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NOTES ON A NEW GROUNDPLAN HYPOTHETICAL DIPTERA WING

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Abstract

The Chironomidae is now recognised as the most basal and oldest known family in the Culicormopha.The wing venation is the most recent chironomids may in some respects appear simplified, when compared to some other culicomorphan families (e.g. Dixidae, Chaoboridae), which does not reflect its true basal position. However, when a broad spectrum of Chironomidae are examined, ranging from the oldest fossils (†Aenneinae) and including both extant basal and more recently evolved subfamilies, it is evident that the wings show much greater variation than is found in any other family of Culicomorpha or even in any single family of Diptera. The venation within the Culicomorpha shows considerable variation between the different families. By examining the groundplan hypothetical Diptera wing and comparing it with features present in the wings of oldest known fossil adult culicomorphan (†Aenneinae – Chironomidae), other Chironomidae and in other seven extant families it is possible to produce a groundplan hypothetical Culicomorpha wing.

Key words: Diptera, Chironomidae, Culicomorpha, fossil, groundplan, hypothetical wing.

Introduction

In the nematocerous and higher Diptera one of the most significant structural features used in determining relationships between and within families is the wing venation. It is important therefore, in order to make proper comparisons, that the names and abbreviations used for the different wing components (veins, cells, etc.) are consistent and correctly applied across the whole Order Diptera and to the outgroup, the Order Mecoptera, from which the earliest Diptera evolved. The wing terminology and abbreviations used are given in Appendix 1 and the colour coding of the wing venation in Appendix 2.

In the adult morphology and terminology chapter (McAlpine, 1981, Fig. 2.67) in the *Manual of Nearctic Diptera* the groundplan hypothetical primitive Diptera wing is illustrated and labelled with abbreviations showing all the different veins, cells and other structures (Fig. 1). However, there are problems with this "ground-plan hypothetical Diptera wing" because it is based on wings of two extant species (McAlpine, 1981, Figs 4.1, 4.2) of the families Tanyderidae (*Protoplasa fitchii* Osten Sacken) and Psychodidae (*Pericoma marginalis*

(Banks)). Some of the components on this wing are not primitive or basal in origin because these two modern streamlined wings have already been subjected to 250 million years of evolution. Changes proposed in the wing vein terminology, see Saigusa (2006) heading below, mean that the McAlpine groundplan wing no longer has two anal veins but only one (**A_1**) because "**A_1**" = **CuP** and "**A_2**" = **A_1** and the wings of *P. fitchii* and *P. marginalis* have no anal veins because what is labelled "**A_1**" is actually **CuP**. The groundplan Diptera wing should have three anal veins and a U-shaped Cubital Fork as in the Diptera-like Mecoptera. It is therefore necessary to produce a new groundplan hypothetical Diptera wing based in part on Saigusa (2006) and a comparison between the wings of the oldest known fossil Diptera, extant basal Diptera and fossils of the Diptera-like Mecoptera (Fig. 2).

Saigusa (2006) (Fig. 3)

During the 6th International Congress on Dipterology (in Fukuoka, Japan), Saigusa (2006) distributed to all delegates a privately published paper entitled *Homology of wing venation of Diptera* (now freely available online) revising the wing terminology of Diptera and resolving conflicting opinions relating in particular to the posterior veins including part of the Medial, Cubital and Anal veins. The changes proposed by Saigusa (2006) included: confirmation that the vein **CuA_1** of McAlpine (1981) is **M_4** [**Note**: except in Diptera which have lost **M_4** – i.e. in most basal and higher Diptera it is **M_{3+4}** – see next paragraph]; and **CuA_2** is now **CuA**; the "vein" labelled **CuP** (of McAlpine 1981) is not a true vein but a **Pseudovein**; that **A_1** is now **CuP**; and that **A_2** is now **A_1** – the names of the corresponding cell names are also affected and changed. These changes are clearly identified in Saigusa (2006, Fig. 8A) and can be easily compared with the outdated McAlpine figure reproduced in Saigusa (2006, Fig. 8B) (Fig. 2)

Note that **CuA_1** of McAlpine (1981) is not always **M_4** as indicated in Saigusa (2006) – it only applies to the modified McAlpine ground-plan wing given in Saigusa (2006, Fig. 8A) and to various mostly basal Diptera where **M_4** is retained (e.g. Tanyderidae, many Tipulidae, Pachyneuriidae, Psychodidae, Pelecorhynchidae, Tabanidae). In the majority of Diptera separate **M_3** and **M_4** veins are lost and instead what remains is a single fused **M_{3+4}** vein (e.g. all Culicomorpha families, Deuterophlebiidae, Axymyiidae, Bibionidae, Mycetophilidae, Sciaridae, Ptychopteridae, some Tipulidae).

Saigusa (2006: 3) says "In addition to the extreme reduction of crossveins, the presence of CuP and reduced number of anal veins (less than 3) have been considered the most fundamental autapomorphies in the wing venation of the order Diptera and some of the most important characters in discussing the origin of the Diptera". This is no longer the case for **CuP** or the number of anal veins because in Mecoptera **CuP** is present (Saigusa, 2006, Fig. 3A) and there are three Anal veins (**A_1**, **A_2** and **A_3**) in his modified groundplan Diptera wing (Saigusa, 2006,

Fig. 8A). However, two of these Anal veins (**A_2** and **A_3**) are very short and in a very basal position on the wing because Saigusa used what he found and illustrated in the wings of an extant Diptera (*Trichocera* sp.) and an extant Mecoptera (*Bittacus* sp.) and believed that (*op. cit.*, p. 9) "the ancestors of the Diptera had proximally narrowed forewings". We believe that in the earliest Diptera the wings were not proximally narrowed but broader as in †*Grauvogelia* and the Diptera-like Mecoptera. Therefore, all three Anal veins in the earliest Diptera would have been well developed and elongate and that **A_2** and **A_3** would not have been restricted to a very basal position. In the *Manual of Afrotropical Diptera* chapter on 'Adult morphology and terminology' (Cumming and Wood, 2017: 111) under **anal vein**, they state that "Wootton and Ennos (1989) and Saigusa (2006) essentially recognise only one anal vein (A_1) in the groundplan of Diptera". This is incorrect at least for Saigusa (2006, Fig. 8A) where his groundplan wing clearly shows the presence of three anal veins. Saigusa (*op. cit.*, p. 9, points 4 and 5 respectively) also clearly states in the text that "(true vein A2) . . . is retained in many groups of Diptera" and "True vein A3 appears as a remnant in some Diptera".

Saigusa (2006) also states that there is a considerable loss in the number of crossveins in Diptera compared to Mecoptera. A **Pseudovein** in the earliest Diptera is probably associated with the presence of fewer crossveins basally. The **Pseudovein**, which Saigusa (2006) calls (p. 9) "the sclerotised ridge behind CuA" and (p. 24) "a thickened cuticular line (pseudovein)" is not present in Mecoptera but is an autapomorphy for and would have been present in the earliest Diptera.

At the 8th International Congress on Dipterology (2016 in Potsdam, Germany) the accepted position for chapters in the then forthcoming *Manual of Afrotropical Diptera* was that all authors would use the older and partially outdated wing terminology first given in the *Manual of Nearctic Diptera* (McAlpine, 1981) which was little changed apart from a few slight modifications in *Contributions to a Manual of Palaearctic Diptera* (Merz and Haenni, 2000) and in the *Manual of Central American Diptera* (Cumming and Wood, 2009). In Potsdam, the senior author lobbied delegates that, for the *Manual of Afrotropical Diptera*, the wing terminology proposed by Saigusa (2006) should be adopted in recognition of the accepted fact that the Mecoptera are the outgroup for the Diptera. By the end of the Potsdam conference it was agreed that all prospective authors of the *Manual of Afrotropical Diptera* would use the revised newer terminology. However, in the adult morphology and terminology chapter in the *Manual of Afrotropical Diptera* the crossvein labelled as "**m-cu**" in Cumming and Wood (2017, Fig. 43a) is incorrect – what is labelled is **not** the crossvein but merely the base of **M_4** – the real **m-cu** is correctly indicated and labelled in McAlpine (1981, Fig. 2.67), Merz and Haenni (2000, Fig. 47) and Saigusa (2006, Fig. 8A) but is incorrectly labelled as "**bm-cu**" in Cumming and Wood (2009, Fig. 43).

The Cubital Fork

It has recently become generally acceptable in Diptera that the “cubital fork” includes both a medial component (the anterior branch) and a cubital component (the posterior branch). The anterior branch of the “cubital fork” is somewhat variable and may comprise **M_4+part of M_{3+4}** or consist only of **M_{3+4}** (in most extant Diptera) or consist only of **M_4** (found in some extant Diptera; more common in older basal fossil nematocerous Diptera). The posterior branch of the “cubital fork” is the distal part of **CuA** for which we use the abbreviation **CuA_d**. Although this fork includes both a medial and a cubital component it is not necessary to change its name and the term “cubital fork” (**CuFk**) is retained.

A change proposed in Ashe *et al.* (2018), which is elaborated in greater detail here, that appears not to have been recognized before, is that the **Cubital Fork** (**CuFk**) occurs as two distinct types. It can be either: *U-shaped Cubital Fork (U-sCuFk)* (Fig. 4) or *V-shaped Cubital Fork (V-sCuFk)* (Fig. 5).

(1) U-shaped Cubital Fork (U-sCuFk) (Fig. 4)

An **U-shaped Cubital Fork** (**U-sCuFk**) consists of the anterior branch (**M_4+part of M_{3+4}** / or **M_4** / or **M_{3+4}**) + the crossvein (**m-cu**) + the posterior branch (**CuA_d** – the distal part of **CuA**). The presumed plesiomorphic condition in basal Diptera (e.g. Krzemiński and Krzemińska, 2003, Fig. 1G, †*Grauvogelia*) is: **M_4+part of M_{3+4}** + **m-cu** + **CuA_d** – the same condition is found in some Diptera-like Mecoptera with four medial branches, e.g. *op. cit.*, Figs 1C, 1E). In some basal Diptera where **M_4** is retained the U-shaped Cubital Fork may consist of either: (a) **M_4+part of M_{3+4}** + **m-cu** + **CuA_d** or (b) **M_4** + **m-cu** + **CuA_d**. In those Diptera with a U-shaped Cubital Fork where a separate **M_4** is lost and only a fused **M_{3+4}** vein remains the fork components are: **M_{3+4}** + **m-cu** + **CuA_d** – this is found in some basal Chironomidae (e.g. †Aenneinae, *Afrochlus* Freeman).

In the outgroup Mecoptera with dipteroidal venation illustrated in Krzemiński and Krzemińska (2003) the cubital fork is **U-shaped** but is more variable, especially in relation to the medial branch component which can be formed by the base of either **M_4**, or **M_4+part of M_{3+4}** or **M_6+part of M_{5+6}**. Examples of these Mecoptera with dipteroidal venation are: **M_4 + m-cu + CuA_d** (*op. cit.* Figs 1D, 1F); **M_4+part of M_{3+4} + m-cu + CuA_d** (*op. cit.* Figs 1C, IE); or **M_6+part of M_{5+6} + m-cu + CuA_d** (*op. cit.* Figs 1A-B). **Note** that **M_5**, **M_6** and **M_{5+6}** do **not** occur in Diptera.

(2) V-shaped Cubital Fork (V-sCuFk) (Fig. 5)

A **V-shaped Cubital Fork** (**V-sCuFk**) consists of two components: the anterior branch (**M_{3+4}**) + the posterior branch (**CuA_d** – the distal part of **CuA**) together forming a V-shaped fusion point where they meet while the crossvein component is lacking. This is the apomorphic (advanced or derived) condition found in the majority of Diptera which have only **M_{3+4}** and **no**

Discal cell. It occurs in most Chironomidae (except some basal taxa).

In those Diptera which possess both a Discal cell + a separate $\mathbf{M_4}$ vein or a Discal cell + a fused $\mathbf{M_{3+4}}$ vein there is no evidence that a V-shaped Cubital Fork exists or has yet evolved. However, in the wings of some extant Diptera there is an indication that evolution towards a V-shaped Cubital Fork may eventually happen

Crossvein(s) between the Media (M) and the Anterior Cubitus (CuA)

Note also that when there are two clearly defined crossveins between **M** and **CuA** the anterior crossvein is called **bm-m** and the posterior crossvein is **m-cu**.

Changes to the terminology of the crossvein "**m-cu**" are also proposed here because between the Media (**M**) and the Anterior Cubitus (**CuA**) there can be (i) two distinct crossveins (an anterior and a posterior crossvein) or (ii) one distinct crossvein. It is not appropriate to only use "**m-cu**" for both alternatives above.

(i) Two distinct crossveins. For the anterior crossvein we use the abbreviation **bm-m** (= basal medial-medial crossvein) – this crossvein originates in **M** (or more rarely in $\mathbf{M_{1+2}}$) and terminates in $\mathbf{M_{3+4}}$ or $\mathbf{M_4}$. In those Diptera with a Discal cell the **m-m** crossvein forms the anterior boundary/closure of the cell and logically the **bm-m** crossvein must form the basal boundary/closure of the cell. Note that the **bm-m** crossvein is frequently retained when the discal cell is lost. While **bm-m** functions as a crossvein the same piece of vein has a separate function – it is also part of the Media (usually part of the base of $\mathbf{M_{3+4}}$) and therefore forms a direct connection back to **M** for $\mathbf{M_{3+4}}$.

For the posterior crossvein we use the abbreviation **m-cu** (= medial-cubital crossvein) which originates at the junction where the apical part of **m-cu**, the basal part of **bm-m** and the base of a Medial branch ($\mathbf{M_{3+4}}$ or $\mathbf{M_3}$ or $\mathbf{M_4}$) all meet. The basal part of **m-cu** terminates in **CuA**. When both crossveins (**bm-m** and **m-cu**) are present the formation of the base of the cubital fork is always distinctly **U**-shaped.

(ii) One distinct crossvein. When only a single crossvein remains between **M** and **CuA** it must be called **bm-cu** (= basal medial-cubital crossvein) because it is the result of fusion (between **bm-m** and **m-cu**) and the two crossveins are no longer distinguishable from one another. This fusion causes the loss of the respective "**-m**" component in **bm-m** and the "**m-**" component in **m-cu**. The **bm-cu** crossvein originates in **M** (or more rarely in $\mathbf{M_{1+2}}$) and terminates in **CuA**. When only one crossvein (**bm-cu**) is present the formation of the cubital fork is distinctly **V**-shaped which consists of only two components, the anterior component is formed by the base of $\mathbf{M_{3+4}}$ while the posterior component is formed by the base of $\mathbf{CuA_d}$. Note that the **bm-cu** crossvein does not form part of the **V**-shaped Cubital Fork.

Evolution of the cubital fork

(i) Diptera without a Discal cell but with vein M_{3+4}. (Fig. 6)

It is necessary to explain how, in those Diptera without a Discal cell, vein $\mathbf{M_{3+4}}$ migrates from being an integral part of the Media vein complex to fuse with and become an integral part of the Anterior Cubitus (**CuA**). This migration occurs in a series of evolutionary steps which are explained as follows.

Step 1. This is the starting point where the base of $\mathbf{M_{3+4}}$ is positioned between the bottom of crossvein **bm-m** and the top of crossvein **m-cu**. In the illustrated example, **bm-m** is vertical and **m-cu** is at an acute angle. The junction point where $\mathbf{M_{3+4}}$, **bm-m** and **m-cu** all meet would represent the bottom left corner of the Discal cell if a Discal were present. The Cubital Fork is distinctly **U-shaped** (formed by $\mathbf{M_{3+4}}$ + **m-cu** + $\mathbf{CuA_d}$).

Step 2. The base of $\mathbf{M_{3+4}}$ is starting to slide down crossvein **m-cu** towards **CuA**. The evolutionary process is gradual as $\mathbf{M_{3+4}}$ gets closer and closer to **CuA**. Both crossveins **bm-m** and **m-cu** are clearly distinguishable from one another. The Cubital Fork is still distinctly **U-shaped**.

Step 3. The two crossveins **bm-m** and **m-cu** are no longer distinguishable and have fused together to form a single **bm-cu** crossvein between **M** and **CuA**. The base of $\mathbf{M_{3+4}}$ has now fused with **CuA** to form a **V-shaped Cubital Fork** ($\mathbf{M_{3+4}}$ + $\mathbf{CuA_d}$). The bottom of the **bm-cu** crossvein is also located at the fusion point between $\mathbf{M_{3+4}}$ and **CuA**.

Step 4. After $\mathbf{M_{3+4}}$ has fused with **CuA** the crossvein **bm-cu** remains mobile. The **bm-cu** crossvein can: (a) move to a more proximal position away from the fusion point to terminate in $\mathbf{CuA_p}$ (Step 4a) or move to a more distal position away from the fusion point to ride up onto and terminate in $\mathbf{M_{3+4}}$ (Step 4b). The crossvein remains mobile in order not to impede any future evolutionary flight potential or wing development. A crossvein fixed permanently in the wrong position, such as a part of the wing which should be flexible, would instead create a stiff point that would impede flight. The position of the **bm-cu** crossvein on the wing can be quite variable between genera within a family (near the wing base, intermediate, or more distal) but among species within a genus the position is generally quite similar with mostly only slight variation.

Step 5. The final stage is the complete loss of the **bm-cu** crossvein. There is no indication, without the evolutionary scenario detailed above, to explain how $\mathbf{M_{3+4}}$ managed to move from the Medial sector to the Cubital sector and form the anterior branch of the Cubital Fork .

(ii) Diptera with a Discal cell and with either vein M_4 or M_{3+4}. (Fig. 7)

In those Diptera with a Discal cell and either $\mathbf{M_4}$ or $\mathbf{M_{3+4}}$ there is some evidence of a partial evolutionary scenario which is incomplete and has yet to completely evolve. In the McAlpine (1981, Fig. 2.67) version of the groundplan Diptera wing it has both a Discal cell and "$\mathbf{CuA_1}$" [= $\mathbf{M_4}$] is fused with and forms a **V-shaped Cubital Fork** with "$\mathbf{CuA_2}$" [= **CuA**]. In the modified McAlpine groundplan wing in Saigusa (2006, 8A) there is a significant change because it now has a **U-shaped Cubital Fork** – in this figure $\mathbf{M_4}$ has moved away from the Discal cell and has travelled down the anterior part of **m-cu** by about one fifth the length of the crossvein. The basal condition in Diptera shows $\mathbf{M_4}$ attached to the bottom of the Discal cell (Fig. 2) while that figured in Saigusa is close to what we call Step 3 (Fig. 3). The following are the evolutionary steps which have so far occurred and are explained as follows.

Step 1 (Fig. 7.1). This is the starting point where the base of $\mathbf{M_4}$ or $\mathbf{M_{3+4}}$ is positioned at or close to the mid-point on the bottom of the Discal cell. In the following text and figures we only use $\mathbf{M_4}$ as the example to avoid confusion but the same senario can also occur if there is only a fused $\mathbf{M_{3+4}}$ vein. In the illustrated example (Fig. 7.1) there are two crossveins between **M** and **CuA**: (i) **bm-m** forms the basal closure of the Discal cell and is at an obtuse angle where it connects to vein **M** and (ii) **m-cu** connects to **CuA** at an obtuse angle. The junction point where **bm-m** and **m-cu** meet one another forms an obtuse angle. The Cubital Fork is distinctly **U-shaped** (formed by $\mathbf{M_4}$**+part of** $\mathbf{M_{3+4}}$ + **m-cu** + $\mathbf{CuA_d}$).

Step 2 (Fig. 7.2). The base of $\mathbf{M_4}$ has moved to the baso-posterior corner of the Discal cell at the same junction point where **bm-m** and **m-cu** meet. The position of the two crossveins (**bm-m** and **m-cu**) relative to each other remains the same. The Cubital Fork is distinctly **U-shaped** (formed by $\mathbf{M_4}$ + **m-cu** + $\mathbf{CuA_d}$).

Step 3 (Fig. 7.3). The base of $\mathbf{M_4}$ has move away from the junction with the two crossveins on the corner of the Discal cell and has started sliding down crossvein **m-cu** towards **CuA**. Both crossveins **bm-m** and **m-cu** are clearly distinguishable from one another but as $\mathbf{M_4}$ slides down towards **CuA** it bisects the **m-cu** crossvein in two parts. The Cubital Fork is distinctly **U-shaped** (formed by $\mathbf{M_4}$ + **part of m-cu** + $\mathbf{CuA_d}$).

Step 4 (Fig. 7.4). This is essentially the same as **Step III** except that $\mathbf{M_4}$ is closer to **CuA** while other features remain the same. Among extant Diptera with a Discal cell there appears to be none that have yet evolved where $\mathbf{M_4}$ fuses with **CuA** to form a **V-shaped Cubital Fork** (Fig. 7.5). Thus **Step 4** appears to be the point that the evolutionary scenario has reached. Future possibilties are shown in Fig 7. (steps 6A and 6B).

The oldest known fossil adult Diptera, mostly wing compressions, are from the Middle Triassic of France, *circa* 240 Mya (Krzemiński and Krzemińska 2003). In one of these, †*Grauvogelia arzvilleriana* Krzemiński, Krzemińska & Papier, the wing is illustrated and labelled (Krzemiński and Evenhuis, 2000, Fig. 14.8) and a colour coded version of the same wing in Krzemiński and Krzemińska (2003, Fig. 1G) clearly shows that **M** has four branches ($\mathbf{M_1}$ to $\mathbf{M_4}$) and **Cu [= CuA]** is a single vein. However, in the wing figures of †*Grauvogelia* there is no indication of the presence of either the **Pseudovein** or **CuP**. A **Pseudovein** should be present but may be too close to **CuA** to be separated from the latter or may not be discrenable due to poor preservation on the fossil. In all the Diptera-like Mecoptera figured in Krzemiński and Krzemińska (2003) **CuP** is present. However, it is difficult to imagine that the presence of **CuP** could have been missed in †*Grauvogelia* and we therefore presume that the vein labelled as "$\mathbf{A_1}$" must be **CuP** and that labelled "$\mathbf{A_2}$" must be $\mathbf{A_1}$, while just above $\mathbf{A_1}$ there is a very short unlabelled vein terminating in the wing margin which must be $\mathbf{A_2}$. Using colour coding for the veins (Krzemiński and Krzemińska, 2003, Fig. 1) show the origin of the venation in Diptera from the Mecoptera and use the same terminology for both insect orders. We have taken the wing of †*Grauvogelia* and used it with some modifications, by examining wing figures of Diptera-like Mecoptera as well as basal and fossil Diptera, to create a new template for the hypothetical ground-plan Diptera wing (Fig. 8).

Groundplan hypothetical Culicomorpha wing (Fig. 8)

The Chironomidae is now recognised as the most basal and oldest known family in the Culicormopha (Ashe and O'Connor, 2012; Borkent, 2012). The wing venation is the most recent chironomids may in some respects appear simplified, when compared to some other culicomorphan families (e.g. Dixidae, Chaoboridae), which does not reflect its true basal position. However, when a broad spectrum of Chironomidae are examined, ranging from the oldest fossils (†Aenneinae) and including both extant basal and more recently evolved subfamilies, it is evident that the wings show much greater variation than is found in any other family of Culicomorpha or even in any single family of Diptera.

The venation within the Culicomorpha shows considerable variation between the different families. By examining the groundplan hypothetical Diptera wing (Fig. 8) and comparing it with features present in the wings of oldest known fossil adult culicomorphan (†Aenneinae – Chironomidae), other Chironomidae and in other seven extant families it is possible to produce a groundplan hypothetical Culicomorpha wing (Fig. 8). These features are:-

(i) **Costa**. A continuous **Costa** surrounding the entire wing margin but strongest and thickest on the anterior margin is the plesiomorphic condition in Diptera and in the earliest Culicomorpha.

Within the Culicomorpha a continuous **Costa** is retained in all four families of the Superfamily Culicoidea (i.e. Dixidae, Culicidae, Chaoboridae and Corethrellidae).

In three of the remaining four Culicomorpha families of the Superfamily Chironomoidea the **Costa** is not continuous beyond the wing apex, ending at or extending a little beyond the apex of R_{4+5}, leaving the hind margin of the wing membranous – this is the apomorphic condition which is found in the families Chironomidae, Ceratopogonidae and Simuliidae. An exception is the Thaumaleidae in which the **Costa** encircles the hind margin of the wing to some degree (Wood and Borkent in McAlpine and Wood (1989: 1359)).

(ii) **Subcosta**. Long, well developed and terminating in the costa (on the anterior wing margin).

(iii) **Radius**. With four branches ($\mathbf{R_1}$, $\mathbf{R_2}$, $\mathbf{R_3}$ and $\mathbf{R_{4+5}}$) of which at least three, with the possible exception of $\mathbf{R_2}$, terminate in the wing margin. There is some evidence from fossil Chironomidae (†*Aenne*) and Dixidae (†*Syndixa* Lukashevich) and extant Chironomidae (most Tanypodinae) and some basal Ceratopogonidae (†*Lebanoculicoides* Szadziewski as figured in Borkent 2019: Fig. 3D) that $\mathbf{R_2}$ terminating in $\mathbf{R_1}$ is the pleisomorphic condition in Culicomorpha. The elongation and narrowing of the wings in extant Dixidae, Corethrellidae, Chaoboridae and Culicidae probably caused $\mathbf{R_2}$ in the ancestors of these families to separate from $\mathbf{R_1}$, with $\mathbf{R_2}$ becoming more elongate and parallel to $\mathbf{R_3}$ and $\mathbf{R_{4+5}}$ with all three veins terminating in the wing margin.

(iv) **Media**. With three branches ($\mathbf{M_1}$, $\mathbf{M_2}$ and $\mathbf{M_{3+4}}$) all of which reach the wing margin. In all extant culicomorphan families (except Chironomidae) $\mathbf{M_1}$, $\mathbf{M_2}$, and $\mathbf{M_{3+4}}$ are retained whereas in all described fossil and extant Chironomidae only two veins $\mathbf{M_{1+2}}$, and $\mathbf{M_{3+4}}$ are present which extent towards but may or may not reach the wing margin.

(v) **Anterior Cubitus** (**CuA**). The **Anterior Cubitus** (including the anterior **CuA** portion) is well developed and terminates in the wing margin.

(vi) **Pseudovein**. A weak vein-like fold, more or less parallel and close to the **Anterior Cubitus** (**CuA**) for most of its length, which was previously wrongly believed to be the posterior cubitus vein.

(vi) **Posterior Cubitus** (**CuP**). The first true vein below the **Anterior Cubitus**. It was previously confused with the **Pseudovein** and in many published works is wrongly labelled as the first anal vein ($\mathbf{A_1}$). The Posterior Cubitus terminates in the wing margin.

(vii) **Anal**. With three veins ($\mathbf{A_1}$, $\mathbf{A_2}$ and $\mathbf{A_3}$) of which at least one ($\mathbf{A_1}$) reaches the wing margin but with $\mathbf{A_2}$ and $\mathbf{A_3}$ possibly weaker apically and stopping short of the margin (Fig. 8).

Although three anal veins are apparently not known to occur in any extant or fossil Cucicomorpha we expect that in the ground-plan there would have been three veins. Evidence for at least two anal veins (within the Culicomorpha) is found in some extant Chironomidae (e.g. *Heptagyia* Philippi, *Murraycladius* Ashe & O'Connor) both of which phylogenetically belong to more apomorphic subfamilies.

(viii) **Cubital Fork** (**CuF**). Within most Culicomorpha, the presence of a distinctly **V**-shaped cubital fork (formed by the fusion of M_{3+4} and CuA) and the presence of a single crossvein (**bm-cu**) is regarded as the apomorphic condition. The pleisomorphic state is the presence of a distinctly **U** –shaped cubital fork and two crossveins (**bm-m** and **m-cu**) in some basal fossil chironomids (e.g. †*Aenne*) and in the extant families Dixidae and Corethrellidae. These two crossveins are: (a) the anterior crossvein (**bm-m**) which is vertical and connects **M** (or $\mathbf{M_{1+2}}$) to

M$_{3+4}$ and (b) the posterior crossvein (**m-cu**) which forms an oblique angular connection between **M$_{3+4}$** and **CuA**. There is no evidence to indicate that a discal cell has every existed within the Culicomorpha but its presence in the very earliest members of the infraorder cannot be ruled out.

(ix) **Crossveins.**

In some extant Chironomidae, of which the clearest example is found in the genus *Afrochlus* Freeman (subfamily Podonominae), both crossveins are clearly present and the cubital fork is distinctly **U**-shaped. There are other examples, especially among the more primitive subfamilies (e.g. Podonominae, Tanypodinae, Diamesinae), where both crossveins are sometimes clearly present but in others it is indistinct due to considerable shortening of the **m-cu** crossvein as **M$_{3+4}$** approaches the fusion point with **CuA** – in such cases the cubital fork is still distinctly **U**-shaped. Previous authors apparently treated wings displaying the two crossveins among extant species as an anomaly usually without any comment or explanation or treated the entire two crossvein complex as representing a single "m-cu" crossvein.

However, the presence of the two crossveins and a **U-shaped Cubital Fork** is much more common in chironomid fossils, particularly in basal subfamilies, e.g. †Aenneinae, †*Dungeyella* (Buchonomyiinae).

FIGURE 1. The groundplan hypothetical primitive Dipter wing according to McAlpine (1981).

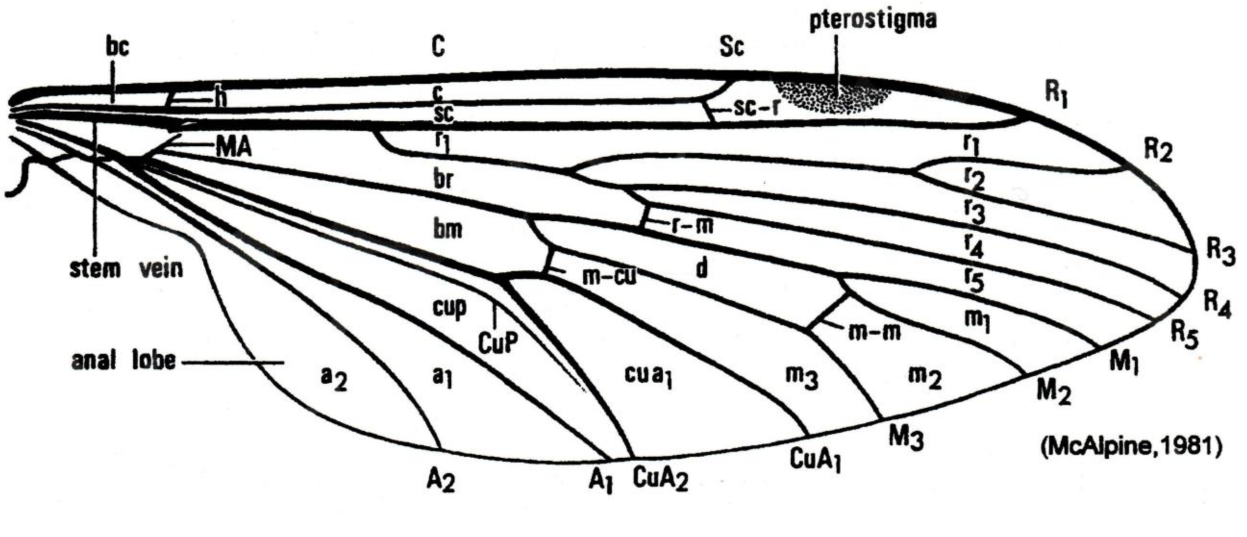


FIGURE 2. Fossil wing of *Prochoristella megaloprepia* (Mecoptera) from the Upper Permian of Australia (From Krzemiński and Krzemiński (2003)).

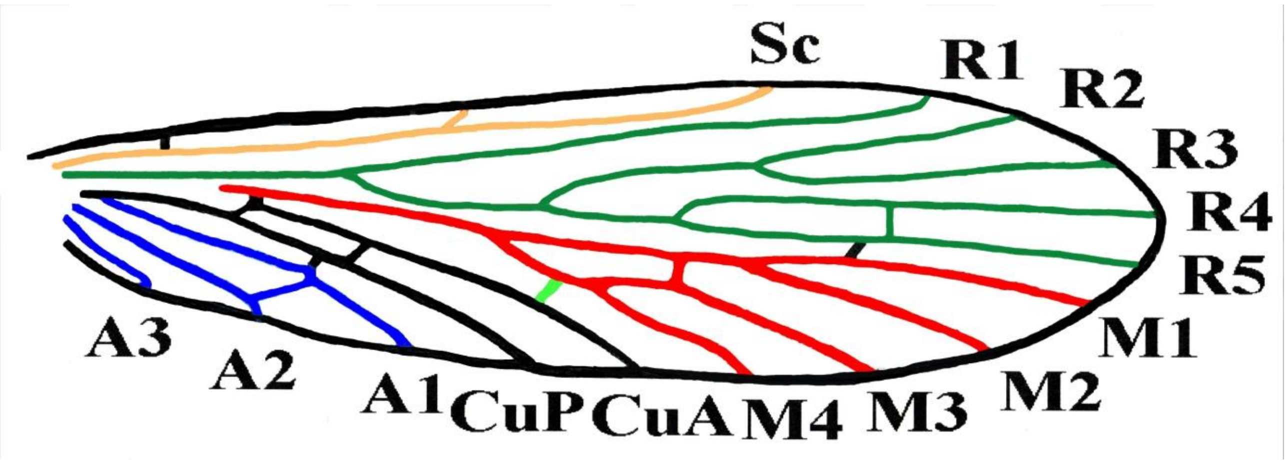


FIGURE 3. The groundplan hypothetical primitive Dipter wing according to Saigusa (2006).

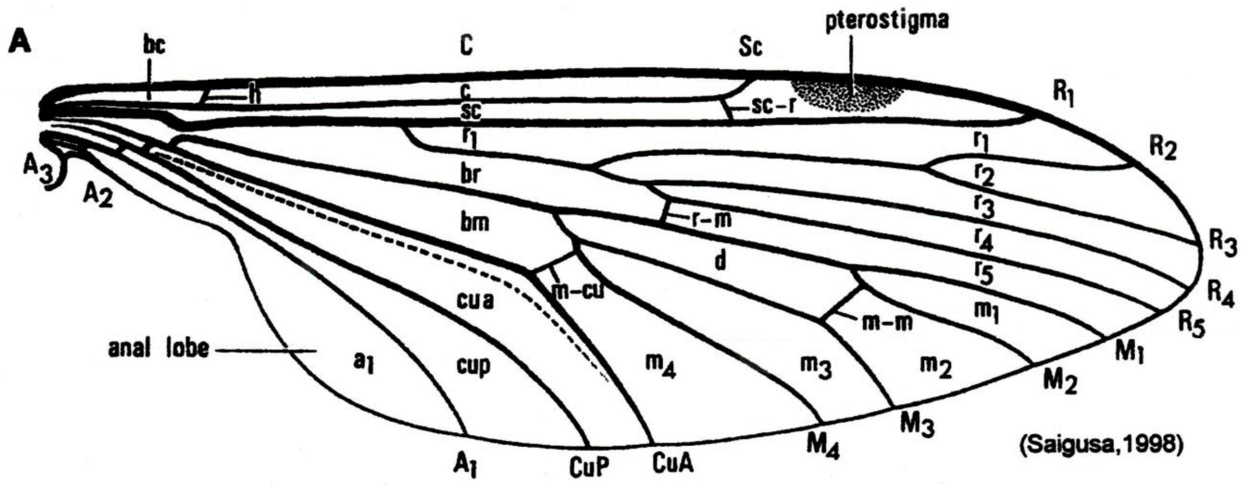


FIGURE 4. Wing of adult female of †*Dungeyella gavini* showing the U-shaped Cubital Fork (U-sCuFk) (redrawn after Jarzembowski *et al*. 2008, Figure 3A). Wing is modified and colour-coded.

BLACK = for the entire outer wing margin (proposed here).
ORANGE = for the Costa (proposed here).
YELLOW = for all Scutal veins (as in Krzemiński and Krzemińska, 2003).
GREEN = for all Radial veins (as in Krzemiński and Krzemińska, 2003).
RED = for all Medial veins (as in Krzemiński and Krzemińska, 2003).
PURPLE = for all Cubital veins (proposed here).
BLACK DASHED LINE = for the pseudovein (proposed here).
SKY BLUE = for all Anal veins (as in Krzemiński and Krzemińska, 2003).
DARK BLUE = for all Crossveins (proposed here).

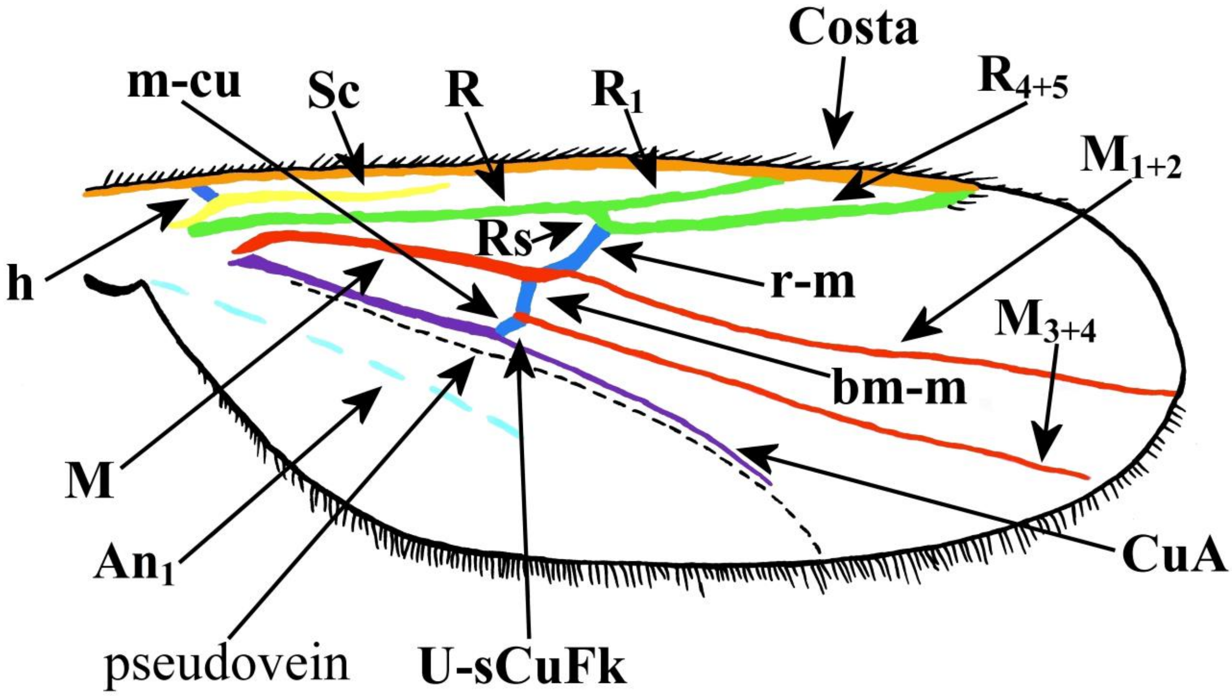


FIGURE 5. Wing of adult male of †*Cretodiamesa taimyrica* showing the V-shaped Cubital Fork (V-sCuFk) (redrawn after Kalugina, 1976a). Wing is modified and colour coded.
BLACK = for the entire outer wing margin (proposed here).
ORANGE = for the Costa (proposed here).
YELLOW = for all Scutal veins (as in Krzemiński and Krzemińska, 2003).
GREEN = for all Radial veins (as in Krzemiński and Krzemińska, 2003).
RED = for all Medial veins (as in Krzemiński and Krzemińska, 2003).
PURPLE = for all Cubital veins (proposed here).
BLACK DASHED LINE = for the pseudovein (proposed here).
SKY BLUE = for all Anal veins (as in Krzemiński and Krzemińska, 2003).
DARK BLUE = for all Crossveins (proposed here).

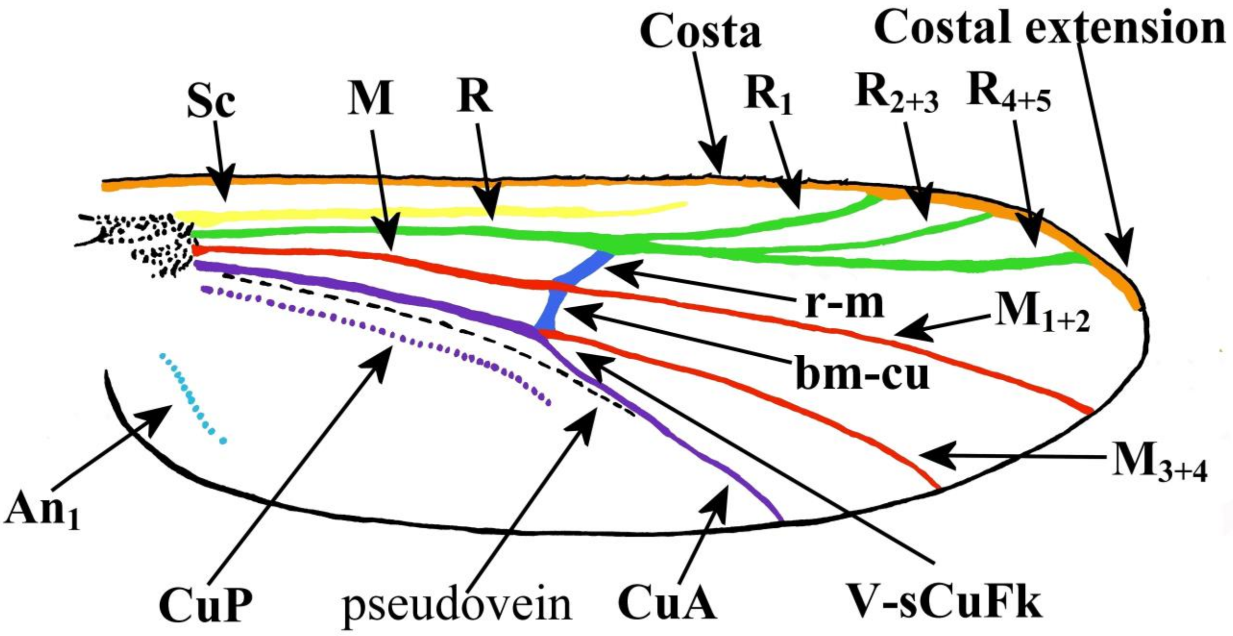


FIGURE 6. Evolution of the Cubital Fork (Redrawn by JPOC from a sketch by PA).

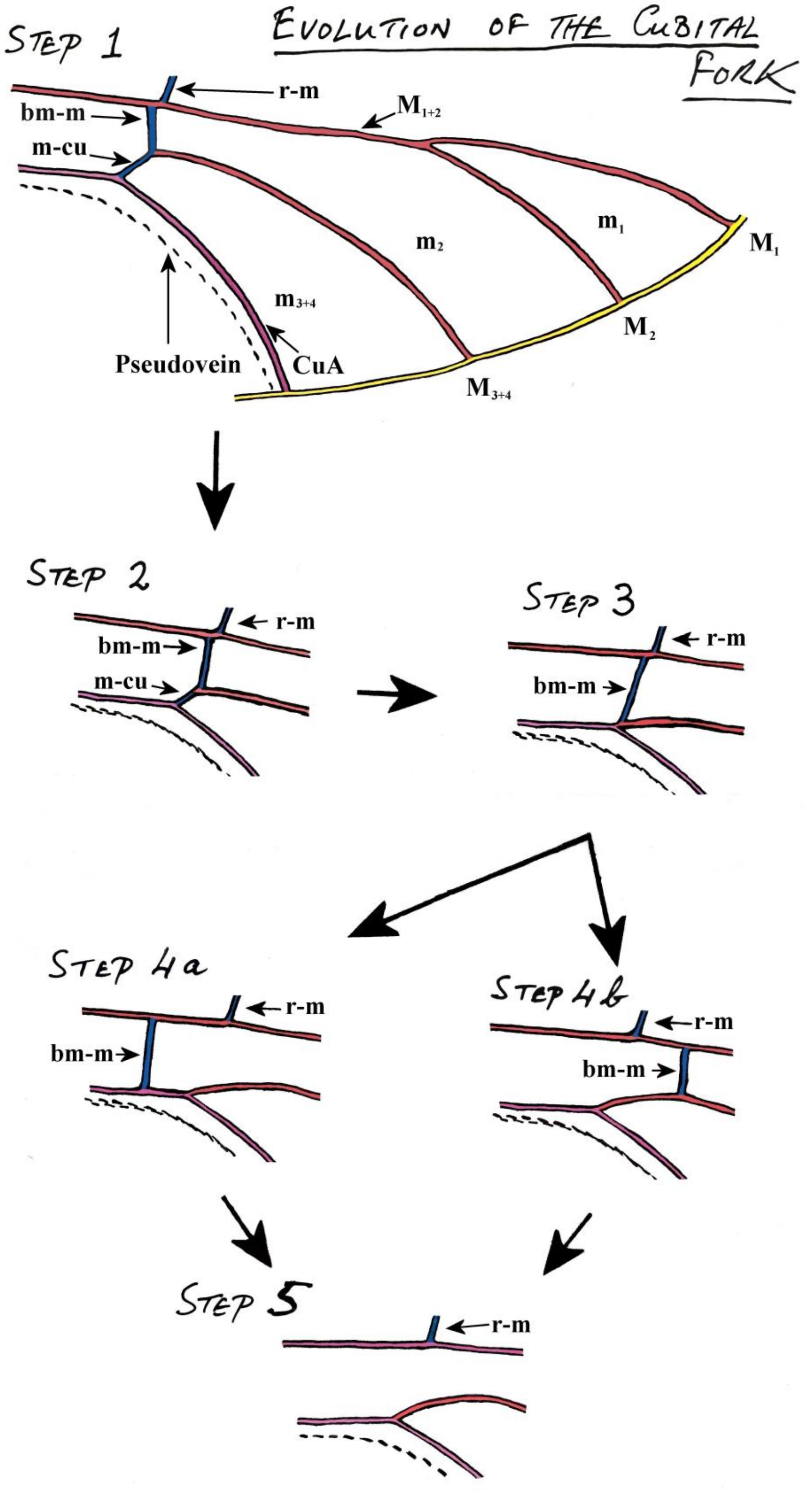


FIGURE 7. Partial evolution of the Cubital Fork in Diptera with a discal cell (Redrawn by JPOC from a sketch by PA).

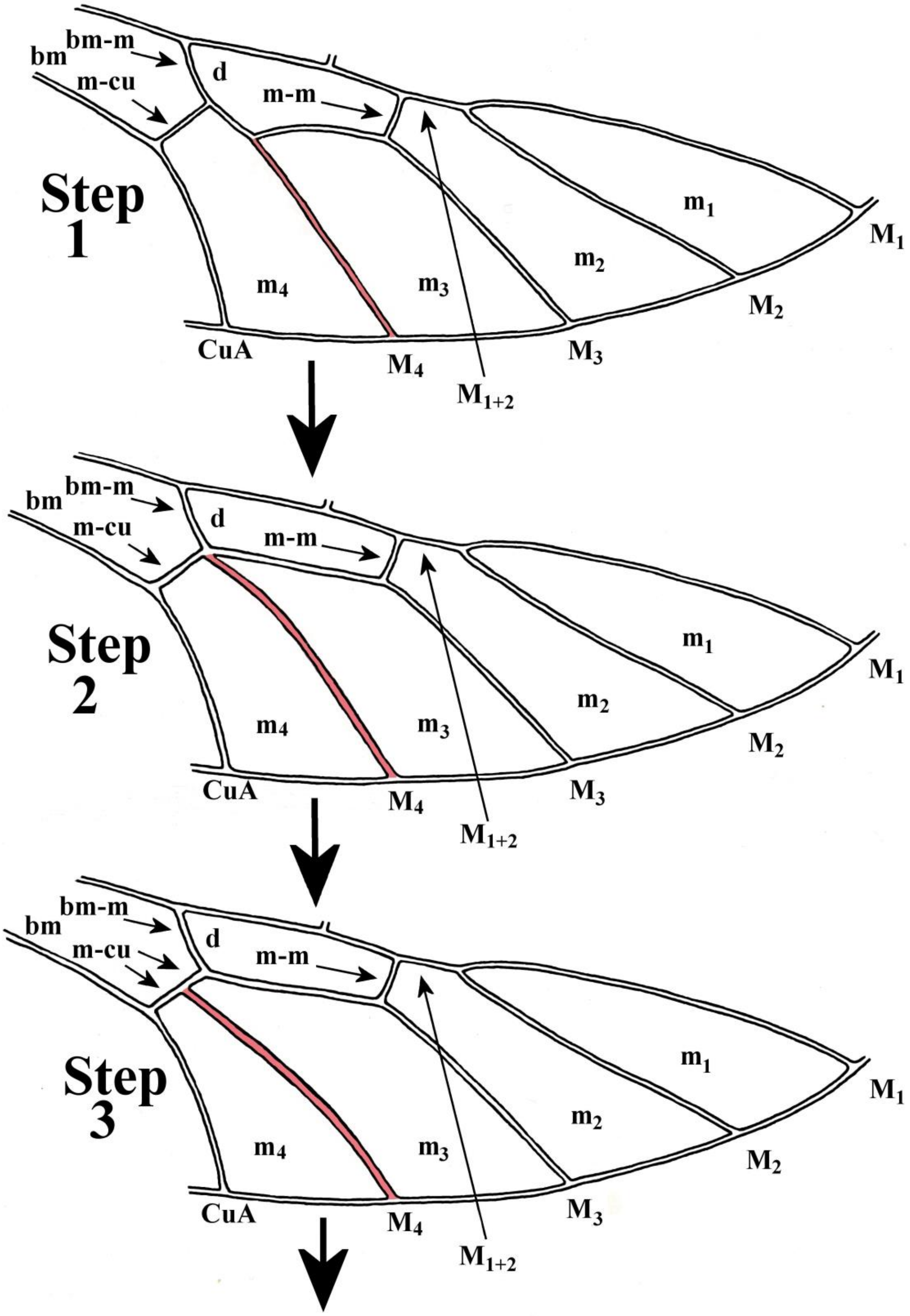


FIGURE 7 (continued).

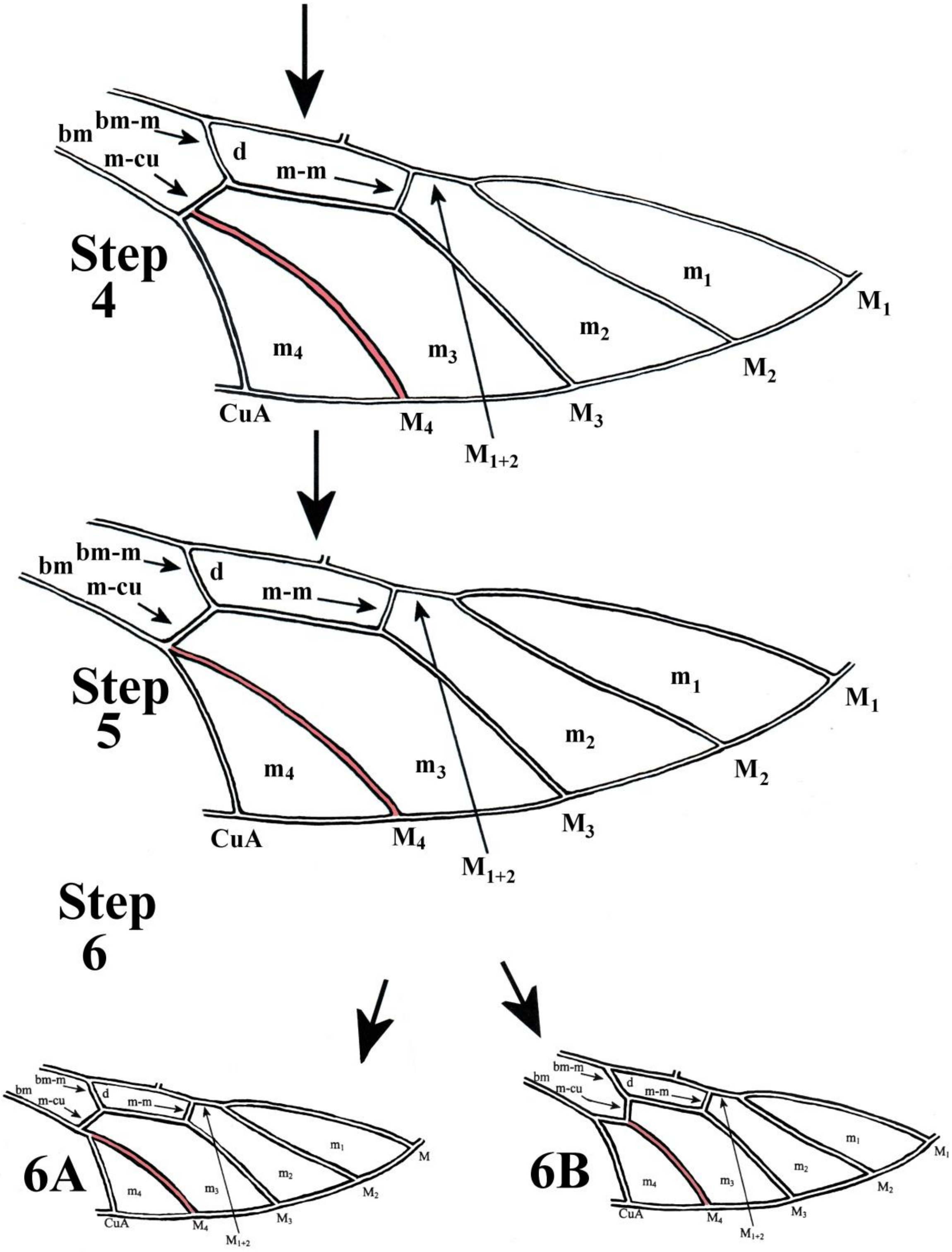
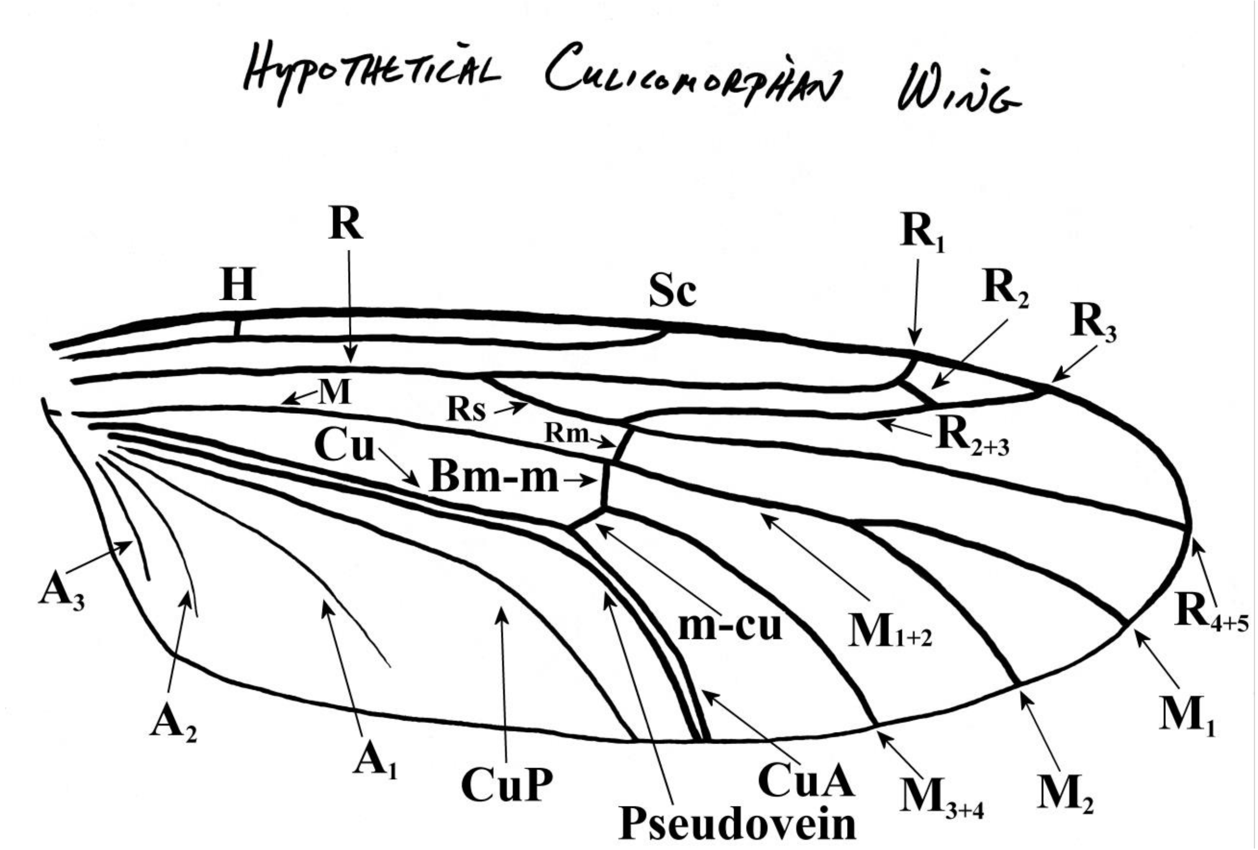


FIGURE 8. Groundplan hypothetical Culicomorpha wing.



Ackknowlegements

Dr Patrick Ashe became ill in the autumn of 2021, was hospitalised in December that year and sadly died six months later on 19 June 2022. Before his death, he mentioned that he wanted his theories about a groundplan hypothetical Culicomorpha wing to be published. Following his passing, with the kind cooperation of the Ashe family, particularly his brother Fergus, Professor Declan Murray and JPOC were given access to Patrick's computer, files and documents in his home office. Draft fragments of text, in printed and electronic format, that he had prepared concerning his wing theory were located. This article was prepared by JPOC based on these fragments.

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APPENDIX 1. Wing terminology and abbreviations used.

The following is a list of the wing vein terminology and abbreviations used. The abbreviations are used whenever necessary in both the text and in the wing figures to facilitate the discussion

Veins

$\mathbf{A_1}$, $\mathbf{A_2}$, $\mathbf{A_3}$ = Anal

C = Costa

CuA = Anterior Cubitus – we divide it into a distal part ($\mathbf{CuA_d}$) and a proximal part ($\mathbf{CuA_p}$) – see below. The **CuA** vein is incorrectly labelled as $\mathbf{CuA_2}$ in many taxonomic works (e.g. McAlpine, 1981, Fig. 2.67, Cumming and Wood, 2009, Fig. 2.43).

$\mathbf{CuA_d}$ = the distal part of the Anterior Cubitus (**CuA**) forms the posterior branch of the Cubital Fork and extends from the fork towards the wing margin.

$\mathbf{CuA_p}$ = the proximal part of the Anterior Cubitus (**CuA**) which extends from its origin near the wing base and terminates just before the Cubital Fork.

CuP = Posterior Cubitus. In many taxonomic works the vein-like fold (= **Pseudovein**) behind **CuA** was incorrectly treated as vein **CuP**. Consequently, the next true vein after the **Pseudovein** which is often incorrectly labelled "$\mathbf{A_1}$" is the real **CuP** vein.

M = Media

$\mathbf{M_1}$, $\mathbf{M_2}$, $\mathbf{M_3}$, $\mathbf{M_4}$ = posterior (sectoral) branches of media ($\mathbf{M_1}$ and $\mathbf{M_2}$ or $\mathbf{M_3}$ and $\mathbf{M_4}$ can fuse partially or completely creating respectively $\mathbf{M_{1+2}}$ and $\mathbf{M_{3+4}}$). The vein incorrectly labelled as $\mathbf{CuA_1}$ in McAlpine (1981) can be either $\mathbf{M_{3+4}}$ or $\mathbf{M_4}$

Pseudovein = The **Pseudovein** is the vein-like fold just behind the Anterior Cubitus (**CuA**). In many taxonomic works it was wrongly believed to be the Posterior Cubitus (**CuP**). Its status was resolved by Saigusa (2006) who proved that it is not a true vein but merely a vein-like fold

R = Radius

$\mathbf{R_1}$ = anterior branch of the radius. It consists of a single vein, $\mathbf{R_1}$

$\mathbf{R_2}$, $\mathbf{R_3}$, $\mathbf{R_4}$, $\mathbf{R_5}$ = posterior (sectoral) branches of the radius. In many Diptera some of these veins can fuse together to form a single vein, e.g. $\mathbf{R_{2+3}}$, $\mathbf{R_{4+5}}$, but other options are possible. When there is a single fused vein present (e.g. $\mathbf{R_{2+3}}$) the name of the corresponding cell below the vein also changes it name (i.e. $\mathbf{r_{2+3}}$)

Rs = radial sector, posterior branch of the radius. It consists of a maximum of four veins ($\mathbf{R_2}$, $\mathbf{R_3}$, $\mathbf{R_4}$ and $\mathbf{R_5}$) but the number is often reduced in many Diptera due to fusion between some of the veins (e.g. $\mathbf{R_{2+3}}$, $\mathbf{R_{4+5}}$)

Sc = subcostal

V-sCuFk = V-shaped Cubital Fork, consists of two components: (i) the anterior branch is either $\mathbf{M_{3+4}}$ or $\mathbf{M_4}$ and (ii) the posterior branch is $\mathbf{CuA_d}$ – the distal part of **CuA**

U-sCuFk = U-shaped Cubital Fork, consists of three components: (i) the anterior branch is either $\mathbf{M_{3+4}}$ or $\mathbf{M_4}$ and (ii) the posterior branch is $\mathbf{CuA_d}$ (the distal part of **CuA**)

cells

$\mathbf{a_1}$, $\mathbf{a_2}$, $\mathbf{a_3}$ = anal
bc = basal costal
bm = basal medial
br = basal radial
c = costal
cua = anterior cubital
cup = posterior cubital
d = discal
$\mathbf{m_1}$, $\mathbf{m_2}$, $\mathbf{m_3}$, $\mathbf{m_4}$ = medial
$\mathbf{r_1}$, $\mathbf{r_2}$, $\mathbf{r_3}$, $\mathbf{r_4}$, $\mathbf{r_5}$ = radial
sc = subcostal

crossveins

Two crossveins between M and CuA

(i) bm-m = basal medial-medial. This is the anterior crossvein when there are two clearly defined crossveins between **M** and **CuA**.

(ii) m-cu = medial-cubital. This is the posterior crossvein when there are two clearly defined crossveins between **M** and **CuA**. The terminal position is quite variable and it may end in **Cu**, in $\mathbf{M_4}$ or in $\mathbf{M_{3+4}}$)

One crossvein between M and CuA

bm-cu = basal medial-cubital. The correct term to apply is **bm-cu** when only a single crossvein remains between **M** and **CuA** it is the result of fusion between **bm-m** and **m-cu**.

h = humeral
m-m = medial-medial
r-m = radial-medial
sc-r = subcostal-radial

APPENDIX 2. Colour coding of wing venation.

Krzemiński and Krzemińska (2003, Figs 1A-G) used colour coded diagrams of the wing venation and used different colours for specific longitudinal sector veins (e.g. green for all radial veins, red for medial veins and black for cubital veins) although the colours used for the crossveins were not consistent (either black or green) and black was also used for the wing margin (including the Costa). Since the Order Mecoptera is considered to be the group from which Diptera evolved, this colour coding was used to demonstrate how the basal Diptera wing (*op. cit.* Fig. 1G) evolved from those Mecoptera with dipteroidal venation (*op. cit.* Figs 1A-F).

The same colour coding of Krzemiński and Krzemińska (2003) is used here with some modifications given in Ashe *et al.* (2018): (i) to account for more recently adopted changes in terminology of some veins, (ii) acceptance that the "vein" previously termed the **Posterior Cubitus** (**CuP**) is **not** a true vein but merely a fold in the wing that is now designated the **Pseudovein** – the real **CuP** vein is the next posterior vein after the **Pseudovein**, and (iii) the recognition that a continuous **Costa** around the entire perimeter of the wing is the plesiomorphic basal condition in Diptera, although in most extant, primitive and fossil taxa it is not continuous but is thickened and usually terminates in either the anterior wing margin or near the wing apex.

The colour coding given here is partially based on that given in Krzemiński and Krzemińska (2003) with additions colour selections in Ashe *et al.* (2018). The complete colour coding proposed for the Diptera (including Chironomidae) and those Mecoptera with dipteroidal venation was given in Ashe *et al.* (2018) and is outlined below. To facilitate discussion of relevant features on the respective wings of two fossil chironomids this colour coding was used by Ashe *et al.* (2018). This colour coding may also be applicable to other insect orders but may require some modification for more complex wing venations:-

Black = for the entire outer wing margin (as in Ashe *et al.*, 2018).
Orange = for the Costa (as in Ashe *et al.*, 2018).
Yellow = for all Scutal veins (as in Krzemiński and Krzemińska, 2003).
Green = for all Radial veins (as in Krzemiński and Krzemińska, 2003).
Red = for all Medial veins (as in Krzemiński and Krzemińska, 2003).
Purple = for all Cubital veins (as in Ashe *et al.*, 2018).
Black dashed line = for the Pseudovein (as in Ashe *et al.*, 2018).
Sky Blue = for all Anal veins (as in Krzemiński and Krzemińska, 2003).
Dark Blue = for all Crossveins (as in Ashe *et al.*, 2018).