

The tergal and pleural wing base sclerites – homologous within the basal branches of Pterygota?

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The Ephemeroptera are usually regarded as the sister group of the remaining Pterygota. Their wing base sclerites and pterothoracic musculature are compared with that of other basal pterygote lineages. It is shown that most elements of the neopteran wing base are also present in Ephemeroptera and Odonata. The wing base in the ground plan of Pterygota is presumably composed of three axillaries and a proximal median plate. The first axillary is provided with two muscles. The third axillary is equipped with one short muscle in the ground plan of Pterygota. A second muscle, which inserts at the third axillary and originates from the episternum, is most likely an autapomorphic character of Neoptera. The results imply that the wing base of Plecoptera is close to the pterygote ground plan. It is assumed that the wing bases of Ephemeroptera and Odonata are secondarily stiffened. The so-called basalare and its associated muscles in Ephemeroptera and Odonata are probably not homologous to the basalare and respective muscles in Neoptera. Though the wing bases of both Ephemeroptera and Odonata show similar modifications their specialisations may have evolved independently from each other.

Keywords: axillaries; flight muscles; basalare; subalare; Ephemeroptera; Plecoptera

Introduction

The development of wings in insects was one key character for the evolutionary success of this diverse group. It opened up new ecological niches and increased the efficiency of dispersal. Other advantages of the ability to fly were certainly better chances to escape from predators and to detect new food resources.

To date there is no general agreement on the derivation of wings and the evolution of wing base sclerites. It is often assumed that insect wings are leg derivatives (Kukalová-Peck 1983), or derived from lateral tergal expansions, the paranota (Hamilton 1971, 1972a,b,c), or rather originate from both tergites and pleurites (Snodgrass 1935).

The number and homology of axillary plates in basal Pterygota has always been controversial. The hypothesis that assumes only one axillary plate in Ephemeroptera, two axillary plates in Odonata, and three axillary plates in Neoptera,

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representing the apomorphic character state in the latter group (Hamilton 1971) is only rarely maintained nowadays (Gullan and Cranston 2005). Grandi (1947) even assumed that the wing base sclerites of Ephemeroptera are ‘pseudopteralia’ without homology to the wing base sclerites of other Pterygota. Most authors today agree on a homology between the axillaries of at least Ephemeroptera and Neoptera. However, it is not clear which element of the mayfly wing base is the homologue to which of the wing base elements of Neoptera (e.g. Brodsky 1970, 1974, 1994; Matsuda 1956; Tsui and Peters 1972). According to Kukalová-Peck (1983, 1987, 1991), the wing base in the pterygote ground plan consists of 32 sclerites, which are secondarily fused in different ways in extant Pterygota. Boudreaux (1979) also suggested that the sclerites of the wing base in Ephemeroptera are probably a result of a secondary fusion correlated with weak flight abilities. The paleopterous wing resting position was assumed to be a primitive character by Boudreaux (1979). In contrast, Brodsky (1994), Kukalová-Peck (1991), Rasnitsyn (2002) and Willmann (1998) assumed that Odonata and Ephemeroptera secondarily lost the ability to fold their wings horizontally over the abdomen.

The basalare and subalare are assumed to be of pleural origin. Most authors have no doubt that the basalare and the subalare of Ephemeroptera are the homologue of the respective sclerites in Neoptera (Matsuda 1970; Brodsky 1974; Hasenfuß 2008).

According to these different opinions on the derivation of wings and wing base morphology, the phylogenetic relationships among the three basal clades of Pterygota are likewise controversially discussed (e.g. Börner 1909; Martynov 1925; Lemche 1940; Schwanwitsch 1943; Hennig 1953; Kristensen 1975, 1981, 1991; Fürst von Lieven 2000; Gorb et al. 2000; Staniczek 2000, 2001; Bechly et al. 2001; Hovmöller et al. 2002; Ogden and Whiting 2003, 2005). Recently, Willkommen (2008) presented a homology of wing base sclerites and flight muscles based on morphological investigations.

Materials, methods and abbreviations

Material examined

Ephemeroptera (imagines): *Siphonurus aestivalis* (Eaton, 1903); *Baetis fuscatus* (Linnaeus, 1761), *Centropilum luteolum* (Müller, 1776); *Cloeon dipterum* (Linnaeus, 1761); *Habroleptoides confusa* Sartori & Jacob, 1986; *Habrophlebia lauta* Eaton, 1884; *Paraleptophlebia submarginata* (Stevens, 1836); *Ecdyonurus submontanus* Landa, 1969; *Ecdyonurus venosus* (Fabricius, 1775); *Epeorus assimilis* Eaton, 1885; *Heptagenia coeruleans* (Rostock, 1878); *Heptagenia sulphurea* (Müller, 1776); *Rhithrogena semicolorata* (Curtis, 1834); *Serratella ignita* (Poda, 1761); *Ephemerella danica* Müller, 1764; *Caenis horaria* (Linnaeus, 1758); *Caenis rivulorum* Eaton, 1884; *Ephoron virgo* (Olivier, 1791); *Exeuthyplocia minima* (Ulmer, 1916).

Ephemeroptera (larvae): *Baetis* sp.

Plecoptera (imagines): *Pteronarcys reticulata* Burmeister, 1839; *Isoperla grammatica* Poda, 1761; *Isoperla goertzi* Illies, 1952; *Perlodes microcephalus* Pictet, 1833; *Capnia vidua* Klapálek, 1904; *Brachyptera seticornis* (Klapálek, 1902).

Plecoptera (larvae): *Brachyptera seticornis* (Klapálek, 1902).

Odonata (imagines): *Sympetrum* cf. *striolatum* Müller, 1764.

Most specimens were preserved in 70–80% ethanol and subsequently dissected under a Leica MZ16 stereomicroscope. Drawings were made by using a drawing tube on a Leica MZ16 stereomicroscope. Photographs were made with a Nikon Coolpix camera.

The terminology of muscles primarily follows Matsuda (1970). The terminology of sclerites of Ephemeroptera generally follows Kluge (1994, 2004) except for the wing base sclerites that are termed axillaria (1Ax, 2Ax, 3Ax) herein. Roman numbers indicate mesothoracic (II) or metathoracic (III) elements. Unless otherwise noted, the head is directed to the top in specimens figure in dorsal view, and to the left in specimens figure in lateral view.

Abbreviations

ANP	anterior notal wing process
ASA	anterior subalar apodeme
Ax	axillary sclerite (1Ax, 2Ax, 3Ax = first, second, third axillary sclerite)
A1	anterior anal vein
BA	basalare
BA.Cm	basalar-coxal muscle (sensu Kluge 1994, 2004)
BSc	basisubcostale
BA.SmI	basalar-sternal muscle inferior (sensu Kluge 1994, 2004)
BA.SmS	basalar-sternal muscle superior (sensu Kluge 1994, 2004)
BA.Trm	basalar-trochanteral muscle (sensu Kluge 1994, 2004)
C	costal vein
Cx	coxa
fwp	forewing pad
hwp	hind wing pad
LPs	lateroparapsidal suture
MA	anterior medial vein
p	pleural muscle
PMP	proximal median plate
PNP	posterior notal wing process
PSA	posterior subalar apodeme
PWP	pleural wing process
p-s	pleurosternal muscle
p-ti (cx)	pleurotrochantinal (coxal) muscle
p-tr	trochanteral muscle
R	(anterior) radial vein
Rs	radial sector
SA	subalare
SA.Cm	subalar-coxal muscle
Sc	subcostal vein
t-cx	tergocoxal muscle
t-p	tergopleural muscle
t-s	tergosternal muscle

Results and discussion

Axillary sclerites

The wing base of Ephemeroptera (Figure 1a) is composed of elements which are homologous with the first, second and third axillary (1Ax, 2Ax and 3Ax; Figure 1) of Neoptera (Willkommen 2008). The basal plate of the wing base of Ephemeroptera is most likely the homologue of the neopteran proximal median plate (PMP; Figure 1a) (Willkommen 2008).

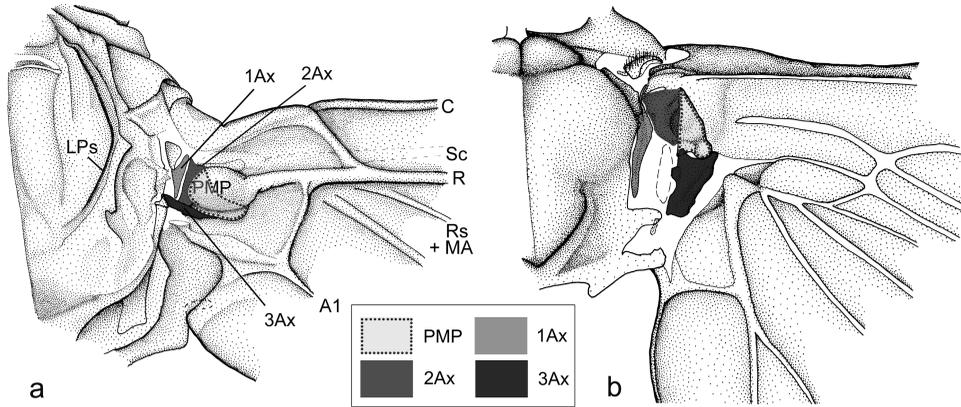


Figure 1. Homology of the axillary sclerites of Ephemeroptera and Neoptera (modified after Willkommen 2008). (a) *Habroleptoides confusa* (Ephemeroptera), right forewing. (b) *Perlodes microcephalus* (Plecoptera), right hind wing.

The 1Ax of Neoptera (Figure 1b) is sclerotised only in the dorsal layer of the wing membrane. It articulates with 2Ax distally and is connected to the subcostal vein (Snodgrass 1935). In the examined Plecoptera there is a muscle attached to the 1Ax, which runs to the pleural ridge (t-p 11; Figure 4b). This muscle is even present in *Capnia vidua*, a brachypterous stonefly. A muscle running from the 1Ax (homology after Willkommen 2008) to the pleural ridge is also present in *Siphonurus aestivalis* (t-p 11 in Figure 2f), *Siphonurus columbianus* McDunnough, 1925 (see Matsuda 1956), and other basal Ephemeroptera (*Parameletus chelifera* Bengtsson, 1908; *Ametropus fragilis* Albarda, 1878; *Metretopus norvegicus* (Eaton, 1871)) (see Brodsky 1974). In most Ephemeroptera there is a second muscle, which extends between 1Ax and the furca. According to Matsuda (1970), this muscle is a plesiomorphic character in Pterygota and homologous with muscle 45 of *Lepisma* sp. (*Zygentoma*). Among adult Pterygota it has been retained only in Ephemeroptera (Matsuda 1970).

The 2Ax of Neoptera is sclerotised in both the dorsal and ventral layer of the wing membrane. It is connected to the 3Ax, the PMP, and the anterior radial vein. On its ventral side the 2Ax articulates with the pleural wing process (PWP) (Snodgrass 1935). A convex axillary flexion line is located proximally to the 2Ax (Wootton 1979). In the ground plan of Neoptera there is no muscle attached to the 2Ax. The 2Ax of Ephemeroptera shows all the above mentioned characters, but it is additionally fused with PMP.

The 3Ax is sclerotised in both the dorsal and ventral layer of the wing membrane. It is connected to the 2Ax, PMP, anal veins, and to the posterior notal wing process (PNP) (Snodgrass 1935). At least one muscle is attached to the 3Ax. In Plecoptera there are two muscles attached to the 3Ax. The first muscle (t-p 14; Figure 4c) is ventrally attached to the pleuron posterior to the PWP. The second muscle (t-p 13; Figure 4c) is attached to the episternum anterior to the pleural ridge.

The 3Ax of nearly all examined Ephemeroptera is tightly connected to the PMP. In *E. danica* for example there is a suture between those elements. There is one muscle (t-p 14, Figure 2e, f) between the 3Ax and the pleuron posterior to the PWP in all examined Ephemeroptera.

Most elements of the wing base of Neoptera are present in the ground plan of Pterygota, namely 1Ax, 2Ax, 3Ax, and PMP. Contrary to previous hypotheses (Snodgrass 1935), two muscles are attached to 1Ax in the ground plan of Pterygota – the axillar-pleural muscle (t-p 11; Figures 2f, 4b) and the axillar-furcal muscle (t-s 3; Figure 2e, f). Among adult Pterygota, the axillar-furcal muscle has been retained only in Ephemeroptera. It is possible that the reduction of the axillar-furcal muscle is an autapomorphic character of Metapterygota (Odonata + Neoptera). It cannot be entirely ruled out that the reduction of the axillar-furcal muscle has happened convergently in Odonata and Neoptera; the Odonata are adapted to a manoeuvrable hunting flight.

Most likely only a single muscle between the 3Ax and the upper part of the pleuron is present in the pterygote ground plan (t-p 14).

On the basis of their different flight adaptation it is more likely that the wing bases of Ephemeroptera (2Ax and PMP fused; Figure 1a) and Odonata (2Ax, PMP and 3Ax fused) are secondarily fused and do not represent the ancestral condition.

The enigmatic question whether the ability to fold the wings horizontally over the abdomen is a ground plan character of Pterygota or rather represents an apomorphic character of Neoptera is still unresolved. The differently specialised flight apparatuses of the two basal lineages of Pterygota (Ephemeroptera and Odonata) together with their different flight behaviour (Ephemeroptera: specialised mating flight; Odonata: adapted to a manoeuvrable hunting flight) suggest that these taxa are more advanced from the groundplan of Pterygota than previously assumed. The inability to fold the wings horizontally over the abdomen could be a result of secondary stiffening in consequence of a partial fusion of the wing base sclerites. The Plecoptera, a basal lineage within the Neoptera, are most likely very close to the pterygote ground plan regarding many aspects of their flight system (Willkommen and Hörnschemeyer 2007; Willkommen 2008). Other than in Ephemeroptera and Odonata, two muscles are attached to the 3Ax in Plecoptera (t-p 13, t-p 14; Figure 4c). The first muscle (t-p 14) extends between the 3Ax and the pleuron next to the PWP. This muscle is also present in Ephemeroptera and Odonata (t-p 14; Figure 2e, f, 3c–e). The second muscle, however, extends between the 3Ax and the episternum (t-p13). This muscle is not present in Ephemeroptera and Odonata. It is either present in the groundplan of Pterygota and reduced in Ephemeroptera and Odonata, which may be associated with the flight adaptations in these groups, or this muscle is a new character of the Neoptera. In the outgroup Zygentoma there are several tergo-pleural muscles present (Barlet 1953, 1954). According to Matsuda (1970), t-p 13 is a new formation of the Pterygota, but Matsuda gives no reasoning for this assumption. It would need a thorough re-examination of the thoracic muscles in primitive Zygentoma to assess this character.

In any case there is not only one muscle attached to the 3Ax in the ground plan of Neoptera as previously assumed, but there is a second muscle (t-p 13) present, extending between the 3Ax and the episternum. The presence of t-p 13 in Neoptera could be the key-character for the ability to fold the wings horizontally over the abdomen.

Pleural wing base sclerites

There are two pleural wing base sclerites present in Pterygota. The basalar (BA) is located anteriorly to the PWP. It articulates with the basisubcostale (BSc) (Brodsky

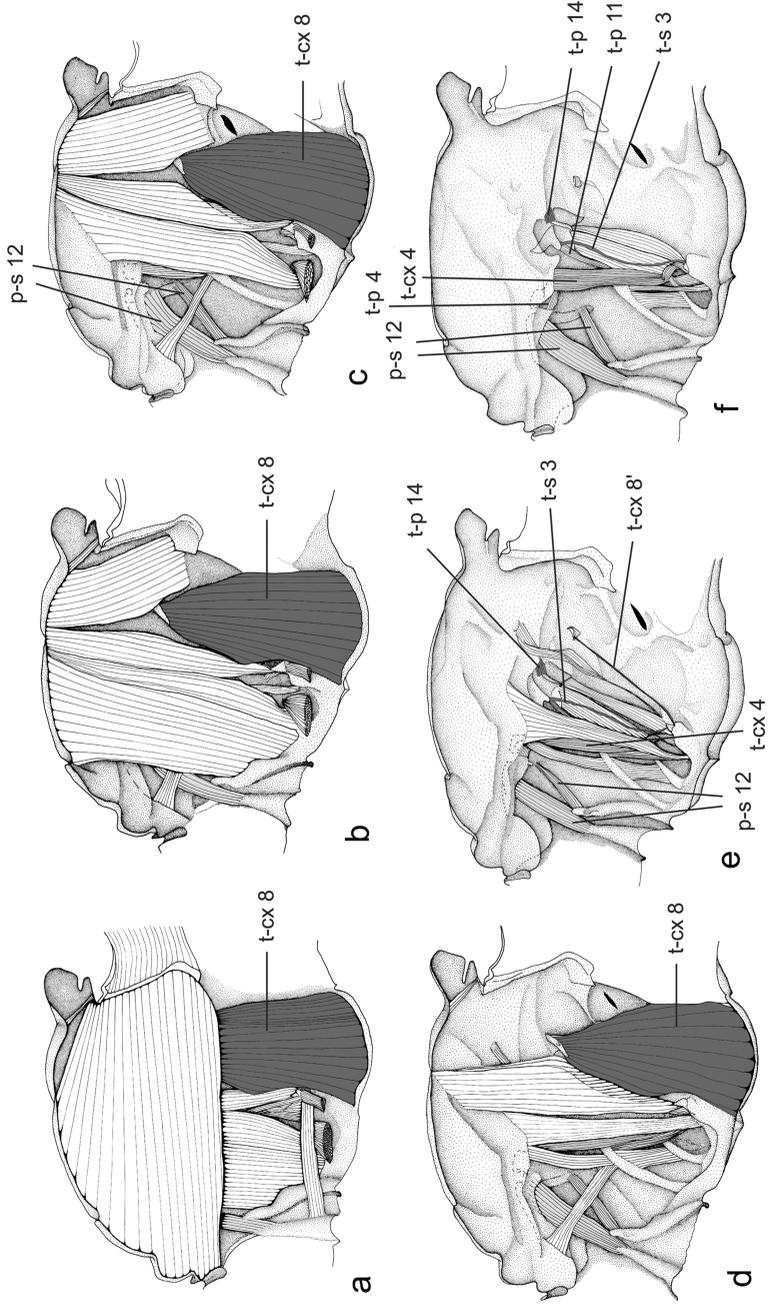


Figure 2a-f. Direct flight muscles of Ephemeroptera (*Siphonurus aestivalis*). Muscle homology after Willkommen 2008 (modified after Willkommen 2008).

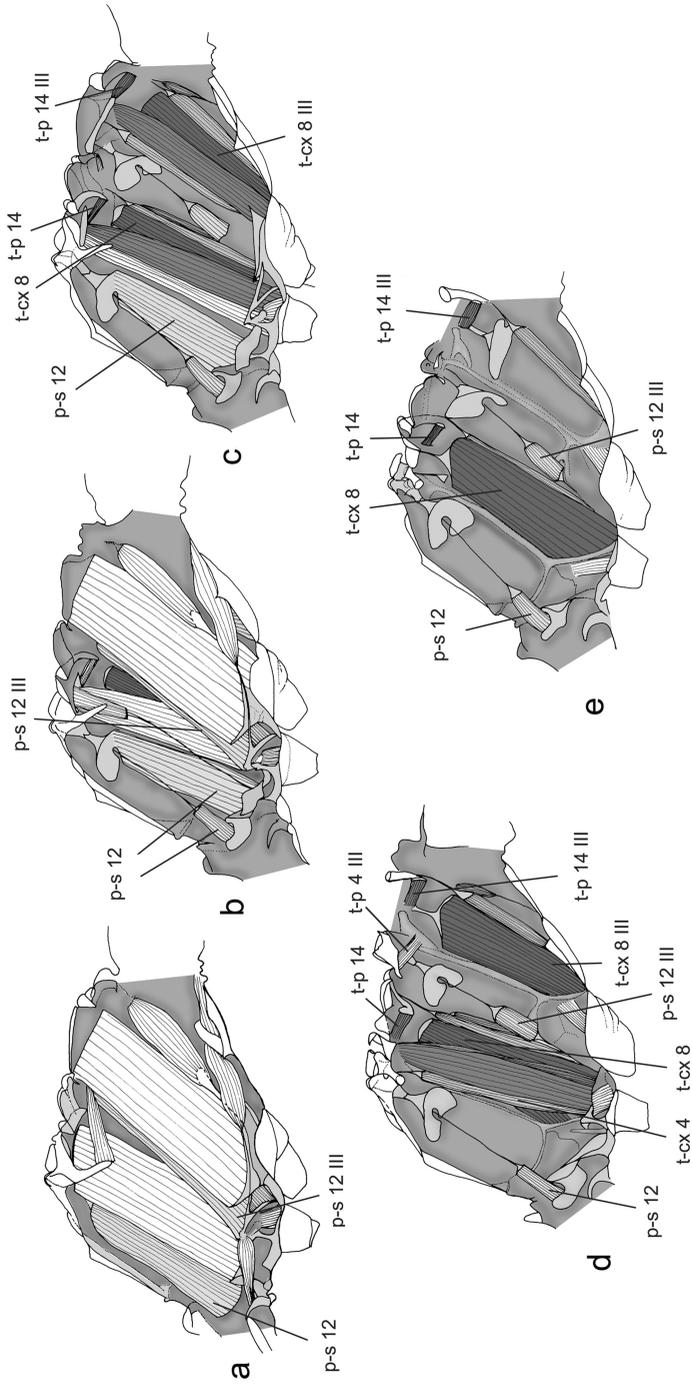


Figure 3a–e. Direct flight muscles of the synthorax of Odonata (*Sympetrum* cf. *striolatum*). Muscle homology after Willkommen 2008 (modified after Willkommen 2008).

1994). The basalare is assumed to be a pleural element (Snodgrass 1935; Matsuda 1970; Hasenfuß 2008). The subalare is located posterior to the pleural wing process. Usually it is also supposed that the subalare is derived from the pleuron (Snodgrass 1935; Hasenfuß 2008), but according to Matsuda (1970), the subalar-coxal muscle is termed t-cx 8 (tergo-coxal muscle), which would imply a tergal origin of the subalare. This terminology was used by Matsuda (1970), because Maki (1938) has shown that this muscle is attached to the lateral part of the tergum in larvae of *Leucophaea* sp. (Blattaria).

Basalare

The basalare is not detached from the episternum in Plecoptera. It articulates anteriorly with the basicostale and posteriorly with the basisubcostale. There are two muscles attached to the basalare. The first muscle is ventrally attached to the coxa, and the second one to the trochanter (Willkommen 2008). There is no generally accepted interpretation of the basalare and its associated muscles in the Ephemeroptera (Table 1).

According to Knox (1935) there are five muscles attached to the basalare in Ephemeroptera: Pm1 and Pm2, which is the paired muscle p-s 12 sensu Matsuda (1970); Pm3, a basalar-trochanteral muscle; Pm4, which is t-cx 4 sensu Matsuda (1970) and Pm5, which is p 5 sensu Matsuda (1970).

Matsuda (1956) mentions only three muscles attached to the basalare of Ephemeroptera (p 5 and the paired p-s 12), but Matsuda (1970) also suspects that p 5 could be t-p 4 (a muscle extending between the laterophragma or the subtegula and the pleural ridge). Matsuda (1970) also mentions a basalar-trochanteral muscle (p-tr 2), which is also listed as an axillar-trochanteral muscle (t-tr 2, see above and Table 1).

Kluge (1994) lists five muscles that are attached to the basalare: BA.Cm – t-cx 4 sensu Matsuda 1970; BA.Pm – p 5 sensu Matsuda 1970; BA.SmI and BA.SmS – the paired p-s 12 sensu Matsuda 1970; BA.Trm.

According to Tsui and Peters (1972) four muscles are attached to the basalare: II-8, II-9, which are the paired p-s12 sensu Matsuda 1970; II10, which is p 5 sensu Matsuda 1970; II-12a.

Brodsky (1974) specifies five muscles attached to the basalare: TTrm2; TCxm5, which is t-cx 4 sensu Matsuda 1970; TSm1 and TSm2, which is the paired p-s 12 sensu Matsuda 1970; TPm3, which is p 5 sensu Matsuda 1970. However, in a compilation (Brodsky 1974, Tables 1, 2) Brodsky lists TTrm2 as absent in all examined Ephemeroptera. Matsuda (1970) also contradicted himself in stating that

Table 1. Different hypotheses on the presence (+), absence (–), or different interpretation (1Ax) of basalar muscles in Ephemeroptera. For explanations of “**” and “***” see text.

	Knox 1935	Matsuda 1956	Matsuda 1970	Tsui and Peters 1972	Brodsky 1974	Kluge 1994
BA.SmS (p-s12)	+	+	+	+	+	+
BA.SmI (p-s 12)I	+	+	+	+	+	+
BA.Pm (p 5)	+	+	+	+	+	+
BA.Cm (t-cx 4)	+	– (1Ax)	– (1Ax/2Ax*)	– (1Ax)	+	+
BA.Trm (p-tr 2)	+	–	– (basalare/1Ax**)	–	?	+

't-cx 4 is attached to the 1Ax in Ephemeroptera' (Matsuda 1970, p. 120, 125), but also mentioning that 't-cx 4 is attached to 2Ax in Ephemeroptera, but to 1Ax in *Ecdyonurus*' (Matsuda 1970, p. 66) (see * in Table 1). Matsuda also interpreted the basalar-trochanteral muscle differently in Ephemeroptera. It is either attached to the basalar and named p-tr 2 (Matsuda 1970: 76, 124), or attached to the 1Ax and named t-tr 2 (Matsuda 1970, p. 75, 120) (see ** in Table 1).

All previous authors agree that the muscles p-s 12 and p 5 are attached to the basalar in Ephemeroptera (Knox 1935; Matsuda 1956, 1970; Tsui and Peters 1972; Brodsky 1974; Kluge 1994). Some authors assume that t-cx 4 is an axillary muscle (Matsuda 1956, 1970; Tsui and Peters 1972) or a basalar-coxal muscle (Kluge 2004). This leads to the question how the basalar is really defined and how many muscles are attached to it in Ephemeroptera.

Most authors have regarded the crescent-shaped sclerite at the anterior wing base of Ephemeroptera as basalar (BA; Figure 5). The morphological study by Willkommen (2008) however revealed that only two of the above mentioned five muscles are attached to this sclerite. In *Siphonurus aestivalis*, the first muscle is dorsally attached to the upper part of the crescent-shaped sclerite and runs to the profurca. The second muscle is stretched between the ventral part of the crescent-shaped sclerite and the presternite (Willkommen 2008). Both muscles correspond to p-s 12 sensu Matsuda (1970) who regarded these two muscles as a unit. The third muscle (p 5), which is generally interpreted as a basalar muscle in Ephemeroptera (Knox 1935; Matsuda 1956, 1970; Tsui and Peters 1972; Brodsky 1974; Kluge 1994), is attached to a separate sclerite. Matsuda (1970) mentioned that p 5 could be t-p 4. The muscle p5 is attached to a sclerite located at the anterior base of the wing, in between tegula and tergum, and posterior to the posterior arc of the prealar bridge. This short muscle is also present in Odonata, where it is assumed to be attached to the 1Ax (Tannert 1958, t-p 11 sensu Matsuda 1970). I assume muscle t-p11 of Odonata (sensu Matsuda 1970) and p 5 of Ephemeroptera to be homologues. These muscles are not basalar or axillar muscles, but rather one and the same muscle (t-p 4 sensu Matsuda 1970) running from the subtegula (or the prescutum in Odonata) to the upper part of the pleuron (Willkommen 2008).

The muscle t-cx 4 is either assumed to be a basalar muscle (Brodsky 1974; Knox 1935; Kluge 1994, 2004) or an axillar muscle (Matsuda 1956, 1970; Tsui and Peters 1972). This muscle is attached to a sclerite lying anteriorly to ANP. It is located posterior to t-p 4, which is not a genuine basalar muscle (see above).

In mayfly larvae, both p-s 12 and t-cx 4 are attached to the tergum (Figure 6), whereas in larvae of Plecoptera the basalar-coxal muscle is attached to the anterior part of the pleural sclerite. The muscles p-s 12 of Ephemeroptera are most likely homologous with two muscles present in Odonata (21, 22 sensu Asahina 1954; p-s 12; Figure 3a-e), which are stretched between the anterolateral part of the humeral plate and the pre-episternal apodeme (Willkommen 2008).

Consequently, the crescent-shaped sclerite at the anterior wing base of Ephemeroptera is most likely homologous to a part of the humeral plate of Odonata. In contrast to Hasenfuß (2008) I assume that these sclerites of Ephemeroptera and Odonata are most likely not homologous with the basalar of Neoptera (Willkommen 2008). Likewise, Kukulová-Peck et al. (2009) assume that the dorsal part of the basalar sclerite of Ephemeroptera (sensu Knox 1935) is homologous to the anterior plate of the wing base of Odonata. The basalar sensu

Knox (1935) is however composed of different sclerites, namely the crescent-shaped sclerite, and two tergal sclerites. The morphological studies by Willkommen (2008) reveal that only the crescent-shaped sclerite is the homologue to a part of the anterior plate of the wing base of Odonata. I assume the anterior tergal sclerite to be the homologue of the subtegula of Neoptera. In the three basal pterygote lineages there is a tergopleural muscle attached to it (t-p 4) (see above). The posterior tergal sclerite is located anteriorly to ANP and posteriorly to the last mentioned sclerite. The muscle t-cx 4 is attached to this sclerite.

Hasenfuß (2008) homologised the basalare of Neoptera with a detached part of the anteriormost of three subcoxal sclerites of *Lepisma saccharina* Linnaeus, 1758 (Iv sensu Hasenfuß 2008). He assumes the homology of trochantinus and pleuron (including basalare) in Lepismatidae (Zygentoma) and Neoptera. Hasenfuß consequently assumes the presence of the trochantinus and basalare in the groundplan of Dicondylia. However, in my point of view the status of the trochantinus and also the presence of the basalare (and the basalar-trochanteral muscle) in Ephemeroptera and Odonata is not confirmed. Furthermore, it is not known if the sclerite Iv is also present in *Tricholepidion gertschi* Wygodzinsky, 1961, which is generally regarded as the basal clade within Zygentoma or even Dicondylia (Bitsch and Bitsch 2000; Staniczek 2000). Barlet (1980) in his investigation of the thorax of *T. gertschi* does not recognise a detached part of the anteriormost of three subcoxal sclerites in this species. To clarify the origin and homology of the trochantinus and the basalare (with the associated muscles) it is necessary to re-examine the plesiomorphic *T. gertschi* in this respect.

Subalare

According to Knox (1935), Kluge (1994) and Matsuda (1956, 1970), three muscles are attached to the subalare of Ephemeroptera – a subalar-coxal muscle (t-cx 8 sensu Matsuda 1970), a subalar-sternal muscle (t-s 5 sensu Matsuda 1970), and a subalar-furcal muscle (t-s 4 sensu Matsuda 1970). Matsuda mentioned that t-s 5 could be a derivative of t-cx 8, but without reasoning. According to Brodsky (1974) four muscles are attached to the subalare of Ephemeroptera because he classified the bipartite subalar-coxal muscle as two separate muscles. Tsui and Peters (1972) also classified the subalar-coxal muscle as two separate muscles, but according to Tsui and Peters (1972) another muscle which is attached to the posterior part of the median plate originates from the subalare in Ephemeroptera. The last mentioned muscle is in fact t-p 14. It is stretched between the 3Ax and the upper part of the pleuron in Ephemeroptera, Odonata and Neoptera. Most authors have no doubt that the subalar-coxal muscle of Ephemeroptera is homologous to the subalar-coxal muscle of Neoptera (Matsuda 1970, Brodsky 1994). The homology of the subalar-sternal muscle and the subalar-furcal muscle is, however, controversial.

In larvae of Plecoptera the future subalare (SA) develops from the membrane above the pleural sclerite, and it is also located there in the imago. A large subalar-coxal muscle (t-cx 8; Figure 4a–c) is attached to the subalare of Plecoptera. In the larvae of Ephemeroptera, the subalar-coxal muscle is attached to the upper part of the pleural sclerite (SA.Cm; Figure 6). The subalar-sternal muscle of Ephemeroptera (t-cx 8; Figure 6) shows the same development as the subalar-coxal muscle in Plecoptera. In the winged stages of Ephemeroptera the subalar muscles are attached

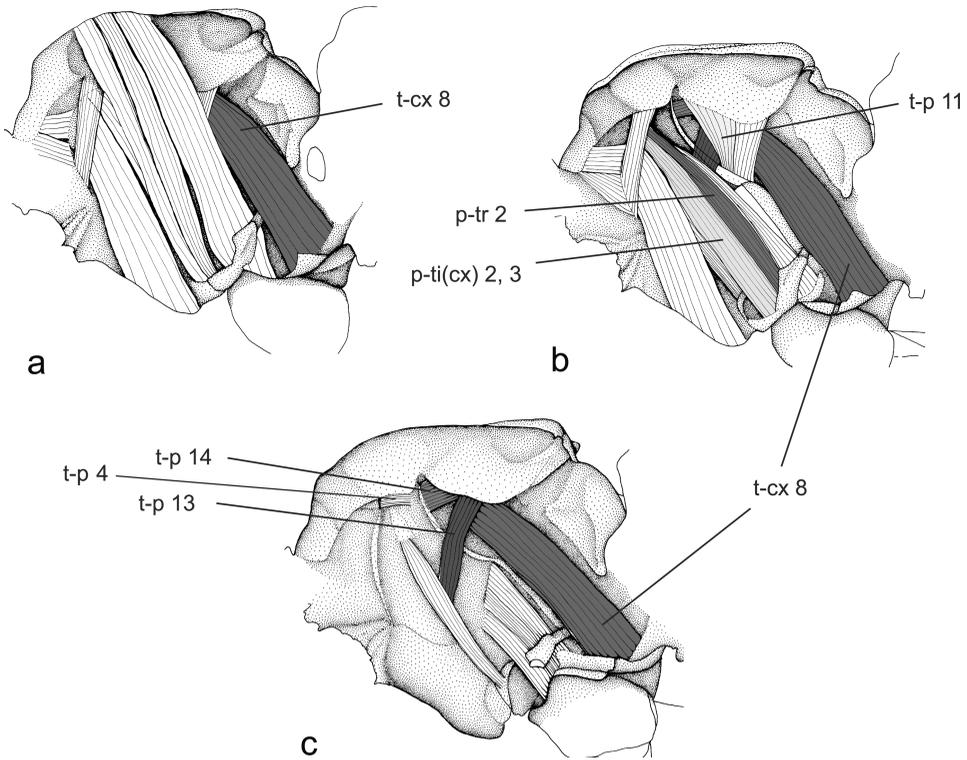


Figure 4a–c. Direct flight muscles of the mesothorax of Plecoptera (*Brachyptera seticornis*). (modified after Willkommen 2008).

to a large sclerite, previously termed subalare, which is located in the membrane above the pleural sclerite (SA; Figure 5). Most likely this sclerite in alate mayflies is a product of a fusion of two sclerites. The subalar-sternal muscle is attached to one of these sclerites. The other sclerite represents the anterior part of the larval pleuron to which the subalar-coxal muscle is attached. So only the posterior part of the subalare of the winged stages of Ephemeroptera is the homologue of the subalare of Plecoptera. The subalar-sternal muscle of Ephemeroptera (t-cx 8; Figure 2a–d) is homologous with the subalar-coxal muscle of Neoptera, but the subalar-coxal muscle of Ephemeroptera (SA.Cm) is most likely not homologous to the subalar-coxal muscle of Neoptera. The subalar-furcal muscle of Ephemeroptera (t-cx8; Figure 2e) is attached to the posterior subalar apodeme (PSA; Figure. 5). Its origin is the same as the origin of the subalar-sternal muscle in mayfly larvae. This indicates that the subalar-furcal muscle could be a derivate of the subalar-sternal muscle of Ephemeroptera, and both muscles together are most likely homologous with the subalar-coxal muscle of Neoptera.

The position of the ventral attachment of the subalar-sternal muscle in the groundplan of Pterygota is not clear. In Ephemeroptera, this muscle is attached to the furcasternum, while in Odonata and Neoptera it is attached to the posterior coxal rim. According to Matsuda t-cx 8 is probably homologous to a tergo-coxal muscle of *Lepisma saccharina*. Brodsky (1974) assumed that the sternal attachment of the subalar-sternal muscle of Ephemeroptera represented a specialisation of the mayfly wing apparatus. Indeed, the subalar-sternal muscle, the subalare, and the

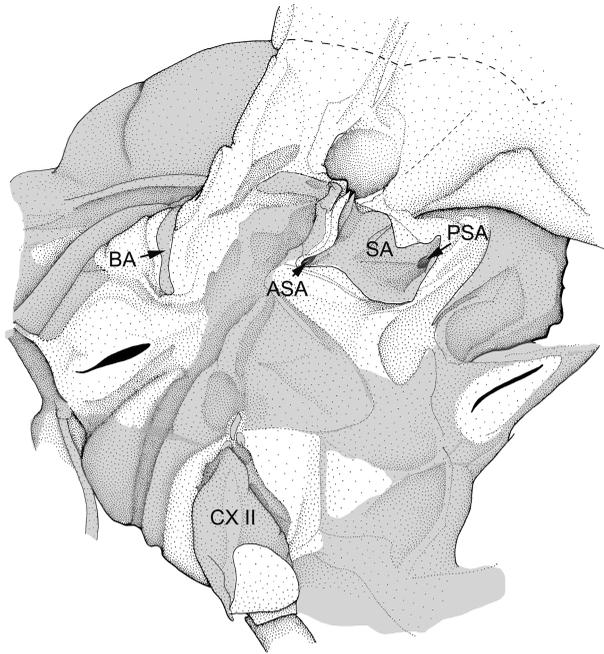


Figure 5. Mesopleuron of a male imago of *Siphonurus aestivalis*. BA – basalare of Ephemeroptera sensu Kluge 2004 (grey areas sclerotised; modified after Willkommen 2008).

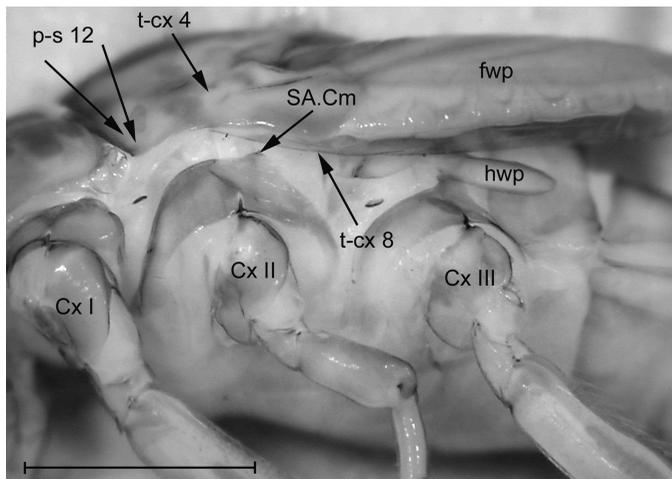


Figure 6. Mesopleuron and metapleuron of a late larva of *Baetis* sp., the arrows show the attachments of the basalare and subalar muscles. SA.Cm – subalar-coxal muscle of Ephemeroptera (terminology sensu Kluge 2004); fwp – forewing pad; hwp – hind wing pad. Scale: 1 mm (modified after Willkommen 2008).

furcasternite of Ephemeroptera are obviously enlarged. Correlated with these specialisations it is likely that the ventral attachment of the pterygote subalar-coxal muscle has shifted to the furcasternum in Ephemeroptera. From this, it is concluded that the loss of the subalar-sternal muscle can no longer be considered an

autapomorphy of Metapterygota as a homologue of this muscle is present in both Odonata and Neoptera (Willkommen 2008).

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