Sc2 and sometimes R1+2, with the position of sc-r being identical in both cases. Different names are given to the same veins within one subgenus, *Limonia* (*Metalimnobia*) (Fig.13).

In my opinion the "ground plan" of subcostal veins should be applied to Tipulomorpha, too. It is less risky to consider sc-r a true cross-vein, not homologous to Sc2 of Mecoptera, since two subcostal long veins were never found in the fossil Diptera. The only group that could be taken under consideration when discussing this homology, is the Diarchineura. In Neoneura sc-r is absent and probably arises independently in Polyneura and some Oligoneura. Its position is very variable and seems to support this hypothesis.

b) Radial field - For Tipulomorpha the authors of MND applied their system after ALEXANDER (1927, 1929), who divided Tipulidae (= Tipulidae in his system)

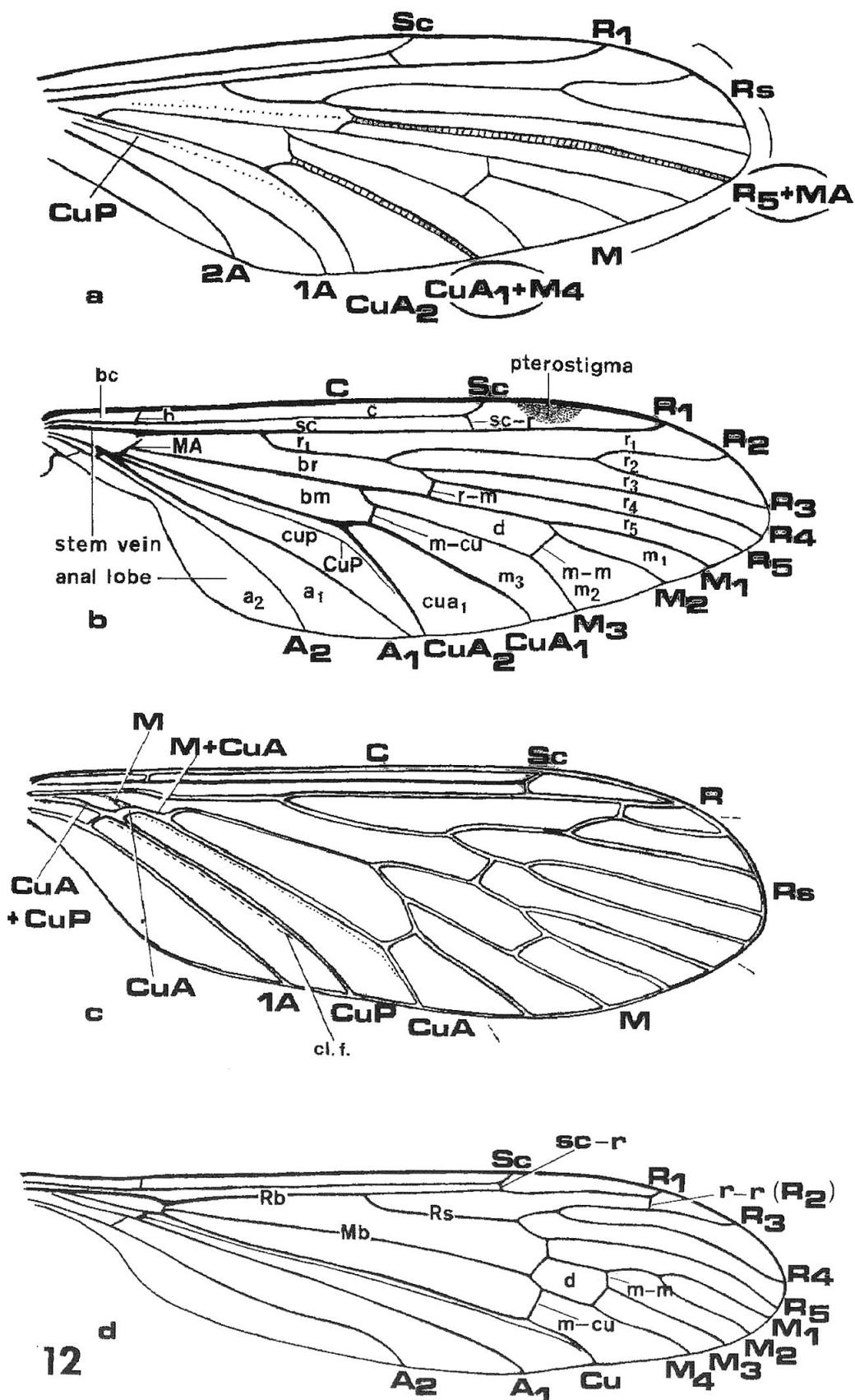


Fig. 12. Ground plans of Diptera wing venation being in use: a.- after HENNIG, 1973, b.- after MND(I), c.- after WOOTTON & ENNOS, 1989, d.- system applied in the present paper.

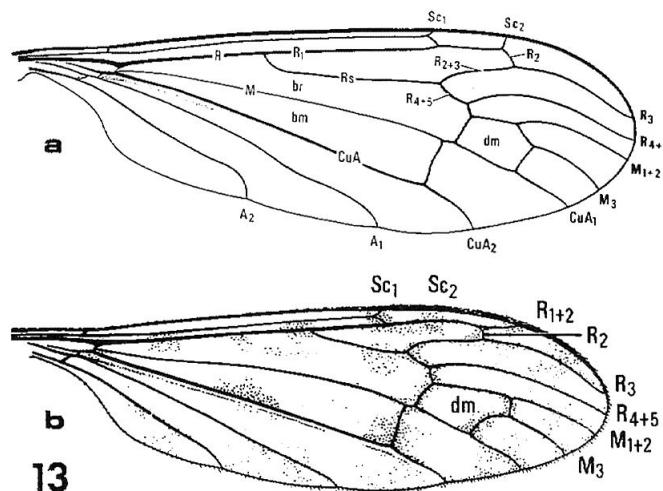


Fig. 13. Different names given to R1 within one subgenus, after MND(I): a.- *Limonia (Metalimnobia) triocellata* (O.-S.), b.- *Limonia (Metalimnobia) immatura* (O.-S.).

into two lines of specialization. One is characterized by 5 radial veins, with R2 taking the position of the cross-vein (cross-vein homologous to R2 Fig.14). Here were included: Pediciinae, Hexatominae and Eriopterinae of the family Limoniidae (= Pediciini, Hexatomini, Eriopterini within the Limoniinae, according to ALEXANDER). In the second group the cross-vein is not homologous to R2, and there are four

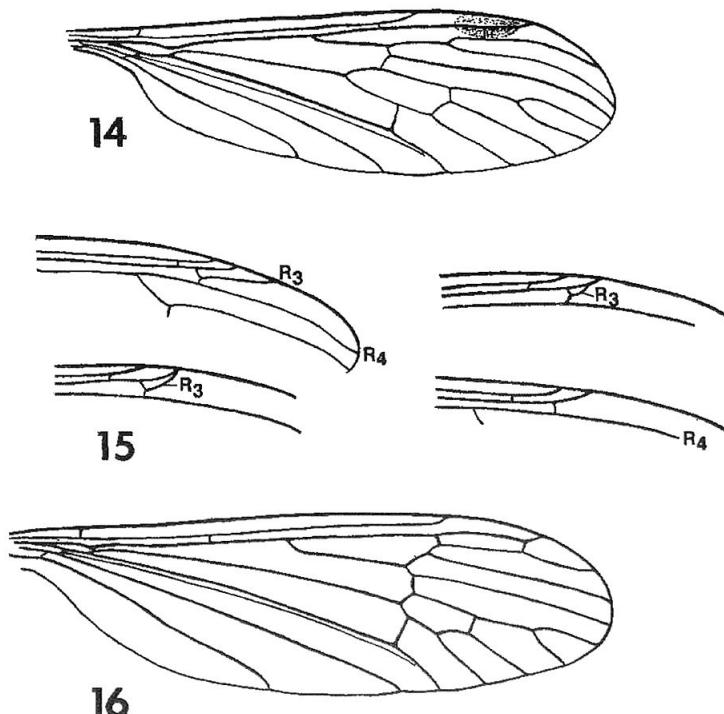


Fig. 14-16. Examples of radial field venation in Limoniidae: Fig. 14. *Prolimnophila areolata* (O.-S.), Hexatominae (after ALEXANDER, 1927). Fig. 15. Reduction of R3 in the genus *Psaronius* ENDERLEIN (after ALEXANDER, 1927). Fig. 16. Two cross-veins in r1 cell, *Dicranota (Eudicranota) pallida* ALEXANDER, after MND(I).

long radial veins: R1, R2, R3 and R4+5. Here belong Architipulinae, Techriinae and Limoniinae from the family Limoniidae, and also families Tipulidae and Cylindrotomidae (Architipulinae, Lechriini and Limoniini from the subfamily Limoniinae, Tipulinae and Cylindrotominae according to Alexander).

The ALEXANDER's idea of two lines of specialization in Tipulomorpha is not consistent with the following facts. The family Architipulinae (2nd line) undoubtedly belongs to Limoniidae and comprises the oldest representatives of this family known from Triassic. In the wing venation, palpi, legs and genital organs shape, Architipulinae show greatest resemblance to Hexatominae (unpublished data, in preparation), who is classified to 1st line. If in the oldest Limoniidae r-r is a cross-vein, it could not be homologous with R2 in the younger families (Tipulidae and Cylindrotomidae).

In the next member of 2nd line, subfamily Limoniinae, which is the youngest of the Limoniidae subfamilies, the reduction of the next radial vein is observed and only three radial veins terminate in wing margin. Whenever the cross-vein r-r is present, its position is like in Architipulinae and Hexatominae, regardless how this reduction was executed (Fig.13). The presence and position of cross-vein r-r is not fixed within the family, it is often absent (as in genera *Gonomyia* MEIGEN and *Helius* LEPELETIER ET SERVILLE), fused with R3 (Fig.15) and may probably arise independently. Besides, in the r1 cell two cross-veins may occur (Fig.16). Summarizing, the origin of this cross-vein in Diptera can be only the subject of speculation and

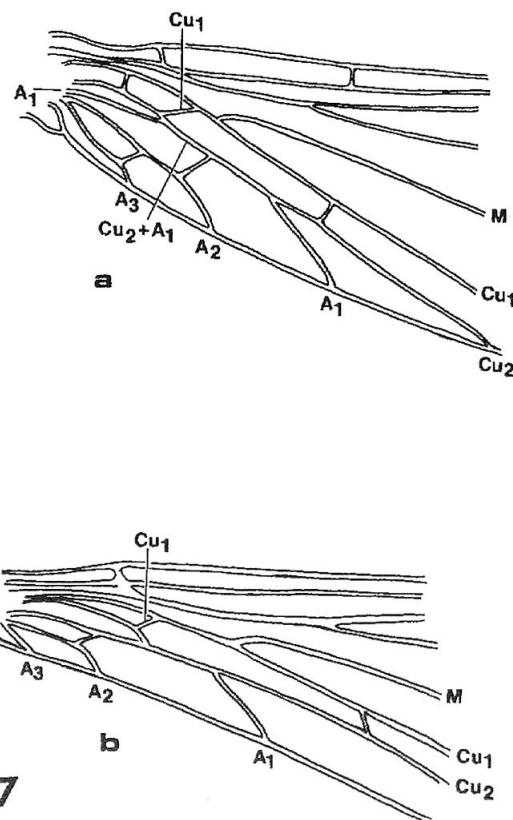


Fig. 17. Fusion of Cu2 with A1 in Mecoptera: a.- *Panorpodes paradoxa* McLACHLAN - hind wing, b.- *Neopanorpa furcata* (HARDWICKE) - hind wing. Both after WILLMANN, 1989a.

the idea of ALEXANDER as well as other arbitrarily introduced conceptions rather have no chance to be proved. Basing on the venation of Diarchineura, we can only suppose that if whenever the cross-vein $r-r$ is homologous to R_2 , it is so in the oldest Tipulomorpha (Architipulinae).

c) Medial, cubital and anal field - In MND, vein M_4 is called CuA_1 . This idea was already criticized by BYERS (1989). Quite contrarily, WOOTTON & ENNOS (1989) proposed four medial veins in Diptera and for the second cubital vein they have taken A_1 (Fig. 12c). Since none of these propositions is sufficiently evidenced, it is sensible to leave the traditional nomenclature of medial, cubital and anal veins after TILLYARD (1926) who assumed only one, fully developed cubital vein in Diptera. The loss of one cubital vein of Mecoptera could happen by one of three ways: fusion of two cubital veins, reduction of one vein or its transformation into CuP , or fusion of cubital CuP and A_1 which is often observed in this group, however mainly in hind wings (Fig. 1b, 17). In this case the veins A_1 and A_2 of Diptera would be homologous to A_2 and A_3 of Mecoptera, respectively.

ACKNOWLEDGEMENTS

I am very grateful to Dr. Ch. L. REMINGTON (Peabody Museum of Natural History, Yale University) for a loan of Triassic specimens. Comments of an anonymous referee are also acknowledged. I am also deeply indebted to Dr J. STARY (University of Olomouc, Czechoslovakia) and to late Dr V. KOVÁLEV (Paleontological Institute, Moscow, USSR) for the long and spirited discussions that provoked me to start more profound studies on the phylogeny of Diptera. However, only I am responsible for the results of these studies, presented here.

RÉSUMÉ

Ce travail est consacré à l'étude de quelques Diptères du Triassique supérieur provenant des Etats-Unis (Caroline et Virginie, Dan River group). Les représentants de quatre familles sont décrits: Eoptychopteridae (spécimen incertain, infra-ordre Ptychopteromorpha), *Yala argentata* n.sp. (Procramp-tonomyiidae, infra-ordre Anisopodomorpha), *Alinka cara* n.sp. (Alinkidae n.fam., infra-ordre Tabanomorpha), *Architipula youngi* n.sp. (Limoniidae, infra-ordre Tipulomorpha). Un nouveau système phylogénique des Diptères, basé sur des matériaux du Triassique et du Jurassique inférieur, est proposé. L'ordre des Diptères est divisé en quatre sous-ordres: Diarchineura n. sous-ordre, Neoneura n. sous-ordre, Oligoneura et Polyneura.

REFERENCES

ALEXANDER, C.P. 1927. The interpretation of the radial field of the wing in the nematocerous Diptera, with special reference to the Tipulidae. *Proc. Linn. Soc. N.S.W.* 52: 42-72.

ALEXANDER, C.P. 1929. A comparison of the systems of nomenclature that have been applied to the radial field of the wing in the Diptera. *IV. Int. Congr. Ent. (Ithaca, N.Y., 1928)* 2: 700-707.

BODE, A. 1953. Die Insektenfauna des ostniedersächsischen oberen Lias. *Palaeont.* 103(A): 1-375.

BRODIE, P.B. 1845. *A history of the fossil insects in the secondary rocks of England*. London, pp. 33-34, 121-122.

BYERS, G.W. 1989. Homologies in wing venation of primitive Diptera and Mecoptera. *Proc. Entomol. Soc. Wash.* 91(4): 497-501.

EVANS, J.W. 1971. Some Upper Triassic Hemiptera from Mount Crosby, Queensland. *Mem. Queensl. Mus.* 6 (1): 145-152.

HANDLIRSCH, A. 1906-1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen*. Engelmann, Leipzig, 1430 pp.

HANDLIRSCH, A. 1909. Zur Phylogenie und Flügelmorphologie der Ptychopteriden (Dipteren). *Annalen des k.k. Naturhistorischen Hofmuseums* 23: 263-272.

HANDLIRSCH, A. 1937-1939. Neue Untersuchungen über die fossilen Insekten. *Ann. Naturhist. Mus. Wien* 48: 1-140; 49: 1-240.

HEER, O. 1849. Die Insektenfauna der Tertiärgebilde von Oeningen und Radoboj in Kroatien. II. Heuschrecken, Florfliegen, Aderfliegen, Schmetterlinge u. Fliegen. *Neue Denkschr. Allg. Schweiz. Ges. Wissensch.* 11: 1-264.

HENNIG, W. 1968. Kritische Bemerkungen über den Bau der Flügelwurzel bei den Dipteren und die Frage nach der Monophylie der Nematocera. *Stuttg. Beitr. Naturk.* 193: 1-23.

HENNIG, W. 1981. *Insects Phylogeny*. Chichester, New York, Brisbane, Toronto, 514 pp.

KALUGINA, N.S. 1986. Infraotriady Tipulomorpha i Culicomorpha. In: NAUKA, M. (ed.) *Nasekomye v rannemelowykh ekosistemakh Zapadnoy Mongolii*, pp.112-115 [In Russian].

KALUGINA, N.S. 1989. Novye psikhodomorfnye dwukrylye nasekomye mezozoya Sibiri (Diptera: Eoptochopteridae, Ptychopteridae). *Paleontol. J.* 1: 65-77 [In Russian].

KALUGINA, N.S. & KOVALEV, V.G. 1985. *Dvukrylye yury Sibiri*. M., Nauka, 198 pp. [In Russian].

KOVALEV, V.G. 1983. Novye danye o natchalnykh etapakh evolucii dvukrylykh. In: *Dvukrylye nasekomye, ikh sistematika, geografitcheskoe rasprostranenie i ekologija*. pp.60-66. L., Zool Inst. AN USSR [In Russian].

KOVALEV, V.G. 1986. Infraotriady Bibionomorpha i Asilomorpha. In: NAUKA, M. (ed.) *Nasekomye v rannemelowykh ekosistemakh Zapadnoy Mongolii*, pp.138-153 [In Russian].

KOVALEV, V.G. 1987. *Klassifikaciya dwukrylykh w svete paleontologicheskikh dannykh*. pp.40-48. L., Zool. Inst. AN USSR, [In Russian].

KRIVOSHEINA, N.P. 1988. Approaches to solutions of questions of classification of the Diptera. *Rev. Ent. URSS*, 67(2): 378-389 [In Russian].

KRZEMINSKI, W. & KOVALEV, V.G. 1988. The taxonomic status of *Architipula fragmentosa* (BODE) and the family Eoasiliidae (Diptera) from the Lower Jurassic. *Syst. Entomol.* 13: 55-56.

KRZEMINSKI, W. & ZESSIN, W. 1990. The Lower Jurassic Limoniidae from Grimmen (Diptera Nematocera). *Dtsch. Entomol. Z.*, N.F. 37(1-3): 39-43.

LOEW, H. 1850. Über den Bernstein und die Bernsteinfauna. *Programm der Königlichen Realschule zu Meseritz*: 3-44.

MCALPINE, J.F. et coll. 1981. *Manual of Nearctic Diptera*. Vol. 1, Research Branch, Agr. Canada Monogr. 27, Quebec, 1-674.

MCALPINE, J.F. et coll. 1989. *Manual of Nearctic Diptera*. Vol. 3, Research Branch, Agr. Canada Monogr. 32, Quebec, 1333-1581.

OLSEN, P.E. et coll. 1978. Cyclic change in Late Triassic lacustrine communities. *Science* 201: 729-733.

PRESL, J.S. 1822. *Additamenta ad Faunam protogaeam, sistens descriptiones aliquot animalium in succino inclusorum*. Deliciae Pragenses historia naturalem spectantes, 191 pp.

RIEK, E.F. 1977. Four-winged Diptera from the Upper Permian of Australia. *Proc. Linn. Soc. N.S.W.* 101(4): 250-255.

ROHDENDORF, B.B. 1961. Drevneyshye infraotriady dvukrylykh iz triasa Sredniey Azii. *Paleontol. Zh.* 3: 90-100. [In Russian].

ROHDENDORF, B.B. 1964. The historical development of the Diptera. *Tr. Paleont. Inst.* 100: 1-311 [English translation by University of Alberta Press, Edmonton, Canada, 360 pp. 1974]

SCUDDER, S.H. 1894. Tertiary Tipulidae with special reference to those of Florissant, Colorado. *Proc. Amer. Phyl. Soc.* 32: 163-245.

TILLYARD, R.J. 1919. A fossil insect wing belonging to the new order Paramecoptera, ancestral to the Trichoptera and Lepidoptera, from the Upper Coal Measures of Newcastle, N.S.W. *Proc. Linn. Soc. N.S.W.* 44: 231-256.

TILLYARD, R.J. 1926. *The Insects of Australia and New Zealand*. Angus & Robertson, Sydney, 560 pp.

TILLYARD, R.J. 1929. Permian Diptera from Warner's Bay, N.S.W. *Nature* 123: 778-779.

TILLYARD, R.J. 1933. The panorpoid complex in the British Rhaetic and Lias. *Fossil Insects* 3: 1-78.

TILLYARD, R.J. 1937. The ancestors of the Diptera. *Nature* 139: 66-67.

USATCHEV, D.A. 1968. Novye yurskiye Asilomorpha (Diptera) fauny Karatau. *Entomol. obozr.* 47(3): 617-628.

WOOTTON, R.J. & ENNOS, A.R. 1989. The implication of the origin and homology of the dipterous wing. *Syst. Entomol.* 14: 507-520.

WILLMANN, R. 1989a. Evolution und Phylogenetisches System der Mecoptera (Insecta: Holometabola). *Abh. Senckenb. Naturforsch. Ges.* 54: 1-153.

WILLMANN, R. 1989b. Rediscovered: *Permotipula patricia*, the oldest known fly. *Naturwissenschaften* 76: 375-377.

(received November 22, 1990; accepted in revised form August 13, 1991)

