

WING VENATION PATTERN OF PLECOPTERA (INSECTA: NEOPTERA)

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ABSTRACT

Some consider the order Plecoptera as the sister-group of all neopterous insects. Hence the interpretation of Plecoptera wing venation has critical implications for character polarization among basal neopterous taxa, *i.e.* polyneopterous insects, and especially for fossil taxa, mainly known after isolated wings. However, no consensus ever emerged from the previous interpretations, partly contradicting. This study provides a detailed morphological comparative study of the wing venation of the order Plecoptera, based on modern taxa. It reveals that 1) the arculus is not a posterior branch of the media but a secondarily strengthened cross-vein, always present in hind wings and very generally in forewings; 2) the media is primitively two-branched in both wing pairs; 3) in hind wings the stems of the radius and the media are basally distinct, but a fusion of the posterior radius (RP) with the media (M) occurs distal to the wing base, both branches diverging further; and 4) the vannus is composed of branches belonging to the anterior analis sector (AA) only (*i.e.* the analis posterior and jugal areas are lacking). A new nomenclature is proposed for describing the branches of AA2. Character states presence of an arculus in both fore- and hind wings, media two-branched, and in hind wings, presence of fusion of RP with M are diagnostic of the order, based on outgroup comparison with other polyneopterous insects. Similarities are noticed between most basal Archaeorthoptera (*i.e.* insects close related to Orthoptera) and Plecoptera concerning the organization of the anal area, although an AP area is retained in the former and absent in the latter. Additionally, wing characters susceptible of being informative for the resolution of the inner phylogeny of the Plecoptera are proposed throughout the paper.

Keywords: Polyneoptera, order, arculus, trachea, anal fan

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INTRODUCTION

Wing venation characters have long been used in systematics of winged insects, from specific to supra-ordinal ranks. Although they are presumably insufficient to provide a reliable phylogenetic signal by themselves (Grimaldi 2001), some complex characters of the wing venation of fossil orders related to Orthoptera and Odonata turned out to be highly discriminative (Béthoux & Nel 2002; Béthoux et al. 2004; Huguet et al. 2002). Characters of wing venation have the significant advantage of being applicable on fossil taxa, mostly recorded after isolated wings. However, the use of these characters in large scale insect phylogenies is premature, because the homologization of each insect order wing venation is a matter of debate yet.

The position of the order Plecoptera within insect phylogeny is critical: it might be sister-group related with all other polyneopterous orders, or even to all

other neopterous orders (all extant orders except mayflies and dragonflies; Kristensen 1991; Hennig 1981; Zwick 1980; but see Grimaldi & Engel 2005; Wheeler et al. 2001a, b). It is unfortunate that, despite its phylogenetic importance, no consensus has been achieved about the homologization and diagnostic characters of the wing venation of the order (Hennig 1981; Needham & Claassen 1925; Sharov 1962a, translated in Sharov 1991; Theischinger 1991; Tillyard 1923; Zwick 2000). As a result, the assignment of some Paleozoic protorthopterous taxa, *i.e.* a group including possible ancestors of polyneopterous orders, is difficult to assess. It directly impacts our understanding of Paleozoic insect evolution, because monophyletic extinct groups are, in some cases, difficult to define with certainty.

Here I provide a comparative study of the wing venation of the Plecoptera, and propose venational traits of the order. The fossil record of the Plecoptera

s. stricto is particularly incomplete, especially in Paleozoic: the oldest stonefly is recorded from Lower Permian (Kungurian; Sinitshenkova 2002), while the putative sister-groups of the order (e.g. *Blattaria sensu* Grimaldi 2001, *Archaeorthoptera* Béthoux & Nel 2002, *Grylloblattida sensu* Storozhenko 2002) are recorded 80 millions years earlier. Therefore, the morphology of the earliest stoneflies is unknown. Moreover most of Paleozoic fossil stoneflies are very incomplete. Hence, I based my review solely on modern material.

MATERIAL AND METHODS

Preparation of the specimens

Wings were removed from specimen preserved in alcohol by piercing the body cuticle surrounding the wing base, gently pull the wing apart from the body, and then cut the muscles and cuticle still attached to the sclerite. Then isolated wings were mounted in Euparal medium. Unfolding the vannus can be difficult when wings are placed in Euparal on their ventral side. It was made possible in delicately stretching the vannus with a mounting needle slipped between the remigium and the vannus, along the claval furrow (*sensu* Wootton 1979) and other folds of the vannus, in dragging the vannus by moving the remigium within the medium, and/or in applying gentle pressure on the wing base. In order to realize this operation in an easier way, wings were also mounted on their dorsal side. This alternative mounting allows us to observe ventral sides with better optical conditions. Eventually, mounting forewings on their dorsal side is more capable of preserving the dorsal cambering of wings at rest (the cambering of forewings mounted on their ventral side is usually altered, probably matching their cambering during upstroke). The preparation was completed with a cover glass, carefully pressed down on the wings, in order to expand them as much as possible.

The specimen figured on Fig. 22 was a particular case. It was made available for dissection and study by the Monte L. Bean Museum of Life Sciences, Brigham Young University (Provo, Utah; loan and dissection approval by R. Baumann). After a preliminary observation, it turned out that, in the postero-basal area of the left hind wing, the two

epidermic layers constituting the wing were not fused. The specimen was probably captured and killed very early after emergence, before complete fusion of the layers. In order to facilitate the separation of the two layers, the apical and basal areas of the wing were cut apart. The posterior wing margin was also removed. Then the layers were tentatively separated. They were fully fused in the anterior part and could not be separated without damage to the layers. Hence the layers were mounted folded apart in Euparal, still joined by the anterior part of the wing. The wing apex and base were mounted next to the dissected area. The upper layer is disrupted along M, and the lower layer is disrupted across the imprint of two anal veins.

Observation and photographs of wings

Wings were observed with a stereomicroscope Leica MZ16. Photographs were made with an Optronics MicroFire digital camera mounted on the stereomicroscope. Digital images were processed with the MicroFire user interface and Adobe Photoshop software. Drawings were made using a drawing tube (camera lucida) mounted on the stereomicroscope, then scanned.

Light settings turned out to be of critical importance for observation and illustration of finite details of the wing venation. Various combinations of transmitted light from standing base and/or optic fibers light sources were experienced and used for different purposes. Slides were placed on supports in order to set appropriate razing light. A peculiar lighting was obtained with the optic fibers light source placed almost parallel to the slide (itself placed on supports), and right above the observed area. With this setting, the light source is actually made of an elliptical projection of the top of the optic fiber, passing vertically throughout the slide, and reflected on the glass of the standing base. The photographs presented on Fig. 18 were obtained with this peculiar light setting. However, these hand-made settings turned out to be hardly reproducible.

Generalized insect wing venation pattern

Main vein and cross-vein definitions

Although widely used in entomological literature, the structure labeled vein, applied to wings, is not

easily defined unambiguously. Of course, cross-vein definition largely relies on that of main-vein. There is a substantial amount of literature on this subject and a review is out of the scope of this paper. The reader could refer to the reviews of Carpenter (1966), Hamilton (1972), Kukalová-Peck (1978), and Wootton (1979).

There are several methods for discriminating a main-vein from a cross-vein. All rely on the assumption that a set of longitudinal main veins, formed after, and following the course of blood lacunae and/or tracheae, is the *primary* constituent of the wing venation in insects. Cross-venation is a secondary structure with respect to main veins.

The tracheal approach relies on the course of the tracheae in nymphal and adult insect wings. This is the pretracheation theory of Comstock & Needham (1898a, b, c, d, e, f, g, h, 1899a, b, c), summarized in Comstock (1918), which implies that the location of the tracheae precedes and determines the course of the blood lacunae. This opinion has been largely criticized. However, the axiom "the principal veins are formed along the course of the tracheae, while in most cases the cross-veins have no tracheae within them" (Comstock & Needham 1898a: 47), or, more appropriately, "all main longitudinal veins were originally provided with tracheae" (Leston 1962: 140), might be true. However, because tracheae cannot be distinguished in fossils there is little chance that this axiom could ever be tested. Another method relies on the relief of the structure. One can distinguish secondarily acquired structures if their relief is opposite to that of the surrounding main-veins. For example the convex veins occurring between the branches of concave main veins, as in various orders (*e.g.* Orthoptera, †Palaeodictyoptera, Odonata, Ephemeroptera), are made of aligned cross-veins. Lastly, the topological approach determines that a structure does not belong to the main-veins system if, in regard of a hypothetical archetypical main-vein pattern, the structure is supernumerary. The obvious problem with the two last approaches is the determination of the archetypical pattern. However, correct results could be expected at an infra-ordinal rank, assuming a comprehensive set of taxa and a robust phylogenetic frame. As suggested by Hamilton (1972), all methods should be used

jointly. In the following, vein will refer to main-veins structures only.

Nomenclature

In the following I use a generalized insect wing venation pattern implying that (1) at least the veins C (Costa), Sc (Subcosta), R (Radius), M (Media), Cu (Cubitus), A (Analis), and J (Juga) are primitively present in winged insects; (2) the first fork of each main vein separates two sectors, an anterior one labeled A, and a posterior one labeled P, (3) anterior sectors are convex, *i.e.* located on ridges, and on the upper layer of the wing, and posterior sectors are concave, *i.e.* located in depressions, and on the lower layer of the wing. Herein the term system encompasses the stem vein and its two main branches (sectors). Basically, this proposal is in accordance with numerous previous authors (Carpenter 1966, 1992; Labandeira et al. 1988; Lameere 1917; Wootton 1979; among others). It is also in accordance with Kukalová-Peck (1991: fig. 6.3C) except on the following points: (1) because photographic evidence of the existence of a precostal vein (PC) in the literature is missing, I consider the occurrence of this vein hypothetical; (2) I consider that the hypothesis of primitively distinct origins of main vein sectors (*i.e.* main veins not stemmed) needs further demonstrative evidence.

Some paleontologists use this nomenclature unaltered but most neontologists and some paleontologists prefer the label R₁ rather than RA, and Rs rather than RP. The labels RA and RP refer to the serial homology between the main veins sectors, which is very generally admitted (Carpenter 1992; Kukalová-Peck 1991; Laurentiaux 1953; Séguéy 1959; Wootton 1979; among others). Therefore, these abbreviations are more proper to describe the radial system relative to other vein systems and should be preferred.

Although the label Sc was previously understood as a sector of the vein C (see Wootton 1979), Kukalová-Peck (1991) erected it as a vein name, incidentally using sector labels ScA and ScP. Although this is an incorrect use of previous labels, this nomenclature has been used unchanged by several authors (including the author of this paper). Providing a corrected version would only improve

the confusion of the current situation. I recommend preferring the label ScP rather than Sc when referring to the concave vein anterior to RA. The label ScA should be preferred (rather than C) when referring to the convex vein anterior to ScP (ScA is well identifiable in several orders, e.g. Orthoptera, †Palaeodictyoptera). Evidence of a costal system *sensu* Kukalová-Peck (1991) is present in Orthoptera (family †Elcanidae), with a concave vein anterior to ScA, justifying the label CP. The presence of a CA sector distinct from the anterior wing margin has yet to be described after more demonstrative evidence, with reference to actual specimens. Possibly, CA has never been a free sector but the primary constituent of the anterior wing margin.

Béthoux & Nel (2003a: fig. 4) described a convex sector, posterior to AP, in forewings of Palaeozoic Permothemistidae (Palaeoptera). It has been interpreted as a part of the jugal system, therefore labeled JA. Some Palaeozoic Palaeodictyoptera also possess a JA sector in forewings (unpubl. data). It gives support to the opinion that a jugal system is primitively present in insect wings, although the presence of a posterior sector of the Jugal (JP), distinct from the wing margin, has never been properly illustrated and identified on the basis of a clear concavity. A JP sector could have never been free, but the primary constituent of the posterior wing margin.

The following abbreviations will be used: ScP, posterior Subcosta; RA, anterior Radius; RP, posterior Radius; M, Media; CuA, anterior Cubitus; CuP, posterior Cubitus; AA, anterior Anal; AP, posterior Anal; J, jugal area. Abbreviations referring to strengthened cross-vein follow Needham & Claassen (1925), with lower case letters referring to the veins involved, e.g. rp-m is the cross-vein located between RP and M (or its anterior branch). The m-cua cross-vein is named arculus. Basically, these settings are in accordance with Kukalová-Peck & Lawrence (2004).

One can notice that another insect wing venation pattern is currently in use in Belayeva et al. (2002) (used in Tillyard 1923, abandoned in Tillyard 1935), referred to as M₅ pattern. Its pertinence has been discussed and it was discarded elsewhere (Béthoux et al. 2005; Kukalová-Peck 1991). A detail of stonefly

wing venation provides additional clues of its irrelevance. The M₅ pattern implies a concave CuA “unless and until CuA merges with M₅” (Rasnitsyn 2002b: 76). However, in stoneflies, the basal stem of Cu, easily recognizable and independent from the basal stem of M, gives rise to an anterior branch CuA that is *convex from its origin, before any connection with another structure* (e.g. the arculus, interpretable as the convex M₅ under the so-named pattern).

Species sample

The wing venation of the following species has been examined after actual specimens. Specimens illustrated herein belong to my personal collection, essentially made of gifts from various collections (see below). Although not exhaustive, my study covers most of the winged families of Plecoptera. Literature data provided valuable additional information. In the following, NZAC refers to the New Zealand Arthropod Collection (Auckland, New Zealand), CSUC refers to Colorado State University Collection (Fort Collins, CO, USA), BYUUC refers to the Brigham Young University Collection (Provo, UT, USA), YPMC to the Yale Peabody Museum Collection (New Haven, CT, USA), and MCC refers to Mississippi College Collection (Clinton, MS, USA).

Antarctoperlaria:

Autroperlidae: *Austroperla cyrene* (Newman, 1845) (Figs. 1, 14-17) (provided and identified by I. McLellan, 2004; and NZAC).

Eustheniidae: *Stenoperla prasina* (Newman, 1845) (Figs. 2, 18) (provided and identified by I. McLellan, 2004; and NZAC); *Stenoperla maclellani* Zwick, 1979 (NZAC; T. K. Crosby; identified by P. J. Leaf, 1974).

Gripopterygidae*: *Zelandobius macburneyi* McLellan, 1993 (Fig. 3); *Zelandobius uniramus* McLellan, 1993; *Taraperla ancilis* (Harding, 1995) (Fig. 4) (all provided and identified by I. McLellan, 2004).

Arctoperlaria: Euholognatha

Taeniopterygidae: *Taeniopteryx burksi* Ricker, 1968 (Fig. 5) (provided and identified by B. Kondratieff, 2004; CSUC).

Leuctridae: *Megaleuctra kincaidi* Frison, 1942 (Fig. 6) (provided and determined by B. Kondratieff,

2004; CSUC); *Leuctra major* Brinck, 1949; *Leuctra braueri* Kempny, 1898 (Fig. 7); *Leuctra nigra* (Olivier, 1811); *Leuctra digitata*, Kempny, 1899; (all *Leuctra* species provided and identified by P. Zwick, 2004).

Nemouridae: *Malenka coloradensis* Banks 1897; *Amphinemura banksi* Baumann & Gaufin, 1972 (Fig. 22); *Protonemura auberti* Illies, 1954 (all Nemouridae, loan BYUC; identification by R. W. Baumann)

Arctoperlaria: Systellognatha

Pteronarcyidae: *Pteronarcys californica* Newport, 1851 (Figs. 8, 19, 23-26) (provided and determined by B. Kondratieff, 2004); *Pteronarcys proteus* (YPMC), *Pteronarcys biloba* (YPMC); *Pteronarcella badia* (loan BYUC; identification by R. W. Baumann).

Peltoperlidae: *Yoraperla nigrisoma* (Banks, 1948) (Fig. 9); *Tallaperla maria* (Needham, 1916) (Figs. 27-30) (all provided and identified by B. Kondratieff, 2004; CSUC).

Perlidae: *Hesperoperla pacifica* (Banks, 1900) (Figs. 31-34); *Acroneuria abnormis* (Newman, 1838) (Figs. 13, 35-36); *Calineuria californica* (Banks, 1905) (all identified and determined by B. Kondratieff, 2004; CSUC); *Anacroneuria litura* (Pictet, 1841) (Fig. 11) (provided and identified by B. Stark, 2004; MCC); *Claassenia sabulosa* (Banks, 1900) (loan BYUC; identification by R. W. Baumann).

Perlodidae: *Isopterla phalerata* Smith, 1917 (Fig. 12); *Setoena bradleyi* (Smith, 1917) (all provided and identified by B. Kondratieff, 2004; CSUC).

Chloroperlidae: *Kathroperla perdita* Banks, 1920 (provided and identified by B. Kondratieff, 2004; CSUC).

Phylogenetic frame

A reference to the inner phylogeny of the order Plecoptera was needed for assessing the polarity of characters states. I mainly based my discussion on Zwick (2000) who recognizes three major clades, Antarctoperlaria, Euholognatha, and Systellognatha, from morphological evidence. This proposal received partial support by Terry & Whiting (2004), based on the most comprehensive phylogenetic analysis of the Plecoptera, using both molecular and morphological data, and a large taxon sample. The familial

composition of the three main clades is consistent with Zwick's proposal. Nevertheless, the inner phylogenies of the three major clades are partly contradictory. I disagree with the position of the genus *Megaleuctra*, placed as sister group of the remaining Plecoptera by Terry & Whiting (2004), and follow Zwick who places it within the Euholognatha (in the Leuctroidea). Wing venation characters support Zwick's opinion: in both wing pairs of *Megaleuctra*, ScP approaches the anterior wing margin, before abruptly reaching RA (as in the genus *Leuctra*, at least; unknown in Antarctoperlaria and Systellognatha); in hind wings of *Megaleuctra*, RP and M diverge at the level of the arculus (as in the genus *Leuctra*, at least; unknown in Antarctoperlaria and Systellognatha). Terry & Whiting (2004) found the family Gripopterygidae paraphyletic with respect to the remaining Antarctoperlaria. I will refer to this assemblage as Gripopterygidae*, implying that the monophyly of this taxon is uncertain. However, I provide additional characters in favor of a monophyletic Gripopterygidae.

MORPHOLOGICAL COMPARATIVE STUDY

Various interpretations of the Plecoptera wing venation (Table 1) differ in the interpretation of few structures. Discussing these central issues will allow me to complete the homologization of the wing venation of the order (Figs. 1-12). The less controversial or unresolved issues will be addressed later in the discussion.

The arculus

Hypotheses

Determining the actual nature of the arculus, a structure situated in the area between M and CuA, usually present in both fore- and hind wings in stoneflies, is a debated issue. It is unarguably the most critical point in any attempt to homologize stonefly wing venation pattern with respect to that of winged insects. The arculus could be defined as the first sclerotized structure occurring in the area between M and CuA. Sharov (1962a), Theischinger (1991), and Carpenter (1992), among other authors, interpreted it as the posterior sector of the median vein (*i.e.* MP; Table 1). Nevertheless this arculus is

Table 1. Correspondences between the pattern of Plecoptera wing venation proposed in the present work and those by relevant previous authors. See text for abbreviations and references.

Present work				Tillyard, 1923				Needham and Claassen, 1925 (Fig. 1)				Sharov, 1962 Carpenter, 1992			
Forewing		Hind wing		Forewing		Hind wing		Forewing		Hind wing		Forewing			
ScP		ScP		Sc		Sc		Sc		Sc		Sc			
R	RA	R	RA	R	R ₁	R+	R ₁			R	R ₁	R+M	R ₁	R	
	RP		RP		RP		Rs (R ₂₋₅)	Rs	Rs+M		RS				
M		M	RP+M	M	M ₁₋₄	M	Rs+M	M ₁₋₄	M ₁₋₄	M ₁₊₂	M	M	M ₁₊₂	MA	
					M ₃₊₄					M ₃₊₄			M ₃₊₄		
arculus		arculus			M ₅ (M ₅ +)		(M ₅ +) Cu ₁			arculus		arculus		MP	
Cu	CuA	Cu	CuA	Cu	Cu ₁	Cu	Cu ₁				Cu	Cu ₁	Cu	Cu ₁	MP+CuA
	CuP		CuP		Cu ₂		Cu ₂	Cu ₂	Cu ₂	Cu ₂	CuP				
AA	AA1		AA	AA1		A	1A		A	1A		A	1stA		A ₁ / 1A
				2A			2A			2dA			2dA		A ₂ / 2A
	αAA2									3dA			3dA		
	βAA2			χAA2									4thA		
	γAA2														
δAA2												5thA			

Table 1 (continued).

Present work					Theischinger, 1991 (Fig. 18.5)					Haas and Kukalová-Peck, 2001 (Fig.14)			Kukalová-Peck and Lawrence, 2004 (Fig. 2)				
Forewing		Hind wing			Forewing		Hind wing			Forewing			Hind wing				
ScP		ScP			Sc		Sc			ScP			ScP				
R	RA	R	RA		R	R ₁	R ₁			R	RA		R	RA			
	RP		RP	RP		RP	RP	RP	RP								
M		M	RP+M	M	M	MA		R _S +M	M	MA	MA	M	RP+M	M	M	RP+M	M
arculus		arculus				MP	MP+CuA		MP	MP+CuA	m-cua (arculus)			m-cua (arculus)			
Cu	CuA	Cu	CuA		Cu	CuA	Cu	CuA	Cu	CuA	MP+CuA	Cu	CuA	Cu	CuA	Cu	CuA
	CuP		CuP			CuP		CuP		CuP	CuP		CuP		CuP		
AA	AA1		AA	AA1		1A		1A			A	AA	AA1		AA1+2		
	AA2	AA2			2A			2A		AA2			AA3+4				
					3A (?)			3A (?)		AA3			AP (?)				
					J			J		AA4			J				
										AP							
											JA						
									JP								

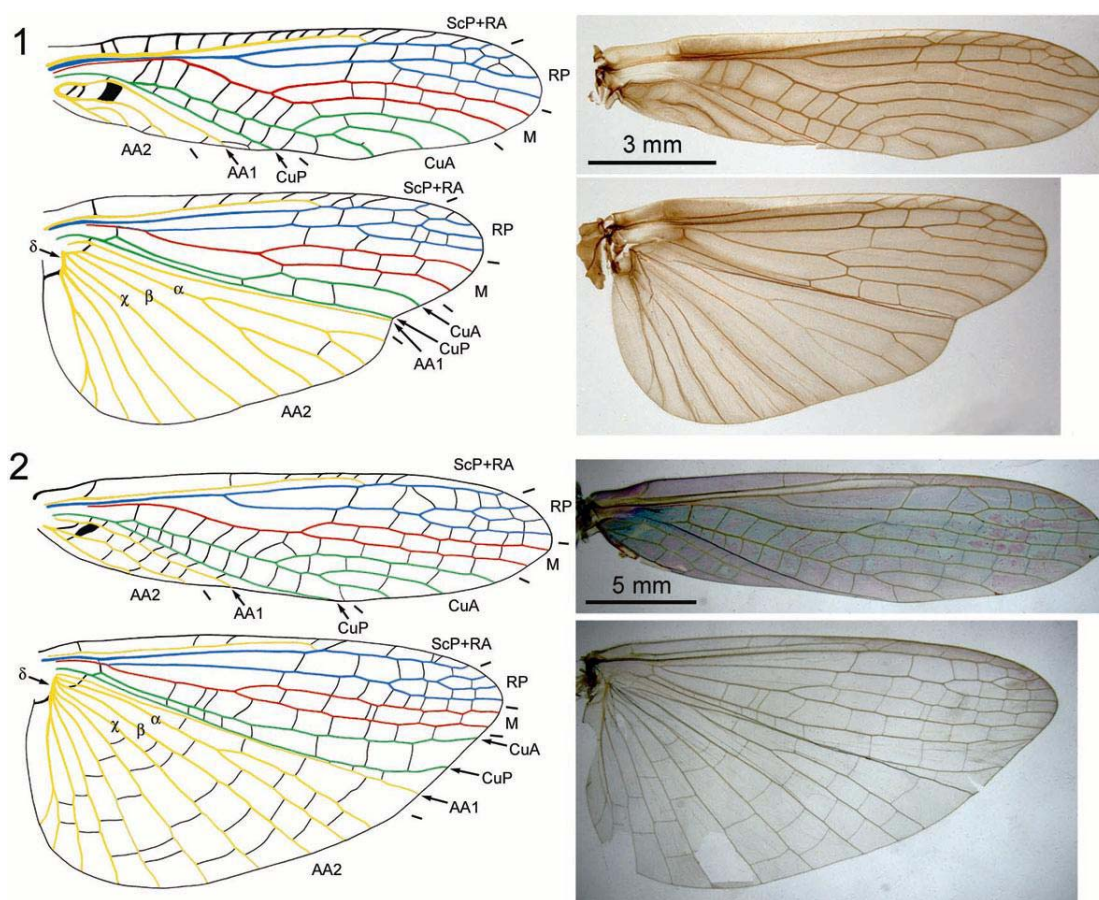
not concave, as should be MP, but convex. This is a strong argument for discarding this interpretation. Additionally, the angle that makes the arcus with

M never suggests that it is an actual branch of M. From M, the arcus is *always* oriented towards the wing base (as are oriented other cross-veins in the

area between M and CuA), although a true vein, at least in some basal taxa, would be oriented towards the apex.

Another homologization of this arculus as part of CuA, consistent with the convexity of this structure, is defensible. Carpenter (1966), while describing species belonging to the extinct family Blattinopsidae Bolton, 1925, probably related to the Blattaria *sensu* Grimaldi (2001), proposed a pattern with two basal

stems, M + CuA1 and CuA2. Later, CuA1 (possibly the arculus in Plecoptera) diverges from M + CuA1 and fuses with CuA2. Basal fusion of CuA (or one of its anterior branches) with M is present in several families of non-archaeorthopterid Protorthoptera (Béthoux et al. 2005; Storozhenko 1998) that might have plecopteroid affinities. Another opinion is provided by Kukalová-Peck (1991) who considers the arculus as a secondarily strengthened cross-vein.



Figs. 1-2. Wing venation in Antartoperlaria. Color-coding following Kukalová-Peck & Lawrence (2004): yellow for the Subcosta (Sc) system; blue for the Radius system (R); red for the Media system (M); green for the Cubitus (Cu) system; yellow for the Analis system (A). Abbreviations as follows: ScP, posterior Subcosta; RA, anterior Radius; M, Media; CuA, anterior cubitus; CuP, posterior cubitus; AA1, first anterior Analis; AA2, second anterior Analis; α , β , γ , and δ are labels newly proposed for the branches of AA2. **1.** *Austroperla cyrene* (Newman, 1845) (Austroperlidae), drawing and photographs of fore- and hind wing. **2.** *Stenoperla prasina* (Newman, 1845) (Eustheniidae), drawing and photographs of fore- and hind wing.

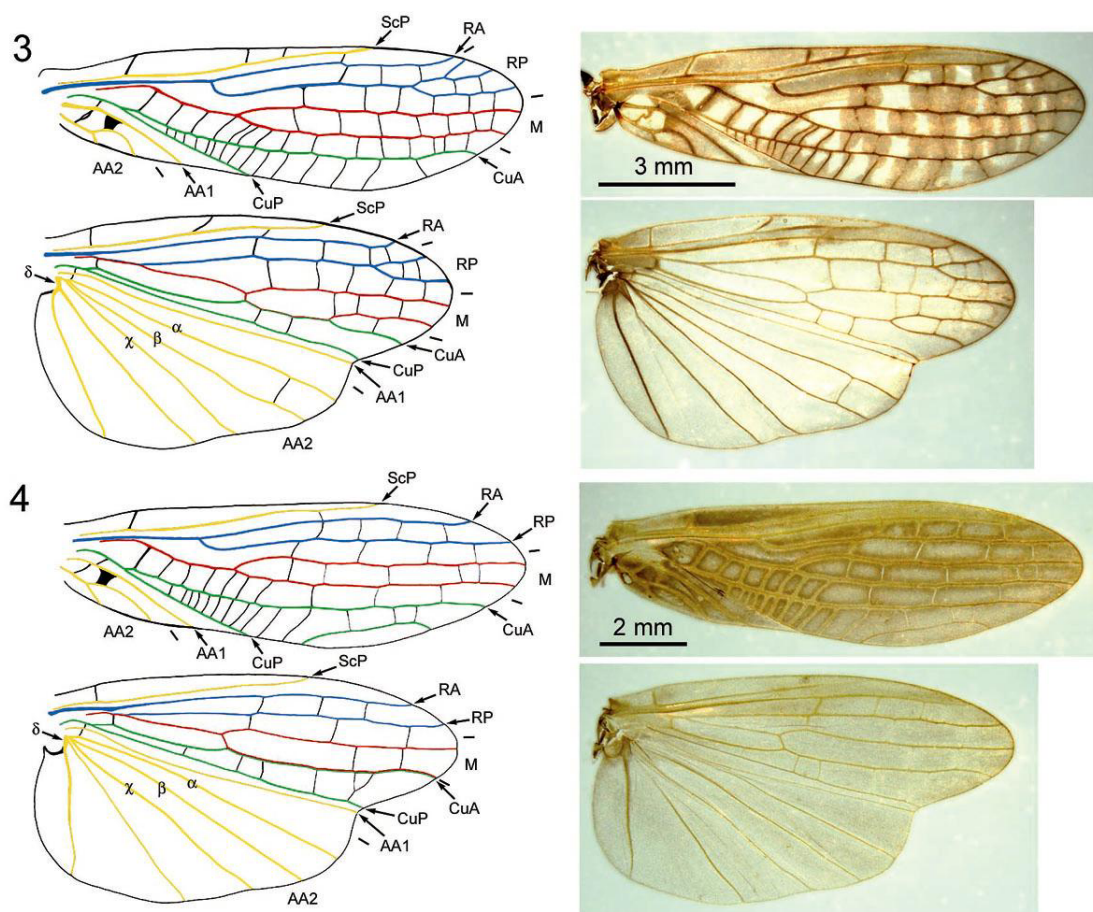
Trachea and blood lacunae

There is no trachea passing through the arculus in nymphs of *Nemoura*, *Taeniopteryx*, or *Pteronarcys* (Comstock & Needham 1898f; Holdworth 1940). I made observations on an adult specimen of *Acroneuria abnormis* (Newman, 1838) (Fig. 13) showing lacunae passing through the veins R, M, and CuA, I interpret as tracheae. There is no such trachea passing through the arculus. Hence the arculus has the same anatomy as surrounding cross-veins and differs from main veins.

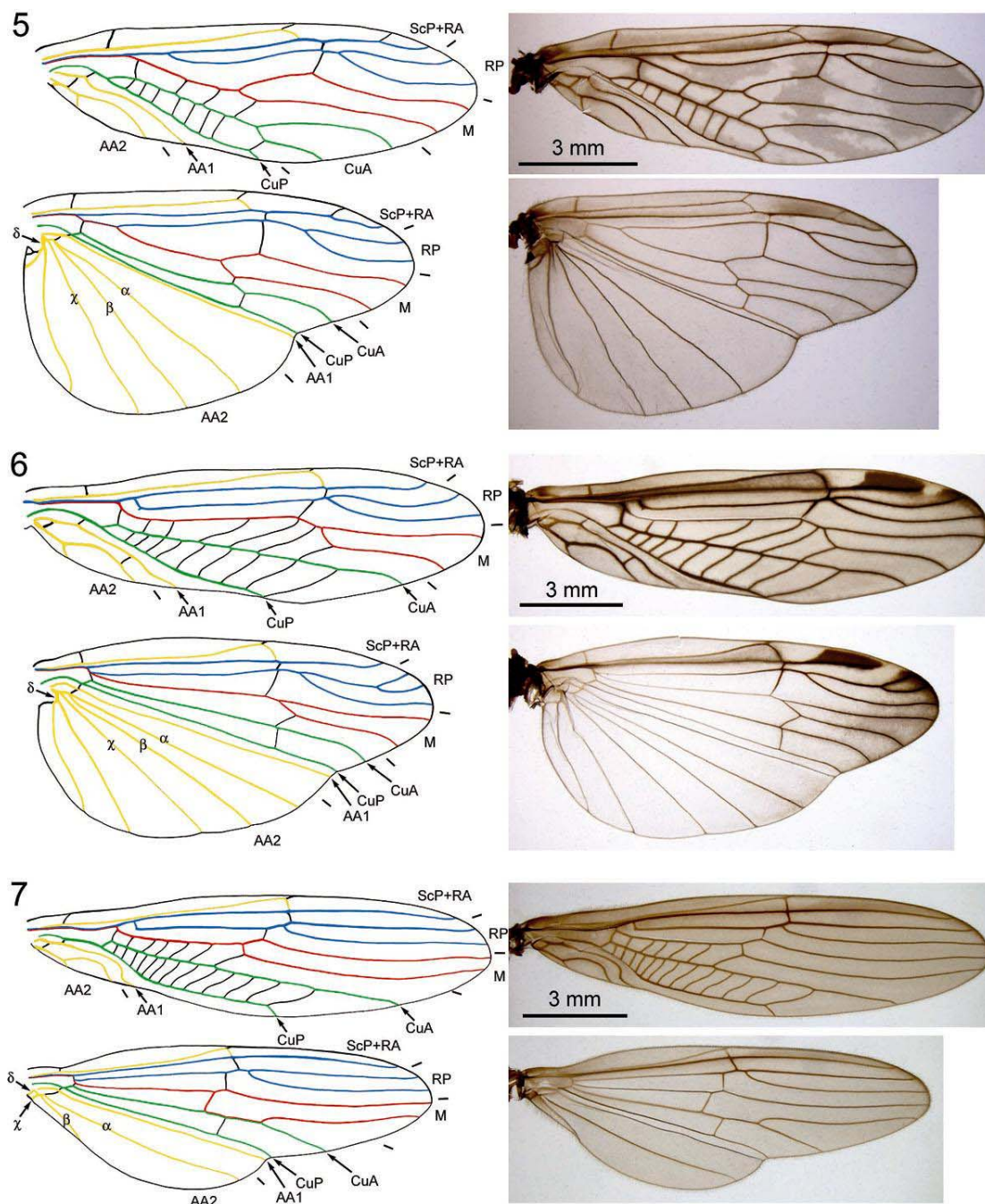
Morphology of the arculus in *Antarctoperlaria*

Although a well-differentiated arculus is generally present in wings of *Antarctoperlaria* (Figs. 2-4), it is not occurring in forewings of *Austroperla*

cyrene (Newmann, 1845) (Figs. 1, 14-17). In this species there is no strong strut between M and CuA but only identical cross-veins. If one considers that the first of these cross-veins is the arculus, the variability in its position and organization provides clues about its origin. The usual position of this structure is illustrated in Fig. 14, connecting CuA, just distal of its origin, with M, basal to the divergence of M from R (R and M are parallel but distinct). It is demonstrated in Fig. 15 that this structure is not a branch of CuA, because it arises before the origin of CuA from Cu. It is demonstrated in Figs. 16-17 that this structure can be forked, a feature that could be expected from a cross-vein-based structure. Such a fork is very unlikely to occur if the arculus would have originated from a



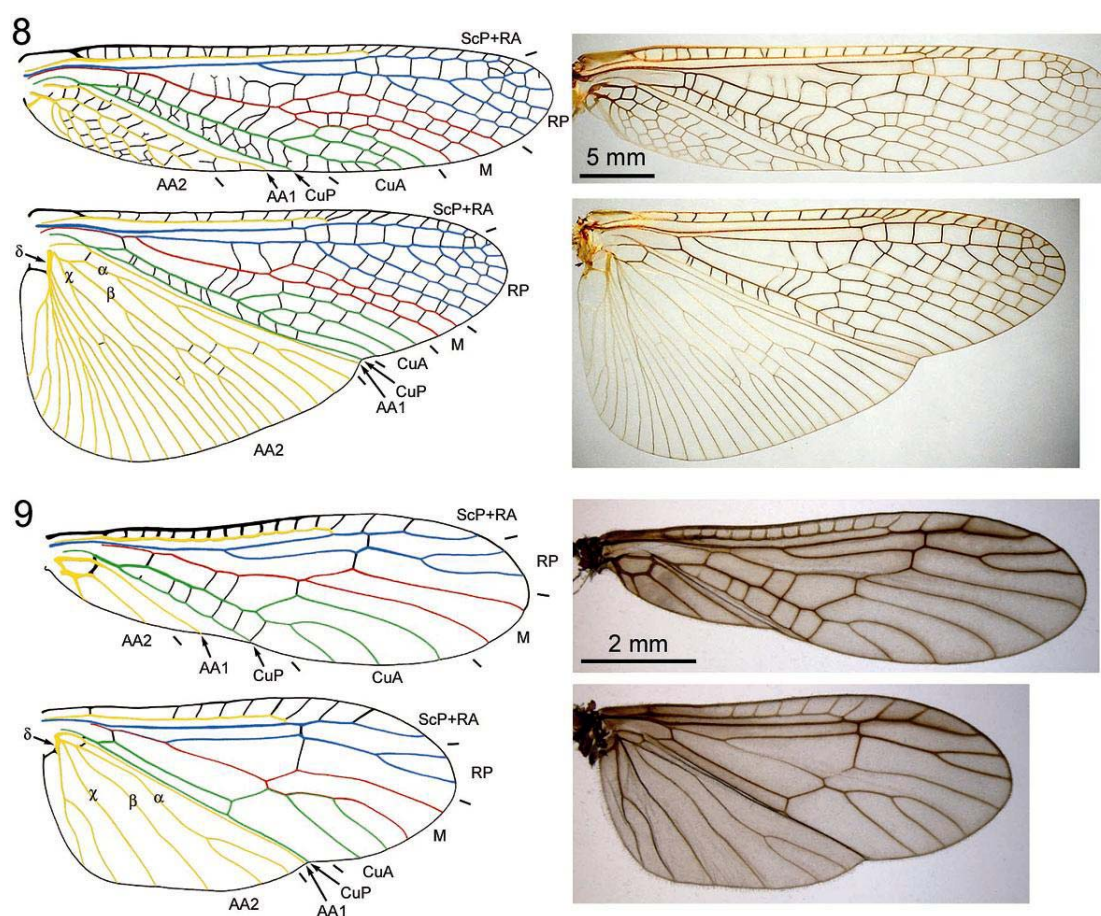
Figs. 3-4. Wing venation in *Antarctoperlaria*. Color pattern and abbreviations as in Fig. 1. **3.** *Zelandobius macburneyi* McLellan, 1993 (Gripoterygidae), drawing and photographs of fore- and hind wing. **4.** *Taraperla ancilis* (Harding, 1995) (Gripoterygidae), drawing and photographs of fore- and hind wing.



Figs. 5-7. Wing venation in Euholognatha. Color pattern and abbreviations as in Fig. 1. 7. *Taeniopteryx burksi* Ricker, 1968 (Taeniopterygidae), drawing and photographs of fore- and hind wing. 6. *Megaleuctra kincaidi* Frison, 1942 (Leuctridae), drawing and photographs of fore- and hind wing. 7. *Leuctra braueri* Kempny, 1898 (Leuctridae), drawing and photographs of fore- and hind wing.

main vein, especially in such a basal position, where main veins organization is more constrained than in the distal parts in insect wings (pers. obs.). The absence of a well-differentiated arculus in forewings is likely to be the case of several Austroperlidae, as suggested by illustrations provided by Illies (1969) and Mclellan (2001). In Eustheniidae, after observations made on specimens belonging to the genus *Stenoperla* McLachlan, 1866, and after

illustrations provided by Zwick (1979), the arculus is moderately stronger than other cross-veins and is sometimes only recognizable after the slight curvature of M and CuA at the point where these veins are connected to it. Interestingly, in some Gripopterygidae* (Figs. 3-4), from the base to the apex of the wing, cross-veins are progressively less sclerotized.



Figs. 8-9. Wing venation in Systellognatha. Color pattern and abbreviations as in Fig. 1. **8.** *Pteronarcys californica* Newport, 1851 (Pteronarcyidae), drawing and photographs of fore- and hind wing. **9.** *Yoraperla nigrisoma* (Banks, 1948) (Peltoperlidae), drawing and photographs of fore- and hind wings.

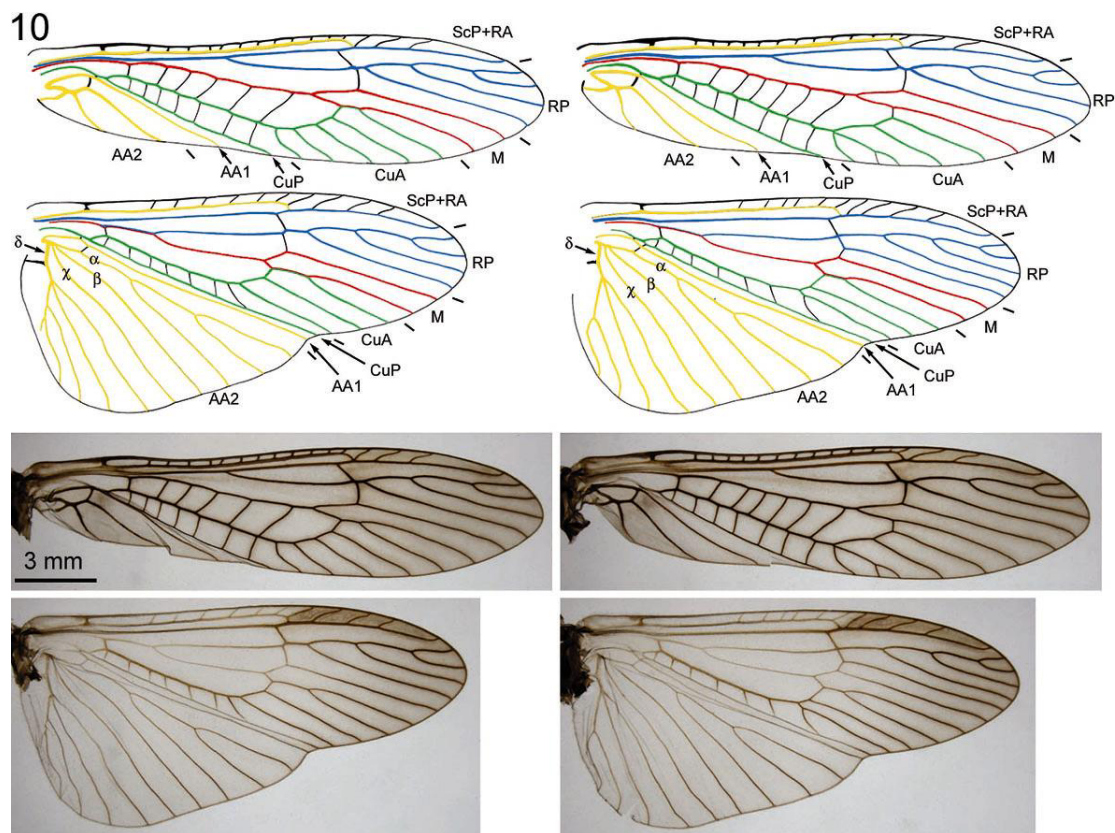


Fig. 10. Wing venation in Systellognatha. Color pattern and abbreviations as in Fig. 1. *Calineuria californica* (Banks, 1905) (Perlidae), drawing and photographs of left and right fore- and hind wings, same individual.

Morphology of the arculus in Euholognatha

A differentiated arculus is virtually present in all Euholognatha. However, in the forewing of one specimen of *Pteronarcys californica* (Pteronarcyidae; Fig. 8), I observed *two* arcules, which would be a very unlikely variation of a main vein. A similar variation was illustrated by Grimaldi & Engel (2005: fig. 7.7) in Pteronarcyidae, with a reticulated arculus. Such variations affecting a cross-vein-based structure are likely to occur in larger species such as *P. californica*, in which cross-veins are more numerous.

Morphology of the arculus in Systellognatha

Among other Systellognatha, *Anacroneuria litura* (Perlidae) (see Stark 1995, 1999 for other species in this genus; see also Stark & Lentz 1992 for the fossil genus *Dominiperla* Stark and Lentz, 1992) has no differentiated arculus in forewing. In virtually all stoneflies having an arculus in forewings, this

structure is precisely located near the origin of CuA and the point of divergence of M from R (R and M could be undistinguishable from each other in some cases), or at the point where the sclerotization of M starts (see species of the genera *Dinotoperla* Tillyard, 1921, *Trinotoperla* Tillyard, 1924, *Illiesoperla* McLellan, 1971; see McLellan 1971; Yule 1984). Interestingly, if cross-veins occur basal to this area, as in *Anacroneuria* (Fig. 11) or *Dominiperla*, there is no arculus. This suggests that the presence of a single strengthened structure near this location has some mechanical properties, and is likely to be a secondary acquisition. This assumption is supported by the convergent acquisition of a similar structure, in a similar location, and similarly cross-vein-based, in several fossil taxa unrelated to Plecoptera (e.g. †Blattinopsidae and †Strephocladidae, see Carpenter 1992; Blattodea: †Archimylacridae, see Schneider 1983).

Conclusion

All these arguments support the opinion of Kukalová-Peck (1991), *i.e.* the arculus is a secondarily strengthened cross-vein. An arculus is always present in hind wings of Plecoptera, that I also consider as a strengthened cross-vein (after an argument of serial homology between wing pairs).

The median system and its relation with the cubitus system

Neopterous insects do not possess a clearly convex MA (for a discussion on this issue see Hennig 1981: 163-165). Some possess a clearly concave sector interpreted as MP, as in Orthoptera and taxa attributed to the Grylloblattida *sensu* Storozhenko (2002). It is not the case of Plecoptera, in which branches of the median system (red vein in Figs. 1-12) show a homogenous neutral relief. Several previous authors interpreted the arculus as MP (see above), hence the remaining part of the median system as MA. But it is demonstrated above that the arculus is not a main vein but a cross-vein-based structure.

The absence of a convex / concave pair in the median system renders the homologization of its branches difficult. Moreover, the dissection presented in Fig. 22 suggests that no parts of the median system are present on the upper epidermic layer of the hind wing of *Amphinemura banksi* (Nemouridae). Hence there would be no MA at all in Plecoptera. Obviously, this fundamental issue needs further evidence. I will follow the conservative approach of Needham & Claassen (1925), naming the complete visible branches of the media M, without distinction of MA and MP (see also the first recommendation in Wootton 1979).

The median system has long been considered to have only two branches (Tillyard 1923). At least, authors who interpreted the arculus as MP considered that MA has only two branches (Sharov 1962a, translated in English in Sharov 1991). However, Grimaldi (2001) suggested that the fossil Permian family Lemmatophoridae Sellards, 1909 belongs to the plecopteroid lineage, partly based after the character M three-branched. Besides this important point, some peculiar veins fusions involving the median system in Plecoptera must be

discussed with details.

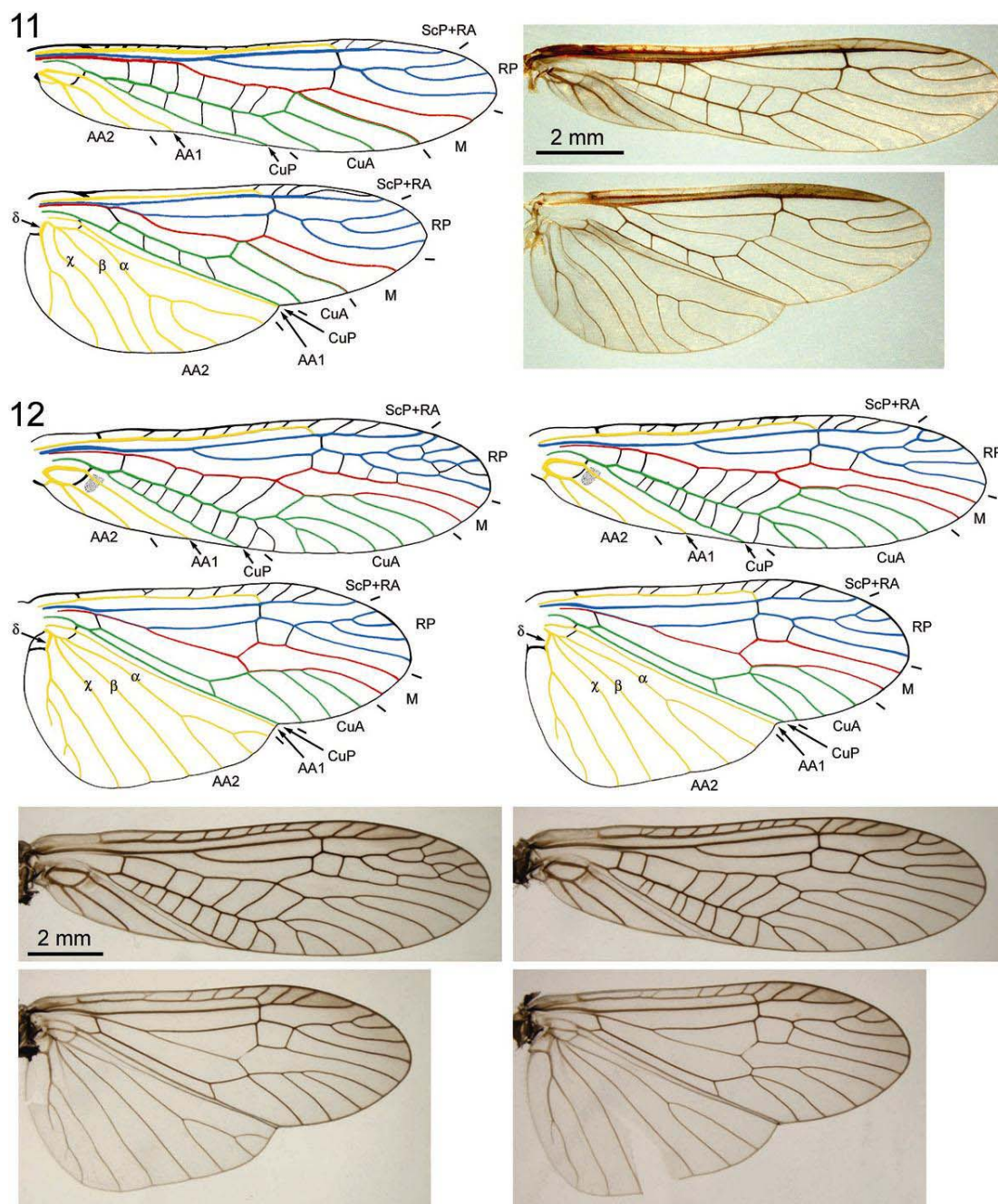
Median system in *Antarctoperlaria*

In virtually all *Antarctoperlaria*, in forewings, the median vein has two branches, always distinct from the cubital system (Figs. 1-4; Illies 1969; McLellan 1969, 1971, 1998, 1999, 2001; Theischinger 1991; Tillyard 1923, 1935; Yule 1984; Zwick 1979). It is also the case in the hind wings of the representatives of the families Austroperlidae, Eustheniidae and Diamphipnoidae.

McLellan (1971: 5) proposed that, in several genera of the Gripopterygidae* group, a partial (Fig. 3) or complete (Fig. 4) fusion of the posterior branch of M_{3+4} [M] with Cu_1 [CuA] occurs. Nevertheless, an alternative hypothesis can be proposed, with a median system simple in the whole Gripopterygidae* group, and with a CuA distally branched in some taxa (for example in *Zelandobius macburneyi*, Fig. 3). However, the median system is branched and CuA is simple in hind wings of all putative sister-groups of the Gripopterygidae (Eustheniidae, *Antarctoperlaria*, Diamphipnoidae) and in virtually all Gripopterygidae forewings, which makes this last hypothesis unlikely. I also favor McLellan's hypothesis because, in genera in which the posterior branch of M and CuA do not diverge distally (for example *Leptoperla* Newman, 1839, *Newmanoperla* McLellan, 1971, *Cardioperla* McLellan, 1971; *Taraperla ancilis*, see Fig. 4), the branching of M is yet easily identifiable: the free part of the posterior stem of M is usually stronger than surrounding cross-veins and the branching usually occurs at the same level as M branches in other *Antarctoperlaria* (basal to the first rp-m cross-vein). Further clues for McLellan's hypothesis might arise from the study of individual variations in species where the points of fusion and divergence of the posterior branch of M and CuA are close together (for example species of the genera *Trinotoperla* Tillyard, 1924, and *Illiesoperla* McLellan, 1971). However, under my opinion, McLellan's hypothesis is well grounded.

In conclusion, the median system has two branches in all members of *Antarctoperlaria*. Additionally, the presence of a fusion between the posterior branch of M and CuA is an apomorphic state character and support, in my opinion, a

monophyletic family Gripopterygidae.



Figs. 11-12. Wing venation in Systellognatha. Color pattern and abbreviations as in Fig. 1. **11.** *Anacroneuria litura* (Pictet 1841) (Perlidae), drawing and photographs of fore and hind wings. **12.** *Isoperla phalerata* (Smith, 1917) (Perlodidae), drawing and photographs of left and right fore- and hind wings, same individual.

Median system in Euholognatha

The morphology of the median system in Euholognatha is interesting to analyze under the light of that of Antarctoperlaria. It is virtually unquestionable that M is primitively two-branched in the Euholognatha (Figs. 5-7), but the presence of a unique cross-vein, distal to the branching of M, in the area between M and CuA, is confusing. It might be interpreted as an anterior branch of CuA fusing with M. Nevertheless, in one specimen of *Leuctra nigra* (Olivier, 1811) this structure is reticulated, a feature that is unlikely to occur with a main-vein-based structure. Moreover, as far as I am aware, there is not any example of a distal re-emergence of a putative branch of CuA from the posterior branch of M, in any forewing of Euholognatha.

In Leuctridae (see *Leuctra braueri*, Fig. 7) a fusion of the posterior branch of M with CuA occurs in hind wings. Following the phylogenetic framework of Terry & Whiting (2004), the family Leuctridae is sister-group related to the other Euholognatha, and a similar fusion occurs in the Gripopterygidae* (Figs. 3-4; fusion characterized by a straight CuA and an oblique posterior branch of M), a group basal within Antarctoperlaria. Nevertheless, I consider that these fusions have been acquired independently and do not constitute a primitive trait of the order Plecoptera. If present in Systellognatha, such a fusion involves an oblique anterior stem of CuA (a proper naming would be fusion of the anterior branch of CuA with M) and a straight branch of M, *i.e.* is not homologous with the organization in Gripopterygidae* and Leuctridae. Following Terry & Whiting (2004), *Megaleuctra*, which has no such fusion (Fig. 6), is sister-group related to the rest of the Plecoptera. Finally, at best, the polarization of the character at the base of the tree is ambiguous. Following Zwick (2000)'s phylogenetic framework, these fusions have been acquired independently.

Median system in Systellognatha

Assessing the ancestral number of branches of M in the Systellognatha (Figs. 8-12) requires a detailed review, because a more or less complete fusion of anterior branch(es) of CuA with the posterior branch of M is very common in the group, leading Séguy (1959: fig. 57), followed by Hennig (1981: fig. 36), to

propose a 3-branched free median system in Perlidae. Unfortunately, the various phylogenetic proposals of the inner phylogeny of the Systellognatha are contradictory for the basal relationships (Terry & Whiting 2004; Uchida & Isobe 1989; Zwick 1973), though families Pteronarcyidae, Styloperlidae, Peltoperlidae, and the super-family Perloidea (Perlidae, Chloroperlidae, Perlodidae) are universally accepted as monophyletic groups. I will discuss the morphology of the median system in each of these groups successively.

The family Pteronarcyidae comprises two genera, *Pteronarcys* Newman, 1838, and *Pteronarcella* Banks, 1900 (Nelson, 1988; Stark & Szczytko, 1982). In forewings of *Pteronarcys californica* (Fig. 8) the posterior branch of M is usually branched (see also *Pteronarcys dorsata* in Needham & Claassen 1925: fig. 10). This can also occur, although less frequently, in the hind wings of the species. Nevertheless, in other species of this genus, some individuals can have two- or three-branched M. In conclusion, the character state in *Pteronarcys* is polymorphic, two- and three-branched. In *Pteronarcella* M is two-branched, at least in forewings, in which no connection between M and CuA occurs (see Comstock 1918: fig. 251; Needham & Claassen 1925: 41, fig. 11, and pl. 2 fig. 2). I conclude from this review that the ancestral state in the Pteronarcyidae is a two-branched M.

Unfortunately no specimens of Styloperlidae were made available for my study. I rely on Uchida & Isobe (1989: fig. 6) to determine that the ancestral state in this family is a two-branched M, at least in forewings. In hind wings the posterior branch of M is connected with the anterior branch of CuA and the available information is not sufficient to determine to which system belong the distal branches.

In forewings of Peltoperlidae (such as *Yoraperla nigrisoma*, Fig. 9) the very last structure occurring in the area between CuA and M is certainly not an anterior branch from CuA but a cross-vein. First, except in the case of *Tallaperla anna* (Needham and Smith, 1916) (see Needham & Claassen 1925: pl. 15 fig. 5), Peltoperlidae have a simple posterior branch of M, *i.e.* a putative branch from CuA never emerges distally (see Needham & Smith 1916: fig. 1; Needham & Claassen 1925: pl. 15 Figs. 1-2; in *Tallaperla maria*, pers. obs.). Additionally, the orientation of this

structure never suggests that it could be a branch of CuA, but a regular cross-vein perpendicular to the surrounding veins. No intermediate state exists exhibiting this structure oriented towards the apex.

A fusion of the anterior branch of CuA with the posterior branch of M occurs in hind wings Peltoperlidae. In the specimen of *Yoraperla nigrisoma* illustrated herein (Fig. 9) the resulting composite vein gives rise to three veins, and is posteriorly pectinate. It is the usual condition in this species. While the most basal branch belongs to CuA, and the most distal one to M, the nature of the middle one is uncertain. Another specimen (pers. coll.) demonstrates that this central branch belongs to CuA: the composite vein [(posterior branch of M) + (anterior branch of CuA)] gives rise to two branches only, the first one being forked (a somewhat similar variation occurs in hind wings of *Isoperla phalerata*, see Fig. 12). The two branches resulting from this fork are homologous with the two first posterior branches of M + CuA of the specimen figured on Fig. 9, and they emerge from the same basal stem, that obviously belongs to CuA. Hence, in hind wings of *Yoraperla nigrisoma*, the two first branches emerging from M + CuA both belong to CuA. Finally, these observations suggest that the median vein is two-branched in fore- and hind wings of the Peltoperlidae.

Although the ancestral state of the Systellognatha can now be established as two-branched M, whichever phylogenetic frame is preferred, several cases in Perlidae and Perlodidae deserve some attention. In forewings of *Calineuria californica* (Fig. 10) the connection between the posterior branch of M and the most anterior branch of CuA is variable. In case where CuA and M are distinct, M is clearly two-branched. The M + CuA fusion is more stable in hind wings of this species.

Because a labile fusion of the posterior branch of M with the anterior branch of CuA is apparently present in all Perlidae, it can be expected that it is also the case in *Anacroneuria litura* (Fig. 11), a derived species in the family (Terry & Whiting 2004). Nevertheless, in this species, the putative composite stem [(posterior branch of M) + (anterior branch of CuA)] is always simple, in fore- as well as in hind wings (Fig. 11) (but see Devyatkov 2003: fig. 2, who

illustrated a distal fork of this stem in forewings of *Yoraperla altaica* Devyatkov, 2003). I propose that a fusion actually occurs as in other Perlidae, and that the two stems do not diverge distally, *i.e.* stay fused. Though the most distal structure between M and CuA has the appearance of a cross-vein, it is slightly stronger, it is never reticulated, and it is oriented like a branch of CuA (toward the wing apex). CuA is distally branched in hind wings of all Perlidae (Needham & Claassen 1925: pl. 13, fig. 4 figured a hind wing of *Claassenia sabulosa* with a simple CuA; after my personal observation of specimens of this species, CuA is always branched). Hence I hypothesize that CuA is also branched in *Anacroneuria litura*. Because only one branch of CuA reaches the hind wing posterior margin free of any fusion, I consider that the structure located between M and CuA is an actual branch of CuA. If so, the presence of a complete fusion of the posterior branch of M and the anterior branch of CuA could be an apomorphy of a sub-clade within the Perlidae.

Based on the previous inferences, I propose that M is also two-branched in Perlodidae (see *Isoperla phalerata*, Fig. 12), though the number of branches emerging from the common stem [(posterior branch of M) + (anterior branch of CuA)] is higher than in other taxa. The variation shown by individuals reveals that the common stem can give rise to two branches only, easily interpretable as 1) the posterior branch of M, 2) the most anterior branch of CuA. Finally, the median vein is ancestrally two-branched in Systellognatha, in fore- and hind wings.

Median system in Plecoptera

In conclusion the three major clades of the order Plecoptera, namely Antartopterlaria, Euholognatha, and Systellognatha, have ancestrally a two-branched median vein.

The course of RP in hind wings

One of the most intriguing characters of stoneflies wing venation is the relative course of the sector RP and the vein M in hind wing (see a brief discussion in Zwick 2000). There is virtually no doubt about the actual nature of veins in the distal area of the wing, since RP and M have very generally the same number of branches and a similar course as in

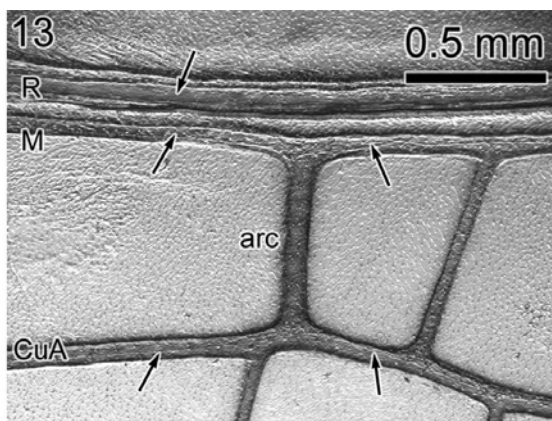


Fig. 13. *Acroneuria abnormis* (Newman, 1838), detail of the arcus. Abbreviations as in Fig. 1 and: arc, arcus. Arrows indicate the course of main veins lacunae. The arcus has no lacuna.

forewings (Figs. 1, 2, 4-5, 7, 9, 11), or closely similar (Figs. 3, 6, 8, 10, 12). Furthermore, the *rp-m* differentiated cross-vein, present in both wing pairs in Euholognatha and Systellognatha, allows us to easily distinguish RP from M in hind wings. However the origin of the common stem RP + M is an unresolved issue. Sharov (1962a: 134) followed by Sinitshenkova (2002: 281) described it as “in hind wing RS [RP] joined with M at the base”, implying that R and M stems are basally distinct. Statements positing that, in hind wing, “the basal section of MA+ is fused with the basal section of R and RS [RP]” (Hennig 1981: 163), and “M originating [...] from Rs [RP]” (Theischinger 1991: 311-312) are ambiguous, as they possibly implies the existence of a common stem RA + RP + M(A) in the ground-plan of the order.

Sharov’s statement is correct and is supported by the presence, at least in two extant and phylogenetically distant stoneflies, of a short oblique unsclerotized oblique structure diverging from R and fusing with M further (arrows in Figs. 18-19). This structure was made visible on specimens belonging to the species *Stenoperla prasina* (Eustheniidae) under a peculiar light setting (see above). This is an unsclerotized blood lacuna. It is located between the stem leading to RA, and the stem giving rise to RP + M (later RP and M). Hence I interpret it as the base of RP diverging from R and fusing with M. As a consequence stems of R and M are basally distinct

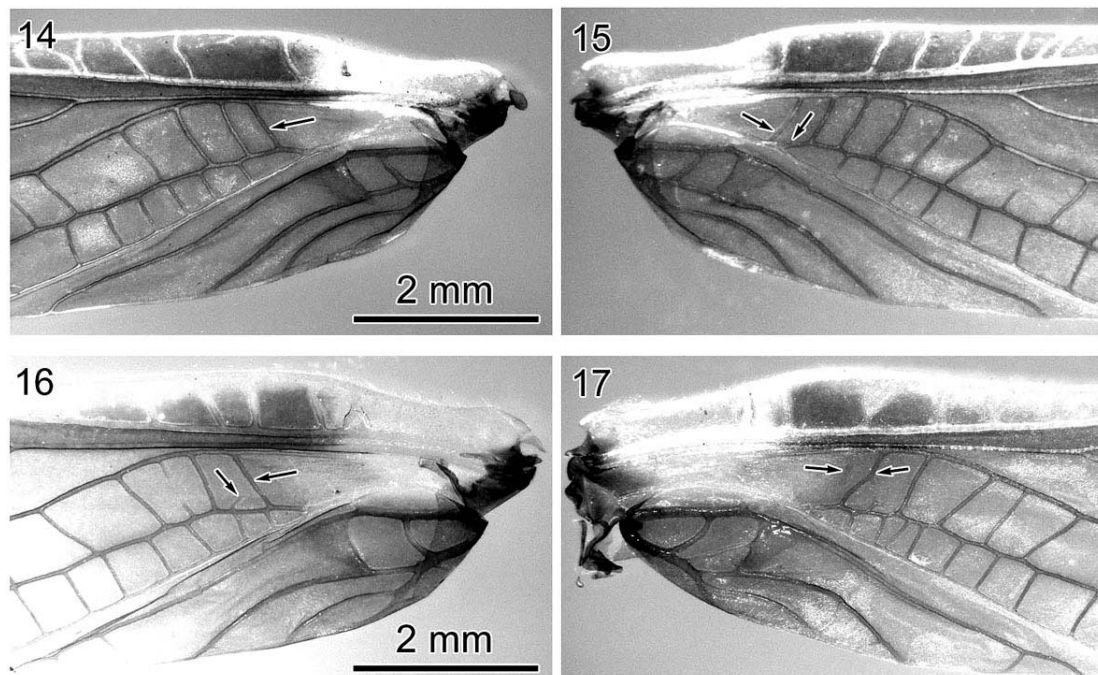
from each other, and RP joins M distal to the wing base. Haas & Kukalová-Peck (2001: fig. 14) also noticed this free part of RP before its fusion with M in a representative of Eustheniidae, but their assertion was not based upon a photographic clue, I provide herein.

I also observed this oblique lacuna in a hind wing of *Pteronarcys californica* (Pteronarcyidae), in which it is located more basally (Fig. 19). Concerning this genus, Holdworth (1940) provided additional support in favor of the R and M stems distinct at the wing base hypothesis, based on an alternative interpretation of his drawings of the wing venation of instars (Figs. 20-21). Holdworth’s M1 in hind wings is simply RP, clearly connected at length with M, from the ninth instar.

Direct observation, while modifying the orientation of optic fibers, provides a composite binocular view that revealed the origin of RP in additional taxa. Unfortunately these composite views were not photographable. Anyway, the occurrence of a visible distinct origin of RP from R, in two phylogenetically distant taxa (a representative of Antartoperlaria and one of Systellognatha) is a sufficient clue to ascertain that R and M are, ancestrally in Plecoptera, distinct in hind wings, and that RP fuses with M distal to the wing base, but basal to the arcus. The presence of basal distinct stems of R and M conforms to the pleisiomorphic condition in winged insects, and was indeed predictable in hind wings of Plecoptera.

The venation of the vannus

Haas & Kukalová-Peck (2001) provided the most comprehensive recent review of the neopterous hind wing venation pattern. The authors emphasized on the homologization of the vanal area for a phylogenetic prospect. They distinguish the full anojugal lobe of Pleconeoptera (including Plecoptera and Embiidina) and Orthoneoptera, in which the AA area is well developed, from the partial anojugal lobe of Blattoneoptera, Hemineoptera, and Endoneoptera, in which the AA area is narrower (see Haas & Kukalová-Peck 2001; Kukalová-Peck & Lawrence 2004, for compositions of super-ordinal groups). However, in both cases, the authors suggest that AP and J areas occur (differentiated JA and JP in



Figs. 14-17. *Austroperla cyrene* (Newmann, 1845) (Austroperlidae). Details of the arcus, all dorsal view. **14.** Left forewing; the arrow indicates the arcus, usual morphology. **15.** Right forewing, same individual as in 14; the left arrow indicates the base of the arcus, *i.e.* the first cross-vein between M and Cu(A), basal to the base of CuA (itself indicated by the right arrow). **16.** Left forewing; the left arrow indicates a vestigial cross-veins directed towards the arcus (itself indicated by the right arrow). **17.** Right forewing, same individual as in 16; the left arrow indicates a vestigial cross-vein occurring basal to the arcus (itself indicated by the right arrow); the arcus is reticulated.

Haas & Kukalová-Peck 2001: fig. 14; undifferentiated J area in Kukalová-Peck & Lawrence 2004). Unfortunately, the presence of these areas in Plecoptera is presented without grounded evidence and is in contradiction with nearly all previous works (Table 1). Additionally it has been demonstrated that the primitive condition in the vannus morphology of Archaeorthoptera (including Orthoptera) conforms to that of the Dictyoptera (Béthoux 2003), *contra* Haas & Kukalová-Peck (2001) and Kukalová-Peck & Lawrence (2004). Then, the proper homologization of the vannus in the Plecoptera has critical phylogenetic implications.

Evidences suggest that, in Plecoptera, a strict serial homology exists between the venation pattern of the forewings clavus and the hind wings vannus (terms *sensu* Wootton 1979). In both wing pairs the

first anal vein, herein labeled AA1, is simple and connected to CuP by a aa1-cup differentiated cross-vein (which can be reduced, the two veins being shortly connected). The vein AA1 is connected to a more basal vein (herein considered as the first branch of AA2, labeled α AA2, generally posteriorly pectinate in Antarctoperlaria and Systellognatha, simple in Euholognatha) by a differentiated aa1-aa2 cross-vein (* in Figs. 23-36; closing the anal cell of Needham & Claassen 1925), present in both wing pairs. Hence AA1 and the first anterior branch of AA2 are homologous, strongly convex in both wing pairs. Thereby they belong to the anterior anal sector, as suggested by previous authors (Table 1).

The two epidermic layers constituting the hind wing of an unusual specimen of *Amphinemura banksi* (Nemouridae) (Fig. 22) (provided by BYUC) were

mounted separately (see Preparation of the specimens section). It is well known that main vein anterior sectors are located on the upper epidermic layer of the wing, while posterior sectors are located on the lower epidermic layer (Séguy 1959; see above). As expected, CuP is present on the lower layer, with a faint imprint present on the upper layer. Conversely, AA1 is virtually absent from the lower layer, and is occurring only in the upper one. This specimen undoubtedly demonstrates that *veins of the enlarged postero-basal lobe are located on the upper layer* (though a faint imprint is visible on the lower layer), hence they belong to an anterior sector. Since CuP is the first posterior sector anterior to this area, these veins belong to AA. Interestingly, M is present only on the lower layer. It suggests that MA is absent in Plecoptera. However, the issue concerning the presence of MA in Neoptera is largely far beyond the scope of this paper.

Additional to this straightforward demonstration, a full homologization of AA veins can be achieved after the more complete venation of the Systellognatha. I use a provisional new venation nomenclature in order to describe the venation of the clavus – vannus area, and demonstrate its validity throughout the discussion.

In forewings of *Pteronarcys californica* (Pteronarcyidae) (Figs. 23-24), basal to the vein α AA2, three main stems (β AA2, χ AA2, and δ AA2) diverge posteriorly from a strongly convex stem (AA2). This is also the case in the hind wings of this species (Figs. 25-26). In both wing pairs of *P. californica* β AA2 is branched, though χ AA2 and δ AA2 are simple in forewings and branched in hind wings. Nevertheless, the number of main stems emerging from AA2 is identical. I propose that these veins are homologous. Interestingly, the veins β AA2 and χ AA2 arise successively as posterior branches of the stem leading to α AA2, itself posteriorly pectinate. Hence they can all be considered as posterior branches of AA2. Additionally, they are inarguably convex in forewings. They are also convex in hind wings, although their relief can be altered due to the course of the folds, which can cross them. Finally, the labels α AA2, β AA2, and χ AA2 are proper to describe branches emerging from the basal stem AA2, in Systellognatha. The case of the precise homology of

δ AA2 in fore- and hind wings will be detailed below, but, considering its strong convexity, it undoubtedly belongs to AA2.

In forewings of a single specimen of *Tallaperla maria* (Peltoperlidae) I observed the occurrence of a vestigial supplementary χ AA2 vein in forewings, usually absent in the family (see Figs. 27-28). This let me hypothesize that this vein is lost in other Systellognatha in which only one vein occurs between α AA2 and δ AA2 (which, as a result, is β AA2).

In *Hesperoperla pacifica* (Figs. 31-34) (Perlidae) the branching pattern of AA2 in the clavus (forewing) can be variable (Figs. 31-32). The differentiation of β AA2 and χ AA2 is unclear. As suggested above, χ AA2 is absent in the forewings of *Acroncuria abnormis* (Perlidae). In the right forewing of one specimen of this species (Figs. 35) I observed the occurrence of a vestigial and incomplete posterior branch of δ AA2. I propose that this branch is homologous with the most posterior branch of δ AA2 in hind wing (Fig. 36), directed towards the basal wing margin (strut in Haas & Kukalová-Peck 2001: fig. 14), present in virtually all Plecoptera retaining a developed vannus. As a consequence, the most posterior branch of AA2 in forewings is not homologous with the strut *sensu* Haas & Kukalová-Peck (2001), as suggested by its orientation, but of the whole δ AA2 hind wing vein. In a hind wing of *Pteronarcys californica* I observed that this strut, unlike anal veins, has no trachea (Fig. 37). Therefore it is a secondarily strengthened cross-vein, as suggested by Haas & Kukalová-Peck (2001).

The hind wing pattern and nomenclature proposed above applies to Systellognatha. Among Antartoperlaria, simple AA1, β AA2, χ AA2, and branched α AA2 and δ AA2 can be recognized in Austroperlidae (Fig. 1). Gripopterygidae conforms to this pattern except by their simple α AA2 (Figs. 3-4). It must be noticed that, if wings are not properly stretched out, the folds occurring between α AA2, β AA2, and χ AA2 can obscure the branching pattern of these veins. In Eustheniidae (Fig. 2) the points of emergence of anal veins are concentrated at the wing base and β AA2 and χ AA2 cannot be positively pointed out as posterior branches of the stem leading to α AA2. However, because this pattern can be

widely recognized in other Plecoptera, I suggest that the two first simple branches, basal to the branched α AA2, are the actual β AA2 and χ AA2.

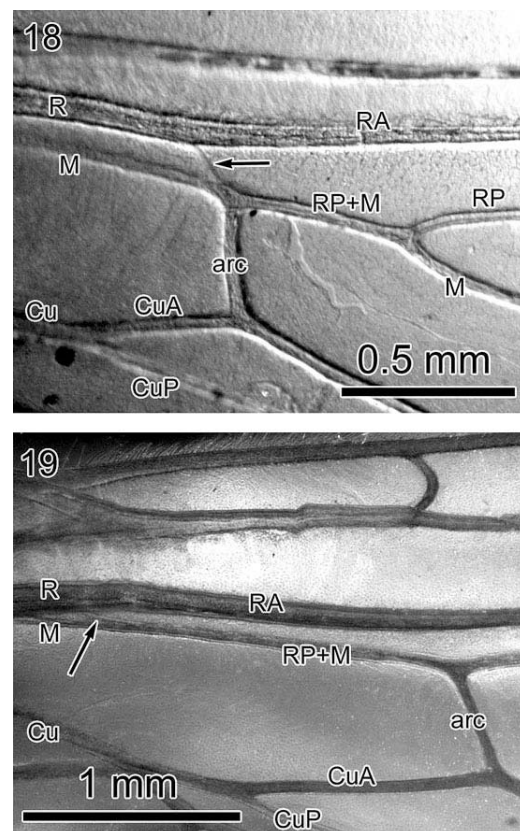
Euholognatha having a well-developed vannus (Figs. 5-6) share the same vannus venation pattern as in Gripopterygidae. I propose a putative interpretation of the vannus of the Leuctridae (Fig. 7), a family in which the vannus area is reduced. The hind wing venation pattern of the family can be conformed to the proposal described above. However, an alternative interpretation is possible: it could be hypothesized that χ AA2 is lost in the Leuctridae, with a δ AA2 branched as usually. This does not affect the validity of the pattern at the level of the order, because the reduction of the vannus is a secondary acquisition of the family.

In forewings of Antartoperlaria and Euholognatha χ AA2 and δ AA2 are difficult to identify. The AA2 stem is usually forked, probably into α AA2 and β AA2, as suggested by the secondary absence of χ AA2 in some Systellognatha.

The rigorous application of the AA2 pattern described above will probably be challenged when less derived taxa will be discovered, in which more numerous posterior branches of AA2 might have occurred without clear differentiation. Nevertheless, this proposal is noteworthy because it properly describes the Plecoptera clavus - vannus area, allowing us to establish serial homology between fore- and hind wings anal veins.

The end of ScP

It is generally admitted that ScP reaches RA at the second third of the wing in Plecoptera. In Gripopterygidae*, ScP runs free from RA until it reaches the anterior wing margin. In this group, unlike most Plecoptera (with the exception of Leuctridae), there are no cross-veins between RA and the anterior wing margin, distal to the end of ScP. This might implies that, in Plecoptera other than Gripopterygidae, ScP actually re-emerges distally from ScP + RA. However, branches occurring between RA and the anterior wing margin could simply be cross-veins. I could not find clear evidence supporting either one of these hypotheses.

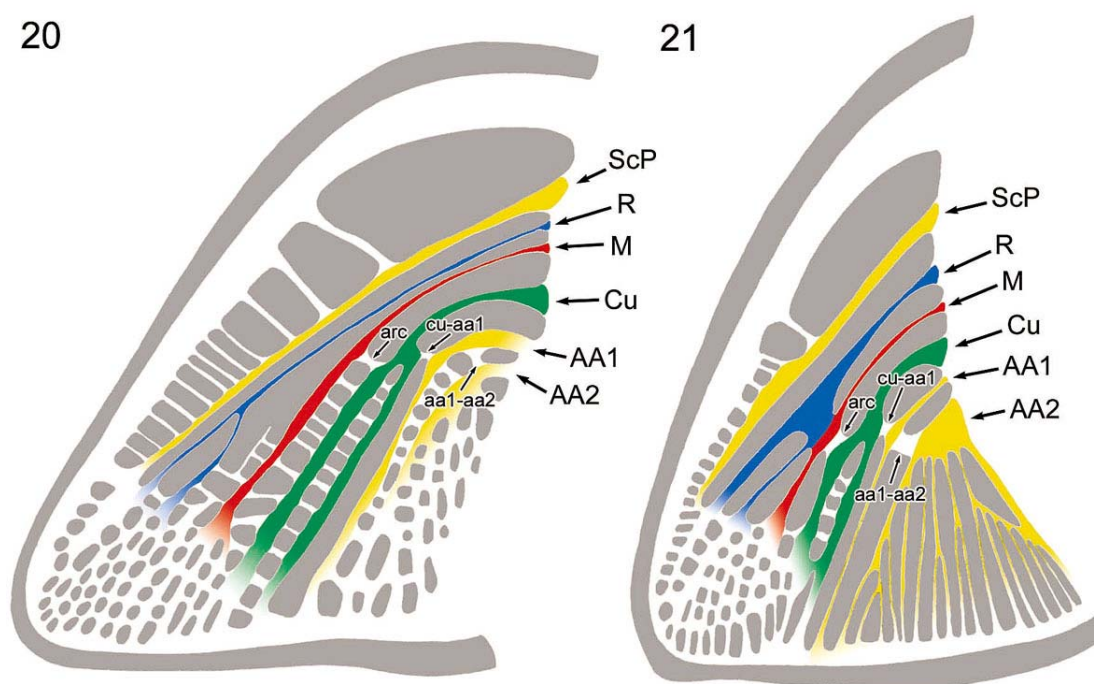


Figs. 18-19. Details of hind wing bases showing the origin of RP (arrows) from R. Abbreviations as in Figs 1 and 13. **18.** *Stenoperla prasina* (Newman, 1845) (Eustheniidae), right hind wing, dorsal view. **19.** *Pteronarcys californica* Newport, 1851 (Pteronarcyidae), right hind wing, ventral view, reversed.

DISCUSSION

Diagnostic characters of the wing venation and phylogenetic implications

Primary homologization of insect orders wing venation carries important phylogenetic implications. Sharov (1961a, 1962a) (discussed in Hennig 1981), after his interpretation of the arculus (as MP), assigned the species *Narkemina angustata* Martynov 1930 and some other Carboniferous fossils (Cacurgidae) to the order Paraplecoptera, assumed to be related to the Plecoptera. Besides the fact that the arculus of the stoneflies is not MP but a strengthened



Figs. 20-21. Eleventh instar wings of *Pternarcys proteus* Newman, 1838 (Pternarcyidae), modified after Holdsworth (1940); color pattern and abbreviations as in Figs. 1 and 13, and cu-aa1: differentiated cross-vein between Cu and AA1; aa1-aa2: differentiated cross-vein between AA1 and AA2. **20.** Left forewing. **21.** Left hind wing.

cross-vein, it turned out that the so called arcus in *Narkemina* Martynov 1930 as well as in Cacurgidae is not MP but CuA emerging from M + CuA (Béthoux in press-a, b). *Narkemina*, the Cacurgidae, and several Carboniferous Protorthoptera (*sensu* Carpenter 1992) belong to the Archaeorthoptera Béthoux & Nel 2002, *i.e.* are related to Orthoptera, and, therefore, have no direct relationships with Plecoptera.

At this point the apomorphic traits of the Plecoptera wing venation can be outlined. First, in hind wings and very generally in forewings, a secondarily strengthened cross-vein, namely the arcus, is present between M and CuA. A similar structure located between M and CuA is present in

various polyneopterous groups. In hind wings of Mantodea, following Smart (1956), a strengthened cross-vein links CuA to M (see also Haas & Kukalová-Peck 2001; Ramsay 1990; Sharov 1962b). The same structure is also present in the order Blattodea (see Haas & Kukalová-Peck 2001; Schneider 1977; pers. obs. on a specimen of *Periplaneta Americana* (L.), pers. coll.). However, this dictyopterid arcus recognized by Haas & Kukalová-Peck 2001 (see Table 6D, Blattoneoptera, characters of the wing venation; absent in Isoptera) actually links CuA to M (MP after Haas & Kukalová-Peck 2001) at the point of divergence of M from R. In hind wings of all Plecoptera but Leuctridae and

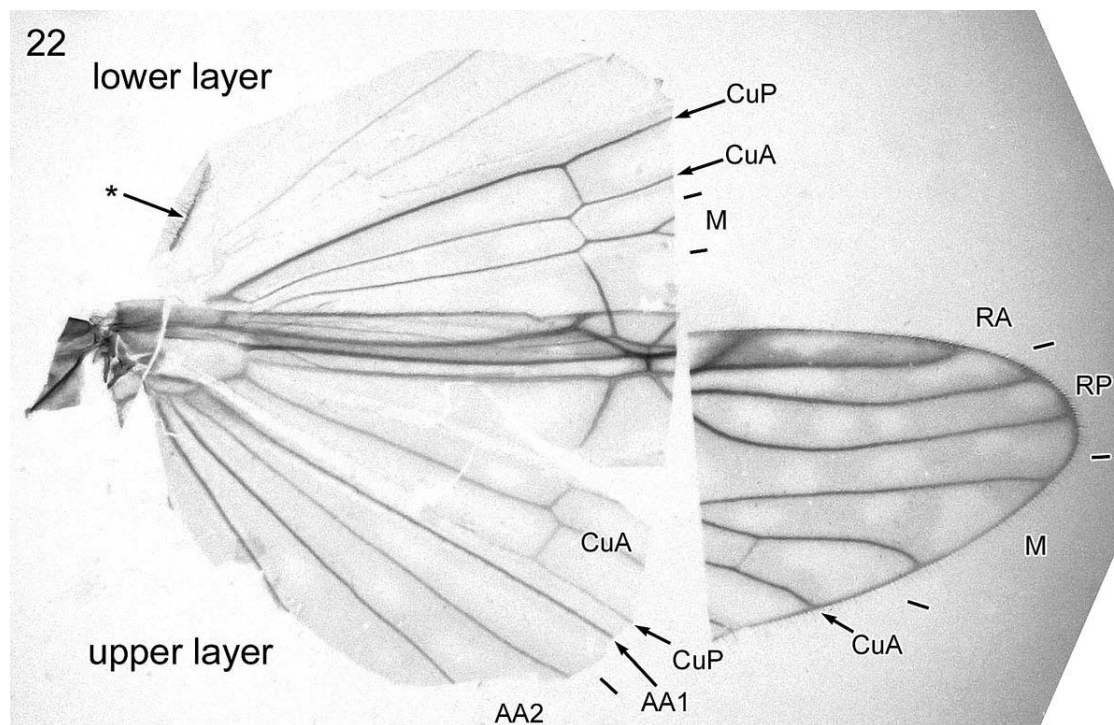


Fig. 22. Dissection of *Amphinemura banksi* Baumann & Gaufin, 1972 hind wing (Nemouridae; left hind wing, dorsal view, reversed) showing the two epidermic layers. Abbreviations as in Fig. 1 and: * indicates a structure that is not a main vein but a remain of the posterior wing margin; lower layer refers to the lower epidermic layer while upper layer refers to the upper one.

Megaleuctridae, the arculus is located basal to the divergence of M and RP. One could argue that the arculus of Plecoptera and of Dictyoptera are not homologous, or at least represent different states. An arculus is present in forewings of various fossil families such as †Blattinopsidae (Béthoux & Nel 2002; Carpenter 1992; Hörnschemeyer & Stapf 2001) and †Archymylacridae (Schneider 1983), belonging to the Dictyoptera. However, characters of the hind wing venation, in these families, are unknown.

The basal representatives of the extinct order †Protelytroptera possess an m-cua arculus in hind wings (Carpenter & Kukalová-Peck 1964). Based upon a new interpretation of the wing venation of *Apachelytron* Carpenter & Kukalová-Peck 1964, Haas & Kukalová-Peck (2001: 454, fig. 3) posited that an arculus is also present in forewings of the basal †Protelytroptera. However, in an earlier work Kukalová-Peck (1991: fig. 6.20A) figured the same

genus without arculus in forewings, and there is no visible arculus on published photographs of *Apachelytron transversum* Carpenter & Kukalová-Peck 1964 (see Carpenter & Kukalová-Peck 1964; Shcherbakov 2002). Hence, I consider the presence of an arculus in protelytropteran forewings as dubious.

From this brief review, the presence of an m-cua arculus is difficult to polarize among polyneopterous insects. This point directly relates to the composition and phylogeny of the Dictyoptera, an issue that overcomes the aim of this paper. However, the co-occurrence of an m-cua arculus in both fore- and hind wings, as in Plecoptera, is unique. Moreover, this arculus is absent in Grylloblattida *sensu* Storozhenko (2002), the putative sister-group or ancestral stock of the Plecoptera (supported by Grimaldi 2001 and Rasnitsyn 2002a). Finally, I propose that the presence of an arculus in both fore- and hind wings is a putative apomorphy of the

Plecoptera.

As a result of the demonstration that the arculus is a secondarily strengthened cross-vein, M is two-branched in both wing pairs (*contra* Grimaldi 2001, character 45). It is also a putative apomorphy, as M has primitively three branches in Embiidina, the possible modern sister-group of the order (Wheeler et al. 2001a, b; in prep.); in Grylloblattida *sensu* Storozhenko (2002), the number of branches of M varies widely, as is in Dictyoptera (Blattodea, Isoptera, Mantodea); in basal Archaeorthoptera M has more than two branches (Béthoux 2003; Béthoux & Nel 2005).

The presence, in hind-wings, of a fusion of RP (originating from R) with M, with a long common stem RP + M, ending with the distal divergence of RP and M, is obviously apomorphic of the Plecoptera. It is absent in all other polyneopterous insects. The RP + MA fusions occurring in Embiidina (see Ross 2000), and in the grylloblattid family †Lemmatophoridae Sellards, 1909 (see Carpenter 1992; revision in prep.) is not homologous, because it involves a different set of sectors, namely MA and RP instead of M stem and RP.

Interestingly Béthoux & Nel (2003b) hypothesized that, in the hind wings of the famous fossil species *Gerarus fisheri* (Brongniart, 1885) (Archaeorthoptera; Upper Carboniferous), a basal stem of RP + (M + CuA) occurs. Again, this fusion is not homologous with the RP + M stem of Plecoptera. *G. fisheri* is a genuine Archaeorthoptera and a significant number of apomorphies separates it from the Plecoptera. Nevertheless, the arrangement of this fusion in Plecoptera provides some help for interpreting the hind wing venation of *G. fisheri*. In this fossil species there is no discernable origin of RP, leading Béthoux & Nel (2003b: 175) to infer that the “base of RP [is located] at the wing base”. However, the base of RP would be, as it is in Plecoptera, constituted of an unsclerotized lacuna, hardly visible even in extant and freshly killed stoneflies. If so, it would be indiscernible on fossil material. In *G. fisheri* the base of RP could well be located more distally than expected by Béthoux & Nel (2003b).

As currently accepted no Protorthoptera *sensu* Carpenter (1992) concurrently possess the three characters mentioned above (presence of an arculus

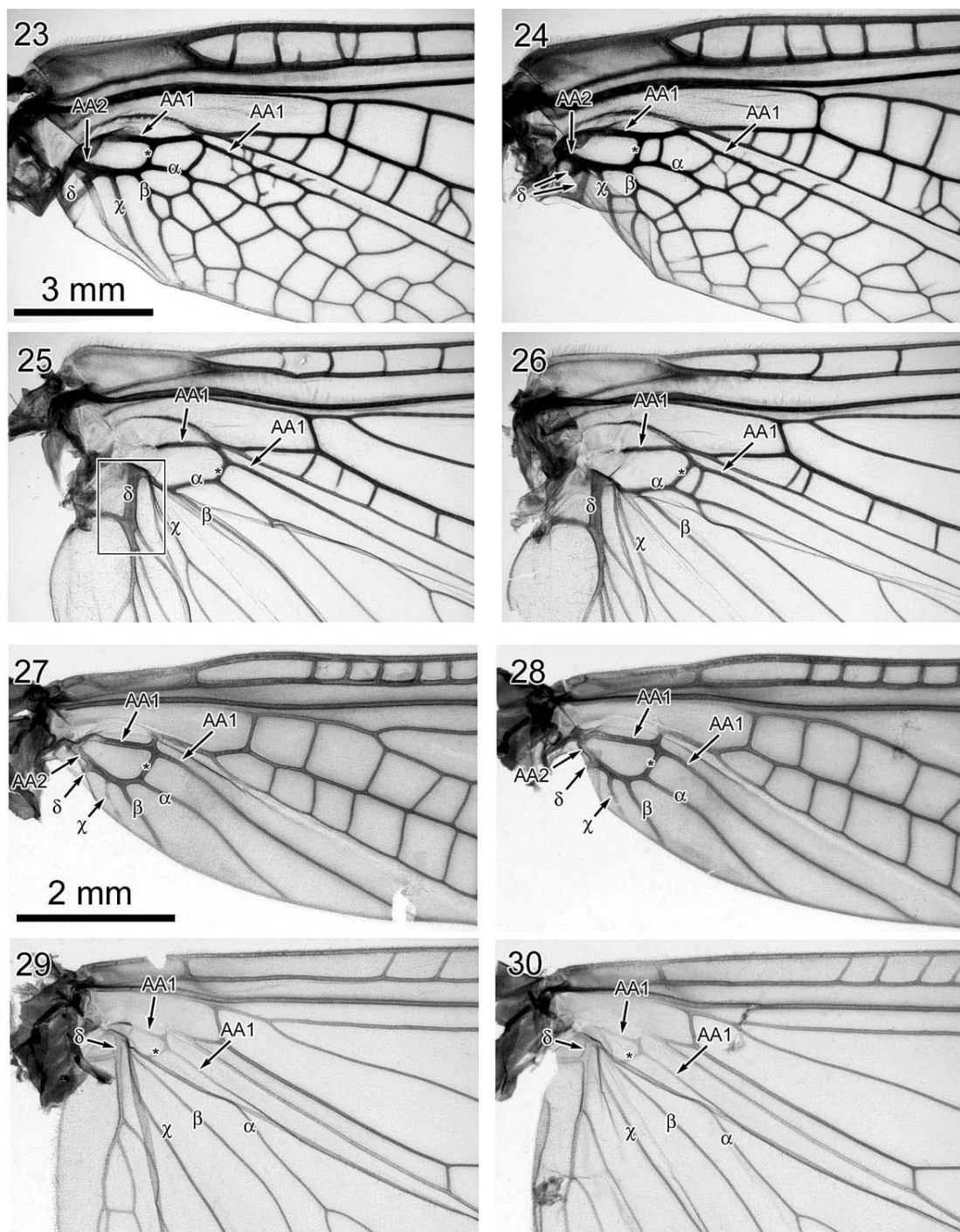
in both wing pairs, Media two-branched, in hind wings, presence of a fusion of RP + M). There is no common stem RP + M in hind wings of *Chelopteryx* Carpenter, 1950 but a usual distal origin of RP from R (*contra* Carpenter 1950; revision in prep.).

Finally it is currently impossible to trace the origin of the Plecoptera further to the latest Early Permian to earliest Late Permian, when undisputable representatives are recorded (Sharov 1961b; Sinitshenkova 2002). Permian taxa have all the apomorphies cited above (hind wings known in *Palaeotaeniopteryx* Sharov 1961b). Palaeozoic stoneflies are so distinct from other contemporaneous or older polyneopterous taxa that, based on our fossil record, no other taxon can reliably be pointed out as potential sister-group.

Full anojugal lobe, partial anojugal lobe, and the vannus morphology in Plecoptera

The interpretation of the clavus - vannus venation proposed herein suggests that, in Plecoptera, the AA sector divides into a simple AA1 and a branched AA2. Interestingly, a similar pattern is present in the forewings of the most basal Archaeorthoptera (*i.e.* insects closely related to Orthoptera) *Protphasma dumasii* Brongniart, 1879 (see Béthoux 2003: 58, fig. 2.1). However, a well-developed AP area is also present in both wing pairs of this last taxa, unlike in Plecoptera. In hind wings of Dictyoptera and *P. dumasii*, two simple AA veins occur (AA1 is lost in derived Mantodea; Smart 1956), separating a wide AP area. Consequently, the vannus in Plecoptera differs from that of the Dictyoptera and *P. dumasii* in the lack of a well-developed AP area and in the extensive branching of AA2.

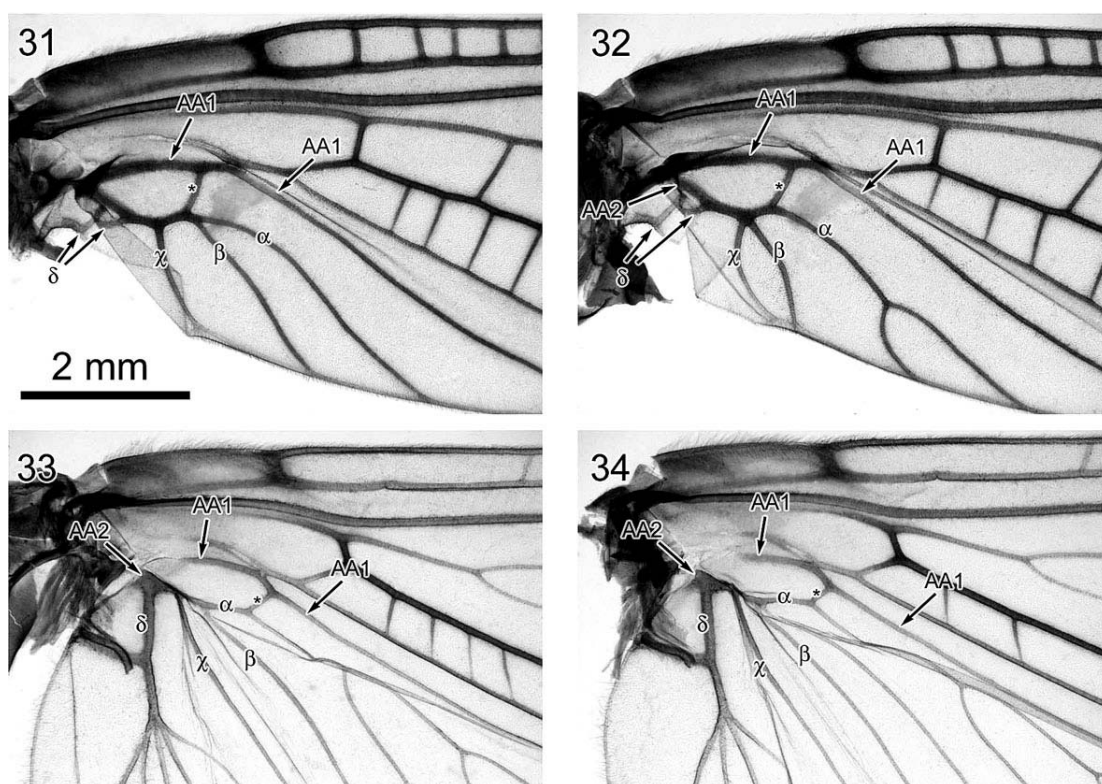
This comparison pictures an evolution of the vannus, in polyneopterous insects, much simpler than that developed by Haas & Kukalová-Peck (2001) and Kukalová-Peck & Lawrence (2004). The full anojugal lobe *vs.* partial anojugal lobe hypothesis (Haas & Kukalová-Peck 2001; Kukalová-Peck & Lawrence 2004) is based on the assumption that ground plan feature, *i.e.* the occurrence of AP and J areas, are rigorously preserved in polyneopterous orders. It is also implicitly based on the assumption that folds are reliable clues for differentiating vein sectors. On this last point, Wootton (1979) already



Figs. 23-30. Vein homologies in the clavus (forewings) and the vannus (hind wings); abbreviations as in Fig. 1 and: * indicates aa1-aa2 differentiated cross-vein. **23-26.** *Pteronarcys californica* Newport, 1851 (Pteronarcyidae), all same individual. **23.** Left forewing, dorsal view, reversed. **24.** Right forewing, dorsal view. **25.** Left hind wing, dorsal view, reversed (frame locates the Fig. 37). **26.** Right hind wing, dorsal view. **27-30.** *Tallaperla maria* (Needham and Smith, 1916) (Peltoperlidae), all same individual. **27.** Left forewing, ventral view. **28.** Right forewing, dorsal view. **29.** Left hind wing, ventral view. **30.** Right hind wing, dorsal view.

demonstrated that, except in the case of the claval and jugal folds, hind wing folds must be used with caution for homologization purposes. I agree with Wootton's opinion, because these folds cross sectors branches, and their course, location, and number, vary. This point has a striking demonstration from literature. Haas & Kukalová-Peck (2001: fig. 14) described, in a representative of the genus *Eusthenia*, a fold occurring between AA2 and AA3, in

addition to the claval fold, the AA4-AP fold, and the jugal fold. Later Kukalová-Peck & Lawrence (2004: fig. 2.A), describing an undetermined species of the same genus, recognized only three folds, the AA2-AA3 fold lacking from their interpretation. Surely, either Haas & Kukalová-Peck (2001) or Kukalová-Peck & Lawrence (2004) did not properly homologize hind wing folds, or folds are not reliable landmarks for vein homologization.

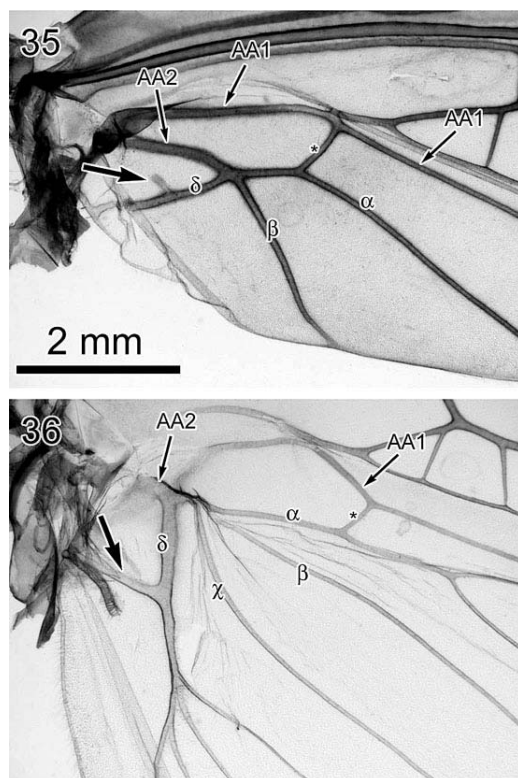


Figs. 31-34. Veins homologies in the clavus (forewings) and the vannus (hind wings). Abbreviations as in Fig. 21. *Hesperoperla pacifica* (Banks, 1900) (Perlidae), all same individual. 31. Left forewing, ventral view. 32. Right forewing, dorsal view. 33. left hind wing, ventral view. 34. Right hind wing, dorsal view.

CONCLUSION

This review shows that wing venation of Plecoptera is neither simple nor primitive. These insects exhibit numerous specializations, leading to confusing situations where cross-veins secondarily strengthened cannot be easily distinguished from main veins branches. Conversely, course of main veins can evolve in a way that follows the location of

a previously existing cross-vein. For example, CuA fuses with M in hind wings of *Leuctra braueri* (Fig. 7) likewise the course of the m-cua cross-vein in less derived taxa. In hind wings of the same taxa, M follows the course of the arcus (*i.e.* a specialized cross-vein) before diverging from it. In Perlidae (Figs. 10-11) and Perlodidae (Fig. 12), the fusion of the anterior branch of CuA with M follows the path of



Figs. 35-36. Veins homologies in the clavus (forewings) and of the vannus (hind wings). Abbreviations as in Fig. 21. The larger arrow indicates the most posterior branch of δ AA2. *Acroneuria abnormis* (Newman, 1838) (Perlidae), all same individual. 35. Right forewing, ventral view, reversed. 36. right hind wing, dorsal view, reversed.

the very last cross-vein occurring between M and CuA in Peltoperlidae (Fig. 9). This phenomenon is the tracheal capture of Leston (1962).

This study also aims to demonstrate that wing venation characters could provide additional support in favor of one or another phylogenetic hypothesis. It is noteworthy that characters “presence of a fusion (posterior branch of M) + (anterior branch of CuA)”, and “ScP reaching the anterior wing margin” (instead of RA), occurring in the Gripopterygidae, might actually support the monophyly of the group, favoring Zwick (2000) *contra* Terry & Whiting (2004). I provided several characters in favor of the inclusion of *Megaleuctra* within the Euholognatha, also supporting Zwick (2000) *contra* Terry & Whiting

(2004). Unfortunately, detailed descriptions of wing morphology in systematic literature of stoneflies are commonly missing. For the great majority of the species, individual and specific variability is unknown (but see Needham & Claassen 1925). With respect to the critical importance of the order Plecoptera in insect phylogeny, and in regard of issues in assignment of fossil taxa to modern lineages, this lack is unfortunate.

This study will be helpful for sorting out the relationships between fossil taxa assigned to the Protorthoptera, debated since decades. A recent phylogenetic hypothesis includes the truly orthopterid Protorthoptera in the clade Archaeorthoptera (Béthoux & Nel 2002, 2005), alongside with the orders Orthoptera, Titanoptera, and Caloneurodea (see Béthoux et al. 2004 for the attribution of the latter). However, a large part of the remaining Protorthoptera, historically referred to as

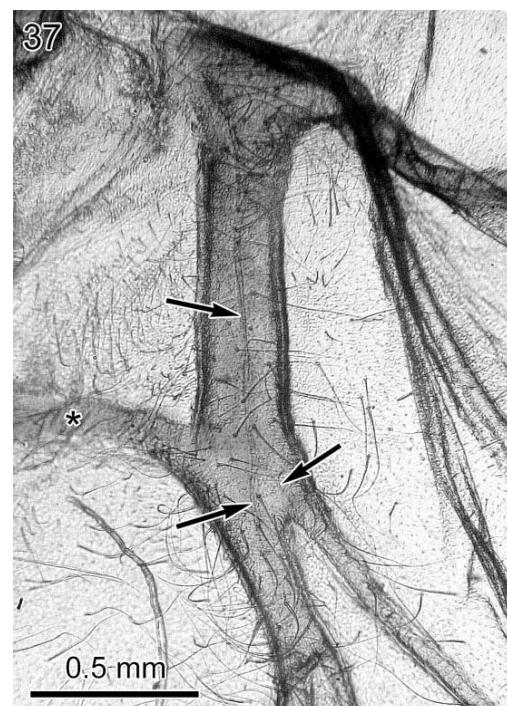


Fig. 37. Detail of a hind wing of *Pteronarcys californica* Newport, 1851 (Pteronarcyidae) (as located on Fig. 25). Arrows indicate the course of δ AA2 trachea. The strut (indicated by *) has no trachea.

Protoperlaria, has still uncertain relationships. Most authors admitted that Protoperlaria are ancestral to or sister-group related to the Plecoptera (Grimaldi 2001; Hennig 1981; Kukalová-Peck 1991; Rasnitsyn 2002a; Storozhenko 2002). This assumption is now testable (in prep.), based on diagnostic characters highlighted above.

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