

A new Triassic family of Diptera from Australia

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LUKASHEVICH, E.D., SHCHERBAKOV D.E. 1999. A new Triassic family of Diptera from Australia. In: AMBA/AM/PFICM98/1.99: 81-89. *Tillyardiptera prima* gen. et sp. nov. (Tillyardipteridae fam. nov.), nearest to ancestral Psychodomorpha, is described from the Upper Triassic of Mount Crosby, Australia. It is the largest Triassic dipteran known up to now. Systematic position of the new family and Triassic Grauvogeliidae, as well as significance of wing proportions for diagnostics of primitive Nematocera, are discussed.

Key words: Diptera, Psychodomorpha, Tillyardipteridae, Upper Triassic, Australia, phylogeny, venation.

Introduction

There is no reliable record of Diptera until the early Middle Triassic (Anisian), and already in the earliest known assemblage from Vosges, France various Nematocera (Grauvogeliidae and undescribed taxa; KRZEMINSKI et al., 1994) coexist with a single undescribed representative of Brachycera (KRZEMINSKI, 1998). An undescribed specimen of Diptera was recorded from the Anisian of Mallorca (SHCHERBAKOV et al., 1995: 78). In the Middle and Late Triassic the dipterans became widespread and diverse, being found in Central Asia, North America and Australia: Ladinian-Carnian and Norian-Rhaetian of Kyrgyzstan and Kazakhstan (4 localities, 13 specimens; SHCHERBAKOV et al., 1995); Cow Branch Formation (Carnian) of Virginia, USA (11 specimens; KRZEMINSKI, 1992); Ipswich group (Carnian) of Australia (1 specimen; KOVALEV, 1983).

Three additional wings from the same Australian locality which already yielded one Triassic find, Mount Crosby (the Ipswich Group of Queensland), were formerly kept in the collection of R.J. TILLYARD and now are housed in the Natural History Museum (Paleontology Dept.), London. Two of them are representatives of the Mesozoic families Paraxymyiidae (first recorded in the Triassic) and Procramptonomyiidae (BLAGODEROV, this issue). The third, large, well-preserved wing bears a label written by TILLYARD: "Order Diptera. New family, genus & species, intermediate between Tanyderidae and Tipulidae." It certainly represents a new family Tillyardipteridae fam. nov. which,

despite numerous 'tipuloid' features, should be included in Psychodomorpha sensu HENNIG.

Following family rank taxa of Diptera are now recorded in the Triassic (number of genera and species in the Triassic in parentheses): Grauvogeliidae (1:1), Vladipteridae (incl. Psychotipinae; 3:4), Gnomuscinae (?Limoniidae; 1:2), Tillyardipteridae (1:1), Crosaphididae (1:1), and Alinkidae (1:1) are all restricted to the Triassic (family status of two latter is still to be proven); Nadipteridae (1:2) include one more Liassic species; Hennigmatidae (2:2) comprise one more relict Cretaceous genus; Protorhynchidae (1:2), Procramptonomyiidae (2:2), Paraxymyiidae (1:1) and possibly also Eoptychopteridae (a doubtful find; 1:1) were common in the Jurassic; Limoniidae (2:2) survived up to the present. These families belong to the infraorders Tipulo-, Psychodo- and Bibionomorpha, whereas Culicomorpha are not found yet (Alinkidae, originally assigned to Brachycera, probably should be included in Bibionomorpha; about the system of Nematocera and vein nomenclature, see SHCHERBAKOV et al., 1995). Most species are known from the holotypes only, except for *Grauvogelia arzvilleriana* described upon some fifty specimens from a single locality, so it is impossible to draw any conclusions about dominant groups. Immature stages of Diptera from the Anisian of Vosges (MARCHAL-PAPIER, 1998), as well as presumed immatures from the Cow Branch Formation (PONOMARENKO, 1993; SHCHERBAKOV et al., 1995), are not described yet.

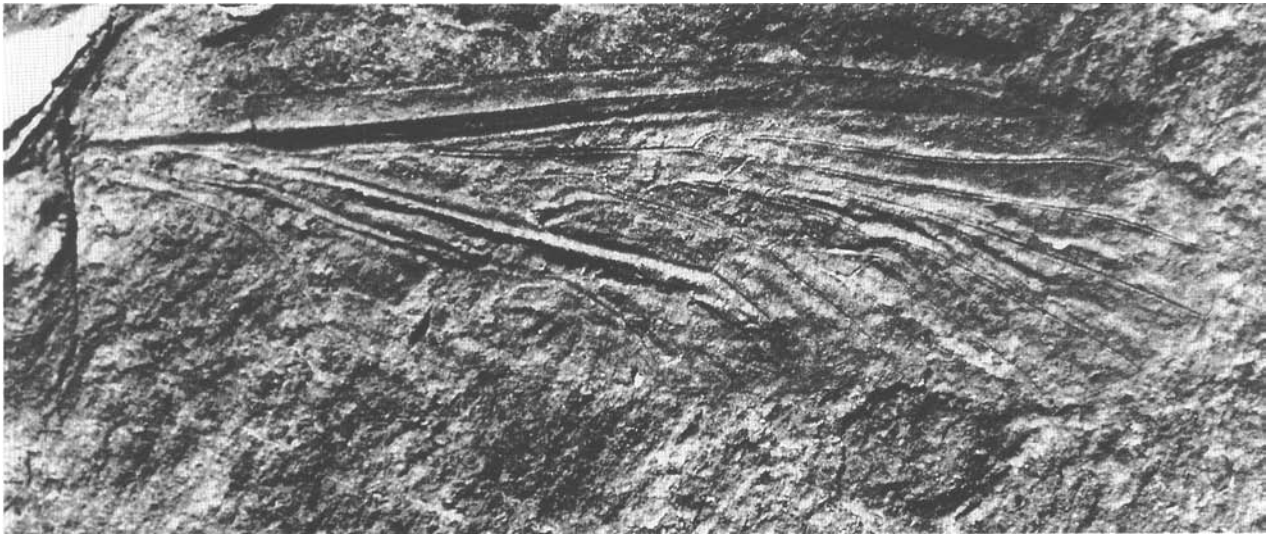


Fig. 1. *Tillyardiptera prima*, sp. nov., holotype In. 44958, wing.

Infraorder Psychodomorpha

Incertae superfamiliae

Tillyardipteridae, fam. nov.

Diagnosis. Wing. Free R2 absent. Sc ending distad of Rs bifurcation; sc-r postsectoral. R distinctly kinked in horizontal plane at humeral level. Rs nearly aligned with short R4+5 and with R4; Rs branches long, markedly diverging; R5 convexity not continued towards wing base. Strong convex M base running nearer to R base, nearly aligned with CuA. M stem somewhat desclerotized, forking symmetrically basad of Rs bifurcation; d cell and M3+4 stem long; m-cu near midlength of d cell, beyond midlength of nearly straight M3+4. CuA bent at m-cu; CuA apex nearly level with Sc apex. CuP not strongly diverging from CuA, entering margin in distal wing half. CuA and CuP ("A1" in traditional dipterological nomenclature; WOOTTON & ENNOS, 1989) curved backwards near margin. 1A ("A2") distad of cu-a reduced, not reaching margin. 2A forming narrow anal loop. Anal lobe somewhat produced, alular incision absent. Wing membrane delicate. Pterostigma well pigmented.

Comparison. Two Triassic families, despite the retention of a short free R2 in both, appear to be nearest to the new one. Nadipteridae (Psychodomorpha Ptychopteroidea) are distinct from it in the Rs not aligned with R4+5 and R4, R5 convexity continued basad, im joining M1+2, m-cu more proximal than r-m, and alular incision devel-

oped. Vladipteridae (Tipulomorpha) are distinct in the long convex 1A reaching wing margin, and sc-r before or just beyond Rs bifurcation. (Of two subfamilies included, Vladipterinae differ additionally in the Sc ending against Rs bifurcation, m-cu joining M3+4 bifurcation or M4 base, and anal loop not formed, whereas Psychotipinae are distinct in the r-m joining R5 base, im joining M1+2, and alular incision developed.) Besides the characters easily seen in the venation diagrams, Vladipterinae are very similar to Tillyardipteridae in the delicate, easily deformable wing membrane, well pigmented pterostigma, and markedly diverging Rs branches. *Dilemmala* (provisionally assigned to this subfamily) is especially similar to *Tillyardiptera* in im joining M2, long shallow R kink opposed to long M+CuA fusion, and MA not inclined (see generic description), and may turn out to agree with the new genus also in the anal venation (not preserved in *Dilemmala* holotype). In the wing proportions (see species description) *Tillyardiptera* is more similar to Vladipteridae (levels of Rs and M bifurcations and of Sc, CuA and CuP apices), except for being intermediate between Vladipteridae and Nadipteridae in the level of R bifurcation. (For further comparison see Discussion and Table 1.)

Tillyardiptera, gen. nov.

Type species. *Tillyardiptera prima*, sp. nov.

Species included. Type species from the Late Triassic Ipswich Group of Queensland, Australia, described herein.

Description. Wing elongate; pterostigma large,

reaching both wing margin and R2+3. R kink long and shallow, opposed to long M+CuA fusion; MA reclined (its anterior end more proximal), probably complete (its junction to M stem not visible). sc-r between the levels of M and Rs bifurcations. r-m joining R4+5 to M1+2 midlength. M stem desclerotized except distal third. M1+2 and M3+4 forks rather long, subequal, im connecting M2 and M3. m-cu level with r-m. Concave fold (iCu) well developed behind entire length of CuA; less pronounced convex fold conspicuous behind proximal half of CuP. Incomplete faint groove in anal lobe may represent remnants of distal 1A.

Etymology. The genus is named in honour of the eminent paleontologist Robin John TILLYARD.

***Tillyardiptera prima*, sp. nov. (Figs.1-3)**

Holotype. In. 44958; positive and negative impressions of a well preserved, slightly deformed wing (membrane between the Rs and M branches crumpled). Mt. Crosby, nr. Ipswich, Queensland, Australia; Triassic, Carnian, Ipswich Group, Insect Bed (R.J. TILLYARD colln.).

Description (initial wing shape restored in Fig. 3). Wing 10.1 mm long, elongate (3.4:1), pale (probably transparent), with darker veins and pterostigma. C thick along anterior margin (except base), narrow beyond R4 apex. Sc terminating distal to R4+5 bifurcation, the latter level with that of M3+4. No trace of free R2 (some crease near R2+3 base is due to membrane crumpling). R4+5 fork about 7 times longer than R4+5 stem. M1+2 fork as long as d cell. Sc apex at 61%, R bifurcation at 29%, Rs bifurcation at 54%, M bifurcation at 45%, CuA apex at 64% and CuP apex at 53% of wing length.

Remarks. The new species is the largest dipteran known from the Triassic, all others described (with wing length 2-6 mm) at most slightly surpassing a half of its size.

Discussion

On the limits of Psychodomorpha. HENNIG (1968) divided nematocerous Diptera into four infraorders: Tipulomorpha, Psychodomorpha, Culicomorpha and Bibionomorpha. WOOD & BORKENT (1989) proposed seven infraorders, dividing the families of HENNIG's Psychodomorpha between Blephariceromorpha and Ptychopteromorpha, except for Psychodidae grouped with several other families on account of

larval similarities (which are most probably symplesiomorphic: OOSTERBROEK & THEOWALD, 1991; SHCHERBAKOV et al., 1995). KRZEMINSKI (1992) divided the order into four suborders (HENNIG'S Psychodomorpha separated between three of them): Diarchineura (incl. Tanyderomorpha and Psychodomorpha), Neoneura (Ptychopteromorpha), Polyneura (Trichoceromorpha and Tipulomorpha), Oligoneura (all remaining Diptera). In both these systems the splitting was intended to receive demonstrably monophyletic higher taxa; however, accepting paraphyletic taxa as no less natural (RASNITSYN, 1996), we can use HENNIG'S infraorders until their polyphyly is proven beyond doubt. Psychodomorpha sensu HENNIG comprise extant Tanyderidae, Psychodidae s.l., Ptychopteridae, Blephariceridae, Deuterophlebiidae, Nymphomyiidae and several Mesozoic families.

On the systematic position of Tillyardipteridae.

Comparative wing morphology and paleontology indicate that modern Tipulomorpha belong to the earliest side branch of Diptera, and, moreover, that the ancestral dipterans could be assigned to the same infraorder (considered paraphyletic). Such Triassic dipterans as Vladipteridae Psychotipinae combining ground-plan characters (free R2), tipulomorphan autplesiomorphies (long convex 1A), and non-tipulomorphan apomorphies (anal loop and alular incision) are difficult to classify, but it is practicable to assign them to Tipulomorpha.

The new family shows most wing characters in common with primitive Tipulomorpha, namely Vladipteridae and Limoniidae (especially Pediciinae), and somewhat less with primitive Psychodomorpha, especially Nadipteridae (Ptychopteroidea) and Ansorgiidae (Jurassic Blephariceroidea). Of 15 characters shared with generalized tipulomorphans, three are restricted to these latter: r-m and m-cu at the same level about midlength of large d cell; both CuP apex and m-cu beyond wing midlength; long, shallow R kink opposed to long M+CuA fusion and bearing reclined MA (see Table 1).

MA, or arculus, a veinal brace between the basal R kink and the base of M stem (often undeveloped in primitive Diptera), probably formed due to the hindwing character of mecopteran ancestors transferred onto the forewing (SHCHERBAKOV et al., 1995). Usually MA is a crossvein, transverse or inclined (i.e. its anterior end more distal; Fig. 4a), sometimes reduced to a stub. However, MA is a spur directed basally from the base of M stem in

Vladiptera (Fig. 4b; analogous spurs from Rs base occur e.g. in some Limoniidae and Culicoidea); it is a longitudinal vein section in Triassic *Dilemmala* (Fig. 4c; incorrectly figured reclined in original description) and living *Ula bolitophila* (Pediinae; SAVCHENKO, 1986, fig. 59); one could assume these configurations to be archaic. When the R kink is long and shallow (turning into vertical plane distally), it could be opposed to equally long basal M+CuA fusion, MA being not developed (e.g. *Dicranota* of Pediciinae) or longitudinal (*Dilemmala*); a configuration with the reclined MA stub from the base of M stem (distad of humeral level) found in *Pedicia* (Fig. 4d) resembles that of *Tillyardiptera* most closely.

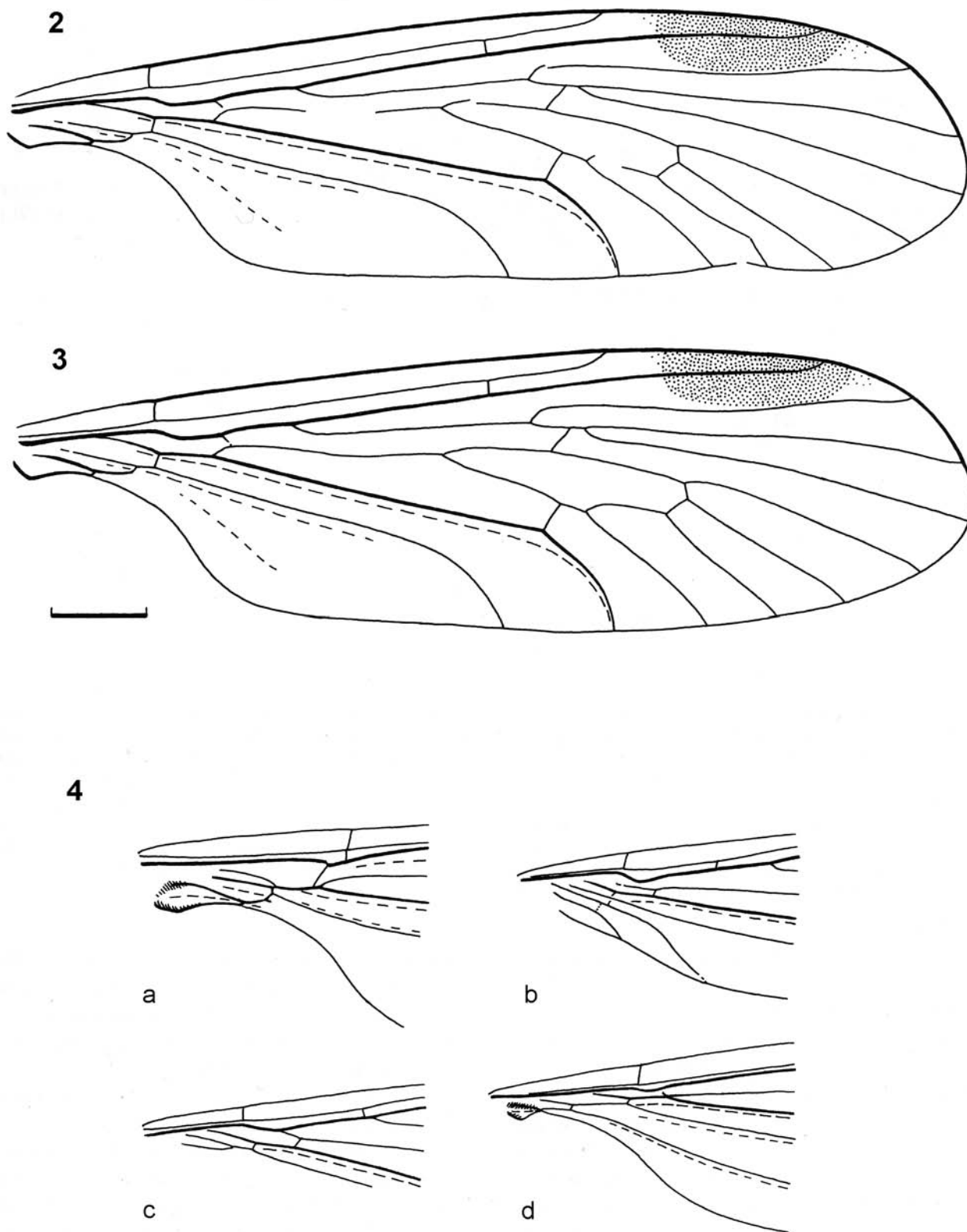
Wing proportions, especially position of the R and M bifurcations and of the CuA and CuP apices along the wing length, were found to be helpful in discriminating between generalized Tipulo- and Psychodomorpha; Psychotipinae retain tipulomorph wing proportions (SHCHERBAKOV et al., 1995). The wing proportions of *Tillyardiptera* relate it to Tipulomorpha (levels of Rs bifurcation and CuP apex) or are intermediate between Tipulo- and Psychodomorpha (levels of R bifurcation and CuA apex). No one single proportion is sufficient to separate nematocerous infraorders. For example, CuP extending beyond the wing midlength is recorded, besides Tipulomorpha, in *Tillyardiptera*, Dixidae, few Bibionomorpha (extant *Pachyneura*, Jurassic *Heterorhynchus*, Triassic *Yala*), and in several Tanyderidae (where could be secondarily elongated, being much shorter in the oldest known genus, Liassic *Nannotanyderus*). However, infraordinal clusters do not overlap in multidimensional character space. Among two- and three-dimensional projections of this distribution the most indicative ones are probably R bifurcation/CuA apex and R bifurcation/Rs bifurcation/CuA apex (Fig. 5), respectively. In the latter 3D distribution some *Eoptychoptera* species lie close to *Tillyardiptera*, but in multiD space they separate from it due to much shorter CuP. The points corresponding to several congeneric species (or to the genera of one subfamily) often group along definite curves, demonstrating the existence of taxon-specific allometric rules (Fig. 6). Probably levels of the R and Rs bifurcations and of the CuA apex are more diagnostic, because they determine the position of two accessory supporting spurs in the dipteran wing: medial spur (along R5) and cubital spur (ENNOS, 1989).

Alignment of R4 and R4+5 with Rs stem is

always associated with a shift of r-m either onto R5 (Psychodoidea, Blephariceroidea, Hennigmatidae, most Limoniidae) or onto the Rs bifurcation (few species of *Crenoptychoptera*, a derived genus of Eoptychopteridae). The condition observed in *Tillyardiptera* seems to be a rare, intermediate one, approached only by that of *Vladiptera* and *Psychotipa predicta* (R4 aligned with Rs, r-m joining R4+5 bifurcation). Possibly the degree of vein alignment in the *Tillyardiptera* holotype is exaggerated by deformation of the wing membrane.

Two other important features indicate rather non-tipulomorph affinities of *Tillyardiptera*. Long unbranched R2+3 not forming a stalk with R4 is characteristic also of Brachycera, most Bibionomorpha, Ansorgiidae (only if a crossvein-like R2 is not present) and few Psychodidae (*Horaiella*). (In other psychodoids, Vladipteridae, Nadipteridae and Hennigmatidae R2 is free, whereas in remaining Ptychopteroidea and most Tipulomorpha it is crossvein-like.) In contrast to this condition, the unbranched R2+3 is always stalked with R4 in Culicomorpha, several families of Bibionomorpha, and in those few limoniids which have the R2 crossvein reduced; in these latter R2+3 is usually oblique and somewhat shortened (not or weakly so e.g. in *Limnophila ctenonycha* and *Atarba subaequalis*; ALEXANDER, 1929, 1979). So the reduction of R2 is not unknown among tipuloids, but the reduction pattern is different from that in *Tillyardiptera*.

The anal veins forming a loop, 1A being reduced beyond it (not reaching margin) is a synapomorphy of all non-tipulomorph Diptera, whereas in Tipulomorpha both 1A and 2A are free and enter the wing margin separately, 2A being extremely reduced in extant families (SHCHERBAKOV et al., 1995). The anal loop and anal margin (without any trace of alular incision) in *Tillyardiptera* are shaped exactly like in *Ptychoptera* (Fig. 4a). Alular incision of the anal wing margin, developed in some Eoptychopteridae, is always suppressed in their derivatives Ptychopteridae (and also in Tanyderidae and some archaic Bibionomorpha); possibly it was lost in *Tillyardiptera* as well. Although 1A is markedly shortened (but reaching margin) in several extant Tipuloidea (*Megistocera* and *Brachypremna* of Tipulidae, *Trentepohlia* and *Pseudoglochina* of Limoniidae) and in most Trichoceridae (apically incomplete in some specimens of Mesozoic trichocerids; pers. obs.), it is entirely reduced only in few tipuloids having narrow



Figs 2-4: 2-3. *Tillyrdiptera prima*, sp. nov., holotype In. 44958, venation: (2) as preserved; (3) initial wing shape restored. Folds in broken line. Scale bar 1 mm; 4. Wing bases (schematized, not to scale): (a) *Ptychoptera contaminata*, recent; (b) *Vladiptera kovalevi*, Triassic; (c) *Dilemmala specula*, Triassic; (d) *Pedicia rivosa*, recent.

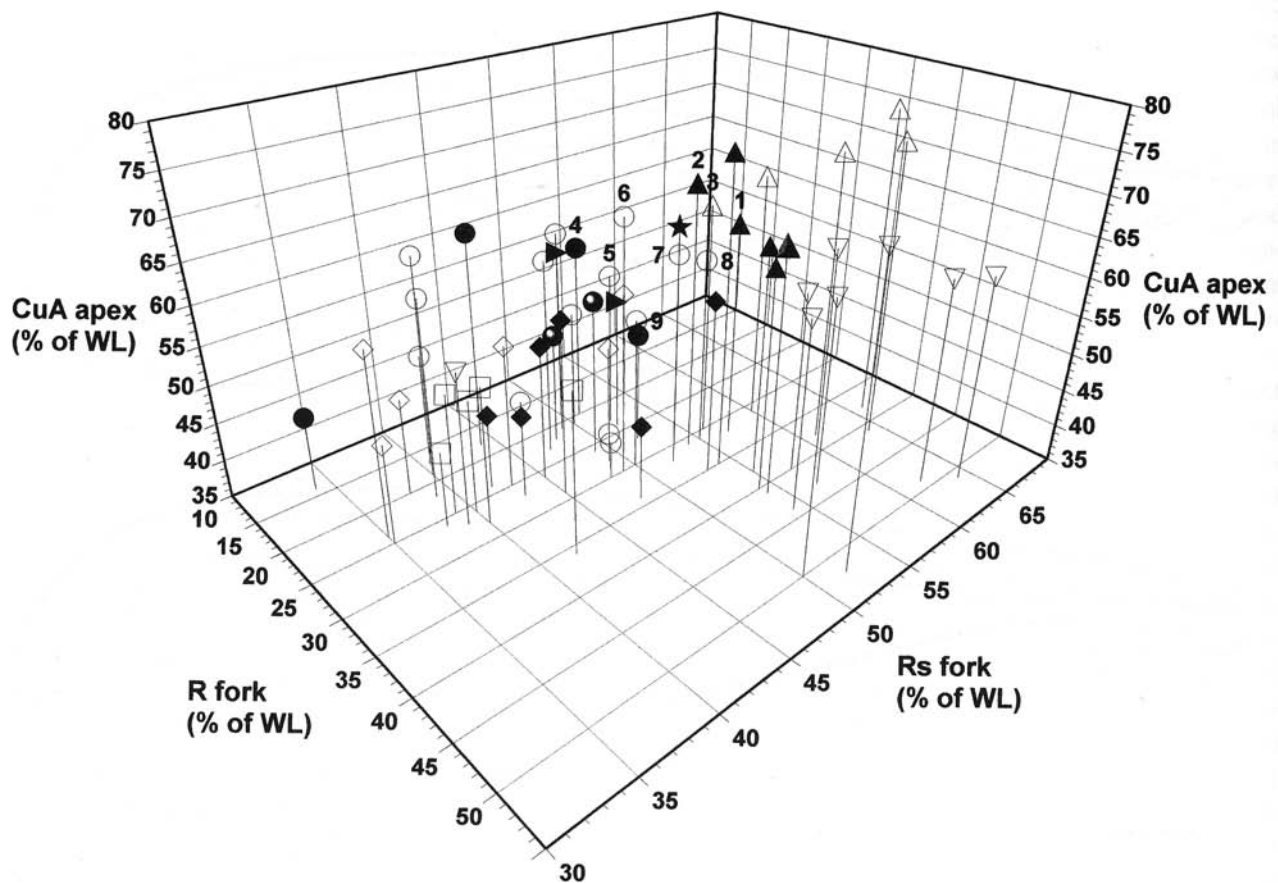


Fig. 5. Correlation between the levels of R bifurcation, Rs bifurcation and CuA apex (% of wing length) for Triassic (filled symbols) and selected Jurassic (open symbols) Diptera Tipulomorpha (triangles), Psychodomorpha (circles), Bibionomorpha (diamonds), Culicomorpha (inverted triangles) and Brachycera (squares): *Tillyardipectera prima* (star), *Vladipectera kovalevi* (Vladipterinae: pyramid), *Psychotipa depicta* (Psychotipinae: 1), *Architipula youngi* (Limoniidae: 2), *Gnomusca* spp. (Gnomuscinae, ?Limoniidae: arrows), *Mailotrichocera jurassica* (Trichoceridae: 3), *Grauvogelia arzvilleriana* (Grauvogeliidae: balls), *Nadipectera kaluginae* (Nadipteridae: 4), *N. anachrona* (5), *Proptychoptera yenisica* (Eoptychopteridae: 6), *Eoptychoptera magna* (7), *E. eximia* (8), *Protanyderus vetus* (Tanyderidae: 9) and 44 more species representing (besides the above families) also Hennigmatidae, Psychodidae, Ansorgiidae, Protorhyphidae, Anisopodidae, Heterorhyphidae, Proqramptonomyiidae, Paraxymyiidae, Alinkidae, Dixidae, Chaoboridae, Chironomidae, Oligophrynidae, Rhagionidae, Protobrachyceridae.

anal lobe (some *Stibadocerella* species of Cylindrotomidae, and *Doaneomyia* of Limoniidae; ALEXANDER, 1965). So far as the anal lobe of *Tillyardipectera* is only a little narrower than in related Psychotipinae, formation of the anal loop (shared with the latter group) and reduction of distal 1A in the new genus are most probably synapomorphic with all higher Diptera, being the only conclusive evidence for its assignment to Psychodomorpha as the most primitive known member. In fact, we classify Psychotipinae as still Tipulomorpha, and Tillyardipteridae as already Psychodomorpha, on account of retention or loss of convex distal 1A reaching wing margin. More psychodomorphan wing proportions, including longer d cell of *Tillyardipectera*, confirm our taxonomic solution.

Similar hypothetical forms with short free R2 added could represent a group ancestral to all the other Psychodomorpha, and to Bibionomorpha as well (more primitive than the node "C" in the phylogram of SHCHERBAKOV et al., 1995: fig. 47).

Two main phyletic lineages of Psychodomorpha s.l. are hypothesized to be (1) Ptychopteroidea (incl. Triassic-Liassic Nadipteridae) + enigmatic Triassic Hennigmatoidea and (2) Psychodoidea s.l. (incl. Tanyderidae) + Blephariceroidea s.l. (incl. Jurassic Ansorgiidae); the second lineage is still to be recorded from the Triassic (SHCHERBAKOV et al., 1995). Within Psychodomorpha, the new family demonstrates maximal similarity to Nadipteridae and Ansorgiidae (Tab. 1), i.e. to the most archaic members of both lineages. Rs aligned with R4, and *im*

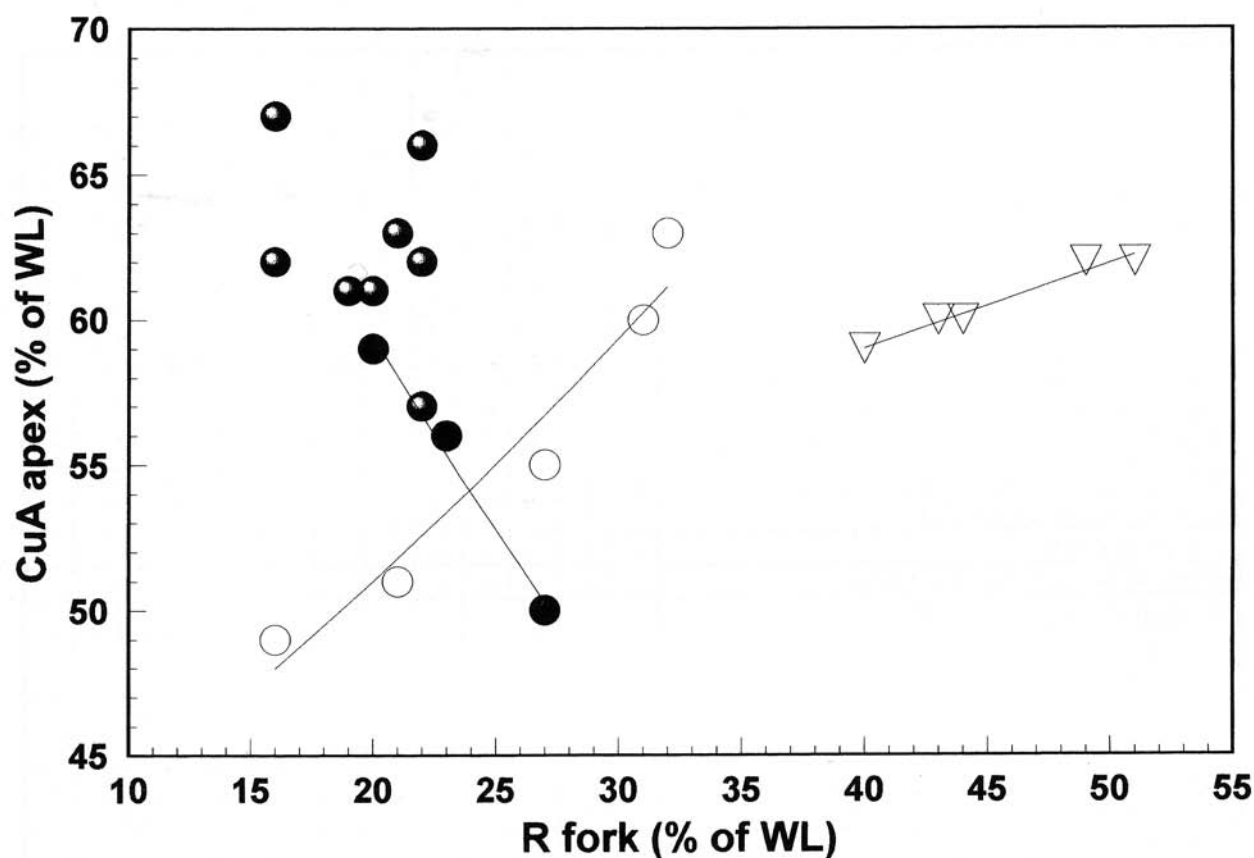


Fig. 6. Correlation between the levels of R bifurcation and CuA apex (% of wing length) in Mesozoic Ptychopteroidea (filled circles, *Nadiptera* spp.; balls, *Proptychoptera* spp.; open circles, *Eoptychoptera* spp.) and Culicoidea (triangles); curves represent exponential trends (not evident for *Proptychoptera*). Figs. 5 & 6 prepared with Harvard ChartXL 2.0.

joining M2 were listed among synapomorphies of Psychodoidea + Blephariceroidea (node "D" in the above phylogram). These characters are susceptible to homoplasy (both met with also in some Pediciinae, Vladipteridae, and Hennigmatidae) and could not be considered sufficient to relate the new family to this lineage. Likewise the simple R2+3 not stalked with R4 is rather a homoplasy with, than a proof of direct relationship to, either Blephariceroidea or Bibionomorpha + Brachycera, so far as all the other characters are concerned. Overall primitiveness and 'tipuloid' proportions of Tillyardipteridae force us to leave it unplaced at superfamily level within Psychodomorpha. Discovery of *Tillyardiptera* annectent between the most primitive Tipulomorpha and Psychodomorpha strengthens the hypothesis that separation of the latter from the former was the first divergence in the history of Diptera.

On the relationships of Grauvogeliidae. Shortly before appearance of our review article on

Triassic Diptera (SHCHERBAKOV et al., 1995) the family Grauvogeliidae was described from the Anisian of Vosges and assigned to Diarchineura as one more infraorder, claimed to combine the features of different dipteran groups from Tanyderidae to Brachycera (KRZEMINSKI et al., 1994). In fact, of the five characters listed, the sc-r crossvein in basal position, very proximal Rs origin, short free R2, and im joining M1+2 are all found in *Proptychoptera* and/or *Nadiptera* (both Ptychopteroidea), whereas the anal loop is not unique but rather universal for Diptera (see SHCHERBAKOV et al., 1995). Furthermore, Grauvogeliidae are similar to most ptychopteroids in the r-m joining R4+5 and the m-cu joining M3+4, and to Eoptychopteridae + Ptychopteridae in the narrow pterostigma, R2+3 approximated to R1 and the M stem continued with M1+2 (excepting some characters, the family runs to Ptychopteroidea in the key to Triassic Diptera: *ibid.*). *Grauvogelia* is more primitive than ptychopteroids in the CuP weakly diverging from CuA,

Table 1. Distribution of *Tillyardiptera-like* character states in various Nematocera (+, present; ±, variable; blank cells, absent)

CHARACTER	Vladipteridae	Limoniidae	Trichoceridae	Nadpteridae	Eoptychopteridae	Hennigmatidae	Grauvogeliidae	Ansorgiidae	Tanyderidae	Psychodidae	Axymyiiformia	Bibioniformia	Anisopodiformia
R kink and M+CuA fusion long; MA not inclined	±	±											
<i>r-m</i> and <i>m-cu</i> about midlength of long <i>d</i> cell		±											
CuP apex and <i>m-cu</i> beyond wing midlength	+	±	+										
Rs branches long, diverging	±	±	±	±	±		+						
<i>m-cu</i> joining straight M3+4	±	±	±	+	±	±							
<i>sc-r</i> postsectoral	±	±	+	+	±	+		+					
strong M base not shifted to Cu base	+	±	+	+	±	±		+					
Rs aligned with R4+5 and R4	±	±			±	±		+	±	+			
anal lobe produced; alular incision absent	±	±	+		±		+		+		+	±	
<i>im</i> joining M2	±	±			±	±		+	+	±		±	±
M forking symmetrically	+	±	±	+	±	+			±	±	±	±	±
long Sc ending at the level of CuA apex	±	±		±	±				±			±	±
<i>r-m</i> joining R4+5	±	±		±	±		+					±	±
CuA bent at <i>m-cu</i> and curved backwards apically	±	±	±								±	±	±
R2 absent		±						+		±	+	+	+
anal loop formed; 1A not reaching margin				+	+	+	+	+	+	+	+	+	+

and peculiar in the M base subtransverse (like in *Psychotipa predicta*, Blephariceridae and some Bibionomorpha). The above characters allow to keep grauvogeliids (like other 'Diarchineura') in Psychodomorpha and treat them as a superfamily Grauvogelioidea, stat. nov. close to Ptychopteroidea.

The wing of *Grauvogelia* was considered the nearest to the dipteran groundplan (KRZEMINSKI, 1994, 1998). Moreover, it's tempting to interpret its broad, unstalked wing base as yet undifferentiated into basiala, and therefore extremely primitive. Nevertheless, the shortened, looped anals, along with basal *sc-r* and M1+2 continuing M stem, are very derived relative to the mecopteran condition and disagree with the above interpretation. Now the other Triassic genera are described in Tipulomorpha, allowing to reconstruct the ground-plan wing as already stalked with long, not yet looped anals, the stalking for better torsion being a component of dipterization process (SHCHERBAKOV et al., 1995). Broad-based wing of *Grauvogelia* seems to be a reversal, possibly due to flying abilities impoverished in some way (mere flapping flight?); if so, Grauvogeliidae may eventually prove to be aberrant

ptychopteroids. The abundance of this dipteran, unusual for the Triassic, could correlate not only with aquatic life mode of immatures (numerous dipteran pupae are found in the same beds) or locality peculiarities but also with a special flight mode of adults.

Acknowledgements

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