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The homology of wing base sclerites and flight muscles in Ephemeroptera and Neoptera and the morphology of the pterothorax of *Habroleptoides confusa* (Insecta: Ephemeroptera: Leptophlebiidae)

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Abstract

The ability to fly is the decisive factor for the evolutionary success of winged insects (Pterygota). Despite this, very little is known about the ground-pattern and evolution of the functionally very important wing base. Here we use the Ephemeroptera, usually regarded as the most ancient flying insects, as a model for the analysis of the flight musculature and the sclerites of the wing base. Morphology and anatomy of the pterothorax of 13 species of Ephemeroptera and five species of Plecoptera were examined and a detailed description of *Habroleptoides confusa* (Ephemeroptera: Leptophlebiidae) is given. A new homology of the wing base sclerites in Ephemeroptera is proposed. The wing base of Ephemeroptera possesses three axillary sclerites that are homologous to the first axillary, the second axillary and the third axillary of Neoptera. For example, the third axillary possesses the axillary-pleural muscle that mostly is considered as a characteristic feature of the Neoptera. Many of the muscles and sclerites of the flight system of the Ephemeroptera and Neoptera can be readily homologised. In fact, there are indications that a foldable wing base may be a ground plan feature of pterygote insects and that the non-foldable wing base of the Ephemeroptera is a derived state.

Keywords: Palaeoptera; Metapterygota; Insect flight evolution

Abbreviations: A, anal vein; A1, anterior anal vein; ab, anal brace; AEM, anepimeron; AES, anepisternum; ALSC, anterolateral scutal costa; ANi, anteronotal transverse impression; ANP, anterior notal wing process; ANp, anteronotal protuberance; AS I, abdominal sternite I; ASA, anterior subalar apodeme; 1Ax, first axillary sclerite; 2Ax, second axillary sclerite; 3Ax, third axillary sclerite; AxC, axillary cord; Ax.Fm, axillar-furcal muscle; axp, axillary plate; Ax.PmI, inferior axillar-pleural muscle; Ax.PmS, superior axillar-pleural muscle; BA, basalare; BA.Cm, basalar-coxal muscle; BAd, dorsal part of basalar sclerite; ban, basanale; BA.Pm, basalar-pleural muscle; BA.SmI, inferior basalar-sternal muscle; BA.SmS, superior basalar-sternal muscle; BA.Trm, basalar-trochanteral muscle; BP, basal plate; BPp, ventral process of basal plate; BS, basisternum; BSc, basisubcostale; C, costal vein; cb, costal brace; Cu, cubital vein; CuA, anterior cubital vein; Cx, coxa (Cx II - coxa of mesothorax / Cx III - coxa of metathorax); DMP, distal median plate; F.CmA, anterior furco-coxal muscle; F.CmP, posterior furco-coxal muscle; Fm, furcal muscle; FS, furcasternum; fw, fore wing; hp, humeral plate (Odonata); HP, humeral plate; hw, hind wing; iFm, intersegmental furcal muscle; KES, katepisternum; LPN, lateropostnotum; LPNC, lateropostnotal crest; LPs, lateroparapsidal suture; M/ MA, anterior medial vein; MLs, median longitudinal suture; MNP, median notal wing process; MNs, mesonotal suture; MP, posterior medial vein; MPs, medioparapsidal suture; MTm, median tergal muscle; P.Cm, pleuro-coxal muscle; PCxsA, anterior paracoxal suture; PCxsP, posterior paracoxal suture; PLs, pleural suture; PLsI, inferior pleural suture; PMP, proximal median plate; PNP, posterior notal wing process; PSA, posterior subalar apodeme; PSL.Cm, parascutello-coxal muscle; PSp, posterior scutal protuberance; PST, presternite; Pt 1, pterale 1; P.Trm, pleuro-trochanteral muscle; PWP, pleural wing process; R, anterior radial vein; Rs, radial sector; S, spiracle; S III, sternum III (sternum of the metathorax); SA, subalare; SA.Cm, subalar-coxal muscle; SA.Fm, subalar-furcal muscle; SAs, subalar suture; SA.Sm, subalar-sternal muscle; Sc, subcostal vein; S.CmA, anterior scuto-coxal muscle; S.CmP, posterior scuto-coxal muscle; S.ESm, scuto-episternal muscle; SL, scutellum; S.LPNm, scuto-lateropostnotal muscle; SrA.Pm, suralar-pleural muscle; S.Trm, scuto-trochanteral muscle; s1, s2, s3, s5, wing base sclerite 1-3, 5; T, tegula.

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1. Introduction

The development of wings in insects was the key to the evolutionary success of this diverse group. Despite the long history of research into wings and their venation (Comstock, 1918; Comstock and Needham, 1898, 1899; Hamilton, 1971, 1972a,b,c) the derivation of the wings and the evolution of the wing base sclerites are still uncertain and the phylogenetic relationships among basal Pterygota remain controversial. For the relationships of Ephemeroptera, Odonata and Neoptera there are at least two hypotheses, each of which is supported by different characters. Based on the current knowledge, it is difficult to arrive at a conclusive decision between the two hypotheses.

The first possibility is the Palaeoptera hypothesis (Fig. 24), which states that Ephemeroptera and Odonata are sistergroups. Supporting characters for this hypothesis are the inability to fold the wings over the abdomen and the similar wing base sclerites (Hennig, 1969; Kukalová-Peck, 1978, 1985, 1991; Martynov, 1925; Rasnitsyn, 2002; Wootton, 1979) in both taxa. Furthermore, the anal brace, the intercalary veins, the proximate stem of the anterior radial vein (RA) and the posterior radial vein (RP) as well as the common stem of anterior medial vein (MA) and posterior medial vein (MP) are plesiomorphic characters of Ephemeroptera and Odonata (Kukalová-Peck, 1983, 1985, 1991, 1998; Kukalová-Peck and Brauckmann, 1990; Riek and Kukalová-Peck, 1984; Staniczek, 2001). The paired penes could be a further supporting character for the Palaeoptera hypothesis (Bechly et al., 2001) but it is controversial if this is an apomorphic character of the Palaeoptera or a plesiomorphic character of the Insecta. The wing base sclerites of Ephemeroptera and Odonata, at first sight, appear very different from those of the Neoptera. The hypothesis that the flight systems of Ephemeroptera and Odonata are plesiomorphic in terms of the few wing base sclerites and the disability to fold the wings over the abdomen seems to be generally accepted. The larger number of wing base sclerites and the presence of an axillary-pleural muscle in Neoptera that allow moving the wings to a resting position over the abdomen are interpreted as derived characters (Matsuda, 1970; Snodgrass, 1935). In contrast, Kukalová-Peck (1983, 1987, 1991) assumed that the few wing base elements in Ephemeroptera and Odonata were a result of a secondary fusion from the pterygotan ground plan of a wing base with 32 sclerites. Hence, this condition is considered to be apomorphic. With reference to Kukalová-Peck (1974b), Boudreaux (1979) presumed that the wing base elements in Ephemeroptera are probably a result of a secondary fusion correlated with their weak flight ability but that the inability to fold the wings back over the abdomen is a primitive character of mayflies. Brodsky (1994) also hypothesised a fusion of sclerites, but originating from a condition that was more similar to the neopteran wing base. A loss of the ability to fold the wings over the abdomen in Odonata and Ephemeroptera is assumed only by Brodsky (1994) and Rasnitsyn (2002).

Conversely, a sistergroup relationship of Odonata and Neoptera (= Metapterygota; Fig. 25) is supported by several apomorphic characters, e.g. the number and position of the articulations of the mandibles, by the loss of several muscles of the mandibles (Börner, 1909; Hennig, 1953; Kristensen, 1975, 1981, 1991; Staniczek, 2000, 2001) and by the absence of the subimago and the terminalfilum (Staniczek, 2001). Odonata and Neoptera lack the ecdysis in the winged stage (Kristensen, 1981; Willmann, 2002).

Regardless of the disagreement on the basal relationships of the Pterygota there remains the question whether the wing base of the Ephemeroptera or of the Neoptera represents the more primitive state.

1.1. The wing base of the Neoptera

In the ground pattern of Neoptera the wing base (Figs. 1, 23a) is composed of three axillary sclerites (1–3Ax), two median plates (PMP, proximal median plate; DMP, distal median plate) and the associated notal wing processes (ANP, MNP, PNP).

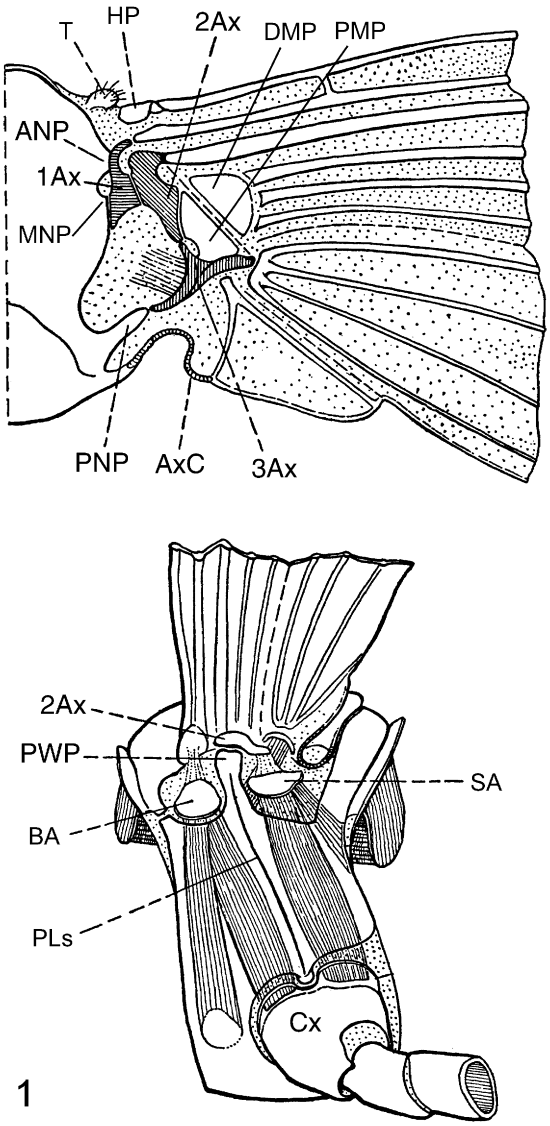


Fig. 1. Schematic representation of neopterous wing base. Top: dorsal view, bottom: lateral view, head to the left [after Snodgrass, (1935: figs. 122, 129 modified)].

Furthermore, there is the basalar sclerite (BA) anterior to the pleural wing process (PWP) and the subalar sclerite (SA) posterior to the pleural wing process (Fig. 1). The first axillary sclerite (1Ax) articulates proximally with the anterior (ANP) and the median notal wing process (MNP) of the associated notum. Distally it is connected to the base of the subcostal vein and to the second axillary sclerite (2Ax). The 2Ax articulates with the base of the radial vein, with the proximal median plate (PMP) and with the third axillary sclerite (3Ax). In Neoptera the 2Ax is also sclerotized in the ventral layer of the wing membrane. A ventral process of this sclerite articulates with the pleural wing process (PWP). The third axillary sclerite (3Ax) is connected to the 2Ax, the proximal median plate (PMP), the posterior notal wing process (PNP) and to the anal veins and jugal veins (Brodsky, 1994; Hörnschemeyer, 2002; Snodgrass, 1935). A muscle (t-p 14, Matsuda, 1970) inserts on the 3Ax and runs to the dorsal part of the pleural ridge. This muscle enables the Neoptera together with the wing base morphology (e.g. shape of the axillary sclerites, flexion-lines) to fold their wings over the abdomen. Furthermore, the 1Ax (Section 4), the ANP and the PNP are each provided with a muscle that runs to the pleurum. Additional direct wing muscles in Neoptera are at least two basalar muscles (basalar-trochanteral muscle, basalar-coxal muscle) and one or two subalar muscles (subalar-coxal muscle, subalar-pleural muscle).

1.2. Current hypotheses on the evolution and homology of wing base sclerites

The wing base sclerites of Ephemeroptera are named first, second, third sclerite and fifth sclerite (s1, s2, s3 and s5, Fig. 2) because the interpretation of the homologies to neopteran axillary sclerites is inconsistent within different works. Their homology will be discussed later in the paper.

Hitherto, the question of the evolution of the flight muscles and of the homology of the wing base sclerites has been answered differently by several authors (Bekker, 1954; Brodsky, 1970, 1974, 1994; Grandi, 1947; Kluge, 1994, 2004; Kukalová-Peck, 1974a,b, 1978, 1983, 1985, 1987; Kukalová-Peck and Brauckmann, 1990; Matsuda, 1956, 1970; Tsui and Peters, 1972).

Grandi (1947) proposed that the sclerites of the ephemeropteran wing base are ‘‘pseudopteralia’’ without homology to the sclerites of the Neoptera. There are three pseudopteralia: the ‘‘pseudopterale prossimale’’ (primo), the ‘‘pseudopterale mediale’’ (secondo) and the ‘‘pseudopterale distale’’ (terzo) (Grandi, 1947).

Bekker (1954) assumes that the movements of the wings are regulated through five sclerites, of which three sclerites are located between the wing and the tergum: the anterior axillary sclerite (aAx), the first axillary sclerite (1Ax) and the fourth axillary sclerite (4Ax). The two further sclerites (2Ax and 3Ax) correspond to the 2Ax and 3Ax of Neoptera. Bekker (1954) hypothesised that the s1 is the anterior axillary sclerite, the s2 is the 1Ax and the whole basal plate is the 2Ax (in difference to Brodsky, 1970) and that the s3 is the 3Ax.

Kluge (1994, 2004) termed the first sclerite (s1) of the ephemeropteran wing base the ‘‘anterior axillary sclerite’’ (term used by Bekker, 1954: aAx), the second sclerite (s2) is termed the ‘‘middle axillary sclerite’’ and the third sclerite (s3) is termed the ‘‘posterior articulatory process’’ on the grounds that there ‘‘is no agreement on homologisation of these sclerites with axillary sclerites of Neoptera’’ (Kluge, 1994: 57).

Kukalová-Peck (1983, 1987) suggested that the wing articulation, namely the axillary sclerites, originated from an additional part of the pleura which was articulated above the subcoxa. In her opinion, there are 32 wing base sclerites in the ground pattern of the Pterygota. These sclerites were arranged in eight rows with the proxalaria, the axalaria, the fulcalaria and the basivenales (from proximal to distal) (Kukalová-Peck, 1983, 1987, 1998). The proxalaria originated from the epicoxa and the axalaria and the fulcalaria probably originated from the wing membrane.

Matsuda (1956) homologised the s1 and s2 (Figs. 2, 6, 7) with the 1Ax and the 2Ax of Neoptera (Fig. 2). Furthermore, the additional sclerite (s5, Fig. 2) in the wing base of Ephemeroptera is interpreted as homologous to the third axillary sclerite (3Ax) of the neopteran wing base. The muscle that is attached to the posterior part of the second free sclerite (s2) (in Matsuda's opinion the homologous sclerite to the 2Ax) was shifted anteriorly from the 3Ax (s5, Fig. 2). Consequently, the absence of the 3Ax in some mayfly species must apparently be secondary. The same homology for the 1Ax and the 2Ax is given by Tsui and Peters (1972).

Two relevant papers of Brodsky (1970, 1974) presented contradictory conclusions. In Brodsky (1970) it was proposed that the s1 is homologous to the ANP of Neoptera and that the s2 is homologous to the 1Ax (Fig. 3). The 2Ax is interpreted as immobile fused with the basal plate and s3 should be the homologous structure to the 3Ax of Neoptera. In the later paper, Brodsky (1974) homologised the sclerites as given in Fig. 4 without a reference to Brodsky (1970). Furthermore, it is assumed that the additional sclerite (s5, Fig. 4) in the wing base of Ephemeroptera is the MNP, which is not homologous to that of Neoptera because it is not articulated with the 1Ax as it is in Neoptera (Brodsky, 1974).

In addition to the above mentioned authors, Knox (1935) examined the thorax of *Hexagenia recurvata* (Ephemeroptera) but she does not interpret the wing base sclerites.

These different interpretations show that the problem of homology of the wing base sclerites is still unsolved.

The aim of our study is to ascertain if, and to what extent the wing base sclerites of the Ephemeroptera can be homologised with the elements of the neopteran wing base. A well-founded hypothesis for this homology would allow a reconstruction of the wing base ground pattern of the Pterygota. The Ephemeroptera, as the most basal extant winged insects, form the basis for this study. These investigations are complemented by studies of the Plecoptera, the taxon that probably represents morphologically the most primitive member of the Neoptera.

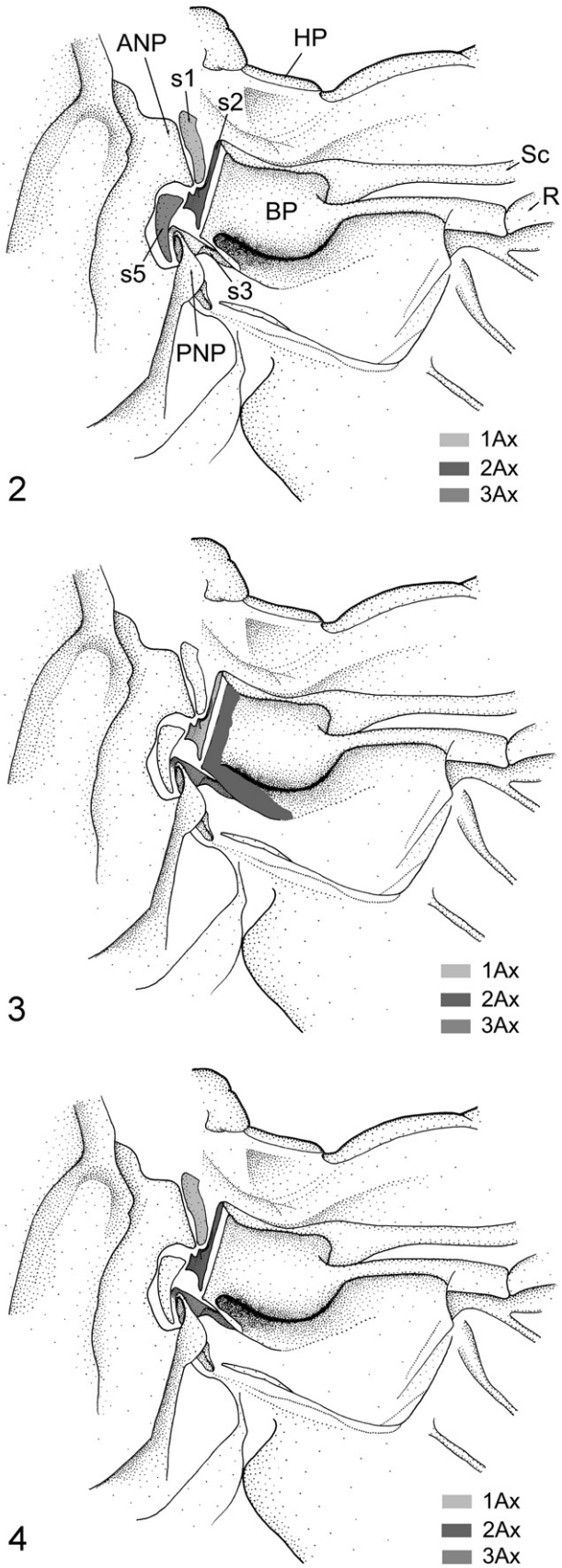


Fig. 2–4. Homology of the ephemeropteran wing base sclerites (right fore wing of *Rhithrogena semicolorata*) with the neopteran wing base sclerites. (2) After Matsuda (1956). (3) After Brodsky (1970). (4) After Brodsky (1974).

2. Materials and methods

2.1. Specimens examined

With the exception of *Siphlonurus aestivalis* (Eaton, 1903) and *Pteronarcys reticulata* (Burmeister, 1839) all specimens were collected in Germany.

Ephemeroptera:
- Leptophlebiidae: *Habroleptoides confusa* Sartori & Jacob, 1986 (Nieme: Lower Saxony; 9 specimens).
- Siphlonuridae: *Siphlonurus aestivalis* Eaton, 1903 (Swiss; J-L. Gattolliat leg.)
- Leptophlebiidae: *Paraleptophlebia* (*Leptophlebia*) *submarginata* (Stevens, 183) (Danube: Baden-Württemberg; 3 specimens)
- Heptageniidae: *Epeorus assimilis* Eaton, 1885 (Nieme: Lower Saxony; 4 specimens), *Ecdyonurus submontanus* Landa, 1969 (Nieme: Lower Saxony; 7 specimens), *Rhithrogena semicolorata* Curtis, 1834; (Goldersbach: Baden-Württemberg; 12 specimens)
- Ephemerellidae: *Serratella ignita* Poda, 1761 (Danube, Neckar: Baden-Württemberg, Nieme: Lower Saxony; 20 specimens)
- Ephemeridae: *Ephemera danica* Mueller, 1764 (Goldersbach, Neckar: Baden-Württemberg; 9 specimens)
- Caenidae: *Caenis rivulorum* Eaton, 1884 (Danube: Baden-Württemberg; 7 specimens)
- Polymitarcyidae: *Ephoron virgo* Olivier, 1791 (Neckar: Baden-Württemberg (A.H. Staniczek leg.), Rhine: (J. Brinkmann leg.); 6 specimens)
- Baetidae: *Baetis* sp. (Neckar: Baden-Württemberg; 20 specimens), *Centroptilum luteolum* O.F. Müller, 1776 (Neckar: Baden-Württemberg; 12 specimens), *Cloeon dipterum* Linnaeus, 1761 (Main: Bavaria; 5 specimens), *Baetis* sp. (larvae, Neckar: Baden-Württemberg; 2 specimens)

Plecoptera:
- Pteronarcidae: *Pteronarcys reticulata* (Australia; P. Zwick leg.)
- Perlodidae: *Isoperla grammatica* Poda, 1761 (Goldersbach: Baden-Württemberg, Nieme: Lower Saxony; 3 specimens)
- Capniidae: *Capnia vidua* Klapálek, 1904 (Oder: Lower Saxony; 3 specimens)
- Taeniopterygidae: *Brachyptera seticornis* Klapálek, 1902 (Nieme, Zorge, Wolfsbach, Kunzenbach: Lower Saxony; 4 specimens)
- Leuctridae: *Leuctra hippopus* Kempny, 1899 (Zorge: Lower Saxony; 5 specimens)

2.2. Methods

The majority of the specimens were collected directly into 80% ethanol. Several specimens were collected into Duboscq-Brasil (Romeis, 1989) and transferred later to 80% ethanol. A minimum of three and up to 20 specimens of each species were examined and dissected under a Leica MZ16 stereomicroscope. Some of the specimens were transferred into 5%

potassium hydroxide solution at room temperature for 1–3 days until the soft tissues dissolved. After rinsing with distilled water, these cleared specimens were transferred again into 80% ethanol for further examination of the sclerites. The examination of the muscles was done with sagittal sectioning of the specimens. The drawings were made with a *camera lucida* on a Leica MZ16 stereomicroscope.

Specimens for scanning electron microscopy (SEM) were transferred gradually into 100% ethanol and dried in a Balzer CPD 030 critical point dryer. The dry specimens were sputter-coated with gold (Balzers SCD050 sputter coater). The examination and photographs were made with a Leo 438VP scanning electron microscope.

Species of which only few specimens were available were investigated by high resolution X-ray tomography (μCT) at the Federal Institute for Materials Research and Testing, Berlin (BAM). These specimens were prepared in the same way as those used for SEM investigation.

The nomenclature of muscles and sclerites primarily follows Kluge (1994, 2004). For comparison, the muscle nomenclature used by other authors is given in Table 1.

3. Results

3.1. Morphology of the pterothorax of Habroleptoides confusa

3.1.1. External morphology of the mesothoracic notum (Figs. 5, 6, 7)

The mesothorax is larger and better developed than the metathorax. The sutures and sclerites are more distinct, the wings are longer and wider and the flight muscles are much stronger in the meso- than in the metathorax.

Table 1
Comparison of muscles names used by different authors

Kluge (1994) and this paper	Brodsky (1974)	Matsuda (1970)
An.Pm	TPm6	
Ax.Fm	TSm5	t-s 3
Ax.PmI	TPm4	t-p 13
Ax.PmS	TPm5	t-p 14
BA.Cm	TCxm5	t-cx 4
BA.Pm	TPm3	t-p 4
BA.SmI	TSm2	p-s 12
BA.SmS	TSm1	p-s 12
BA.Trm	TTrm2	p-tr 2
F.CmA		s-cx 5
F.CmP		s-cx 2
Fm		
iFm		
MTm	Tm1	t 14
P.Cm		p-cx 5
P.Trm		p-tr 1
PSL.Cm	TCxm4	
S.CmA	TCxm1	t-ti 3
S.CmP	TCxm2/3	t-cx 7
S.ESm	TPm1	t-p 5, 6
S.LPNm	Tm2	t 12
S.Trm	TTrm1	t-tr 1
SA.Cm	TCxm6/7	t-cx8
SA.Fm	TSm4	t-s 4
SA.Sm	TSm3	t-s 5
SrA.Pm	TPm2	t-p 10
	Tm3	t 13

The acrotergite at the front of the mesonotum separates the prothorax from the mesothorax. The scutum is divided into several concave and convex areas. The anteriormost convexity is the anteronotal protuberance, which posteriorly ends in a distinct transverse impression (ANp, ANi in Figs. 5, 7). A second convexity is the paired posterior scutal protuberance (PSp in Figs. 5, 7), which is the place of attachment of the scuto-lateropostnotal muscles (S.LPNm in Figs. 13, 14). Posteriorly of this convexity lies the prominent scutellum (SL in Fig. 5).

The median longitudinal suture (MLs in Fig. 5) of the scutum is concave and clearly visible in males and females of *H. confusa*. This suture is absent from the posterior part of the tergum. The medioparapsidal sutures (MPs in Fig. 7) laterad of the median suture are less distinct. These sutures are a little more conspicuous in adult than in subadult specimens. Laterad of the medioparapsidal sutures are the lateroparapsidal sutures (LPs in Figs. 5, 7). These sutures are deep and wide in adults and subadults of male and female specimens. The anterolateral scutal costa (ALSC in Fig. 5) is located anterior of the lateroparapsidal sutures. Across the anterior part of the scutum runs the well developed mesonotal suture (MNs in Fig. 5). A further paired suture, which has its origin in the mesonotal suture, runs posterially (medially of the medioparapsidal sutures and parallel to them) and turns anteriorly again (laterad of the medioparapsidal sutures). This extension is more distinct in adult specimens than in subadult ones. In subadult specimens there is a distinct pigmentation in this area.

Habroleptoides confusa has conspicuous anterior and posterior notal wing processes (ANP, PNP in Figs. 5–7). These structures articulate with sclerites of the wing base. The anterior notal wing process is about as long as wide and articulates with the first free sclerite in the wing base (s1). The posterior notal wing process is more slender and articulates with the third sclerite (s3) of the wing base (Figs. 5–7).

The tegula (T in Fig. 5) is rather elongated and scarcely covered with short, inconspicuous setae in subadult specimens. In adult specimens, these setae are usually missing. Proximally of the tegula lies a sclerite (BAd in Figs. 7 and 9) that is directly associated with the basalar sclerite. This sclerite is the point of the dorsal attachment of a short but robust basalar-pleural muscle (BA.Pm, Fig. 17) and a well developed basalar-coxal muscle (BA.Cm Figs. 15, 16).

The most distinct structure in the wing base is the convex basal plate (BP in Figs. 6, 7). The well-sclerotised base of the subcosta is located on its anterior and ventral side (BSc in Fig. 10). The base of the radial vein is attached to about the middle of the basal plate. There is a flat and well-sclerotised part on the proximal margin of the basal plate that has a ventral process in the anterior area (BPp in Fig. 9). This process articulates with the pleural wing process (PWP in Figs. 9, 10).

The costal vein (C) and the anterior radial vein (R) are coupled by the characteristic costal brace (cb in Figs. 6, 7). The anal brace (ab in Figs. 6–8) is located between the radial vein and the well sclerotised basanale (ban in Figs. 5–7).

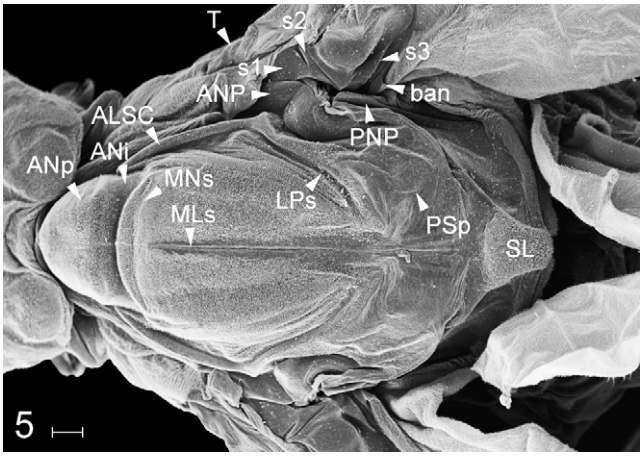


Fig. 5. Mesotergum and wing base of *H. confusa*, SEM image. Dorsal view, head to the left (scale bar 100 μm).

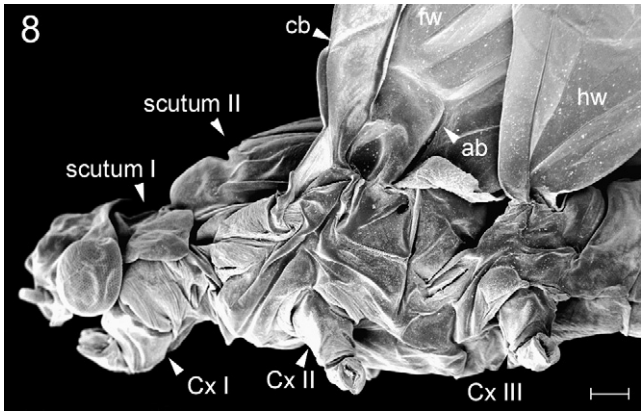


Fig. 8. Pleurum of *H. confusa*. Lateral overview of the pro-, meso- and metathoracic pleurum of a female imago, SEM image (scale bar 200 μm).

Furthermore, there are three sclerites in the wing base (s1, s2, s3 in Figs. 5–7). The first sclerite (s1) articulates with the anterior notal wing process and with the second sclerite. The second sclerite (s2) articulates distally with the basal plate and with the third sclerite on its posterior end. The two sclerites s1 and s2 are rather inconspicuous. The third sclerite (s3) is connected to the posterior part of the basal plate. Proximally it articulates with the posterior notal wing process. About two-thirds of this sclerite are fused with the basal plate. The wing veins have no direct articulation with the three sclerites (s1, s2 and s3) of the wing base.

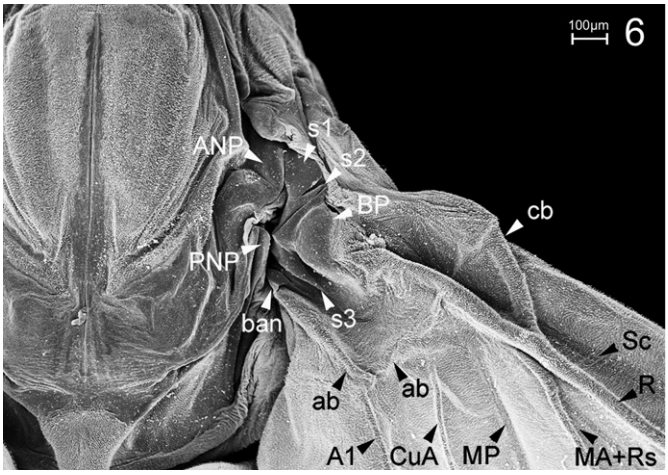
3.1.2. External morphology of the mesothoracic pleurum (overview Fig. 8, and Figs. 9 and 10)

The pleurum in Ephemeroptera is less robust than in most other Pterygota because the sclerites are separated by comparatively large membranous areas.

The dorsal arc of the prealar bridge on the anterior side of the mesothorax is extended ventrally and touches the ventral arc (not pictured). Posteriorly to the prealar bridge is a large membranous area with the spiracle (S in Figs. 9 and 10) and the basalar sclerite (BA in Figs. 9, 10). The most distinct suture in the mesothorax of *H. confusa* is the paracoxal suture, which extends dorsally into the pleural suture. The paracoxal suture (= precoxal suture) is divided into an anterior and a posterior part (PCxsA, PCxsP in Figs. 9, 10). The anterior paracoxal suture divides the anterior anepisternum (AES in Figs. 9, 10) from the posterior katepisternum (KES in Figs. 9, 10). The AES and the KES are about equal in width. The posterior paracoxal suture is slightly less distinct than the anterior paracoxal suture. It divides the dorsal anepimeron from the ventral katepimeron. The anepimeron is slightly more slender than the katepimeron.

The pleural suture (PLs in Figs. 9, 10) is well developed and runs nearly vertically. It is about half as broad as the anterior paracoxal suture. Dorsally the pleural suture extends into the distinct pleural wing process (PWP in Figs. 9, 10). The externally visible condylus of the pleural wing process—the fulcrum—is rather small. It articulates with a ventral process of the basal plate (BPp in Fig. 9). Ventrally the pleural suture ends at the point where the coxa (Cx) is articulated with the pleurum.

The basalar sclerite (BA in Figs. 9, 10) is distinct, and is a small, slender crescent-shaped sclerite at the anterior base



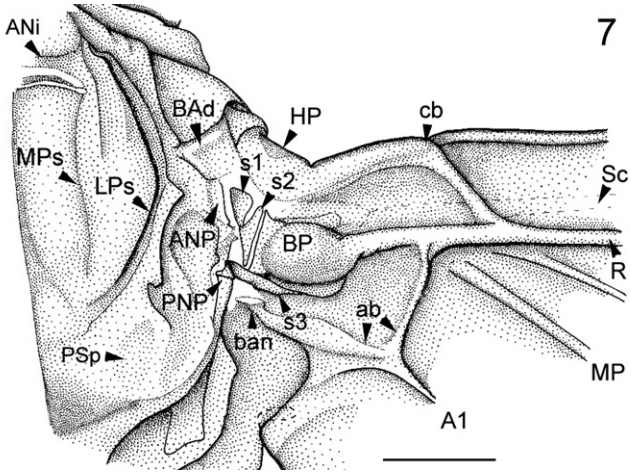
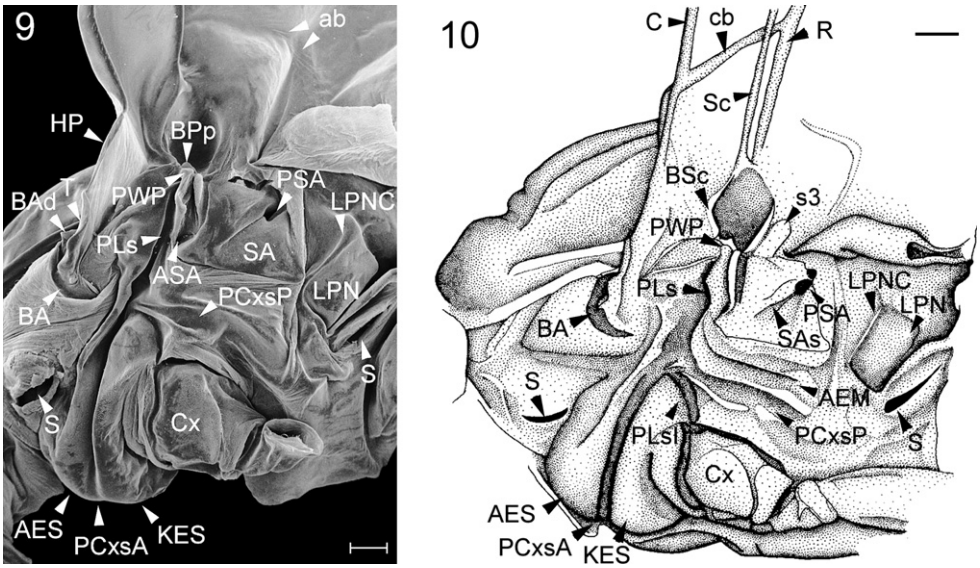


Fig. 6 and 7. Base of right fore wing of *H. confusa* (dorsal view). Scanning electron microscope picture of a female subimago of *H. confusa* (scale bar 100 μm). Drawing of the right fore wing of *H. confusa* (scale bar 0.5 mm).



Figs. 9–10. Pleurum of *H. confusa*. Scanning electron microscope picture of the mesothoracic pleurum of a female imago (head to the left) (scale bar 100 μm). Drawing of the mesothoracic pleurum (head to the left) (scale bar 100 μm).

of the wing. It articulates posteriorly with the tegula (T in Figs. 5, 9) and dorsally with the scutum.

The subalar sclerite (SA in Fig. 9) is a very conspicuous element of the pleurum of the mesothorax. It is about trapezoidal and its anterio-dorsal part is less sclerotised than the posterio-ventral part. The latter is triangular and more pigmented with a distinct suture (SAs Fig. 10) running anterio-ventrad from a distinct pit: the subalar apodeme (posterior subalar apodeme, PSA in Figs. 9, 10). The posterior subalar apodeme is the point of the dorsal insertion of the subalar-sternal muscle (SA.Sm in Figs. 12–15). The anterio-dorsal part of the subalar sclerite is rectangular, with a well sclerotised part that runs alongside the pleural wing process. Ventrally it extends into a distinct suture with a second and smaller apodeme (anterior subalar apodeme, ASA in Fig. 9) at its ventral end where the subalar-coxal muscle inserts (SA.Cm Fig. 17).

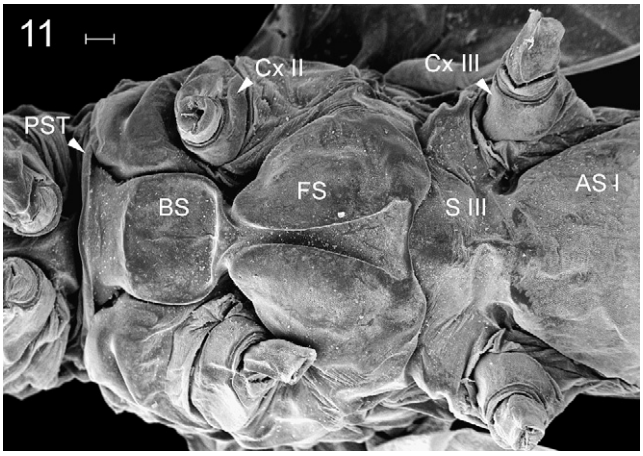


Fig. 11. Ventral view of the meso- and metathoracic sternum of a female imago of *H. confusa* (head to the left, SEM image) (scale bar 100 μm).

The lateropostnotum, (LPN, postalar bridge), which is the ventral point of attachment of the scuto-lateropostnotal muscle (S.LPNm in Figs. 13, 14) and the lateropostnotal crest (LPNC in Figs. 9, 10) are distinct.

3.2. Muscles of the mesothorax (Figs. 12–17)

The muscles can be subdivided into dorsal muscles, dorso-ventral muscles, pleural muscles, ventral muscles and direct flight muscles. The dorsal muscles include the dorsal longitudinal muscles. The dorso-ventral muscles are the muscles with the dorsal point of attachment on the tergum. The pleurum is the dorsal point of attachment of the pleural muscles. The ventral muscles are muscles that are attached only to the sternal elements. Direct flight muscles include all muscles that are associated with the wing base sclerites, the basalar sclerite or the subalar sclerite. Coxal and trochanteral muscles were not investigated in this study.

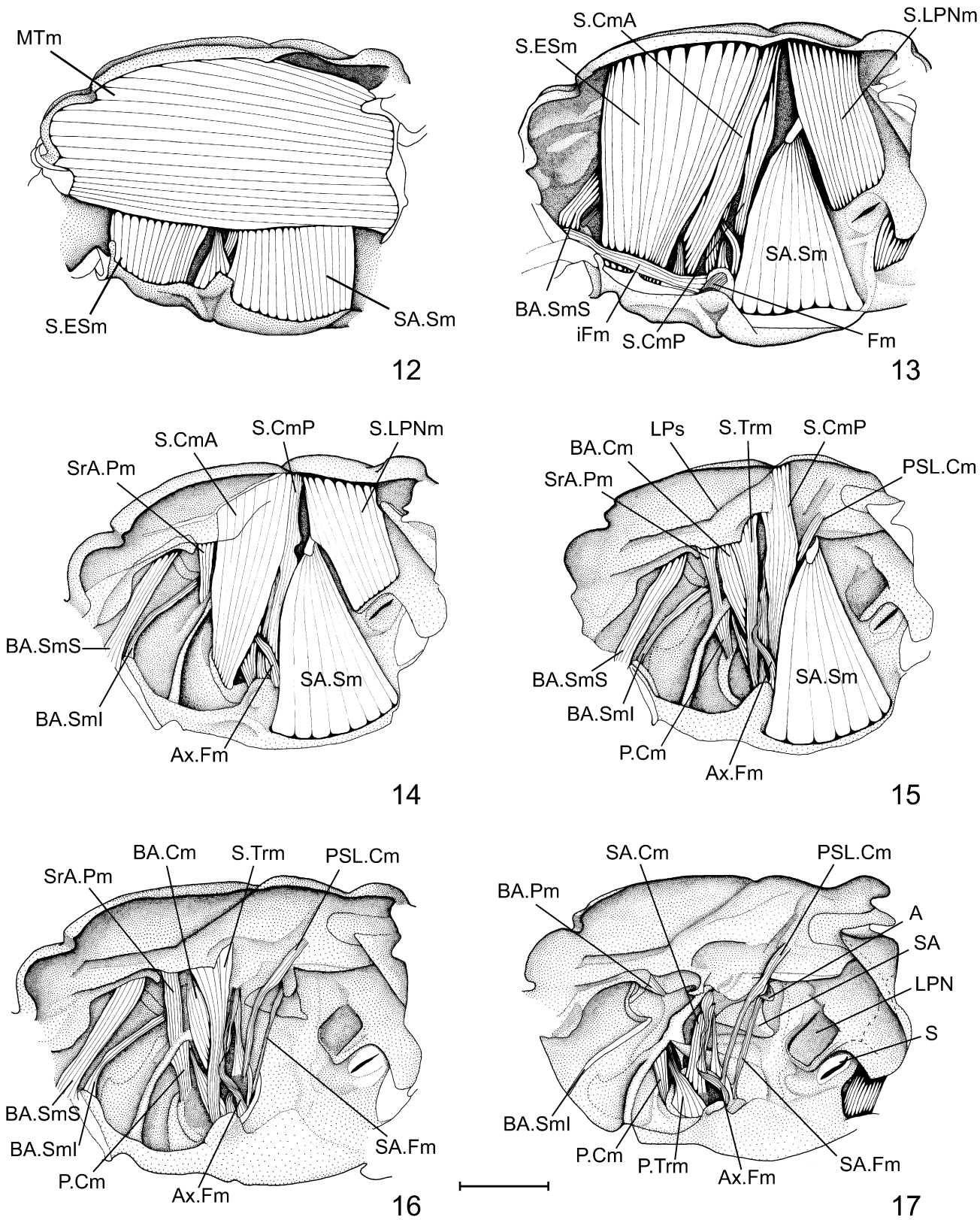
3.2.1. Dorsal muscles of the mesothorax

There are two dorsal longitudinal muscles: The median dorsal muscle (median tergal muscle, MTm in Fig. 12) and the oblique dorsal muscle (scuto-lateropostnotal muscle S.LPNm in Figs. 13, 14). MTm is the largest muscle in the mesothorax. Anteriorly it is attached to the tergum laterally of the median longitudinal suture and posteriorly to the median part of the second phragma.

S.LPNm is a large oblique dorso-ventral running muscle. It goes from the posterior part of the scutum (PSp in Figs. 5, 7) to the latero-ventral part of the phragma between the mesothorax and the metathorax (lateropostnotum, LPN in Figs. 9, 10).

3.2.2. Dorso-ventral muscles of the mesothorax

The scuto-episternal muscle (S.ESm in Figs. 12, 13) is a very large muscle running from the anterior part of the scutum to the anterio-ventral area of the episternum.



Figs. 12–17. Musculature of the right half of the mesothorax of a female imago of *H. confusa* at progressive stages of dissection (head to the left). See also Figs. 13–17. Median muscles (scale bar 0.5 mm). Musculature of the right half of the mesothorax of a female imago of *H. confusa* at progressive stages of dissection (head to the left). See also Fig. 12 and 14–17 (scale bar 0.5 mm). Musculature of the right half of the mesothorax of a female imago of *H. confusa* at progressive stages of dissection (head to the left). See also Figs. 12, 13 and 15–17 (scale bar 0.5 mm). Musculature of the right half of the mesothorax of a female imago of *H. confusa* at progressive stages of dissection (head to the left). See also Figs. 12–14, 16 and 17 (scale bar 0.5 mm). Musculature of the right half of the mesothorax of a female imago of *H. confusa* at progressive stages of dissection (head to the left). See also Figs. 12–15 and 17 (scale bar 0.5 mm). Musculature of the right half of the mesothorax of a female imago of *H. confusa* at progressive stages of dissection (head to the left). See also Figs. 12–16. Most lateral muscles (scale bar 0.5 mm).

The anterior scuto-coxal muscle (S.CmA in Figs. 13, 14) is about half the size of the S.ESm. It runs laterally from the lateroparapsidal suture of the scutum to the anterior side of the coxa.

The posterior scuto-coxal muscle (S.CmP in Figs. 13–15) is attached to the scutum, posteriorly of S.CmA. It runs to the posterior rim of the coxa. This muscle is smaller than the anterior scuto-coxal muscle.

The scuto-trochanteral muscle (S.Trm in Figs. 15, 16) is a slender and flat muscle, which runs from the lateral part of the scutum to the trochanter. The dorsal point of attachment of S.Trm is located laterally of S.CmA and S.CmP.

The parascutello-coxal muscle (PSL.Cm in Figs. 15–17) is a very slender muscle running from the lateral part of the scutellum to the posterior margin of the coxa. This muscle consists of only a few fibres, which are attached to the coxa via a tendon.

The anteronoto-pleural muscle (An.Pm) is a short and flat muscle, consisting only of a few fibres (not pictured). It runs from the anterior part of the scutum, anteriorly of the ANP, to the paracoxal suture above the base of the pleuro-coxal muscle.

The suralar-pleural muscle (SrA.Pm in Figs. 14–16) is only flat but distinct. This muscle runs from the suralare, which contains the anterior notal wing process, to the paracoxal suture.

3.2.3. Pleural muscles of the mesothorax

The pleuro-coxal muscle (P.Cm in Figs. 15–17) is a small and short muscle running from the anterior paracoxal suture (PCxsA) to the anterior rim of the coxa.

The pleuro-trochanteral muscle (P.Trm in Fig. 17) has its dorsal attachment on the anterior paracoxal suture, posteriorly of the pleuro-coxal muscle, and goes to the trochanter. This is only a slender muscle broadened ventrally.

3.2.4. Ventral muscles of the mesothorax

The intersegmental furcal muscle (iFm in Fig. 13) is a slender but distinct muscle. Its anterior attachment is at the posterior side of the profurca. From there it runs to the anterior side of the mesofurca.

The furcal muscle (Fm in Fig. 13) is a transverse muscle that goes from the proximal side of the right sternal apophysis to the proximal side of the left sternal apophysis.

The furco-coxal muscle posterior (F.CmP) is a flat muscle that runs from the posterior margin of the furca to the posterior coxal rim (not pictured).

3.2.5. Direct flight muscles of the mesothorax

The basalar sclerite has four muscles. The superior basalar-sternal muscle (BA.SmS in Figs. 13–16) runs from the dorsolateral part of the basalare to the anterior sternal apophysis. The inferior basalar-sternal muscle (BA.SmI in Figs. 14–17) runs from the ventral margin of the basalar sclerite to the presternite of the mesothorax (PST in Fig. 11). The superior basalar-sternal muscle is considerably larger than the very small inferior one. A third muscle goes from the dorsal part of the basalar sclerite (BAd) to the pleurum near the pleural wing process (BA.Pm in Fig. 17). This is a very short but robust muscle. Furthermore, there is a muscle that is dorsally attached to the basalar sclerite and ventrally to the posterio-medial rim of the coxa (BA.Cm in Figs. 15, 16).

There are three muscles on the subalar sclerite. The largest one is the very robust subalar-sternal muscle (SA.Sm in Figs. 12–15). It attaches dorsally on the posterior subalar apodeme (PSA in Figs. 9, 10) that is clearly visible from outside (see also Sect56n 3.1: subalar apodeme) and on the subalar suture (SAs in Fig. 10). The SA.Sm runs to the furcasternum (FS in Fig. 11).

There is a second, very slender muscle, the subalar-furcal muscle (SA.Fm in Figs. 16, 17), which inserts on the posterior subalar apodeme (PSA in Figs. 9, 10) and goes to the furca.

The third subalar muscle, the subalar-coxal muscle (SA.Cm in Fig. 17) extends between the smaller, anterior apodeme (ASA in Fig. 9) of the subalar sclerite and the rim of the coxa (where the coxa is articulated to the pleurum). This muscle sometimes consists of two parts.

The short and broad axillar-pleural muscle is running from the anterior dorsal part of the subalar sclerite (just posterior to the pleural wing process) to the third sclerite of the wing base (Ax.PmS not pictured).

A further very slender muscle, the axillar-furcal muscle (Ax.Fm in Figs. 14–17) inserts on a ventral projection of the second sclerite of the wing base. It has its ventral attachment on the furca.

3.2.6. External morphology of the metathoracic notum (not pictured)

The hind wings of *H. confusa* are only about half as long as the fore wings; in flight, they are coupled with the fore wings. Consequently, the metathorax is comparatively short and most muscles are distinctly smaller than in the mesothorax. The basalar and the subalar sclerites, the fulcrum and most sutures are inconspicuous.

The reduction of the metathorax includes the shortening of the tergal elements, especially of the scutum. The sutures, concavities and convexities that are distinct in the mesothorax are missing in the tergum of the metathorax. The metathoracic scutum and scutellum are rather flat and nearly equal in length.

The sclerites of the metathroracic wing base are partly reduced. The anterior notal wing process (ANP) is only short and rather indistinct. The posterior notal wing process (PNP) is not clearly distinguishable from the scutellum. The basal plate of the wing base is distinct but rather simple in structure. The proximal flat part, as in the wing base of the mesothorax, is less discernible. The anterior two wing base sclerites are not visible. The third wing base sclerite is a distinct, elongate sclerite. The basanale and the anal brace are missing. The costal brace is developed only as a furrow.

3.2.7. External morphology of the metathoracic pleurum (Fig. 18)

The most distinct suture in the metathoracic pleurum is the anterior paracoxal suture (PCxsA in Fig. 18). The posterior paracoxal suture (PCxsP in Fig. 18) is well developed and becomes carinate posteriorly.

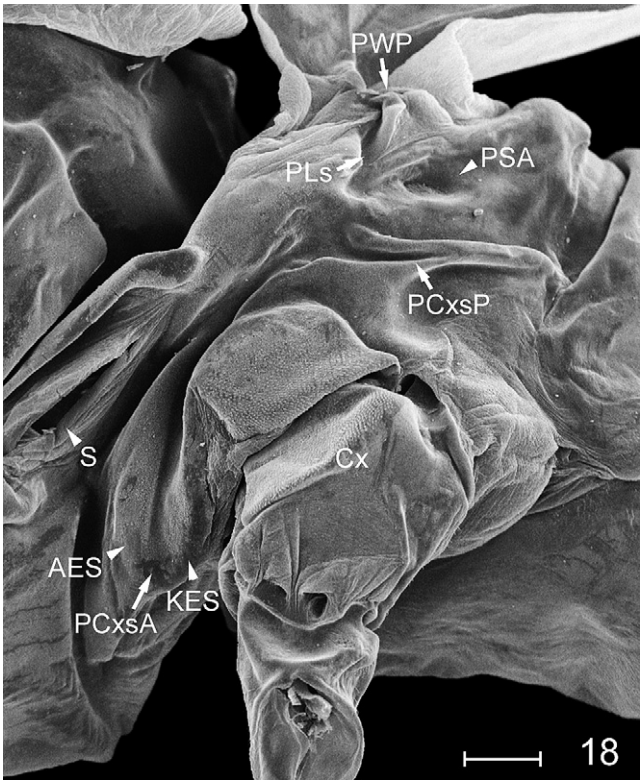


Fig. 18. Scanning electron microscope image of the metathoracic pleurum of a female imago of *H. confusa* (head to the left) (scale bar 100 μm).

Only the dorsal and the ventral parts (directly below the PWP and above the coxal articulation) of the pleural suture are distinct. In between the pleural suture is absent (PLs in Fig. 18).

The pleural wing process (PWP in Fig. 18) is rather small and the fulcrum is not clearly separated. The basisubcostale is clearly discernible on the ventral side of the wing (BSc in Fig. 18).

The anepisternum is narrower than the katepisternum (AES, KES in Fig. 18). The subalar sclerite and the basalar sclerite are reduced in the metathorax and are inconspicuous externally.

3.3. Muscles of the metathorax (Figs. 19-21)

3.3.1. Dorsal muscles of the metathorax

The median dorsal muscle (MTm, Fig. 19) is besides the S.ESm the largest muscle in the metathorax. The MTm runs from the middle phragma to the posterior phragma.

3.3.2. Dorso-ventral muscles of the metathorax

The scuto-episternal muscle (S.ESm, Figs. 19, 20) is a robust muscle that runs from the scutum to the distinct episternum. It is the largest dorso-ventral muscle of the metathorax.

The anterior scuto-coxal muscle (S.CmA, Fig. 20) is a relatively large muscle and is dorsally attached to the middle part of the scutum and ventrally to the anterior rim of the coxa. The posterior scuto-coxal muscle (S.CmP, Fig. 20) is less distinct and very slender. It has its dorsal attachment on the scutum, posteriorly to the S.CmA. At the ventral end it is attached to the posterior rim of the coxa.

The scuto-trochanteral muscle (S.Trm, not pictured) lies laterally to the S.CmP and is about as distinct as the anterior scuto-coxal muscle (S.CmA). Dorsally it is attached to the scutum and ventrally to the trochanter.

3.3.3. Pleural muscles of the metathorax

The pleuro-coxal muscle (P.Cm, Fig. 21) is a flat, wide muscle, which runs from the anterior paracoxal suture to the anterior rim of the coxa. The pleuro-trochanteral muscle (P.Trm, Fig. 21) is rather slender. It originates at the pleural suture and inserts on the trochanter.

3.3.4. Ventral muscles of the metathorax

The furcal muscle (Fm, not pictured) runs between the left and the right furcal arm of the segment. It is a distinct muscle even in the metathorax.

The furco-coxal muscle posterior (F.CmP, Figs. 19, 20) runs from the furcal arm to the posterior rim of the coxa.

3.3.5. Direct flight muscles of the metathorax

Even though the hind wings are coupled with the fore wings in flight, the direct flight muscles are present, although they are quite small.

The basalar-pleural muscle (BA.Pm, Fig. 21) runs from the dorsal part of the basalar sclerite to the pleurum just anterior to the pleural wing process (PWP, Fig. 18).

One subalar muscle runs from the pleurum to the posterior part of the coxa. This muscle consists of two parts: one part (SA.Sm, Figs. 20, 21) is dorsally attached on a broad area of the pleurum that could be the remains of the subalar sclerite and the subalar suture. The point of attachment, the posterior subalar apodeme (PSA in Fig. 18), is distinct only on the outside but reduced interiorly. Ventrally the SA.Sm is attached to the posterior rim of the coxa. The dorsal point of attachment and the fact that there are two distinguishable parts of the muscle show that this is the subalar-sternal muscle (SA.Sm, Figs. 20, 21), even though ventrally the muscle is not associated with the furcasternum. The sternal elements of the metathorax (comprising the furcasternites behind the coxa) are reduced, thus the ventral point of attachment of the SA.Sm is shifted anteriorly onto the coxa.

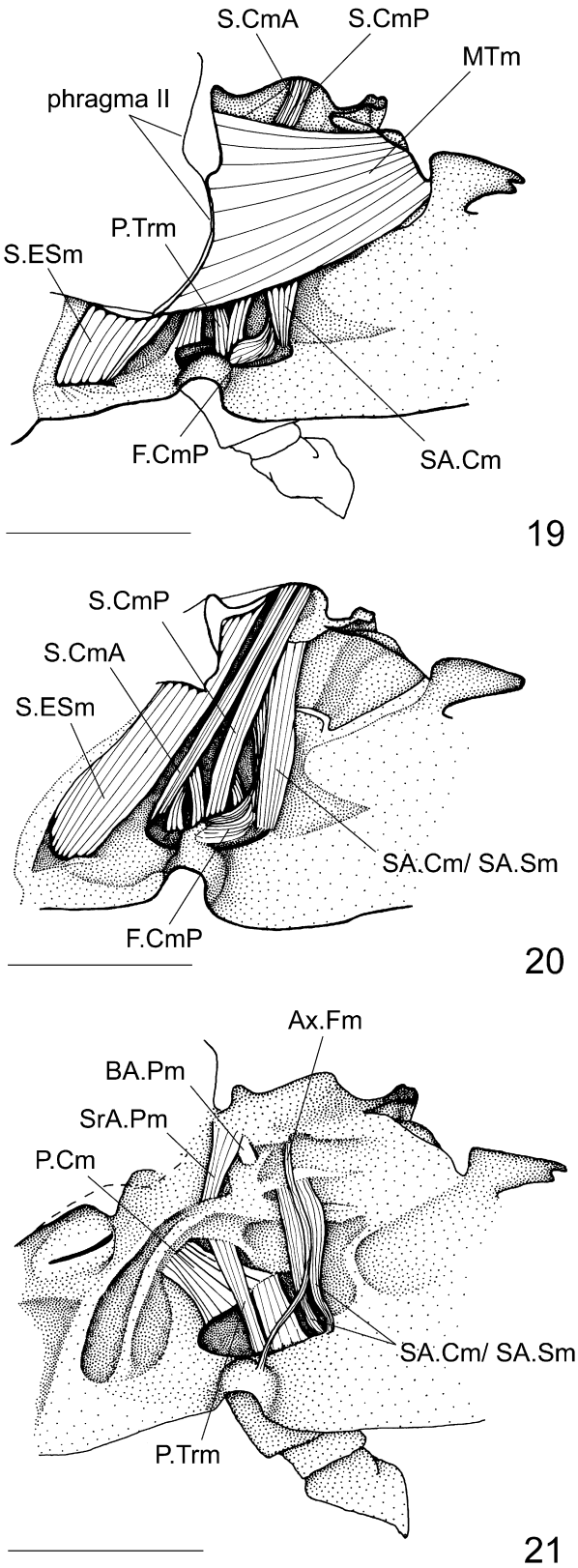
The second part of the muscle is the subalar-coxal muscle (SA.Cm, Figs. 20, 21). It is dorsally attached to the anterior remains of the subalar sclerite just beneath the SA.Sm and runs to the posterior rim of the coxa. The usual point of attachment, the anterior subalar apodeme (ASA) is missing.

The axillar-furcal muscle (Ax.Fm, Fig. 21) is present in the metathorax and is as slender as the Ax.Fm in the mesothorax.

4. Discussion

4.1. Homology of wing base sclerites

Superficially, the wing base of Ephemeroptera seems to be different to that of other Pterygota. However, our study reveals possibilities for the homology of at least some of the wing



Figs. 19–21. Musculature of the right half of the metathorax of a female imago of *H. confusa* at progressive stages of dissection (head to the left). See also Figs. 2 and 21. Median muscles (scale bar 100 μm).

base sclerites of Ephemeroptera and Neoptera, thus a new homology of wing base sclerites is proposed.

The *first free sclerite* (s1, Figs. 2–7) is articulated with the anterior part of the notum. The orientation and the position (e.g. no connection to the subcostal vein) of this sclerite in the wing base of Ephemeroptera indicate that it is a detached part of the ANP instead of the 1Ax as it is in Neoptera. The anterior notal wing process (ANP) in Plecoptera (Fig. 23a) is a concave and clearly demarcated but integral part of the tergum in the same position as the first sclerite (s1) of Ephemeroptera.

The homologous part to the first axillary (1Ax) of Neoptera rather is the *second free sclerite* (s2, Figs. 2–7) of the ephemeropteran wing base. This sclerite is connected anteriorly to the base of the subcostal vein and distally to the flat proximal part of the basal plate, which contains the ventral process that is articulated with the pleural wing process. In the comparatively primitive *S. aestivalis* (Ephemeroptera: Siphlonuridae) there are two muscles attached to this sclerite, which is the plesiomorphic condition (Matsuda, 1970). The first muscle originates ventrally of the pleural suture. The second muscle originates at the tip of the furca and is also present in other Ephemeroptera. The latter is probably homologous to muscle 45 of *Lepisma saccharina* (Zygentoma: Lepismatidae) (Matsuda, 1970). A muscle from the first axillary sclerite to the pleural suture is also present in Plecoptera. The only difference is, that in Plecoptera this muscle inserts nearly on the whole length of the posterior part of the 1Ax. In *S. aestivalis* it arises only from one point on the axillary sclerite. The point of insertion of the two muscles in *S. aestivalis* is developed as a proximoventrad directed projection on the s2. This probably results in a more concentrated power transmission.

In the wing base of some Ephemeroptera a further sclerite (s5, Figs. 2–4) lies between s2, s3 and the posterior notal wing process. The occurrence of this sclerite in many taxa of the Ephemeroptera (*Siphlonurus*, *Rhithrogena*, *Heptagenia* (and *Ametropus*, *Metretopus*, *Parameletus*; Brodsky, 1974)) suggests that it also belongs to the ground pattern of the

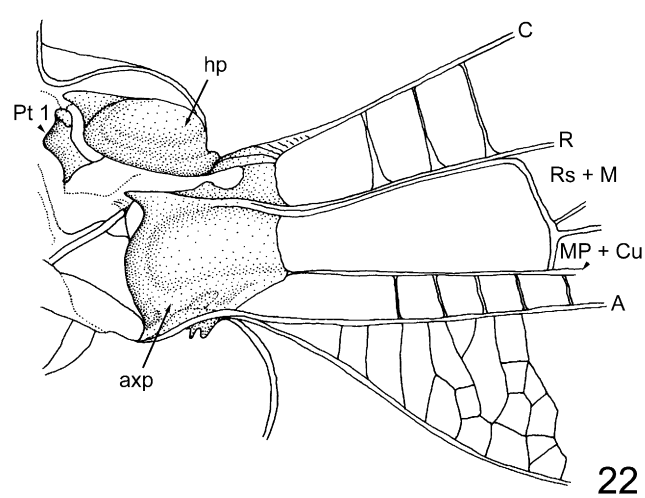


Fig. 22. Wing base of the right fore wing of the dragonfly *Calopteryx virgo*. Drawing after Tannert, (1958: fig. 3); Nomenclature of the wing veins after Riek and Kukalová-Peck (1984); Nomenclature of the wing base sclerites combined after Asahina (1954) and Tannert (1958).

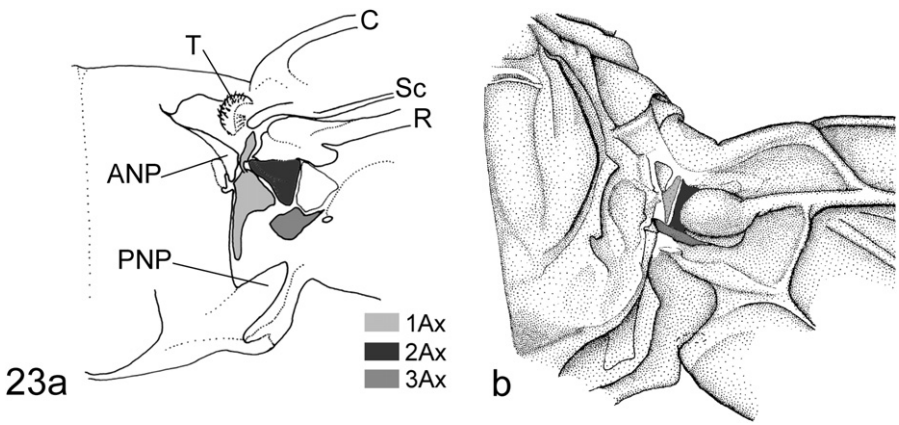


Fig. 23. Homologies of the ephemeropteran wing base sclerites with the neopteran wing base sclerites, this paper. (a) Diagram of the right hind wing base of the stonefly *Pteronarcys reticulata*; (b) right fore wing of *Habroleptoides confusa*.

Ephemeroptera. In *S. aestivalis* this sclerite is not completely detached from the scutum; hence it is probably a part of the MNP that is reduced in other families. Brodsky (1974) assumes that the s5 is a MNP, which is not homologous to the MNP of Neoptera because it is not associated with the 1Ax. However, if the homology of the wing base sclerites is as we assume, it is quite probable that the s5 is homologous to the MNP of Neoptera. Nevertheless, s5 could also be a detached or not yet associated posterior part of the 1Ax as it is present in Neoptera.

The flat and well sclerotised proximal margin of the *basal plate* (BP) in Ephemeroptera is sclerotised in the dorsal and ventral layer of the wing membrane. On the ventral side it has a process (BPp) which articulates with the pleural wing process. Furthermore, it is immobile, connected to the radial vein. Proximally, there is the convex axillary flexion-line between s2 and BP. In the Plecoptera the 2Ax is sometimes fused with the base of the anterior radial vein. In the fore and hind wing of *P. reticulata* (Plecoptera: Pteronarcidae) for example, the anterio-distal part of the 2Ax is fused with the base of the radial vein over about one third of the length of 2Ax. This fusion appears also in the hind wings of other stoneflies and seems to be an apomorphic condition. On the basis of the above mentioned characters the proximal part of the basal plate should be homologised with the second axillary sclerite (2Ax) of the neopteran wing base.

The *third sclerite* (s3) of Ephemeroptera, which is partially attached to the basal plate, is associated with the anal veins via the anal sclerite and the anal brace (Figs. 6, 7). There is also a muscle attached to this sclerite, which runs to the pleurum posterior to the PWP. Matsuda (1956) did not mention this muscle. Consequently, he overlooked the fact that the s3 is other than his 3Ax sclerotised not only in the dorsal membrane but also in the ventral membrane as it is the case in the 3Ax of Neoptera. Therefore Matsuda (1956) homologised the s5 (Fig. 2) with the 3Ax of the Neoptera. The homology of s3 and 3Ax is additionally supported by the following characters: The s3 of Ephemeroptera is ventrally associated with the subalar sclerite (Fig. 10), which is also the case in the 3Ax of Neoptera (Brodsky, 1994). In Neoptera, the 3Ax lies about rectangular to the median line of the insect body (Brodsky, 1994). The s3 lies, in contrast to s5, in the same position relative to the body axis. The 3Ax of Matsuda (1956) has no muscle; it is not associated either with the anal veins or with the subalar sclerite of the pleurum. Moreover, it is sclerotised only in the dorsal layer of the wing membrane. Hence it is the more parsimonious assumption to homologise the s3 of the Ephemeroptera with the 3Ax of the Neoptera.

The third axillary sclerite (3Ax) in Plecoptera is rather simple and without a distinct anterior arm as it is shown, e.g. in the fore wing and in the hind wing of *P. reticulata* (Plecoptera: Pteronarcidae) (Fig. 23a). A muscle runs between a proximal concavity of this sclerite and the pleural ridge near the pleural wing process.

Mostly, the 3Ax of the Neoptera has no very close contact to the proximal median plate (PMP). However, at least in some Plecoptera the third axillary sclerite is fused more or less distinctly with the PMP. This is the case in the hind wings of *P. reticulata*, in the fore and hind wings of *Leuctra hippopus* (Plecoptera: Leuctridae), *Nemoura cinerea* and *Nemoura* sp. (Plecoptera: Nemouridae) and in the hind wings of *Brachyptera seticornis* (Plecoptera: Taeniopterygidae). This fusion of the 3Ax and the proximal median plate is secondary in Plecoptera and could also be a secondary development in Ephemeroptera. In the latter, it could be an adaptation for stability in flight while parachuting and gliding.

In summary, the position of the s3 and its articulation with other elements of the wing base in Ephemeroptera and the fact that there is a pleural muscle attached to this sclerite is evidence of homology of the third sclerite (s3) of Ephemeroptera with the third axillary sclerite (3Ax) of Neoptera.

The morphology of the wing base and musculature of Odonata was examined by several Authors (Asahina, 1954; Maki, 1938; Pfau, 1986, 1991; Snodgrass, 1909, 1935; Tannert, 1958).

The wing base of Odonata (Fig. 22) articulates via the anterior humeral plate (after Asahina, 1954 or costal plate after Tannert, 1958) and the posterior axillary plate (after Asahina, 1954 or radio-analis plate after Tannert, 1958) with the thoracic tergum. The anterior humeral plate is supposed to be a product of a fusion of the humeral plate, which is present in other insects (Tannert, 1958) and the base of the costal vein (Snodgrass,

1909, 1935). The radial and the anterior medial vein originate from the dorsal part of the axillary plate (wing vein nomenclature after Riek and Kukalová-Peck, 1984). The veins of the media sector, the cubitus and analis originate from the ventral part of the axillary plate (Tannert, 1958). The posterior condylus of the PWP articulates with a ventral part of the axillary plate.

Two short muscles run from the posterointernal side of the axillary plate to the membrane just posterior to the pleural wing process (Asahina, 1954). This is the same position as the muscle from the 3Ax to the pleurum (Ax.PmS) of Ephemeroptera and (t-p 14 after Matsuda, 1970) of Neoptera.

Furthermore, Asahina (1954), Tannert (1958) and Pfau, (1986/1991) describe some muscles that could be homologous to basalar muscles in Ephemeroptera and/or Neoptera. However, the available information is not sufficient to homologise individual muscles with certainty. Here further investigations are essential.

4.2. Evolution of the mechanism of folding the wings over the abdomen

Ephemeroptera and Odonata are both adapted to special kinds of flight. Odonata are extremely manoeuvrable flying hunters. Ephemeroptera are adapted to a gliding flight and parachuting and especially males are adapted to persistent vertical mating flight. The dorsal longitudinal muscle of the mesothorax is enlarged and requires at least one-half of the dorso-ventral extent of the mesothorax. The metathorax is small, bearing the short hind wings. Compared to other pterygote insects this is an apomorphic condition.

Thus, we assume that the wing base elements of Ephemeroptera are at least partly a result of secondary fusion for more stability at the wing base in the gliding position. Supporting this hypothesis is the fact that the wing veins in fossil mayflies (Protereismatidae) are distinct even near the wing base (Kukalová-Peck, 1974b). Kukalová-Peck (1974b) assumed that large and apparently functional mouthparts were present in Permian mayflies. Therefore, she assumed that horizontal flight was more important in these taxa.

In this publication the wing base sclerites of Ephemeroptera are homologised to neopteran sclerites as shown in Fig. 23. The 2Ax and the 3Ax are fused with the basal plate. The 3Ax of the ephemeropteran wing base has the axillar-pleural muscle, which is also present in the Neoptera and most likely in Odonata.

The sistergroup relationships among basal Pterygota (Ephemeroptera, Odonata and Neoptera) are still not known with sufficient certainty.

If the Palaeoptera (Fig. 24) are monophyletic and the disability to fold the wings over the abdomen is a plesiomorphic character, it is the question if the fusion of the wing base sclerites in Ephemeroptera and Odonata evolved convergently or if it is a synapomorphy of both taxa. Nevertheless, most likely the wing base sclerites are a product of a secondary fusion (see above). The anterior radial vein is directly connected with the basal plate (Ephemeroptera) and the axillary plate (Odonata) respectively. Unlike Odonata the radial sector, the anterior and posterior medial veins and the cubitus are not directly connected with the basal plate in Ephemeroptera. To answer the question of a homologous or a convergent fusion of the wing base sclerites in the two orders it will be necessary to re-examine the wing base structures and the associated muscles of Odonata.

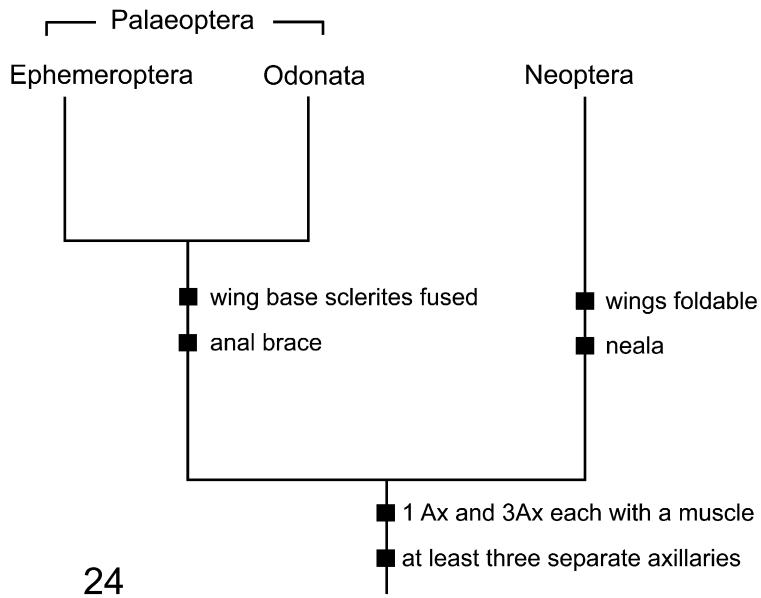
There are more characters supporting the Metapterygota-hypothesis (see Introduction). The Metapterygota are characterised by the absence of the axillar-furcal muscle and the basalar-sternal muscles, the missing terminalfilum and the loss of the moult in the winged stage.

On the assumption that the Metapterygota (Fig. 25) exist, as we assume, the evolutionary pathway could be as follows: In the pterygotan ground plan the wing base was composed of at least three axillary sclerites, which are convergently secondarily fused in Ephemeroptera as an adaptation for mating flight and for gliding. In Odonata the wing base sclerites could have been fused as an adaptation to highly manoeuvrable hunting flight.

In consideration of the special mating flight in Ephemeroptera and the hunting flight in Odonata together with the presence of the axillar-pleural muscle in the these orders, it is a legitimate question if the disability to move the wings to a resting position over the abdomen is a plesiomorphic character or if it is a secondary development. If we assume a wing base configuration similar to the Neoptera as the pterygotan ground plan such movements of the wings may also have been possible.

In fact, the fossil Diaphanopterodea combine the apomorphic character of haustellate mouthparts of the Palaeodictyopteroida with the ability to fold the wings over the abdomen (Kukalová-Peck, 1974a). Kukalová-Peck assumed that the ability to fold the wings "arose at least twice in insects" (Kukalová-Peck, 1974a,b; Kukalová-Peck and Brauckmann, 1990). A convergent evolution of wing folding was also suggested by Wootton (1979) and Wootton and Kukalová-Peck (2000). Willmann (1998) suggested that the ability to fold the wings over the abdomen could be a plesiomorphic condition and that, "there is no need to view wing folding in the Neoptera and Diaphanopterodea as a result of convergence" (Willmann, 1998: 274).

In fact, if the Metapterygota (Odonata + Neoptera) exist, as we and Staniczek (2001) assume, then the ability to fold the wings over the abdomen was lost at least three times during the early evolution of the Pterygota. An indication that this scenario could be possible are the Lepidoptera (Neoptera: Holometabola), where the Papilionoidea also lost the ability to fold the wings (Ivanov, 1996). Nevertheless, this theory is not supported by palaeontological evidence. The fossil pterygotan insects Palaeodictyopteroida (*sensu* Bechly, 1996) are a monophyletic group with haustellate mouthparts (Kukalová-Peck, 1991) which contain the presumably paraphyletic Palaeodictyoptera (Bechly personal communication; Grimaldi and Engel, 2005), the Megasecoptera, the Diaphanopterodea and the Permothemistida. The Diaphanopterodea and Permothemistida have an apomorphically reduced number of tarsomeres (Grimaldi and Engel, 2005). If the phylogenetic relationships are as assumed above, the ability to move the wings to a resting position over the abdomen was reduced several times within the



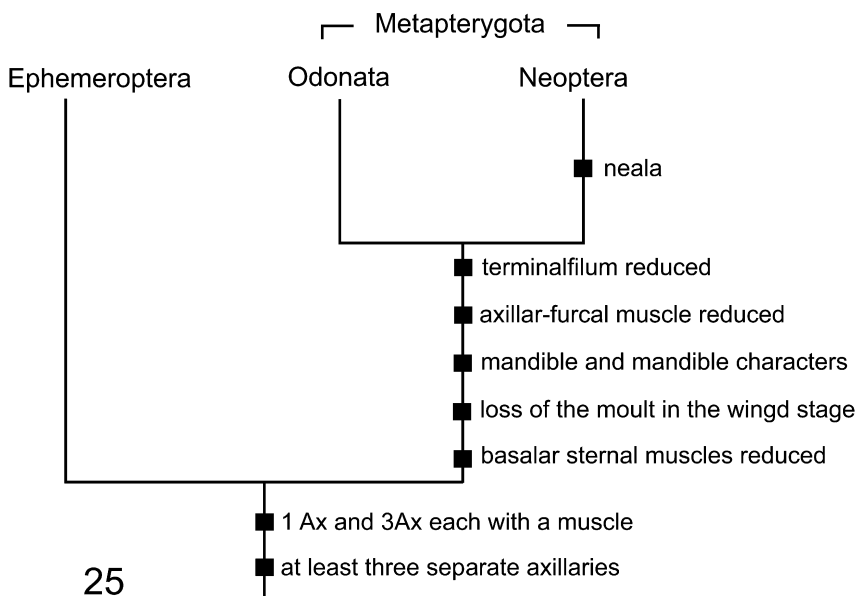


Fig. 24 and 25. Interpretations of character evolution for the Palaeoptera and Metapterygota hypothesis; for further explanations see text.

paraphyletic Palaeodictyoptera, in the Ephemeroptera and in the Odonata.

4.3. Homology of flight musculature in Ephemeroptera and Neoptera

Differences in musculature between adult Ephemeroptera and adult Neoptera are evident in the presence of the subalar-sternal muscle, the subalar-furcal muscle, two basalar-sternal muscles and the axillar-furcal muscle in Ephemeroptera. In Neoptera these muscles are missing.

The musculature of Ephemeroptera differs from that of Neoptera especially in the development of the basalar and subalar muscles. In Plecoptera each of the two basalar muscles (cpm 50, M. basalare-endocoxalis; cpm 51, M. basalare-coxalis, Wittig, 1955; Zwick, 1973) is about equal in proportion to the subalar muscle (cpm 53 M. subalar-coxalis, Wittig, 1955; Zwick, 1973). The subalar sclerite is a simple longish sclerite in Plecoptera but very distinct and specialised in Ephemeroptera. Besides the subalar-coxal muscle (SA.Cm) the Ephemeroptera possess a robust subalar-sternal muscle (SA.Sm) and a slender subalar-furcal muscle (SA.Fm) in the mesothorax. In the metathorax the SA.Sm and the SA.Cm are present but reduced and run close to each other. These two muscles are missing in the Plecoptera. Most probably they were already absent in the ground pattern of the Neoptera (Matsuda, 1970).

There are some difficulties regarding the homology of the muscles of the basalar sclerite and the basalar sclerite itself between the Ephemeroptera and other insects: in the Ephemeroptera there are two basalar-sternal muscles (BA.SmS, BA.SmI; Figs. 14–16), which insert on a crescent-shaped sclerite (BA in Figs. 9, 10) of the mesothorax. This crescent-shaped basalar

sclerite has a dorsal extension (BAd in Figs. 7, 9) that is connected immobile to the tegula. Two further muscles insert on the dorsal part of the basalar sclerite: the basalar-coxal muscle (BA.Cm) and the basalar-pleural muscle (BA.Pm).

The basalar-sternal muscles BA.SmS and BA.SmI do not exist in the mesothorax or in the metathorax of Plecoptera and other Pterygota (Matsuda, 1970), but muscles in the same position are present in Lepismatidae (Matsuda, 1970). These muscles are most likely reduced in the Neoptera. In contrast to the basalar-sternal muscles, a basalar-coxal muscle is present in the Neoptera. The BA.Cm of Ephemeroptera is often classified as an axillary or tergal muscle. Grandi (1947) and Matsuda (1956) classified this muscle as an axillary muscle (m. coxo-ascellare after Grandi, 1947), dorsally attached to the first free sclerite (Ax1 of Matsuda, 1956; Tsui and Peters, 1972 and "pseudopterale prossimale" of Grandi, 1947). Brodsky (1974), in contrast, classified the same muscle as a tergal muscle (TCxm 5). Kluge (1994) designated it as a basalar muscle (BA.Cm) but without further explanation. The BA.Cm inserts in most of the examined species on the sclerite which is directly associated with the crescent-shaped basalar sclerite (BAd in the anterio-dorsal part of the wing base; Fig. 7) or on a sclerotisation in the membrane just posterior to it. We decide to term this muscle BA.Cm because the sclerite BAd is the dorsal extension of the crescent-shaped sclerite which is termed basalar sclerite in Ephemeroptera.

The fact that this muscle has different names demonstrates the uncertainty of its derivation, which is directly connected to the uncertainty about the derivation of the sclerite on which the muscle inserts. BA.Cm of *H. confusa* is dorsally attached to the BAd in the dorsal anterior margin of the mesothoracic pleurum. The BA.Cm runs (below the s1!) to the coxo-pleural articulation point in the pleura. The dorsal point of attachment of this muscle varies in different species of Ephemeroptera. In *Centroptilum luteolum* (Ephemeroptera: Baetidae) for instance this muscle is dorsally attached to a projection of the basal plate. In *Leptophlebia pacifica* (McDunnough, 1933) the insertion is on s1 (1Ax of Tsui and Peters, 1972). In the primitive *Siphlonurus aestivalis* BA.Cm is dorsally attached to the BAd (the point of insertion lies next to the s1).

A further muscle inserts on the dorsal sclerite between the basalare and the tegula, the basalar-pleural muscle (BA.Pm), which is similar to the "m. pleurocondilo-scutale" of Grandi (1947) and t-p4 and p5 of Matsuda (1970). It is also present in *P. reticulata* (Plecoptera: Pteronarcidae) where it inserts dorsally on a small sclerite and runs to the pleurum. This short but distinct muscle is also present in the mesothorax and metathorax of *Perla abdominalis* (tpm 47, Wittig, 1955) and other Plecoptera and is dorsally attached to a small sclerite next to the tegula ("kleine Sklerifikation hinter der Tegula" of Wittig, 1955). Ventrally it is associated with an upper part of the pleural suture. This means that the posterior dorsal part of the basalar sclerite in Ephemeroptera is present also in Plecoptera.

Although the function and the position of the basalar sclerite and the associated muscles are about the same as in Neoptera (Brodsky, 1994) there are some facts that are difficult to interpret. The two muscles of Lepismatidae, which are homologised with the basalar-sternal muscles (BA.SmS and BA.SmI) of Ephemeroptera, are tergo-sternal muscles (Matsuda, 1970). We found first clues that all basalar muscles in Ephemeroptera (BA.SmS, BA.SmI, BA.Cm, BA.Pm) are of tergal origin (Willkommen, unpublished). This means that the basalar sclerite probably is, at least partially, of tergal origin or that it moved upwards in Ephemeroptera. A basalar-trochanteral muscle, which Matsuda (1970) assumed to be present in Ephemeroptera, was not found in any examined ephemeropteran specimens.

The Ephemeroptera possess three or two axillary muscles (for homologisation of the axillary sclerites see above). In basal taxa there are two muscles that insert on the 1Ax of which the axillar-pleural muscle is reduced in higher ephemeropteran taxa but in some Neoptera it is still present. The axillar-furcal muscle seems to be an archaic muscle that is present in Lepismatidae (Matsuda, 1970) and reduced in Neoptera. The third axillary muscle inserts on the 3Ax of Ephemeroptera and runs to the anterior part of the subalar sclerite just posterior to the PWP. This muscle is homologous to the axillar-pleural muscle of Neoptera and therefore it is most likely a ground plan character of Pterygota.

Besides the large median tergal muscle (MTm, dorsal longitudinal muscle) and the dorsal oblique muscle (S.LPNm) there is a third dorsal oblique muscle present in a few taxa of Ephemeroptera (e.g. Ephemerellidae, *Serratella ignita*). It runs from the scutum, just posterio-medially of the S.LPNm to the postnotum. If present, this muscle is only small because the second antagonist to the MTm is the dorsal oblique muscle (S.LPNm) that is enlarged in nearly all Ephemeroptera.

5. Conclusions

As mentioned above, there are some problematic aspects. For instance, it was not possible to elucidate the origin and development of the basalar sclerite and the homologies of the associated muscles remain equivocal between Ephemeroptera and Neoptera. To clarify these aspects, further investigations of the larval development of Ephemeroptera and Plecoptera and detailed studies of larvae and adults of Odonata are necessary.

Well supported results of our investigation are that in the ground plan of the Pterygota the wing base was composed of at least three separate sclerites. Also, at least two of these sclerites, the 1Ax and the 3Ax of the neopterous nomenclature were equipped each with a muscle.

A significant result of this investigation is that the wing base sclerites of Ephemeroptera can be homologised with the wing base sclerites of Neoptera. In the Ephemeroptera the 2Ax and often also the 3Ax are fused with the median plate to form the characteristic basal plate. The 3Ax possesses an axillary-pleural muscle, which is hypothesised to be homologous to the respective muscle of the Neoptera and therefore is a ground plan character of the Pterygota. We also assume that the fusion of the axillary sclerites is a secondary development in Ephemeroptera as an adaptation to their special kind of flight. A fusion of wing base sclerites most likely took place independently in Odonata.

This also leads to the conclusion that probably the ground pattern of the Pterygota included a wing base that was composed of similar sclerites and muscles as the wing base of extant Neoptera.

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