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周长发．蜉蝣翅基纵脉走向模式（昆虫纲：蜉蝣目）（英文）［J］．环境昆虫学报，2024，46（6）：1326-1331．ZHOU Chang-Fa．The running pattern of longitudinal veins at wingbase of mayflies (Insecta: Ephemeroptera)［J］．*Journal of Environmental Entomology*，2024，46（6）：1326-1331．

蜉蝣翅基纵脉走向模式（昆虫纲：蜉蝣目）（英文）

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摘要：由于蜉蝣成虫翅基结构变形大，起始状态难以确定，其原始脉相及其起源过程仍未有清楚呈现。不过，少数中国大型蜉蝣稚虫翅芽的基部却保留着一些原始线索，如中国古丝蜉 *Siphluriscus chinensis*、长茎蜉 *Ephemera pictipennis* 和戴氏短丝蜉 *Siphlonurus davidi*。总体上，它们表明：蜉蝣翅脉中的亚前缘脉弓（Subcostal brace）可能起源于亚前缘脉前支（ScA）；径脉（Radius，R）与中脉（Media，M）在基部就完全合并，后中脉（Media Posterior，MP）最先离开它们的主干，然后是基部合并在一起的径分脉（Radial Section，Rs）和前中脉（Media Anterior，MA）；肘脉（Cubitus，Cu）完全独立；臀脉（Anal，A）的气管起源于肘脉中的气管。在蜉蝣翅中，所有纵脉都有独立的翅基骨片但它们都不能活动，而是与纵脉完全愈合在一起，特别是在径脉（R）与中脉（M）的基部形成一个较大的骨板，所有这些骨片与骨板又因翅基的骨化和硬化而连接成块，因而蜉蝣翅不具有折叠的结构基础。从系统发育的角度看，蜉蝣目内不同的演化支系具有不同的脉相，它缘于各纵脉在翅基的位置不同，如亚前缘脉弓（ScA）与翅前缘的距离以及肘脉（Cu）与中脉（M）的距离。而对于有翅昆虫的三大支而言，蜉蝣似乎与新翅类较接近，因为它们的翅基都具有3块腋片且径脉（R）与中脉（M）在基部合并，而蜻蜓翅基不具腋片且中脉（M）与肘脉（Cu）合并，似乎与蜉蝣的关系较远，故从翅基结构与脉相来看，“古翅类”（=蜉蝣目+蜻蜓目）应该不是单系群。

关键词：脉相；翅基；气管；起源；昆虫
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The running pattern of longitudinal veins at wingbase of mayflies (Insecta: Ephemeroptera)

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Abstract: The original or primitive venation of mayflies was not presented clearly upon living materials before, this mostly results from the deform of mayfly imaginal wingbase. Some nymphs of large mayflies of China, like *Siphluriscus chinensis*, *Ephemera pictipennis* and *Siphlonurus davidi*, however, show some clues. Together, they demonstrate that in mayflies, subcostal brace maybe originated from longitudinal vein Anterior Subcostal (ScA), stems of Radius (R) and Media (M) are always fused at base, Media Posterior (MP) leave them first, then the branch of Rs (Radial Section) +MA (Media Anterior), Cubitus (Cu) disconnected to any other veins. Additionally, all longitudinal veins of mayflies fused with their sclerotized base respectively but without any moveable sclerite. Instead, base of R+M of mayflies sclerotized into a single one big plate, and all sclerites of wingbase are fused together rigidly by sclerotized wingbase, which disables any possible folding of mayfly wings. Phylogenetically, in the order Ephemeroptera, the different positions of ScA and Cu leaded to different and diverse venations and lineages of Ephemeroptera. In the Pterygota, the Ephemeroptera has the same fused pattern of R+M and three axillary sclerites as the

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Neoptera while the Odonata has the fused Cu+M, which disproves the monophyly of Paleoptera.

Key words: Venation; wingbase; trachea; origin; insect

1 Introduction

The basic venation system and sclerites at wingbase of insect had been proposed by Comstock & Needham (1898) and Snodgrass (1927, 1935) (Hamilton, 1972). In a series of papers, mostly in 1991, Kukalová-Peck hypothesized a ground-plan of insect wing and venation to explain the forming reason and pattern of the insect venation. In her hypothesis, originally the insect wing had at least eight pairs of longitudinal veins, named PC, C, Sc, R, M, Cu, A, J. In addition, at the base of wing, there were four columns and eight rows of sclerites. With evolution, those veins and sclerites changed and fused differently in different clades. In Neoptera, they formed three axillaries and two median plates. At the same time, vein R and M fused together. With the help of muscles on those sclerites and plates, neopterans can fold their wings on the dorsal back of body.

The wingbase of dragonflies had been researched by several scholars. For example, Riek and Kukalov-Peck (1984) believed those sclerites of dragonflies formed three big plates, and the bases of M and Cu fused together. Rehn (2003) basically repeated their theory.

Needham *et al*. (1935) and Kluge (1994, 2004) described the thoracic structures of mayflies but did not mentioned the origin of sclerites and veins. Kukalová-Peck *et al*. (2009) reconstructed the anterior articular plate of mayflies. Kluge (1994, 2004) clearly showed that there were three axillary sclerites at the wingbase of mayflies although Needham *et al*. (1935) showed only one. Zhou (2007) observed that the wings of mayfly *Siphluriscus chinensis* was remarkable. It has independent ScA or Sc brace. In most other mayflies, this vein fused with Costal vein. Meanwhile, the traces of R or Rs and M were presented too. The stem or base of Cu was independent and visible. However, at least four points were not mentioned or presented at that time. First, the relationship between R and M; second, the detaching pattern of MA and MP; third, the relationship between A and Cu, and fourth, the sclerites of wings. In real imaginal specimens like *Siphluriscus chinensis*, the bases of mayflies are totally thickened or sclerotized, with several big plates. The trace of longitudinal veins are not clear.

This year, I checked lots of mayfly imaginal wings again. They look similar but without any new clue. So I turn to the nymphs of mayfly. Luckily, in some big mayflies, their wingpads have clear tracheae and venation. Those materials seem provide the necessary information and solve the four points I want to know.

2 Materials and methods

2.1 Materials

Most large mayfly specimens in our collection were checked, including Ameletidae, Ephemeridae, Ephemerellidae, Euthyplociidae, Heptageniidae, Isonychiidae, Polymitarcyidae, Potamanthidae, Siphlonuridae, Siphluriscidae, and Vietnamellidae. Most of them did not show more information but three species of them provided clues.

Siphluriscus chinensis (Ulmer, 1920) (Siphluriscidae): 1♀, Zhejiang Province , Bai-Shan-Zhu, Qingyuan county, 20-IX-1993, leg. WU Hong; 1♂, Zhejiang Province, Tian-Mu-Shan mountain, 2VI-1999, leg. ZHAO Ming-Shui; 1♀ subimago, Guangxi Province, Rongshui County, Jiu-Wan Mt., Wei-Lin-Jiang forestry station, 5-VIII-2003, leg. JIANG Guo-Fang; 1♀ subimago, Zhejiang Province, Tian-Mu-Shan mountain, 2VI-2023, leg. ZHANG Hao-Min; 20 nymphs 1♀1♂, Tian-Ping Mt., Hua-Ping, Guangxi Province, 2023-VIII-2-5, leg. Xin-He Qiang.

Ephemera pictipennis Ulmer, 1924 (Ephemeridae): 2 ♂ imagines, 1 nymph, gate of Tian-Mu-Shan, Zhejiang Province, leg. Chang-Fa Zhou, Yan-Yan Jia and Ping Chen, 2009-IV-26-27; 6 ♀ imagines, Che-Ba-Lin, Guangdong Province, leg. Chuan-Chuan Gu, 1991-IV-26; 12 ♂ imagines, Hua-Wang village, Jing-Xiu, Guangxi Province, leg. Huai-Jun Xu, 2002-IV-13； 2 ♂ and 12 ♀ imagines, Si-Xing logging camp, Wuyi Mt., Fujian Province, leg. Wei Zhang & Zhi-Min Lei, 2012-IV-15; 20 nymphs, Che-Ba-Ling, Shao-Guan, Guangdong Province, 2024-IV-2-14, leg. De-Wen Gong and Xu-Hong-Yi Zheng.

Siphlonurus davidi (Navás, 1932): 1 ♂ 2 ♂♂ subimagos, 4♀♀ subimagos and 25 nymphs, Jing Hai (Mirror pool or lake, alt. 2398 m), 2013-VII-6, leg. Hun He and Guangba Li.

All specimens are in mayfly collections, Nanjing Normal University, China.

2.2 Methods

Specimens were examined under Nikon SMZ18 stereomicroscope. The photographs were taken using Sony Alpha 7R II with a Sony FE 90 mm macro lens and edited with Adobe Photoshop CC 2019. Each structure were taken multiple pictures in different focuses and levels, and then they were overlapped together.

2.3 Abbreviation

Precosta (PC, PCA+, PCP-), costa (C, CA+, CP-), subcoxta (Sc, ScA+ , ScP-), radius (R, RA +=R_1, RP-) , media (M, MA+ , MP-), cubitus (Cu, CuA+ , CuP-), anal (A, AA+ , AP-) and jugal (J, JA+ , JP-). A = anterior, P =posterior, + = convex, -= concave. AxA (anterior axillary sclerite), AxM (middle axillary sclerite).

3 Results

3.1 *Siphluriscus chinensis*

The imaginal wingbase of *Siphluriscus chinensis* has been presented by Zhou (2007) . In this study, a picture of wingbase of this species is presented in figure 1. It shows there is a big plate at the base of R+M, Cu and A each has a sclerite at base too. All those plates and sclerites are fused together and immovable because whole wingbase is hardened or sclerotized (Fig. 1). According to Kluge (1994, 2004), there are three axillary sclerites at mayfly wingbase, two of them (AxA and AxM) can be seen in the figure 1.

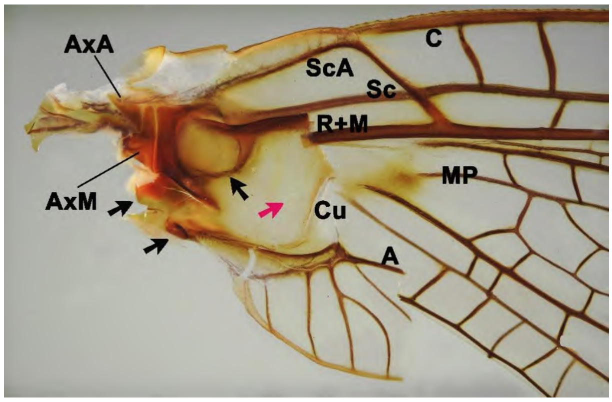

Fig. 1 Forewing base of *Siphluriscus chinensis* male imago
Note: Showing the main sclerotized plates and wingbase; black arrows indicating the sclerotized plates and sclerites, red arrow indicating the sclerotized wingbase; two axillary sclerites AxA and AxM after Kluge, 1994 and 2004.

Some nymphal individuals of this species have clear venation and internal tracheae (Fig. 2). All tracheae of forewings have common stem (Figs 2-A-B), then ScA detached first, then Sc and R, M fused with R, MP detached first, Cu is independent, the trachea of A is a branch of Cu (Figs 2-A-B).

In hindwing (Fig. 2-C), it looks like R and M fused at base shortly, then MP left, then Rs+MA detached. The other points are similar to forewings.

3.2 *Ephemera pictipennis*

In the forewing of this species (Fig. 3), the relationship of M and R is clearer than *Siphluriscus chinensis*. It shows the R and M divided into two clades first, then they fused together for short distance, then MP leave away, after that, MA + Rs leave R_1(Fig. 3-B). The tracheae of Cu and A are from same clade and then detached into two (Cu and A) for a long distance (Fig. 3-B).

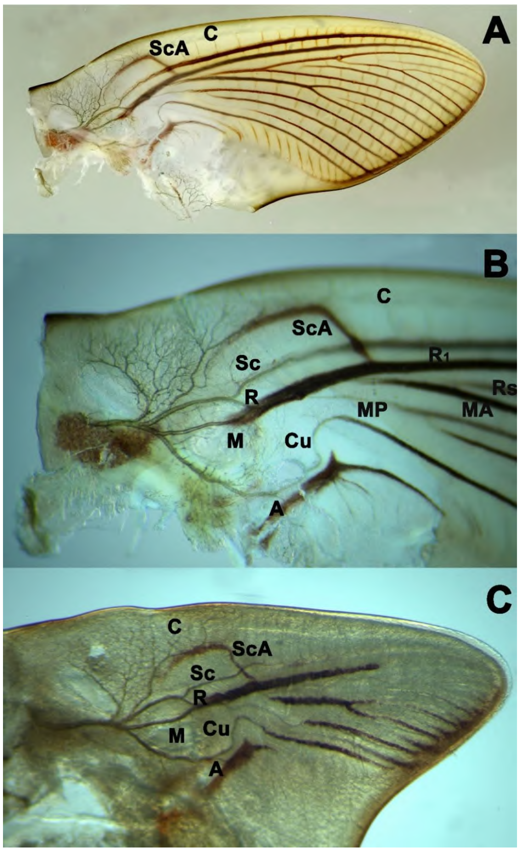

Fig. 2 Tracheal system and venation of *Siphluriscus chinensis* nymph

Note: A, Forewing pad; B, Enlarged base of forewing pad; C, Hindwing pad.

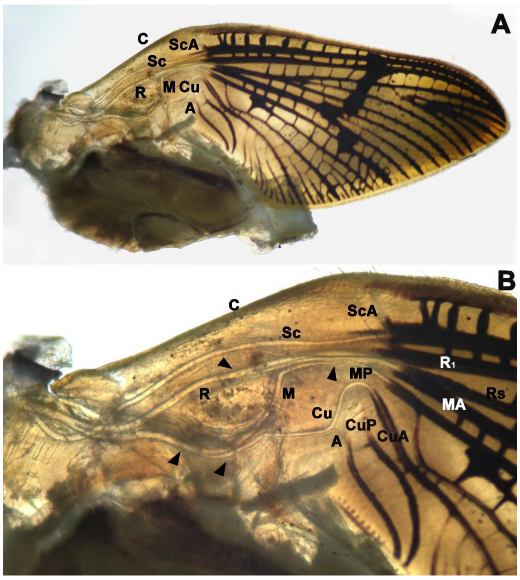

Fig. 3 Tracheal system and venation of *Ephemera pictipennis* nymph

Note: A, Forewing pad; B, Enlarged base of forewing pad (black arrows indicating the forking points of the R, M, M+Cu and Cu+A).

3.3 *Siphlonurus davidi*

In the imaginal hindwing of this species, the stem of Rs and MA run along with R_1 for some distance (Fig. 4).

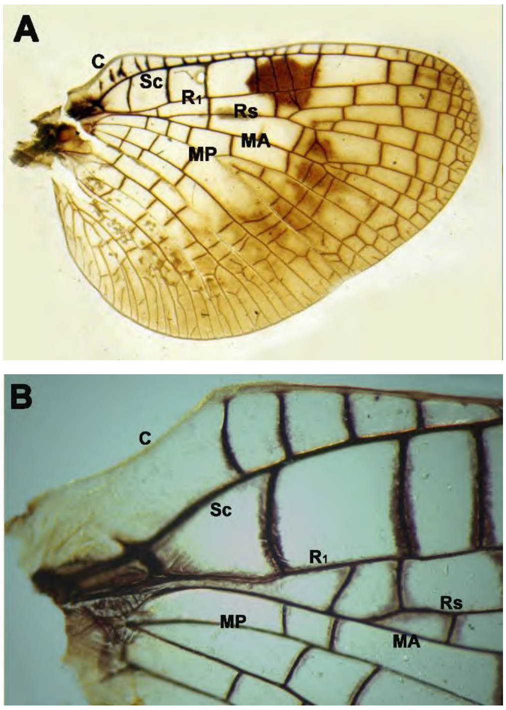

Fig. 4 Hindwing venation of *Siphlonurus davidi*

Note: A, Hindwing; B, Enlarged base of hindwing.

3.4 Characteristics of mayfly wingbase and venation

Based on above pictures and information in Zhou (2007), the main characteristics of mayfly wingbase and venation are: (1) in Ephemeroptera, all tracheae of wing from one common stem (Figs 2–3). This point has been noticed by Chapman (1918), Needham *et al.* (1935) and Written (1962).

(2) From ScA to Cu, each longitudinal vein divided into two clades, the anterior convex one and posterior concave one. This point supports the theory of insect wing and venation proposed by Kukalová–Peck (1991).

(3) In mayflies, R always fused with M at beginning (Figs 1–3). Before (Figs 3–A–B) or after their fusion (Figs 2–A–B), they divided into two clades respectively. Then MP leave, after that, Rs+MA leave the main R_1. Those information can be seen in Figs 2–3.

(4) In real mayfly, the Cu is always independent, without any connection to any other veins at base (Figs 1–3).

(5) The mayflies do not have movable sclerites or plates at the base of R+M, instead, they has a big plate at base (Fig. 1), which is the thickened oval area of nymphal wingpad (Figs 2–3). Additionally, almost whole base formed into one big plate (Fig. 1).

4 Discussion

In the light of this study, some fossil mayflies should be rechecked to see whether they are mayflies or not, such as *Protereisma* (Kukalová-Peck, 1997, 2009). It has connection between Cu and M but unfused M to R, while the fused R+M is the typical character of modern mayflies (Figs 1–3). In the theory presented here, those fossil insects are not real mayfly, at most the protype or ancestor of mayflies.

In Neoptera, the M fused with R, and there are three axillaries at wingbase (Kukalová-Peck, 1991). In Odonata, there are no axillaries there and M fused with Cu (Riek and Kukalová-Peck, 1984). Based on veins and wingbase of mayflies presented above, the taxon Paleoptera (mayflies + dragonflies) does not exist because the mayflies have fused R+M (Figs 1–3), just like the Neoptera but in contrast to Odonata.

In terms of sclerites of winged insects, in Neoptera, there are three axillaries and two median plates (Kukalová-Peck, 1991). In Odonata, there are three big plates (Riek and Kukalová-Peck, 1984). In Ephemeroptera, we can see each longitudinal vein has a sclerite at their base, especially that of R+M (Fig. 1). But all of them are fused together because of sclerotized base of wing (Fig. 1). That means almost whole wingbase, at least from R+M to A, of mayfly form a single one sclerotized plate, this prevents the folding of wings. Furthermore, Kluge (1994, 2004) presented that there are three axillary sclerites at the mayfly wingbase but there is not median plate. The latter point further avoids any possibility of wing folding. In short, although the basic structure or pattern of mayfly wingbase of mayfly is similar to those of Neoptera, they are different in median plate and flexibility of wing. In Odonata, however, there are no median plate nor axillary sclerites.

In addition, if we compare two different wings of mayflies, we can see their wingbase and vein pattern are quite different. In *Siphluriscus* or superfamily Siphlonuroidea (Figs 1, 2), the distance between C and ScA is relatively larger than *Ephemera* (Fig. 3) but its Cu is closer to posterior margin of wings than *Ephemera*. This kind of orientation lead to different venations and clades of mayflies. In Siphlonuroidea, such as *Siphluriscus* (Figs 1, 2–A), it has independent ScA but narrow Cu area. In contrast, in Ephemeridae (Fig. 3–A), the Cu is close to R+M at base, leaving a relatively larger space between Cu to hind margin of wing. So they need curved MP_2 and Cu, and larger Cu area and more intercalaries to support the wing. In short, the different wingbases or running patterns of veins contribute to different evolutionary clades of mayflies.

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