

# The morphology of the pterothorax of Ephemeroptera, Odonata and Plecoptera (Insecta) and the homology of wing base sclerites and flight muscles<sup>1</sup>

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## Abstract

The ability to fly was the decisive factor for the evolutionary success of the most diverse group of insects, the Pterygota. Nevertheless, the ground plan of the functionally important wing base has not been sufficiently clarified.

The aim of this study is to homologise the wing base sclerites of Ephemeroptera, usually regarded as sister group of the remaining Pterygota, with that of other basal pterygote lineages and to reconstruct the ground plan of the wing base of Pterygota. The pterothoracic musculature of representatives of the three basal lineages of Pterygota (Ephemeroptera, Odonata and Neoptera) is also described and discussed.

Contrary to previous hypotheses, 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 axillary sclerites. The proximal median plate is probably also present in the ground plan of Pterygota. The first axillary is provided with two muscles. The third axillary is equipped with a short muscle that originates from the epimeron. This muscle is interpreted as another ground plan character of Pterygota. In Plecoptera a second muscle inserts at the third axillary sclerite. It originates from the episternum and is most likely an autapomorphic character of Neoptera. The results imply that the wing base of the Plecoptera is close to the pterygote ground plan. It is assumed that the wing base of Ephemeroptera and Odonata is 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.

The enlarged subalare and associated muscles, the large dorsal longitudinal muscle, the small metathorax and shortened hind wings in Ephemeroptera suggest that mayflies have a derived flight apparatus in many respects. The Odonata on the other hand show different specialisations, namely a synthorax, large direct flight musculature, and a fusion of second and third axillary with the proximal median plate. Though the wing base in both taxa is secondarily stiffened, the specialisations of Ephemeroptera and Odonata may have evolved independently from each other.

**Key words:** Axillaries, subalare, basalare, flight muscles, basal Pterygota, Palaeoptera, Metapterygota.

## Zusammenfassung

Die Flugfähigkeit der geflügelten Insekten (Pterygota) war der entscheidende Faktor für den evolutiven Erfolg dieser äußerst artenreichen Gruppe. Dennoch ist der Aufbau des funktionell wichtigen Flügelgelenkes im Grundplan der Pterygota noch nicht zufriedenstellend aufgeklärt.

Ziel dieser Arbeit ist es, die Flügelbasissklerite der Ephemeroptera, gemeinhin als Schwestergruppe der übrigen Pterygota angesehen, mit denen anderer basaler Pterygota zu homologisieren und den Grundplan des Flügelgelenkes der Pterygota zu rekonstruieren. Ferner wird die pterothorakale Muskulatur von Vertretern der drei basalen Gruppen der Pterygota (Ephemeroptera, Odonata und Neoptera) beschrieben und diskutiert.

Entgegen früherer Hypothesen sind die Elemente der neopteren Flügelbasis sowohl in der Flügelbasis der Ephemeroptera als auch in jener der Odonata wiederzufinden. Vermutlich ist die Flügelbasis im Grundplan der Fluginsekten aus drei Axillaria aufgebaut. Wahrscheinlich ist auch die proximale Medianplatte im Grundplan der Pterygota vorhanden. Das erste Axillare ist im Grundplan der Pterygota mit zwei Muskeln ausgestattet. Ein weiterer Muskel zieht vom Epimeron zum dritten Axillare. Höchstwahrscheinlich eine Neuerwerbung der Neoptera ist dagegen ein Muskel, welcher bei den Plecoptera vom dritten Axillare zum Episternum zieht. Möglicherweise kommt das Flügelgelenk der Plecoptera dem Grundplan der Flügelbasis der Pterygota sehr nahe. Es wird dagegen angenommen, dass die Flügelbasis der Ephemeroptera und Odonata sekundär versteift ist. Das so genannte Basalare und seine Muskeln der Ephemeroptera und Odonata sind wahrscheinlich nicht mit dem Basalare und den zugehörigen Muskeln der Neoptera homolog.

Das vergrößerte Subalare nebst dazugehörigen Muskeln, der stark vergrößerte dorsale Längsmuskel, der verkleinerte Metathorax und die verkürzten Hinterflügel bei Ephemeropteren legen nahe, dass deren Flugapparat in vielerlei Hinsicht abgeleitet ist. Dagegen besitzen die Odonata andere Spezialisierungen im Pterothorax, beispielsweise einen Synthorax, vergrößerte direkte Flugmuskeln sowie die Verschmelzung des zweiten und dritten Axillare mit der proximalen Medianplatte. Obwohl beide Taxa eine sekundär versteifte Flügelbasis besitzen, sind diese Spezialisierungen bei Ephemeroptera und Odonata wohl unabhängig voneinander entstanden.

<sup>1</sup> Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultäten der Georg-August-Universität zu Göttingen

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## 1 Introduction

Mayflies (Ephemeroptera) are usually regarded as one of the most ancient extant lineages of winged insects (Pterygota). Among the characteristic features of extant mayflies are the moult of a winged subadult stage (the subimago), short antennae, the costal brace, the reduction of metathorax and hind wings, the medial abdominal terminal filament, and in the male prolonged fore legs, a pair of abdominal claspers and paired penes (HENNIG 1969; KRISTENSEN 1975, 1981; STANICZEK 2000, 2001; WILLMANN 2003).

Usually, the adult life span of mayflies is very short lasting from a couple of hours to a few days. Mayflies do not feed in the winged stages, and their mouthparts are atrophied. Due to the short adult life span the emergence of mayflies must be synchronised to ensure mating and reproduction. Male imagines perform characteristic nuptial dances to attract females, and also mating takes place in the air. In several species the female mates as subimago,

but in the majority of species mating takes place in the adult stage.

The fossil record (e. g. GRIMALDI & ENGEL 2005, KLUGE 1993, McCAFFERTY 1990, SINITSHENKOVA & CORAM 2002, SINITSHENKOVA 1984, TSHERNOVA 1970) of mayflies dates back to the Permian, although some fossils that are regarded as close relatives [*Lithoneura lameerei* Carpenter, 1938, *Triplosoba pulchella* (Brongniart, 1893)] are recorded from the Carboniferous (GRIMALDI & ENGEL 2005). The position of the Carboniferous taxon *Triplosoba pulchella* is controversial since the characteristic costal brace is absent (CARPENTER 1963). There is also no general agreement on the position of *Bojophlebia prokopi* Kukalová-Peck, 1985 and *Lithoneura lameerei* that are regarded as earliest stem group representatives of mayflies by some authors (CARPENTER 1987, GRIMALDI 2001, KUKALOVÁ-PECK 1985, WILLMANN 1999).

Prottereismatoidea, known from the Permian, are generally accepted as stem group representatives of Ephemeroptera. The Prottereismatidae are characterised

by fore and hind wings of similar size, though the hind wings are slightly shorter than the fore wings (CARPENTER 1979, 1992). The oldest known representative belonging to the extant crown group is the Jurassic *Stackelbergisca sibirica* Tshernova, 1967 (CARPENTER 1992, HUBBARD 1990, McCAFFERTY 1990, SINITSHEKOVA 1984), which has been assigned to the Siphuriscidae recently (ZHOU & PETERS 2003).

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. The winged insects also take advantage of the flight ability in providing with food and in being able to escape fast from hunters.

Up to date there is no general agreement on the derivation of wings and the evolution of wing base sclerites. The wings are for example assumed to be derivatives of the legs (KUKALOVÁ-PECK 1983), or derived from paranota, which are lateral expansions of the tergites (HAMILTON 1971, 1972a, 1972b, 1972c) or rather originate from both tergites and pleurites (SNODGRASS 1935). Also the problem of the wing base ground plan of Pterygota is unsolved. On the one hand it is assumed that the wing base consists of 32 sclerites in the pterygote ground plan (KUKALOVÁ-PECK 1983, 1987, 1991). According to this author, these sclerites are secondarily fused in different ways in extant Pterygota. Even up to date it is hypothesised, that Ephemeroptera possess only one axillary plate, Odonata have two axillary plates, and Neoptera possess three axillary plates in the wing base, of which the last mentioned condition represents the apomorphic state (GULLAN & CRANSTON 2005). Also the phylogenetic relationships among the three basal clades of Pterygota remain controversial, in spite of a long history of research into wings and their venation (BECHLY 1996, 1999; COMSTOCK 1918; COMSTOCK & NEEDHAM 1898, 1899; EDMUNDS & TRAVER 1954; FORBES 1943; HAMILTON 1971, 1972a, b, c; KUKALOVÁ-PECK 1985; RIEK & KUKALOVÁ-PECK 1984; WOOTTON 1979, 1992). The first hypothesis (Chiastomyaria hypothesis) assumes a sister group relationship between Odonata and Ephemeroptera+Neoptera (LEMICHE 1940, SCHWANWITSCH 1943). The Palaeoptera hypothesis (MARTYNOV 1925) states that Ephemeroptera+Odonata is the sister group to Neoptera, and the Metapterygota hypothesis assumes a sister group relationship between Ephemeroptera and Odonata+Neoptera (BÖRNER 1909; FÜRST VON LIEVEN 2000; HENNIG 1953; KRISTENSEN 1975, 1981, 1991; STANICZEK 2000, 2001).

The musculature and the thoracic sclerites of various insects have been treated in different studies (e. g. BARLET 1967; CRAMPTON 1914, 1918; MAKI 1938; MATSUDA 1970; MICKOLEIT 1969; RÄHLE 1970; SNODGRASS 1927, 1935; WEBER 1924a, 1924b, 1925). The thoracic musculature and sclerites especially of Ephemeroptera, Odonata and Plecoptera were also examined by various authors (ASAHINA

1954; CLARK 1940; CREMER 1934; DÜRKEN 1907; GRANDI 1947; HATCH 1966; MALOEUF 1935; MATSUDA 1956; NELSON & HANSON 1968, 1971; KNOX 1935; KLUGE 1994; BRODSKY 1970, 1974, 1979b; WITTIG 1955; PFAU 1986; ZWICK 1973). Extensive investigations on structure and function of the flight apparatus of insects and insect flight in general were done by BRODSKY (1971, 1975, 1986, 1992), who summarised most of the results in a compendium (BRODSKY 1994). Other major contributions were published by DUDLEY (2002), NACHTIGALL (1966, 1967, 2003), NACHTIGALL et al. (1998), WOOTTON & KUKALOVÁ-PECK (2000) and WOOTTON (1979, 1992). The general morphology of mayflies has been treated by KLUGE (1994, 2004). Several works dealing with the structure of the wing base and its associated sclerites were done by BRODSKY (1970, 1974, 1979a, 1979b), BROWNE & SCHOLTZ (1994, 1995, 1996), GRANDI (1947), HAAS & KUKALOVÁ-PECK (2001), HÖRNSCHEMEYER (1998, 2002, 2004), IVANOV (1995, 1996, 1997), KUKALOVÁ-PECK (1974b, 1983), ONESTO (1959a, 1959b, 1960, 1961, 1963, 1965), PFAU (1977, 1986, 1991), SHARPLIN (1963a, 1963b, 1964), SNODGRASS (1909), TANNERT (1958) and YOSHIZAWA & SAIGUSA (2001).

Morphological and molecular investigations and discussions towards the sistergroup relationships among basal Pterygota and Ephemeroptera have been contributed amongst others by KRISTENSEN (1975, 1981, 1991), OGDEN & WHITING (2003, 2005), WILLMANN (1998, 2003, 2005), WHITING et al. (1997), and WHEELER et al. (2001). The Palaeoptera hypothesis is supported on the basis of morphological data for example by BECHLY et al. (2001), GORB et al. (2000), HENNIG (1969), and WAGNER et al. (1996), and with molecular data by HOVMÖLLER et al. (2002), which is however not clearly supported by OGDEN & WHITING (2003). According to BÖRNER (1909), FÜRST VON LIEVEN (2000), and STANICZEK (2000, 2001) there is evidence for the Metapterygota hypothesis.

There are several different hypotheses on the homology of the wing base sclerites between Ephemeroptera, Odonata and Neoptera (BEKKER 1954; BRODSKY 1970, 1974, 1994; GRANDI 1947; KLUGE 1994, 2004; KUKALOVÁ-PECK 1974a, 1974b, 1978, 1983, 1985, 1987; KUKALOVÁ-PECK & BRAUCKMANN 1990; MATSUDA 1956, 1970; TSUI & PETERS 1972; for detailed explanations see section 4.2). Some of them are mainly based on topographical characteristics, for example the spatial orientation of the sclerites within the wing base. Others rely on the relative position of the sclerites to each other and to the notal wing processes. Even different works of one and the same author resulted in different hypotheses (BRODSKY 1970, 1974). Up to date, no consensus on the different hypotheses was reached so that the problem has to be regarded as unsolved. The aim of the present study is to compare the ephemeropteran wing base with the wing base sclerites of Neoptera, and to reconstruct the wing base ground plan of Pterygota. Previ-

ous hypotheses are discussed and in addition, the pterothoracic musculature is compared.

The Ephemeroptera are often assumed to be the sister-group of the remaining Pterygota. Consequently, this study focuses on Ephemeroptera. It is complemented by investigations on Odonata and Plecoptera. The latter possibly represent the sister group to the remaining Neoptera or rather the remaining Polyneoptera (HENNIG 1969, KRISTENSEN 1991, ZWICK 1980), and most likely retained many primitive characters with regard to the wing base.

#### Acknowledgements

First of all I would like to thank PD. Dr. T. HÖRNSCHEMEYER and Prof. Dr. R. WILLMANN (Göttingen) for their general support and encouragement during the time of my doctoral thesis. Special thanks also to PD. Dr. T. HÖRNSCHEMEYER (Göttingen), Dr. G. BECHLY (Stuttgart) and Dr. A. STANICZEK (Stuttgart) for valuable comments and discussions.

Furthermore, thanks are given to Dr. J. GOEBBELS and J. NÖTEL (Berlin) for the acquisition of the  $\mu$ CT data and to B. WIPFLER and U. KALBITZER (Göttingen) for the 3D-reconstruction of the  $\mu$ CT data.

Sincere thanks to Prof. Dr. P. ZWICK (Schlitz), Dr. A. STANICZEK (Stuttgart), Dr. J.-L. GATTOLLIAT (Lausanne), Dipl. Geol. J. BRINKMANN (Tübingen), Dipl. Biol. F. WIELAND, Dipl. Biol. O. EIKEL, Dipl. Biol. R. KLUG and Dipl. Biol. V. FEUERSTEIN (all Göttingen), PD. Dr. T. HÖRNSCHEMEYER, Dipl. Biol. U. GRIESSER (Stuttgart), Dr. A. GOLUBOVIĆ (Tübingen), and Dr. M. OHL (Berlin) for loan and donation of specimens.

I am grateful to J. REIBNITZ (Stuttgart) for his valuable advice with colour electronic page setting, and to Dr. E. WEBER and Drs. E. and G. MICKOLEIT (Tübingen) for advice regarding methods.

I owe special thanks to K. CRANE (Erlangen) and A. BAXTER (Hull) for their help and the corrections of the English language.

This work was supported by a grant to PD. Dr. T. HÖRNSCHEMEYER from the Deutsche Forschungsgemeinschaft (DFG HO 2306/2-1, 2-3).

## 2 Material and Methods

### 2.1 Materials

The examined material was fixated in 70–80% ethanol. The number of specimens examined is given in square brackets. The list given below includes all examined material, even though it is unquoted in sections 3 and 4.

#### Ephemeroptera, winged stages

##### Siphonuridae

*Siphonurus aestivalis* (Eaton, 1903): Switzerland, Vaud, des Monneaux, 29.IV.1994, leg. J.-L. GATTOLLIAT; Germany, Baden-Württemberg, Schwäbisch Gmünd, 20.V.2005, leg. A. STANICZEK & M. PALLMANN [2 ♂♂, 2 ♀♀ imagines].

##### Baetidae

*Baetis* sp.: Germany, Baden-Württemberg, Tübingen, River Neckar, 12.VIII.2003, leg. J. WILLKOMMEN [20 ♀♀ imagines and subimagines].

*Baetis fuscatus* (Linnaeus, 1761): Germany, Baden-Württemberg, Hirschau, River Neckar, 2.X.2004, leg. J. WILLKOMMEN [1 ♂ imago; 2 ♂♂ subimagines].

*Centroptilum luteolum* (Müller, 1776): Germany, Baden-Würt-

temberg, Tübingen, River Neckar, 12.VIII.2003, leg. J. WILLKOMMEN [3 ♂♂, 9 ♀♀ imagines and subimagines].

*Cloeon dipterum* (Linnaeus, 1761): Germany, Bavaria, Würzburg, River Main, 25.VI.2005, leg. J. WILLKOMMEN [2 ♂♂, 5 ♀♀ imagines; 1 ♀ subimago].

##### Leptophlebiidae

*Habroleptoides confusa* Sartori & Jacob, 1986: Germany, Lower Saxony, Löwenhagen, Nieme creek, 5.VI.2004, leg. J. WILLKOMMEN [15 ♂♂♀♀ imagines and subimagines].

*Habrophlebia lauta* Eaton, 1884: Germany, Baden-Württemberg, Bebenhausen, Goldersbach creek, 10.VI.2004, leg. J. WILLKOMMEN [1 ♂, 2 ♀♀ imagines; 3 ♀♀ subimagines].

*Paraleptophlebia submarginata* (Stevens, 1836): Germany, Baden-Württemberg, Rottenacker, River Danube, 15.V.2004, leg. J. WILLKOMMEN [3 ♂♂ subimagines].

##### Heptageniidae

*Ecdyonurus submontanus* Landa, 1969: Germany, Baden-Württemberg, Munderkingen, River Danube, 6.VIII.2003, leg. A. GOLUBOVIĆ [5 ♂♂, 2 ♀♀ subimagines].

*Ecdyonurus venosus* (Fabricius, 1775): Germany, Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. WILLKOMMEN [2 ♂♂ imagines].

*Epeorus assimilis* Eaton, 1885: Germany, Lower Saxony, Löwenhagen, Nieme creek, 2.VI.2004, leg. J. WILLKOMMEN [4 ♂♂ imagines].

*Heptagenia coerulans* (Rostock, 1878): Germany, Bavaria, Regensburg, 26.VII.2005, leg. U. GRIESSER [2 ♀♀ subimagines].

*Heptagenia sulphurea* (Müller, 1776): Germany, Bavaria, Würzburg, River Main, 2.VII.2005, leg. J. WILLKOMMEN [8 ♀♀ imagines; 2 ♂♂ subimagines].

*Rhithrogena semicolorata* (Curtis, 1834): Germany, Baden-Württemberg, Bebenhausen, Goldersbach creek, 8.V.2004, leg. J. WILLKOMMEN [11 ♂♂, 2 ♀♀ imagines].

##### Ephemerellidae

*Serratella ignita* (Poda, 1761): Germany, Baden-Württemberg, Munderkingen, River Danube, 6.VIII.2003, leg. A. GOLUBOVIĆ; Baden-Württemberg, Tübingen, River Neckar, 19.VII.2003, leg. J. WILLKOMMEN; Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. WILLKOMMEN [24 ♂♂♀♀ imagines and subimagines].

##### Ephemeridae

*Ephemerella danica* Müller, 1764: Germany, Baden-Württemberg, Bebenhausen, Goldersbach creek, 10.VI.2004, leg. A. GOLUBOVIĆ; Tübingen, River Neckar, 10.VII.2003, leg. J. WILLKOMMEN [1 ♂, 2 ♀♀ imagines; 4 ♀♀ subimagines].

##### Caenidae

*Caenis horaria* (Linnaeus, 1758): Germany, Brandenburg, Rheinsberg, lake Rheinsberger See, 6.VIII.2004, leg. J. WILLKOMMEN [1 ♂ imago].

*Caenis rivulorum* Eaton, 1884: Germany, Baden-Württemberg, Rottenacker, River Danube, 15.V.2004, leg. J. WILLKOMMEN [5 ♂♂, 2 ♀♀ imagines; 1 ♀ subimago].

*Caenis robusta* Eaton, 1884: Germany, Brandenburg, Rheinsberg, lake Rheinsberger See, 6.VIII.2004, leg. J. WILLKOMMEN [2 ♂♂ imagines].

##### Polymitarcyidae

*Ephoron virgo* (Olivier, 1791): Germany, Baden-Württemberg, Neckar-Gmünd, River Neckar, 6.VIII.1994, leg. A. STANICZEK; Rhineland-Palatinate, Koblenz, River Rhine, 11.VIII.2004, leg. J. BRINKMANN; Bavaria, Würzburg, River Main, 7.VIII.2005, leg. J. WILLKOMMEN [9 ♂♂ imagines; 7 ♀♀ subimagines].

*Povilla adusta* (Navás, 1912): Mali, Niger Basin, River Niger, Gao, 7.IX.1987, leg. J.-M. ELOUARD [1 ♂ imago].

## Euthyplociidae

*Exeuthyplocia minima* (Ulmer, 1916): Ivory Coast, Cavally Basin, River Cavally, Grié (region Toulepleu), 4.II.1988, leg. J.-M. ELOUARD [2 ♂♂ imagines, 1 ♀].

## Oligoneuriidae

*Elassoneuria* sp.: Madagascar, Mangoro Basin, River Mangoro, Mangoro (pont routier), 2.IV.1992, leg. J.-L. GATTOLLIAT [1 ♂].

*Oligoneuriella rhenana* (Imhoff, 1852): Germany, Baden-Württemberg, Oberriexingen, Enz River, 10.VIII.1996, leg. A. STANICZEK [1 ♂, 1 ♀].

## Palingeniidae

*Palingenia longicauda* (Olivier, 1791): Hungary, Tisza River, 30.VI.1993, leg. M. SARTORI & L. RUFFIEUX [1 ♂, 1 ♀].

## Ephemeroptera, larvae

## Heptageniidae

*Ecdyonurus submontanus* Landa, 1969: Germany, Lower Saxony, Löwenhagen, Nieme creek, 2.V.2004, leg. C. JOACHIM [7 specimens].

## Baetidae

*Baetis* sp.: Germany, Lower Saxony, Goslar, Gose creek, 15.IV.2005, leg. J. WILLKOMMEN [4 specimens].

## Plecoptera, adults

## Pteronarcyidae

*Pteronarcys reticulata* Burmeister, 1839: Russia, Russian Far East, Primorje, Orekhovka River near Marevka, trib. Malinovka, 17.VI.1998, leg. P. ZWICK [1 ♂].

## Chloroperlidae

*Chloroperla susemicheli* Zwick, 1967: Italy, Valnontey, 14.IX.2004, leg. J. WILLKOMMEN [1 ♂].

*Chloroperla tripunctata* Scopoli, 1763: Italy, Valnontey, 14.IX.2004, leg. J. WILLKOMMEN [3 ♂♂].

*Siphonoperla torrentium* (Pictet, 1841): Germany, Lower Saxony, Löwenhagen, Nieme creek, 2.VI.2004, leg. J. WILLKOMMEN [1 ♂].

## Perlodidae

*Isoptera grammatica* Poda, 1761: Germany, Baden-Württemberg, Bebenhausen, Goldersbach creek, 14.VI.2004, leg. A. GOLUBOVIĆ; Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. WILLKOMMEN [1 ♂, 1 ♀].

*Isoptera goertzi* Illies, 1952: Germany, Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. WILLKOMMEN [2 ♂♂, 1 ♀].

*Perlodes microcephalus* Pictet, 1833: Germany, Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. WILLKOMMEN [1 ♂, 1 ♀].

## Capniidae

*Capnia vidua* Klapálek, 1904: Germany Lower Saxony, Harz National Park, Torfhaus, Oder creek, 15.IV.2004, leg. A. GOLUBOVIĆ [3 ♂♂].

## Taeniopterygidae

*Brachyptera seticornis* (Klapálek, 1902): Germany, Lower Saxony, Harz, Hohegeiß, Kunzenbach creek, 17.IV.2005, leg. J. WILLKOMMEN [3 ♂♂, 2 ♀♀].

## Leuctridae

*Leuctra hippopus* Kempny, 1899: Germany, Lower Saxony, Zorge, Zorge creek, 17.IV.2005, leg. J. WILLKOMMEN [1 ♂, 1 ♀].

## Nemouridae

*Nemoura cinerea* Retzius, 1783: Italy, Bormio, 29.V.2004, leg. J. WILLKOMMEN [1 ♀].

*Nemoura* cf. *flexuosa* Aubert, 1949: Germany, Lower Saxony, Harz, Hohegeiß, Kunzenbach creek, 17.IV.2005, leg. A. GOLUBOVIĆ [1 ♀].

*Nemoura marginata* (Pictet, 1836): Germany, Lower Saxony, Börsinghausen, 19.V.2004, leg. J. WILLKOMMEN [1 ♀].

*Nemoura* sp.: Germany, Lower Saxony, Börsinghausen, 19.V.2004, leg. J. WILLKOMMEN [1 ♀].

*Protonemoura intricata* (Ris, 1902): Germany, Lower Saxony, Goslar, Gose creek, 15.IV.2005, leg. A. GOLUBOVIĆ [1 ♀].

*Protonemoura meyeri* Pictet, 1841: Germany, Lower Saxony, Harz, Hohegeiß, Kunzenbach creek, 17.IV.2005, leg. A. GOLUBOVIĆ [1 ♂].

## Plecoptera, larvae

## Taeniopterygidae

*Brachyptera seticornis* (Klapálek, 1902): Germany, Lower Saxony, Zorge creek, 17.IV.2005, leg. A. GOLUBOVIĆ [2 specimens].

## Odonata, adults

## Aeshnidae

*Aeshna mixta* Latreille, 1805: Germany, Lower Saxony, Pevestorf (Lüchow-Dannenberg), River Elbe, 8.V.2005, leg. T. HÖRNSCHEMEYER [1 specimen].

## Libellulidae

*Sympetrum sanguineum* Müller, 1764: Germany, Lower Saxony, Pevestorf (Lüchow-Dannenberg), River Elbe, 8.V.2005, leg. T. HÖRNSCHEMEYER [1 ♀].

*Sympetrum* cf. *striolatum* Müller, 1764: Germany, Brandenburg, Rheinsberg, lake Rheinsberger See, 14.X.07, leg. J. WILLKOMMEN [1 ♂].

## Lestidae

*Lestes barbarus* Fabricius, 1798: Germany, Lower Saxony, Pevestorf (Lüchow-Dannenberg), River Elbe, 8.V.2005, leg. T. HÖRNSCHEMEYER [1 ♂].

*Sympetma fusca* Vander Linden, 1820: Germany, Lower Saxony, Pevestorf (Lüchow-Dannenberg), River Elbe, 8.V.2005, leg. T. HÖRNSCHEMEYER [1 ♂].

## 2.2 Methods

The majority of the specimens was collected into 80% ethanol. Several specimens were first fixated in Duboscq-Brasil (ROMEIS 1989) and after 24 h transferred to 80% ethanol. A few species were fixated in a solution of 95% ethanol, formaldehyde and acetic acid (66 : 33 : 10) and after at least 24 h transferred into 80% ethanol. The examination of dry specimens is not satisfactory, so no dry museum material was used for this study.

Specimens were examined and dissected under a Leica MZ16 stereomicroscope. The muscular preparation was done after cutting specimens sagittally into two halves with a razor blade, while the specimens were fixed onto a prepared cork. Afterwards the halves were each fixed by micro needles in a Petri dish. The thoracic muscles were successively removed from medial to lateral using a pair of Dumont forceps. A few species were dissected after a horizontal cut. The drawings were made using a drawing tube on a Leica MZ16 stereomicroscope.

To examine the thoracic sclerites, some of the specimens were first gradually transferred into 10% ethanol and thereafter to 5% potassium hydroxide solution at room temperature for one to three days until the soft tissues dissolved. Small or fragile specimens were transferred into 15% ethanol for about eight days. After rinsing with distilled water, the cleared specimens were again gradually transferred into 80% ethanol for further examination of the sclerites.

Specimens used for scanning electron microscopy (SEM) were gradually transferred into 100% ethanol and then 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 with only limited material available were investigated by high resolution X-ray tomography ( $\mu$ CT) at the Federal Institute for Materials Research and Testing, Berlin (BAM) (HÖRNSCHEMEYER et al. 2002, HÖRNSCHEMEYER 2004). These specimens were prepared in the same way as those used for SEM investigation except of additional cutting off abdomen, wings, and partly the head of the specimens. The dry specimens were fixed vertically (head upwards) on a rivet with paraffin or Leit-C (usually used for SEM). Some of these specimens were sputter coated for subsequent scanning electron microscopy after examination with  $\mu$ CT.

The photographs (except Figs. 58–60) were made with a Nikon Coolpix camera that was mounted on the stereomicroscope. The pictures 58–60 were made with a Leica Macroscope and processed with Synchroscope Automontage.

### Terminology

Terms with “II” or “III” indicate mesothoracic (II) or metathoracic (III) elements. The term “basal plate” (BP sensu KLUGE 2000) is equivalent to the term “median plate” (sensu TSUI & PETERS 1972) and both terms are used in section 4.2.

The terminology of muscles and sclerites of Ephemeroptera primarily follows KLUGE (1994, 2004). For comparison, the terminology used by other authors is given in Tab. 1. The dorsal muscle “t13” is not treated by KLUGE, so the terminology of BRODSKY (1994) has been used.

The nomenclature of muscles and sclerites of Odonata primarily follows ASAHINA (1954) and that of the Plecoptera follows WITTIG (1955) and ZWICK (1973).

For the most part the discussion (section 4.3) is restricted to the mesothoracic muscles since the metathorax and consequently the metathoracic muscles of Ephemeroptera are reduced whereas the flight muscles and the sclerites of Plecoptera are similar in the mesothorax and in the metathorax.

Since the interpretation of the homologies between the ephemeropteran wing base sclerites and the neopteran axillary sclerites is inconsistent within different papers (e.g. BRODSKY

**Tab. 1.** Comparison of ephemeropteran muscles and terminology used by different authors with the homology partly used by MATSUDA (1970).

Muscle attachments	KLUGE 1994 and this study	BRODSKY 1974	MATSUDA 1970	WITTIG 1955	MAKI 1938	TSUI & PETERS 1972
phragma I–phragma II	MT.m	Tm1	t 14	d1m 35	20	II-1
scutum–postnotum	S.LPNm	Tm2	t 12	d1m 36	21	II-4
scutum–postnotum		Tm3	t 13	d1m 37	–	–
scutum–episternum	S.ESm	TPm1	t-p 5, 6	dvm 40	25	II-6
scutum–trochantinus			t-ti 2	dvm 41		
scutum–Cx anterior	S.CmA	TCxm1	t-ti 3		36	II-11
scutum–trochanter	S.Trm	TTrm1	t-tr 1	dvm 42		II-14
scutum–Cx posterior	S.CmP	TCxm2/3	t-cx 7	dvm 43	39	II-19
scutellum–Cx posterior	PSL.Cm	TCxm4	t-cx 6	–	40	II-21
notum–pleurum	AN.Pm	TPm6	t-p 3	tpm 46a		II-7
subtegula–episternum			t-p 4	tpm 47		
scutum–episternum			t-p 7	tpm 46b		
ANP–episternum	SrA.Pm	TPm2	t-p 8			II-13?
scutum (PNP)–pleurum			t-p 15	tpm 49		
episternum–Cx anterior	P.Cm		p-cx 5	cpm 52		II-15
episternum–trochanter	P.Trm		p-tr 1			II-16
left mesofurca–right mesofurca	Fm		s 16		23	II-29
profurca–mesofurca	iFm		s 13	v1m 38	22	II-3
furca–Cx anterior	F.CmA		s-cx 5			
furca–Cx posterior	F.CmP		s-cx 2			II-26?
“BA”–sternum	BA.SmS	TSm1	p-s 12		33	II-8
“BA”–sternum	BA.SmI	TSm2	p-s 12		34	II-9
notum–pleurum	BA.Pm	TPm3	p 4, t-p 4	tpm 47	30	II-10
BA–coxa	BA.Cm	TCxm5	t-cx 4	cpm 51	31	II-18
BA–trochanter	BA.Trm	TTrm2	p-tr 2	cpm 50		–
SA–furcasternum	SA.Sm	TSm3	t-s 5		26	II-5
SA–furca	SA.Fm	TSm4	t-s 4		27	II-20
SA–coxa	SA.Cm	TCxm6/7	t-cx 8	cpm 53	41	II-22/II-23
posterior SA–pleurum	–	–	t-p 16	ppm 56	–	–
1Ax–pleurum	Ax.PmI	TPm4	t-p 11		–	–
1Ax–furca	Ax.Fm	TSm5	t-s 3		28	II-17
3Ax–epimeron	Ax.PmS	TPm5	t-p 14		32	II-22a
3Ax–episternum			t-p 13	tpm 48		

1970, 1974; GRANDI 1947; KLUGE 1994, 2004; KUKALOVÁ-PECK 1983, 1985; MATSUDA 1956) it necessitates simplification. Therefore, the wing base sclerites of Ephemeroptera are named first, second, third and fifth sclerite (s1, s2, s3 and s5). Their homology will be discussed later.

In this work the terminology of the wing base sclerites of Odonata follows ASAHINA (1954). The terminology of the wing veins follows RIEK & KUKALOVÁ-PECK (1984). The numbers and the terminology of the odonatan muscles follow ASAHINA (1954). The parenthesised numbers refer to the metathoracic muscles.

The arrangement of the mayfly musculature in the descriptions (and in Tabs. 1, 3) is as follows: Dorsal muscles (dorsal longitudinal, tergal muscles) – dorso-ventral muscles (tergo-pleural muscles) – pleural muscles – ventral muscles – direct flight muscles. The musculature of Odonata is described in ascending order (muscle 21 to muscle 41) with the terminology following ASAHINA (1954). The stonefly muscles are arranged according to ZWICK (1973): Dorsal muscles (dorsal longitudinal muscles) – dorso-ventral muscles (tergo-sternal muscles, tergo-coxal muscles) – pleural muscles (tergo-pleural muscles, pleuro-coxal muscles, direct flight muscles).

Unless otherwise noted, the head is directed to the top in figures in dorsal view, and to the left in figures in lateral view.

The total length of the specimens is measured from the anterior margin of the head (without antennae) to the end of the abdomen (without cerci).

#### Abbreviations

A	anal vein
A1	anterior anal vein
ab	anal brace
AEM	anepimeron
AES	anepisternum
ALSC	antero-lateral scutal costa
ANi	anteronotal transverse impression
ANP	anterior notal wing process
ANp	anteronotal protuberance
AN.Pm	anteronoto-pleural muscle
ASA	anterior subalar apodeme
AS I	abdominal sternite I
Ax	axillary sclerite (1Ax, 2Ax, 3Ax = first, second, third axillary sclerite)
AxC	axillary cord
Ax.Fm	axillar-furcal muscle
axp	axillary plate (Odonata)
Ax.PmI	inferior axillar-pleural muscle
Ax.PmS	superior axillar-pleural muscle
BA	basalare
BA.Cm	basalar-coxal muscle
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
CuP	sector of the cubital vein
Cx	coxa (Cx II = coxa of mesothorax; Cx III = coxa of metathorax)

Cx.Cxm	coxo-coxal muscle
DMP	distal median plate
EM	epimeron
ES	episternum
F	furca
F.CmA	anterior furco-coxal muscle
F.CmP	posterior furco-coxal muscle
Fm	furcal muscle
FS	furcasternum
fwp	wing pad of the mesothorax
HP	humeral plate
hp	humeral plate (Odonata)
hwp	wing pad of the metathorax
iFm	intersegmental furcal muscle
KEM	katepimeron
KES	katepisternum
LPN	lateropostnotum
LPNC	lateropostnotal crest
LPs	lateroparapsidal suture
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
PAB	prealar bridge
P.Cm	pleuro-coxal muscle
PCxsA	anterior paracoxal suture
PCxsP	posterior paracoxal suture
PES	preepisternum
PLs	pleural suture
PLsI	inferior pleural suture
PLsS	superior pleural suture
PMP	proximal median plate
PNP	posterior notal wing process
PRS	prescutum
PSA	posterior subalar apodeme
PSL.Cm	parascutello-coxal muscle
PSp	posterior scutal protuberance
PST	presternite
P.Trm	pleuro-trochanteral muscle
PWP	pleural wing process
R	(anterior) radial vein
Rs	radial sector
RSSs	recurrent scuto-scutellar suture
S	spiracle
s1, s2, s3, s5	wing base sclerites 1–3, 5
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
Sct	scutum
S.ESm	scuto-episternal muscle
SL	scutellum
SLS	sublateroscutum
S.LPNm	scuto-lateropostnotal muscle
SrA	suralare
SrA.Pm	suralar-pleural muscle
S.Trm	scuto-trochanteral muscle
T	tegula
Tn	trochantinus

### 3 Results

#### 3.1 General Remarks

In the following, descriptions of pleurum, tergum and muscles of the pterothorax of three species of Ephemeroptera and one species of Odonata are given exemplarily. Additionally, the morphology of tergum and pleurum of the pterothorax of *Pteronarcys* and the muscles of *Brachyptera* (Plecoptera) are described.

*Siphonurus aestivalis* (Siphonuridae), as a rather primordial mayfly (KLUGE et al. 1995) shows plesiomorphic conditions in several respects, whereas *Baetis* sp. (Baetidae), even though also rather primitive among the Ephemeroptera with respect to other morphological features, is characterised by very short and rudimentary hind wings. *Ephoron virgo* (Polymitarcyidae) is an example for a more specialised ephemeropteran taxon, which is characterised by horizontal nuptial dances (BRODSKY 1973, FISCHER 1991).

These investigations are supplemented by a description of a late larva of *Baetis* sp. Additionally, the flight muscles of *Sympetrum* cf. *striolatum* (Libellulidae) are described as an example of Odonata. *Pteronarcys reticulata* (Plecoptera) is a subordinate species among Pteronarcyidae but rather basal among Systellognatha. *Brachyptera seticornis* (Taeniopterygidae) is a basal taxon among Nemouroidea and the remaining Euholognatha.

#### 3.2 Ephemeroptera

##### 3.2.1 General Remarks

The mesothorax of subimaginal and imaginal Ephemeroptera is always larger and more developed than the metathorax. The sutures and sclerites are more distinct, the wings are larger and the flight muscles are much stronger in the mesothorax when compared to the metathorax. The pleurum in Ephemeroptera is less robust than in Plecoptera and other Pterygota because the sclerites are well separated by comparatively large membranous areas.

The hind wings are only about half as long as the fore wings and, in flight, they are often coupled with the fore wings. As a consequence, the metathorax is comparatively short and most of the muscles are considerably smaller than the muscles of the mesothorax. The basalar and the subalar, the fulcrum and most sutures are inconspicuous in the metathorax. In the mesothorax, however, they are all well developed.

Even though the hind and fore wings are coupled in flight, the direct flight muscles are present in the mesothorax and in the metathorax, although they are comparatively smaller in the metathorax.

The diminished size of the metathorax brings about the shortening of the tergal elements, especially of the scutum.

The sutures, concavities and convexities that are distinct in the mesotergum are missing in the metatergum.

The superior axillar-pleural muscle (Ax.PmS) running from the third wing base sclerite to the pleurum is visible only if the specimen is dissected with the wings held down.

##### 3.2.2 *Siphonurus aestivalis*, winged stages (Figs. 1–25) (n = 4)

###### Measurements

Total length: 15.8 mm (♂), 22 mm (♀). – Length of mesothorax: 4.2 mm. – Length of mesothoracic wing: 14.7 mm (♂), 20.8 mm (♀). – Width of mesothoracic wing: 5 mm (♂), 7.5 mm (♀). – Length of metathorax: 1.35 mm. – Length of metathoracic wing: 6.6 mm (♂), 10.25 mm (♀). – Width of metathoracic wing (measured at the tornus): 3.3 mm (♂), 4.8 mm (♀). – Height of mesothorax: 4.2 mm (2.1 mm belong to MTm). – Height of metathorax: 2.38 mm.

###### External morphology of the mesonotum

The tergum is subdivided into the notum and postnotum. The notum is subdivided into the prescutum, scutum and scutellum (SL; Figs. 1, 3, 12). The narrow acrotergite and the anterior phragma at the front of the mesonotum separate the prothorax from the mesothorax.

The narrow prescutum has conspicuous lateral arms, which form the prealar bridge (PAB; Figs. 4, 5). The prealar bridge of the mesothorax is subdivided into three arcs. The dorsal arc is extended ventrally and is connected to the ventral arc. The posterior arc is long and ends next to the sclerite where the basalar-pleural muscle is attached (BA.Pm sensu KLUGE 1994). The large scutum, posterior to the prescutum, is divided into several concave and convex areas that also serve as the attachment points of the dorso-ventral muscles. The anterior convexity is the anteronotal protuberance (ANp; Fig. 1), which posteriorly ends in the anteronotal impression (ANi; Fig. 1). The prominent and paired posterior scutal protuberances (PSP; Figs. 1–3, 12) are the dorsal attachments of the scuto-lateropostnotal muscles (S.LPNm; Figs. 15, 16). Posteromedial to the PSP lies the scutellum (SL; Figs. 1–3, 12). The lateral parts of the scutellum are well developed.

The median longitudinal suture (MLs; Figs. 1–3) is clearly visible from the anterior part of the scutum (from the ANi) and it obliterates towards the posterior third of the scutum, well before the PSP. The medioparapsidal sutures (MPs; Figs. 1–3) lateral to the MLs are rather inconspicuous. The lateroparapsidal sutures (LPs; Figs. 1–3) are located lateral to the MPs. They are conspicuous sutures in *S. aestivalis* and disappear at their postero-dorsal end. The conspicuous antero-lateral scutal costa (ALSC; Fig. 1) is located anterior to the lateroparapsidal sutures.

The mesonotal suture (MNs; Figs. 1–3, 8) proceeds across the anterior fourth of the scutum. It is a distinct suture with a carinate anterior rim.



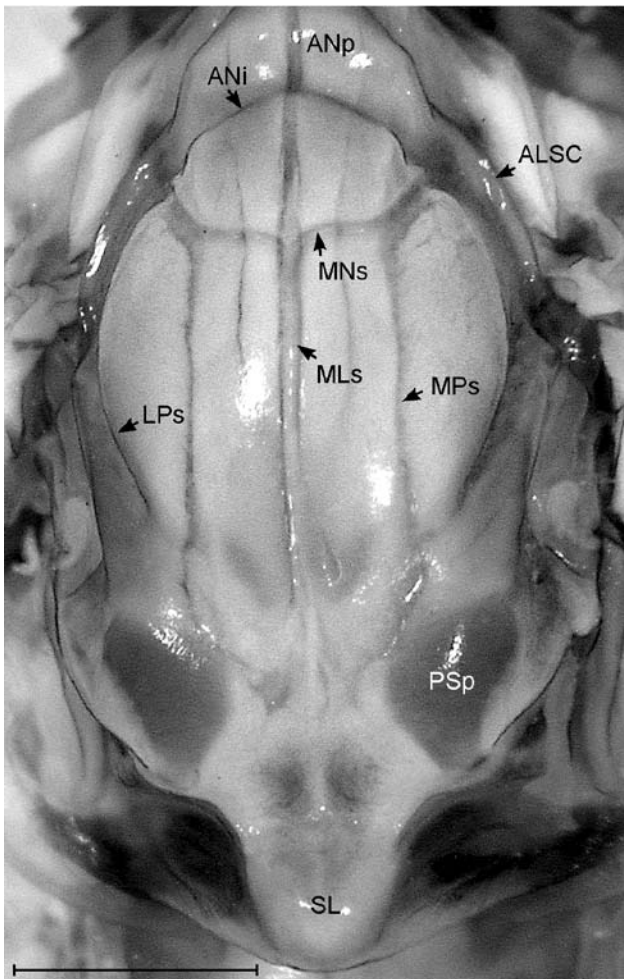


Fig. 1. *Siphonurus aestivalis*, ♀ imago, mesotergum. – Scale: 1 mm.

*Siphonurus aestivalis* has conspicuous anterior and posterior notal wing processes (ANP, PNP; Figs. 2, 3). The anterior notal wing process is long and narrow and is located in direct proximity of the first free wing base sclerite (s1; Figs. 2, 3). The posterior notal wing process is a little less distinct than the anterior one and articulates with the third free wing base sclerite (s3; Figs. 2, 3).

The tegula (T; Figs. 2, 8, 12) is a well separated sclerite, which is located at the anterior base of the wing. Usually, it lacks setae in the imago, but in some male imagines it is sparsely covered with short setae.

Between the tegula and the tergum there are two sclerites. The anterior sclerite is connected to the crescent-shaped sclerite (BA; Figs. 4–8). It is the dorsal point of attachment of the basalar-pleural muscle (BA.Pm sensu KLUGE 1994; Figs. 18, 19). The posterior sclerite is the dorsal point of attachment of the basalar-coxal muscle (BA.Cm sensu KLUGE 1994; Figs. 17–19). The slightly tri-

angular humeral plate (HP; Fig. 8) is distinct in the fore wing. Its anterior tip is well sclerotised.

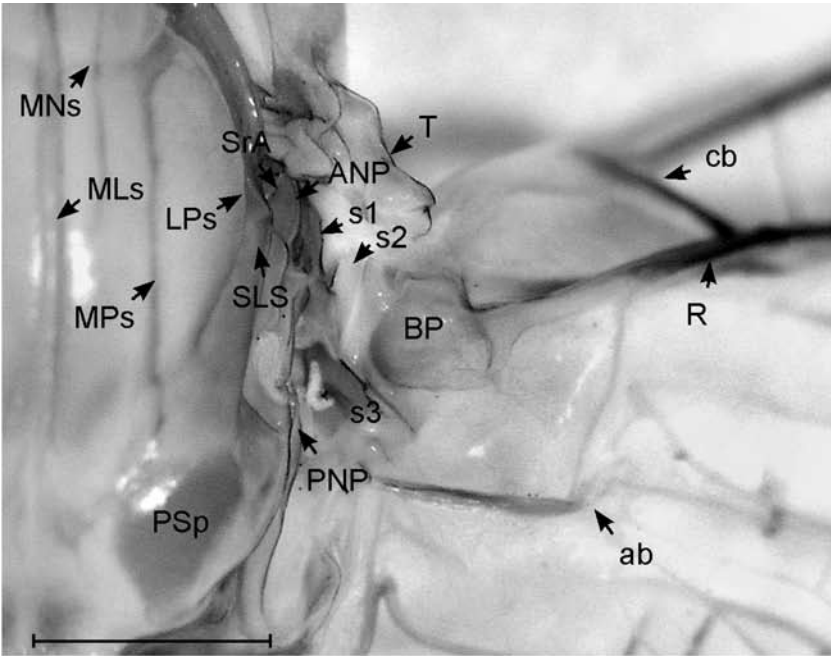
The basal plate (BP; Figs. 2, 3) is a very prominent structure in the wing base. It is sclerotised in both dorsal and ventral layer of the wing membrane. The subcostal vein originates on the antero-ventral side of the basal plate. The radial vein originates almost centrally on the dorsal side of the basal plate. The main part of the BP resembles a convex hemisphere as seen from above. Its postero-medial part is, however, concave with a distinct and well sclerotised posterior edge, which articulates with the s3. The basal part of the BP is flat and anteriorly tapers off into a ventral process (BPp; Fig. 7). This process articulates with the pleural wing process (PWP; Figs. 4–8).

In addition to the basal plate, there are three more sclerites in the wing base. The first free sclerite (s1; Figs. 2, 3) lies distal to the ANP. It articulates distally with the second free wing base sclerite (s2; Figs. 2, 3). The first free sclerite is triangular in shape and narrow. It is only sclerotised in the dorsal layer of the wing membrane. The second free wing base sclerite (s2; Figs. 2, 3) is a distinct, and large sclerite, which is also only sclerotised in the dorsal layer of the wing membrane. The articulation point with the s1 is well sclerotised. The proximal part of s2 is bent inwards. The s2 articulates distally with the basal plate and posteriorly with the third free wing base sclerite (s3; Figs. 2, 3).

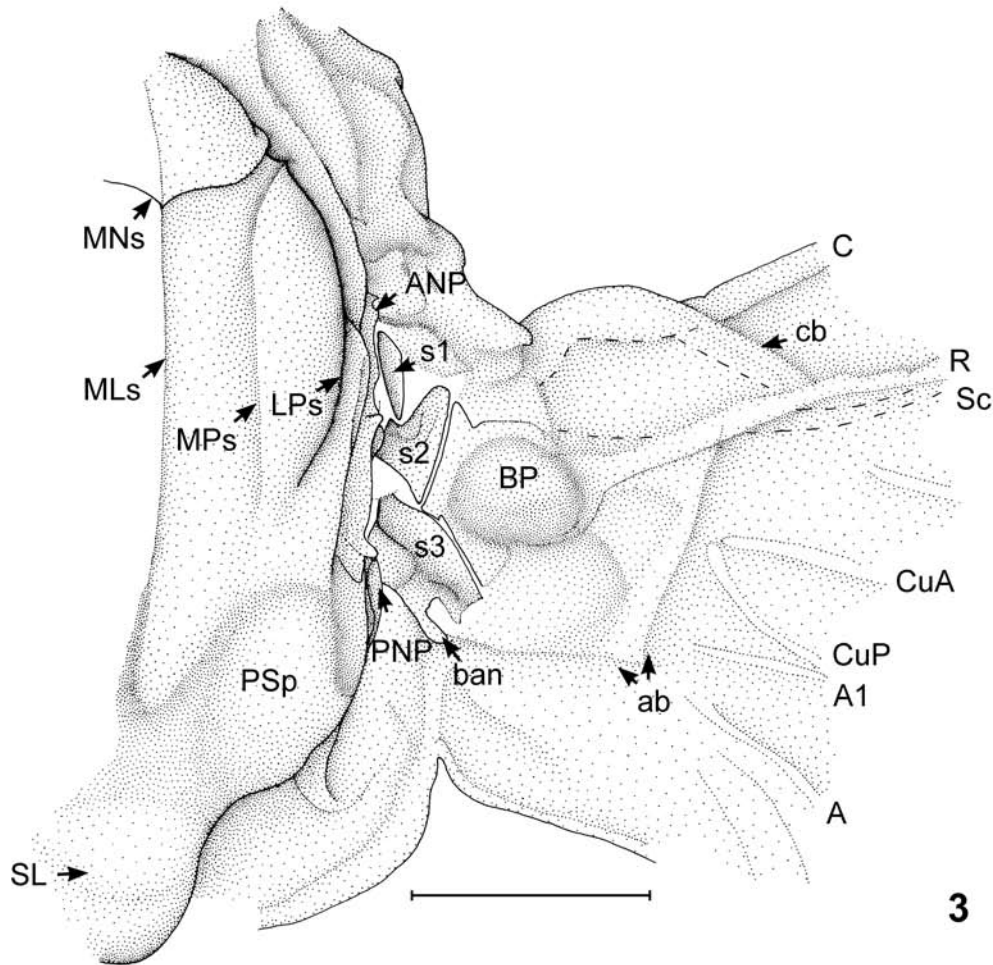
The third free wing base sclerite (s3) is a large sclerite, which is not easily distinguishable from the basanale (ban; Fig. 3). It is sclerotised in the dorsal as well as in the ventral layer of the wing membrane. The antero-lateral ridge of the s3 is connected to the posterior rim of the basal plate. The proximal part of s3 articulates with the posterior notal wing process (PNP). Ventrally, the s3 is connected to the subalare (SA; Figs. 5, 10). A fifth, slightly crescent-shaped sclerite is present in the mesothorax (s5, not pictured, compare Fig. 86), which is associated with the scutum between the ANP and PNP.

The wing veins are not directly connected to the wing base sclerites. The s2 is connected to the subcostal vein (Sc; Fig. 3) via the anterior point of the basal plate. The s3 is connected to the anal veins (A; Fig. 3) via the basanale and the anal brace (ab; Figs. 2, 3).

The prominent costal brace (cb; Figs. 2, 3) at the anterior wing base stretches between the costal vein and the anterior radial vein. The costal brace tapers off into a fold, which ends anterior to the BP. In addition, the costal brace is weakly connected to the subcostal vein, near the connection to the radial vein. The proximal (or posterior) arc of the anal brace (ab; Fig. 2) is conspicuous and the distal (or anterior) arc is rather less distinct. The basanale is well sclerotised and distinct in the wing base of *Siphonurus aestivalis*.



2



3

**Figs. 2–3.** *Siphonurus aestivalis*, ♀ imago, right fore wing. – Scales: 1 mm.

The radial sector (Rs) is basally fused to the anterior medial vein (MA). The anterior medial vein (MA) and the posterior medial vein (MP) are fused to each other at their bases. The radial sector (Rs) branches off from the MA distal to the MA-MP fork. The distinct anal brace is located between the anterior radial vein and the sclerotised basanale (ban).

The lateropostnotum (LPN, postalar bridge; Figs. 4, 5, 8), which is the ventral point of attachment of the scuto-lateropostnotal muscle (S.LPNm; Figs. 15, 16), is distinct and the lateropostnotal crest (LPNC; Fig. 8) is rather inconspicuous in *Siphonurus aestivalis*.

#### External morphology of the mesopleurum (Figs. 4–10, 13)

The most distinct sutures in the mesopleurum are the pleural suture (PLs) and the anterior paracoxal suture (PCxsA; Figs. 4, 5, 8). The pleural suture divides the pleurum into the anterior episternum and the posterior epimeron. The pleural suture is divided into the upper or superior part (PLsS; Figs. 4, 5, 8) and the lower or inferior part (PLsI; Figs. 4, 5, 8). The pleural suture runs almost vertically and extends dorsally into the distinct pleural wing process (PWP; Figs. 4–8). The externally visible condylus of the PWP is rather small. The fulcrum articulates with the ventral process of the basal plate (BPp; Figs. 7, 8). Ventrally, the pleural suture ends at the point where the coxa articulates with the pleurum, the coxo-pleural joint.

The second distinct suture, i. e. the paracoxal suture, is subdivided into the anterior paracoxal suture (PCxsA) and the posterior paracoxal suture (PCxsP; Figs. 5, 8). The anterior suture (PCxsA) is conspicuous, while the posterior suture (PCxsP) is rather inconspicuous. The PCxsA divides the pleurum into a broad anepisternum (AES; Figs. 4, 5, 8) and a narrow katepisternum (KES; Figs. 4, 5, 8). The PCxsP is more distinct in male specimens than in female ones. It divides the dorsal anepimeron (AEM; Fig. 5) from the ventral katepimeron (KEM; Fig. 5).

The basale (BA; Figs. 4–8) is located anterior to the PWP at the anterior base of the wing. It is a crescent-shaped sclerite, which merges posteriorly with the tegula and dorsally with the tergum. Posterior to the PWP lies the subalare (SA; Figs. 5, 10). It is a conspicuous element of the mesopleurum. Its dorsal part is less sclerotised and less pigmented than the ventral part. The latter is of triangular shape. Its dorsal margin forms a distinct suture (SAs; Fig. 8) that separates the dorsal and ventral part of the subalare from each other. The posterior end of the ventral sclerite forms the large posterior subalar apodeme (PSA; Figs. 4–8). The small anterior subalar apodeme (ASA; Figs. 4–8) is mainly formed by the anterior end of the dorsal subalare. The posterior subalar apodeme and the ventral sclerite of the SA is the area of insertion of the subalar-sternal muscle (SA.Sm; Figs. 14–16). The anterior

margin of the dorsal subalare is well sclerotised. The ASA is the insertion point of the subalar-coxal muscle (SA.Cm; Figs. 18, 19).

#### Muscles of the mesothorax

##### Dorsal muscles

**MTm:** The median tergal muscle (Fig. 14) is anteriorly attached to the first phragma and the anterior part of the scutum and runs to the posterior (or second) phragma. It is almost half the height of the mesothorax. The contraction of MTm results in downwards movement of the wings.

**t13:** The second dorsal longitudinal muscle (Figs. 14–17) is anteriorly attached to the scuto-scutellar impression and runs to the scutellum. It is a very small and flat muscle, lying posterior to MTm. It consists of only a few fibres.

**S.LPNm:** The scuto-lateropostnotal muscle (Figs. 15, 16) is attached to the posterior part of the scutum (PSP) and runs in almost vertical direction to the latero-ventral part of the phragma – the lateropostnotum (LPN). Ventrally the muscle is a little wider than dorsally. S.LPNm lies slightly lateral to MTm.

##### Dorso-ventral muscles

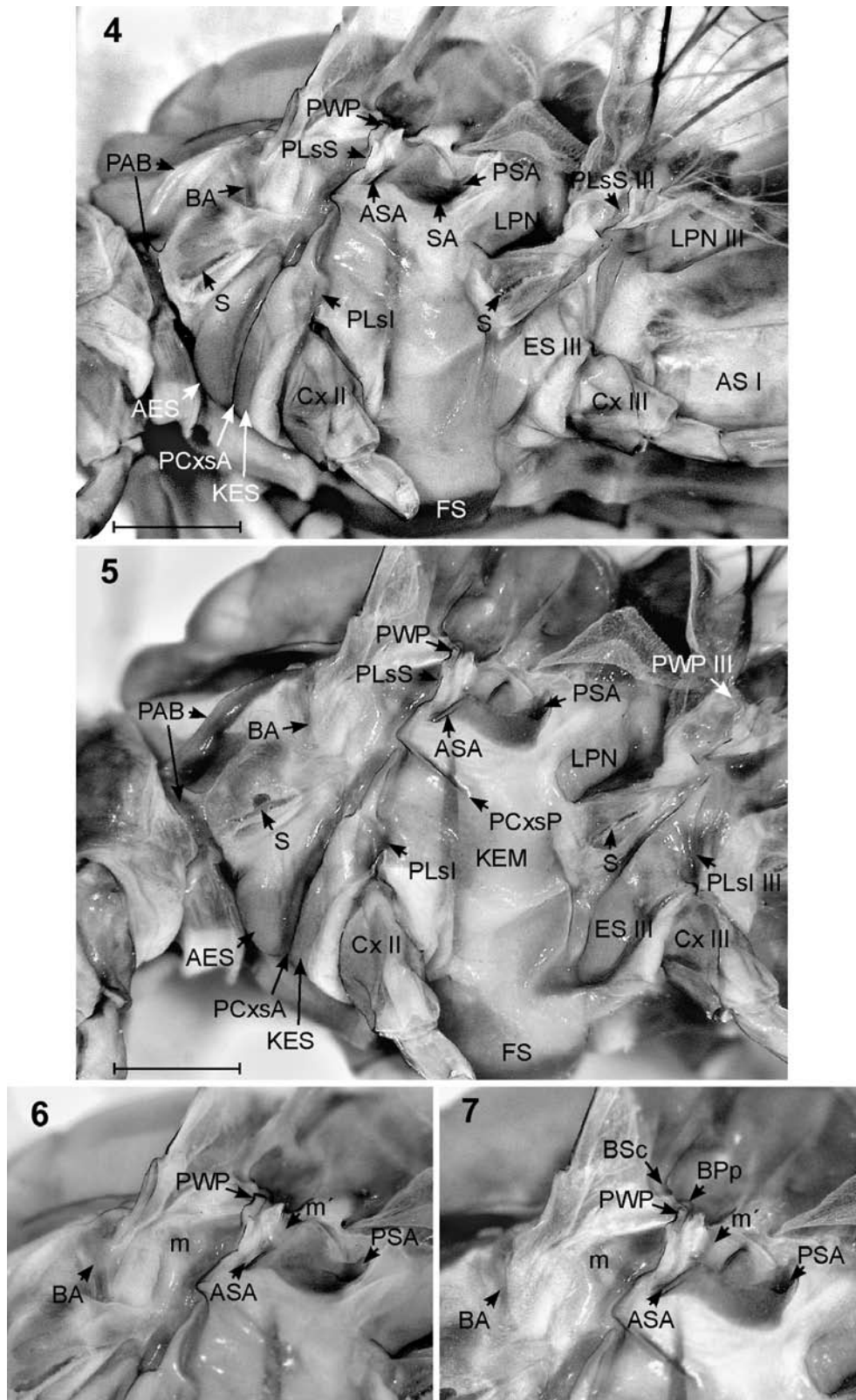
**S.ESm:** The scuto-episternal muscle (Fig. 15) is dorsally attached to the anterior part of the scutum and extends to the ventral part of the episternum. It is a large muscle lying lateral to MTm. It is dorsally wider than ventrally. The dorsal area of attachment is a little less than one third of the length of the mesothorax. S.ESm is the main antagonist to MTm.

**S.CmA:** The anterior scuto-coxal muscle (Figs. 15, 16) is dorsally attached to the lateroparapsidal suture and proceeds to the anterior rim of the coxa. It lies postero-lateral to the S.ESm.

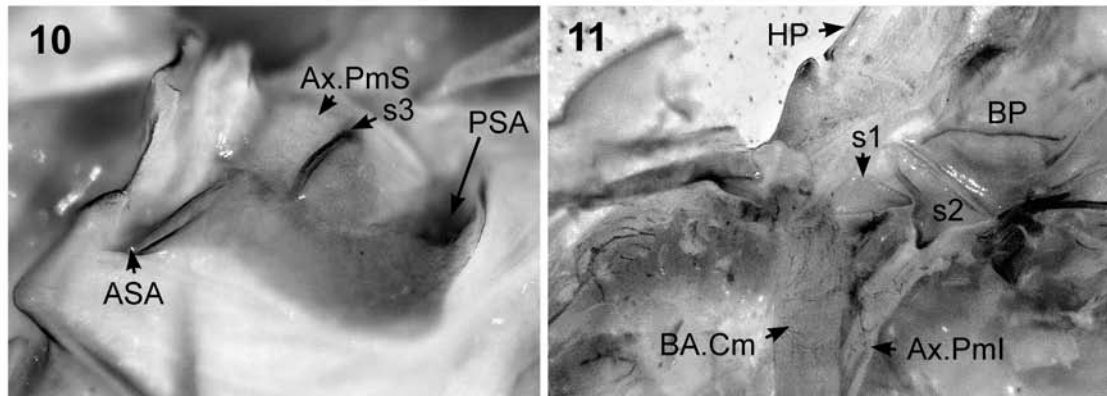
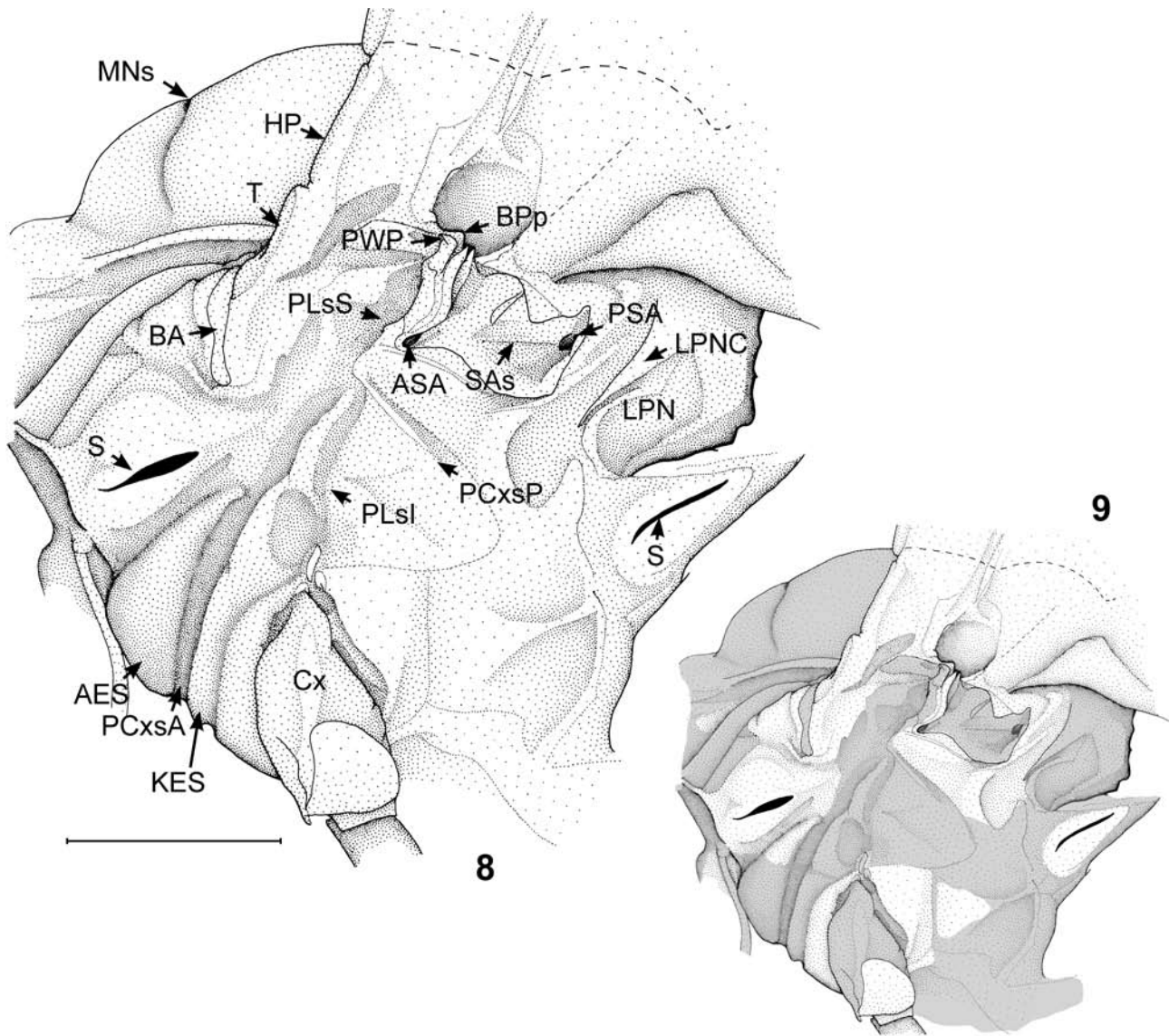
**S.CmP:** The posterior scuto-coxal muscle (Figs. 16, 17) runs from the posterior part of the scutum (anterior part of the posterior scutal protuberance, PSP) to the posterior rim of the coxa. S.CmP is located postero-lateral and in close proximity to S.CmA. This muscle is roughly similar in size as the S.CmA.

**S.Trm:** The scuto-trochanteral muscle (Figs. 17, 18) is dorsally attached to the sublateraloscutum (SLS; Fig. 2) and proceeds to the trochanter. It is a flat muscle, which is thinner than the S.CmA and the S.CmP and lies lateral to the latter.

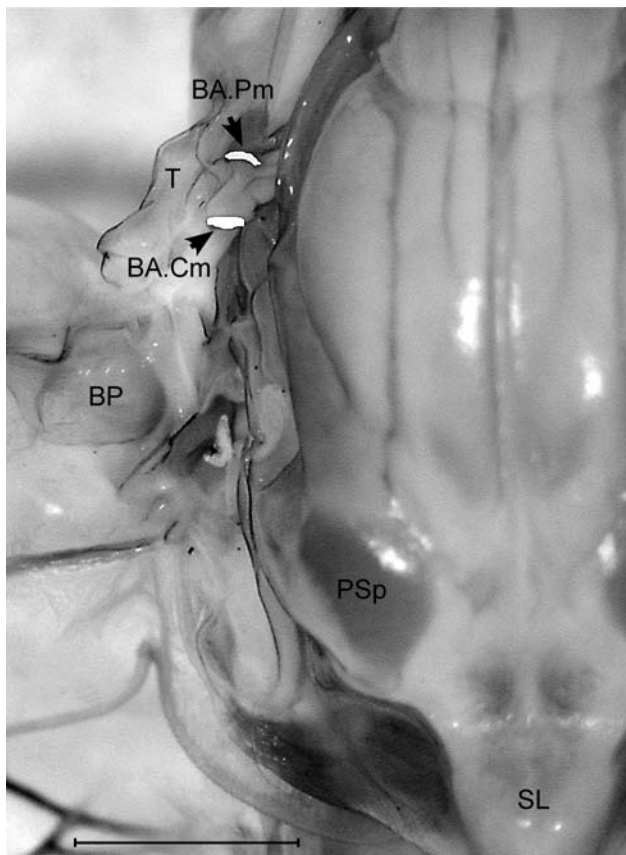
**PSL.Cm:** The parascutello-coxal muscle (Fig. 18) extends from the antero-lateral part of the scutellum, the parascutellum, to the postero-lateral rim of the coxa. The ventral point of attachment lies besides the ventral point of attachment of the subalar-coxal muscle. The PSL.Cm is a flat and slender muscle, which lies lateral



**Figs. 4–7.** *Siphonurus aestivalis*, ♀ (4, 6) and ♂ (5, 7) imago. – 4–5. Pleurum of meso- and metathorax. 6–7. Mesopleurum, upper area. – m = ventral attachment of BA.Pm; m' = ventral attachment of Ax.PmS. – Scales: 1 mm.



**Figs. 8–11.** *Siphonurus aestivalis*, ♂ (8–10) and ♀ (11) imago. – 8–9. Mesopleurum (grey areas sclerotised). 10. SA of the mesopleurum (Ax.PmS and s3 shine through the SA). 11. Mesothorax, internal view, dorsal attachment of BA.Cm and Ax.PmI. – Scale: 1 mm.

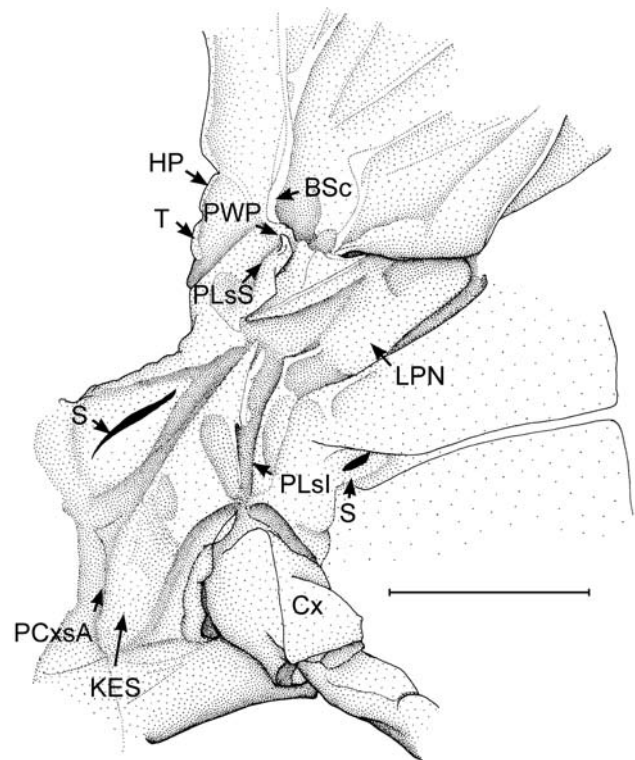


**Fig. 12.** *Siphonurus aestivalis*, ♀ imago, left fore wing base and attachment points of BA.Pm and BA.Cm. – Scale: 1 mm.

to S.LPNm. The dorsal part of this muscle is slender but robust (wider than in most other Ephemeroptera) and is ventrally attached to the coxal rim via a long, probably epidermal tendon.

**AN.Pm:** The anteronoto-pleural muscle (Figs. 16, 17) is dorsally attached to the antero-lateral part of the scutum and extends to the dorsal part of the anterior paracoxal suture. It is a flat but distinct and relatively robust muscle (more distinct than in other Ephemeroptera, e.g. *Habroleptoides confusa*). AN.Pm lies anterior to SrA.Pm and medial to the basalar-sternal muscles (BA.SmS, BA.SmI).

**SrA.Pm:** The suralar-pleural muscle (Figs. 16–18) is dorsally attached to the suralare (SrA; Fig. 2), which includes the anterior notal wing process. Ventrally, it is attached to the paracoxal suture (below the posterior pleural suture). In some specimens the ventral point of attachment is somewhat antero-dorsal: In this case, the muscle is ventrally attached to the dorsal part of the AES. The SrA.Pm is a flat muscle consisting of only a few fibres.



**Fig. 13.** *Siphonurus aestivalis*, ♂ imago, metapleurum. – Scale: 1 mm.

#### Pleural muscles

**P.Cm:** The pleuro-coxal muscle (Figs. 17–19) runs from the anterior paracoxal suture to the anterior coxal rim. It is a short muscle, which is oval in cross section.

**P.Trm:** The pleuro-trochanteral muscle (Figs. 17–19) is dorsally attached to the anterior paracoxal suture and ventrally to the trochanter. It is a slender muscle lying direct posterior to P.Cm. P.Trm is almost round in cross section.

#### Ventral muscles

**iFm:** The intersegmental furcal muscle (Fig. 14) runs from the posterior side of the profurca to the anterior side of the mesofurca. It is a flat but distinct muscle.

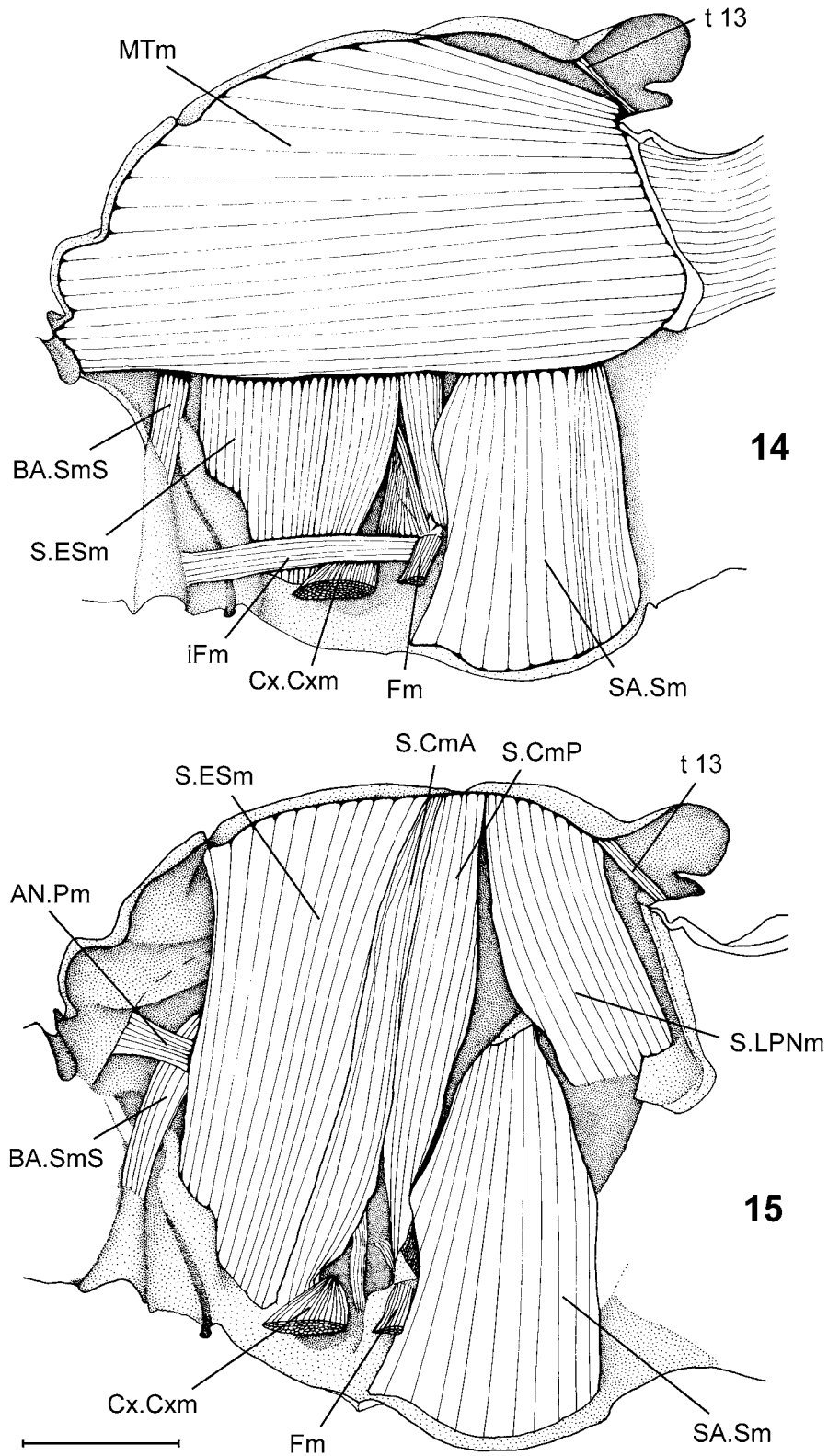
**Fm:** The furcal muscle (Figs. 14–16) runs from the medial side of the right sternal apophysis (right furca) to the medial side of the left sternal apophysis (left furca).

**F.CmP:** The posterior furco-coxal muscle (Figs. 18, 19) is a flat muscle running from the posterior side of the furca to the coxal rim (next to the coxo-pleural articulation and the ventral attachment of the BA.Cm).

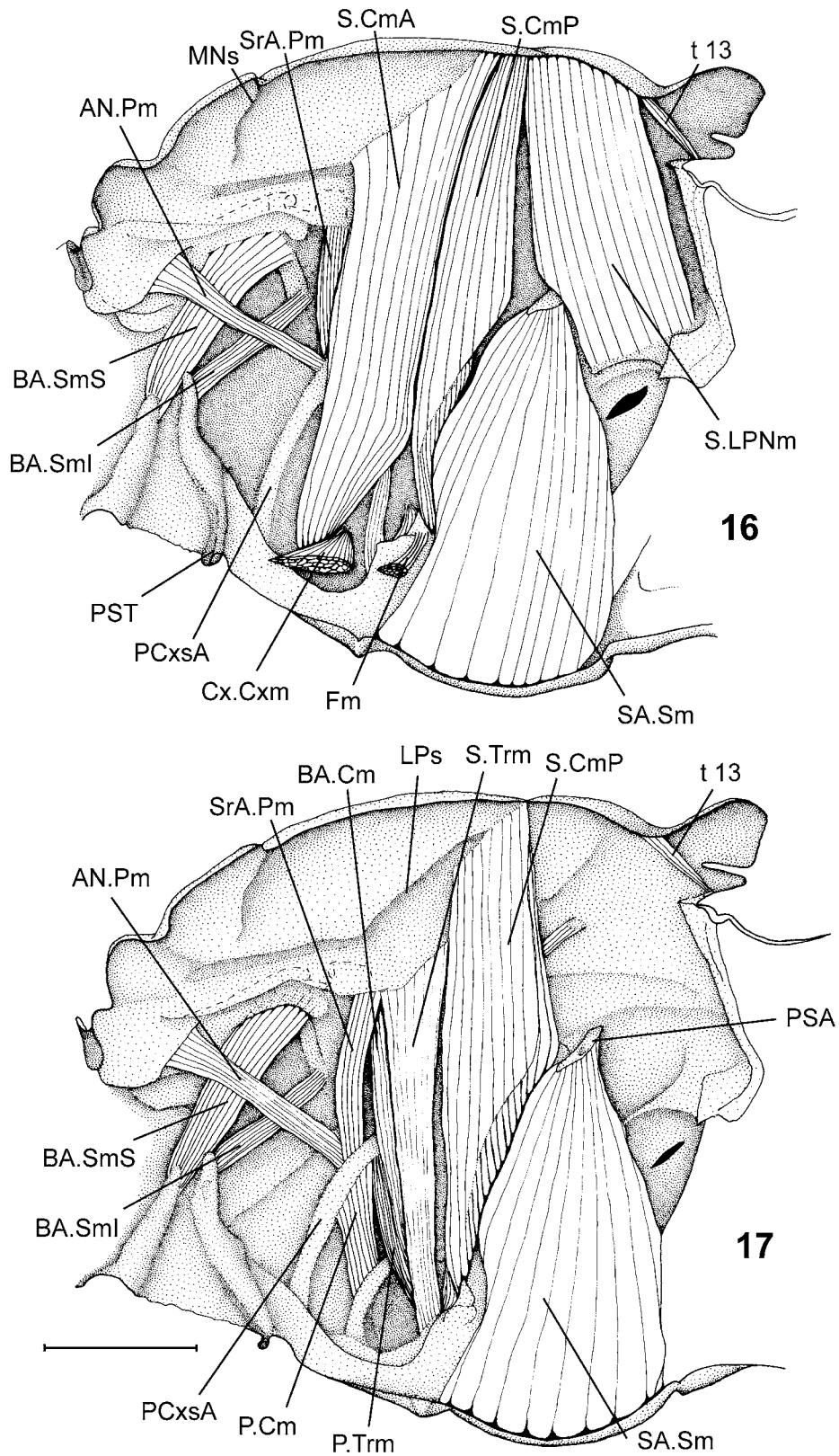
#### Direct flight muscles

**BA.SmS:** The superior basalar-sternal muscle (Figs. 14–19) is dorsally attached to the crescent-shaped basalare



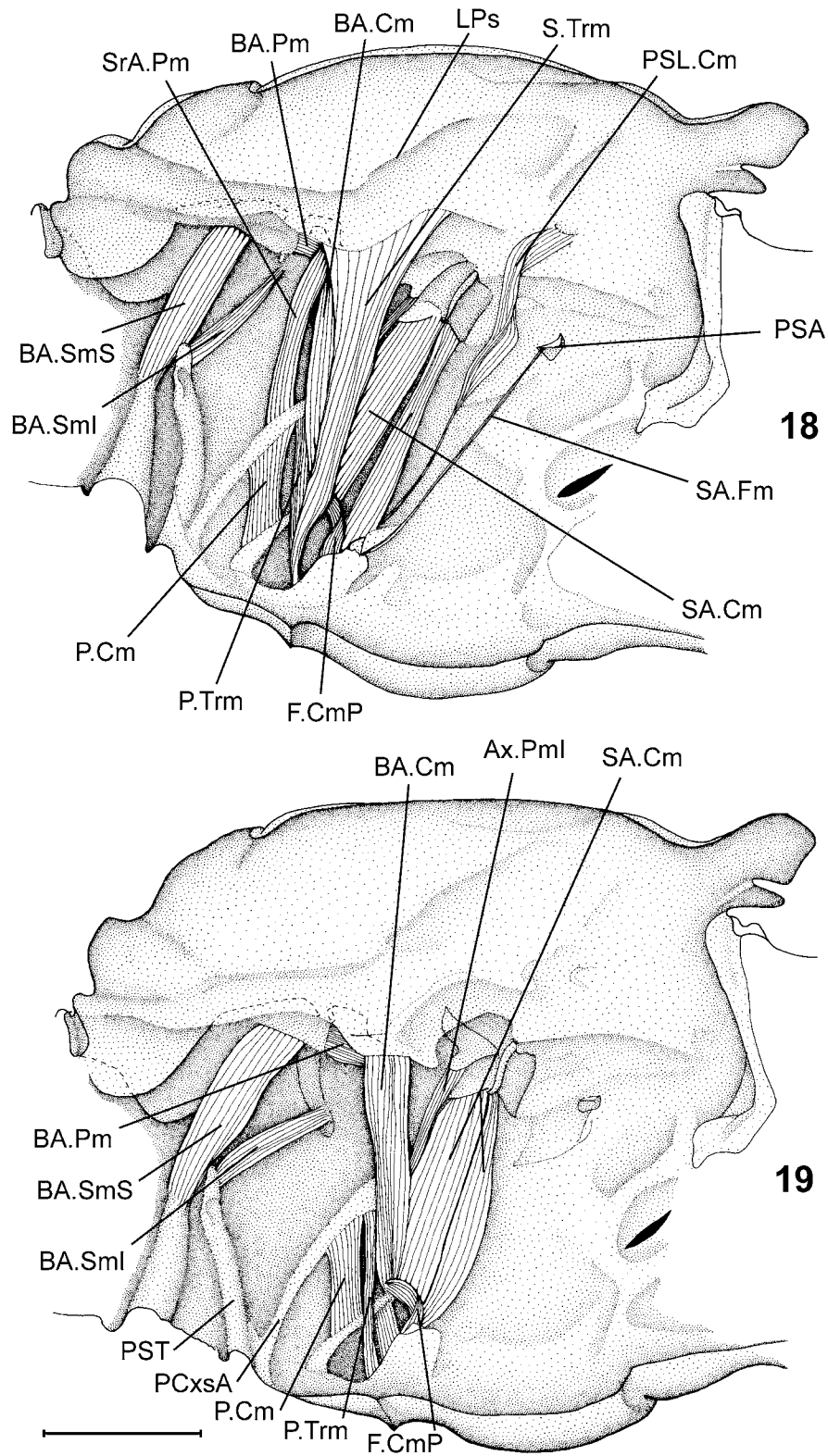


**Figs. 14–15.** *Siphonurus aestivalis*, ♀ imago, musculature of the right half of the mesothorax at progressive stages of dissection, starting with median muscles (14) and progressively proceeding to the most lateral muscles (see Fig. 19). – Scale: 1 mm.

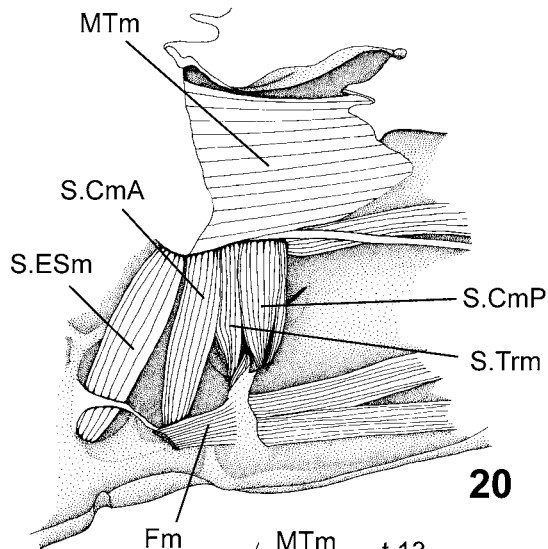


**Figs. 16–17.** *Siphonurus aestivalis*, ♀ imago, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 14–15). – Scale: 1 mm.

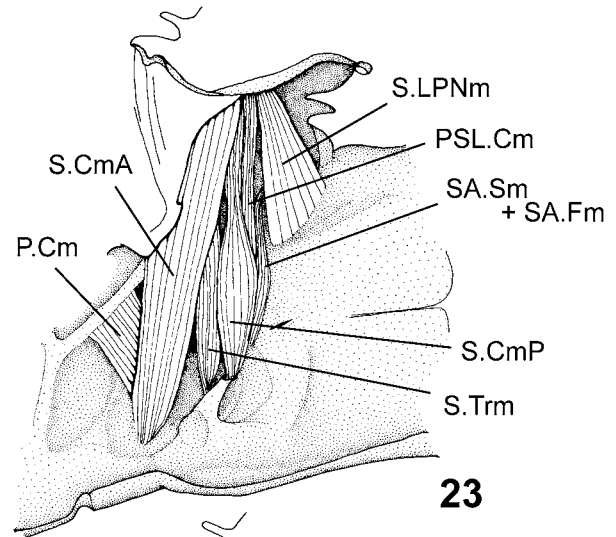




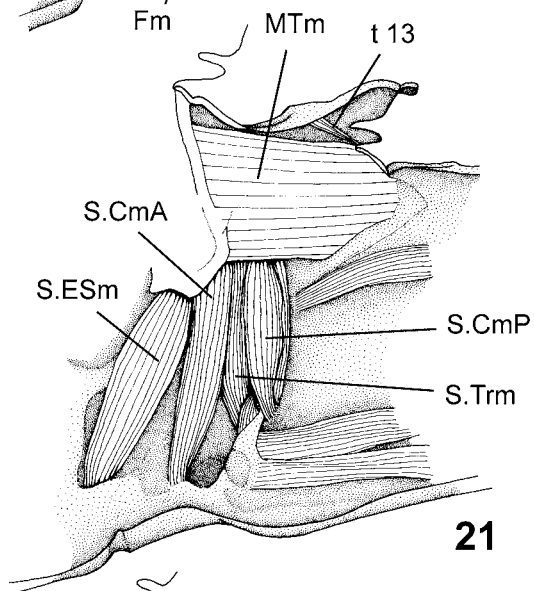
**Figs. 18–19.** *Siphonurus aestivalis*, ♀ imago, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 14–15). – Scale: 1 mm.



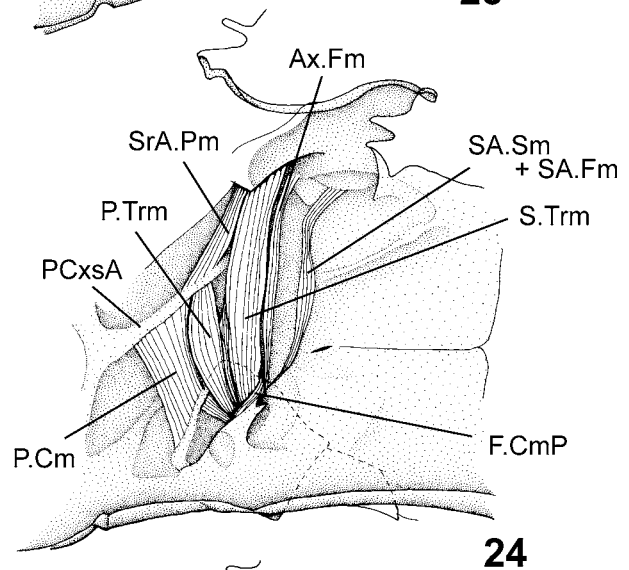
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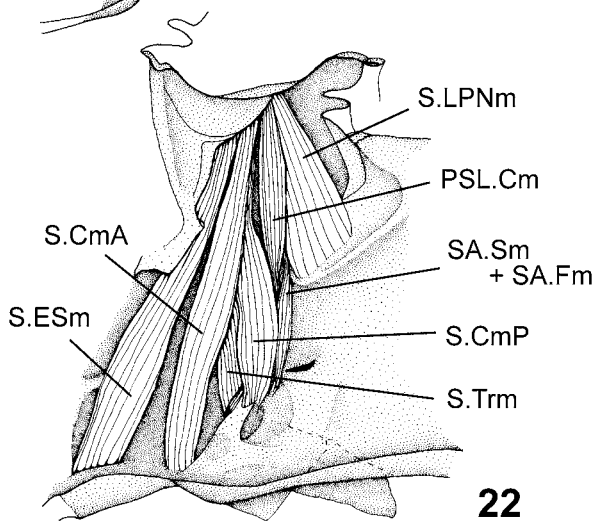
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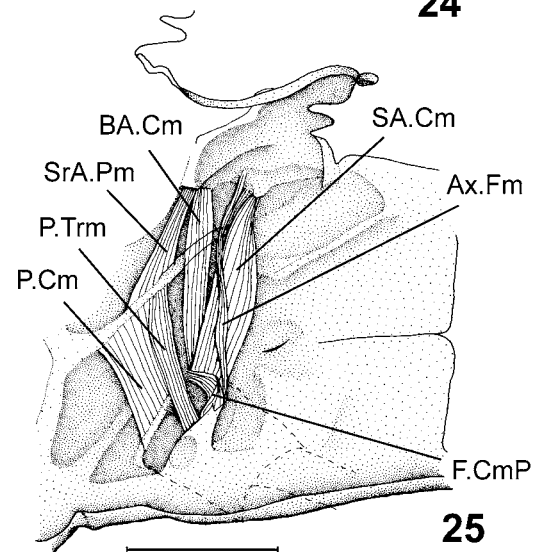
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**Figs. 20–25.** *Siphonurus aestivalis*, ♀ imago, musculature of the right half of the metathorax at progressive stages of dissection, starting with median muscles (20) and progressively proceeding to the most lateral muscles (Fig. 25). – Scale: 1 mm.

and runs to the profurca or directly posterior to it. The superior basalar-sternal muscle is considerably larger than the very small inferior one.

**BA.SmI:** The inferior basalar-sternal muscle (Figs. 16–19) runs from the ventral part of the crescent-shaped basalar to the presternite (PST, compare Fig. 48). It is much smaller than the BA.SmS (only about one quarter of its size).

**BA.Pm:** The basalar-pleural muscle (Figs. 18, 19) is a short but robust muscle running from a sclerite, lying in-between the tegula and the tergum, to the pleurum – anterior to the PWP.

**BA.Cm:** The basalar-coxal muscle (Figs. 17–19) is dorsally attached to a sclerite, lying antero-medial to sl. It proceeds to the coxal rim (adjacent to the coxo-pleural joint). BA.Cm is located antero-lateral to SrA.Pm.

**SA.Sm:** The subalar-sternal muscle (Figs. 14–17) is dorsally attached to the ventral part of the subalare and to the posterior subalar apodeme (PSA). It extends to the furcasternum. It is the largest subalar muscle, ventrally slightly wider than dorsally and located posterior to S.CmP.

**SA.Fm:** The subalar-furcal muscle (Fig. 18) is a very slender muscle running from the posterior subalar apodeme (PSA) to the furca. It is located anterior to SA.Sm.

**SA.Cm:** The subalar-coxal muscle (Figs. 18, 19) is dorsally attached to the anterior part of the subalare, i.e. the anterior subalar apodeme (ASA). The SA.Cm consists of two parts. The first part is more compact and runs to the latero-posterior part of the coxal rim (near the coxo-pleural joint). The second part, which lies lateral to the first part, is rather flat and runs to the posterior rim of the coxa. The insertion as well as the origin of the second part is wide. SA.Cm is located anterior to SA.Sm.

**Ax.Fm:** The axillar-furcal muscle (not pictured, compare Figs. 53, 119–122: t-s 3) is a very slender muscle running from the proximal apodeme of the second wing base sclerite (s2) to the tip of the furca.

**Ax.PmI:** The (inferior) axillar-pleural muscle (Fig. 19) runs from the ventral side of the proximal apodeme of the second wing base sclerite (s2) to the pleural ridge. Both the Ax.Fm and the Ax.PmI are slender but robust muscles that are distinct in the mesothorax.

**Ax.PmS:** The (superior) axillar-pleural muscle (not pictured, compare Figs. 54, 55) is a short but robust muscle running from the third wing base sclerite (s3) to the anterior part of the subalare.

**Cx.Cxm:** The coxo-coxal muscle (Figs. 14–16) is present. It stretches from the antero-lateral interior area of the right coxa to the antero-lateral interior area of the left coxa. The muscle is located anterior to the furco-furcal muscle (Fm) and is about two to three times as large as the Fm.

### External morphology of the metanotum

The metanotum is rather flat. Its sutures are more or less reduced in comparison to the mesonotum. The scutum and the scutellum (SL) are short and approximately equal in length. The posterior scutal protuberances (PSP) are visible. Posterior to the PSP is the scutellum; its dorsal and lateral parts (scutellum, SL, and parascutellum, PSL) are distinct.

The median longitudinal suture (MLs) is indistinct and just visible at the anterior part of the scutum.

The elements of the metathoracic wing base are partially reduced. The anterior and the posterior notal wing processes (ANP, PNP) are distinct in the metanotum. The PNP articulates with the third free wing base sclerite (s3). The tegula is located at the anterior part of the wing base, between the tergum and the humeral plate (HP); it is discernible even in the hind wing. The humeral plate (HP) is located distal to the tegula; it is conspicuous in the metathorax but T and HP are rather membranous and soft.

The major part of the basal plate (BP) is clearly convex and distinct. Its proximal area is flat and clearly distinguishable from the convex area of the basal plate.

The first free (anterior) wing base sclerite (s1) is missing. The second free wing base sclerite (s2) is conspicuous and broad (roughly like the mesothoracic s2). It has a distinct proximal process, which is slightly bent inwards. The third free wing base sclerite (s3) is, like the second sclerite, discernible in the metathoracic wing base.

The basanale of the hind wing is hard to distinguish from s3. The costal brace (cb) at the anterior part of the wing is conspicuous. The anterior part of the anal brace (ab) is arched and rather indistinct. The proximal (or posterior) arc of the anal brace is conspicuous. The distal (or anterior) arc of the anal brace is rather indistinct. The distinct subcostal vein (Sc) originates at the antero-ventral part of the basal plate. The anterior radial vein originates at the antero-dorsal part of the basal plate. The base of the anterior medial vein (MA) is located directly posterior to the anterior radial vein and it is discernable almost to the basal plate.

The lateropostnotum (LPN) is developed as a distinct convex area (similar to the mesothorax).

### External morphology of the metapleurum

The anterior paracoxal suture (PCxsA; Fig. 13) is the most conspicuous suture in the metapleurum. It divides the narrow anepisternum (AES) from the much wider katepisternum (KES; Fig. 13). The posterior paracoxal suture (PCxsP) is indistinct in the metapleurum. A further conspicuous suture is the pleural suture (PLsS, PLsI; Figs. 5, 13). It divides the wider episternum (ES; Figs. 4, 5) from the narrow epimeron. Dorsally the PLsS extends into the distinct pleural wing process (PWP; Fig. 13). The basal part of the subcostal vein (BSc; Fig. 13) is also distinct.

A basalar (BA) is not visible. The dorsal part of the subalar (SA, not pictured) is partly noticeable as a narrow sclerite, while the ventral part is inconspicuous.

#### Muscles of the metathorax

##### Dorsal muscles

**MTm:** The median tergal muscle (Figs. 20, 21) stretches between the two phragmata. It is a very large muscle in relation to the size of the metathorax.

**t13:** The second dorsal muscle (Fig. 21) runs from the notum (in-between the scutum and the scutellum, lateral to the MLs) to the dorsal part of the phragma between the metathorax and the abdomen. The muscle is small, flat and consists of only a few fibres, though it is approximately equal in size to t13 of the mesothorax.

**S.LPNm:** The scuto-lateropostnotal muscle (Figs. 22, 23) runs from the posterior part of the scutum to the small lateropostnotum. It is a relatively large muscle comparable in size to that of the mesothorax. The ventral point of attachment is wider than the dorsal one.

##### Dorso-ventral muscles

**S.ESm:** The scuto-episternal muscle (Figs. 20–23) runs from the antero-median part of the triangular scutum to the episternum. It is a large muscle in the metathorax.

**S.CmA:** The anterior scuto-coxal muscle (Figs. 20–23) is dorsally attached to the scutum – postero-lateral to the dorsal point of attachment of the S.ESm and runs to the anterior coxal rim. It is a large muscle, which is only slightly smaller than S.ESm.

**S.CmP:** The posterior scuto-coxal muscle (Figs. 20–23) runs from the scutum (posterior to the S.CmA) to the posterior coxal rim. The S.CmP is smaller and more slender than the S.CmA.

**S.Trm:** The scuto-trochanteral muscle (Figs. 20–24) is dorsally attached to the lateral part of the scutum (lateral to S.CmA and S.CmP, proximal to the BP of the wing base and at the same level). Ventrally, the muscle is attached to the antero-medial area of the trochanter. S.Trm is almost half the size of S.ESm.

**PSL.Cm:** The parascutello-coxal muscle (Figs. 22, 23) runs from the anterior part of the scutellum to the postero-lateral part of the coxal rim. The dorsal half of PSL.Cm is broad. The muscle is ventrally attached to the coxal rim via a tendon. It is a comparably large metathoracic muscle, which is as large if not larger than its mesothoracic equivalent.

**AN.Pm:** The anteronoto-pleural muscle (not pictured) is dorsally attached to the antero-lateral part of the notum and extends to the dorsal part of the anterior paracoxal suture just dorsally of the P.Trm. It is a flat and wide but distinct and relatively robust muscle.

**SrA.Pm:** The suralar-pleural muscle (Figs. 24, 25) is dorsally attached to the lateral part of the scutum and runs to the dorsal part of the anterior paracoxal suture. It is a very slender muscle consisting of only a few fibres.

##### Pleural muscles

**P.Cm:** The pleuro-coxal muscle (Figs. 23–25) is stretched between the anterior paracoxal suture (PCxsA) and the anterior rim of the coxa. The muscle seems to consist of two parts and it is rather flat but broad.

**P.Trm:** The pleuro-trochanteral muscle (Figs. 24, 25) runs from the PCxsA to the trochanter and is almost round in cross section.

##### Ventral muscles

**Fm:** The furcal muscle (Fig. 20) runs from the medial side of the right sternal apophysis (right furca) to the medial side of the left sternal apophysis (left furca). It is a flat muscle.

**F.CmP:** The flat posterior furco-coxal muscle (Figs. 24, 25) runs from the furca to the coxal rim, where the BA.Cm is attached to the coxo-pleural joint.

##### Direct flight muscles

**BA.SmS:** The superior basalar-sternal muscle (not pictured) is diminished. It is a short and flat muscle running from the anterior part of the wing base to the membrane just posterior and above the stigma.

**BA.SmI:** The inferior basalar-sternal muscle is absent in the metathorax.

**BA.Cm:** The basalar-coxal muscle (Fig. 25) is dorsally attached to a small sclerite in the membrane (just as in the fore wing) and is ventrally attached to the coxal rim (near the coxo-pleural joint). It is a large, robust and distinct muscle.

**BA.Pm:** The basalar-pleural muscle (not pictured) is dorsally attached to a distinct triangular sclerite (anterior to s2) and runs posteriorly to the pleurum, anterior to the pleural suture. It is a robust and short muscle.

**SA.Cm, SA.Sm, SA.Fm:** The subalar is small in the metathorax and its apodemes are inconspicuous externally. Furthermore, the anterior basisternum and the posterior furcasternum are inconspicuous and the first abdominal sternite is located shortly posterior to the metacoxa. The subalar muscles are small and not as conspicuous as in the mesothorax. Two muscles are distinguishable: The first one (SA.Cm; Fig. 25) is dorsally attached to the anterior section of the subalar and is ventrally attached to the coxal rim. It is a flat but relatively broad muscle. Posterior to the SA.Cm is the dorsal point of attachment of the second, slender part (SA.Sm, SA.Fm; Figs. 23, 24). It is ventrally attached

to the posterior rim of the coxa and a few fibres are attached to the tip of the furca.

**Ax.Fm:** The axillar-furcal muscle (Figs. 24, 25) is a very slender muscle running from the process of the s2 to the tip of the furca. It is almost as large as the Ax.Fm of the mesothorax.

**Ax.PmI:** The inferior axillar-pleural muscle (not pictured) is dorsally attached to the process of s2 (anterior to the Ax.Fm) and runs to the pleural suture. It is a slender muscle consisting of only a few fibres.

**Ax.PmS:** The superior axillar-pleural muscle (not pictured) is a short but robust muscle running from s3 to the pleurum (posterior to the PWP).

**Cx.Cxm:** The coxo-coxal muscle (not pictured) is present in the metathorax and runs from the anterior rim of the left coxa to the anterior rim of the right coxa.

### 3.2.3 *Baetis* sp., winged stages (Figs. 26–37) (n = 13)

Measurements (of the described ♀ specimen)

Total length: 6.25 mm. – Length of mesothorax: 1.5 mm. – Length of metathorax: 0.65 mm. – Height of mesothorax: 1.5 mm (0.9 mm belong to MTm). – Height of metathorax: 1 mm.

#### External morphology of the mesonotum

The anteronotal protuberance (ANp; Fig. 26) and the impression (ANi; Fig. 26) posterior to it are distinct. Anterior to the scutellum are the prominent paired posterior scutal protuberances (PSP; Fig. 26), which are approximately in the centre of the scutum. The PSP are longish rather than circular. The scutellum (SL; Fig. 26) and its lateral parts are distinct.

The median longitudinal suture (MLs; Fig. 26) is conspicuous in the centre part of the scutum. It disappears anteriorly next to the ANi and ANp and posteriorly next to the SL. The medioparapsidal sutures (MPs; Fig. 26) are at least as distinct as the MLs and converge posteriorly. Lateral to the MPs run the distinct lateroparapsidal sutures (LPs; Figs. 26–29), which are also posteriorly convergent. The conspicuous antero-lateral scutal costa (ALSC; Fig. 26) is located at the antero-lateral part of the scutum. The mesonotal suture (MNs) is not visible.

The anterior and the posterior notal wing processes (ANP, PNP; Figs. 27–29) of the wing base are distinct. Nevertheless, the ANP is rather short while the PNP is conspicuous. The tegula (T; Figs. 27, 29, 33) at the anterior wing base is densely covered with short setae in subimagines, whereas in adults there are distinctly less setae.

At the anterior base of the wing, a two armed sclerite is visible, which is connected to the crescent-shaped sclerite (BA; Figs. 30–33). The anterior branch lies medial to the tegula and the posterior branch lies anterior to the first

free wing base sclerite (s1; Figs. 27–29). The basalar-pleural muscle (BA.Pm, not pictured) is attached to the anterior part of the sclerite, while the basalar-coxal muscle (BA.Cm, not pictured) attaches to the posterior part of the sclerite.

The basal plate (BP; Figs. 27–29) of the wing base is convex, but in several specimens this was not as distinct as in other Ephemeroptera. The proximal base of the basal plate is clearly demarcated and has a process anteriorly and also a conspicuous process posteriorly. The proximal process is the dorsal attachment point of the axillar-furcal muscle (Ax.Fm, not pictured). The first free wing base sclerite (s1; Figs. 27–29) is a rather large triangular sclerite, which is sclerotised only in the dorsal layer of the wing membrane. It articulates with the ANP proximally. No muscle is attached to it. The second free wing base sclerite (s2, not pictured) seems to be diminished in size. The third free wing base sclerite (s3; Figs. 27–29) articulates with the basal plate anteriorly and with the PNP posteriorly. A muscle is attached to the proximal part of this conspicuous sclerite, and this muscle runs to the pleurum posterior to the PWP. The distinct basanale (ban; Fig. 29) posterior to the s3 is sclerotised.

Most of the wing veins disappear at the wing base. However, the costal vein, the subcostal vein and the anterior radial vein are conspicuous even at their bases. The radial sector and the anterior medial vein converge at their bases but are not distinctly connected. The sector of the medial veins disappears at the base. The anterior cubital vein and the anterior anal vein are discernable next to the anal brace. Both the anal and the costal brace are conspicuous.

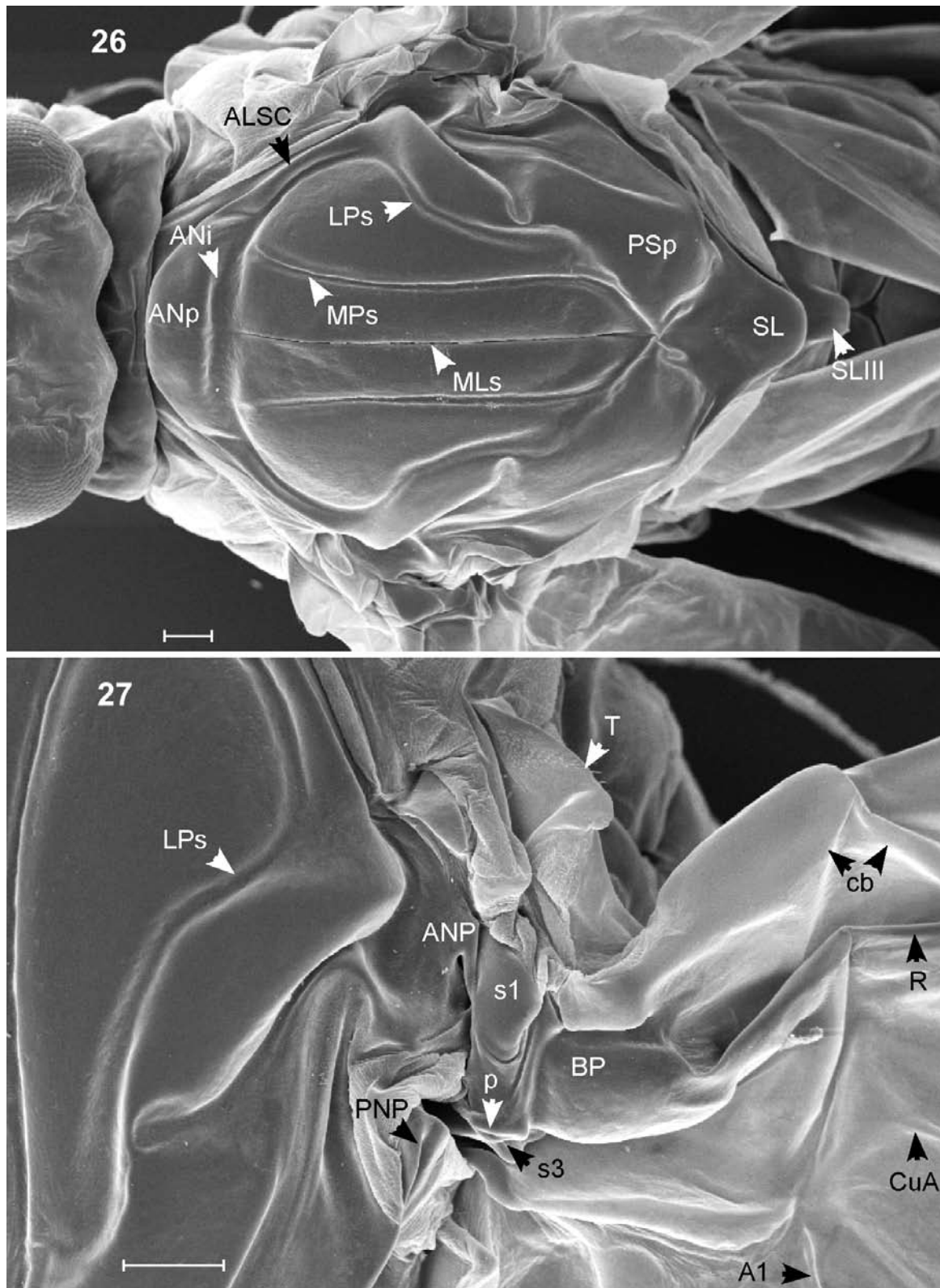
The lateropostnotum (LPN; Fig. 32) is rather small and triangular in shape in the examined specimens.

#### External morphology of the mesopleurum

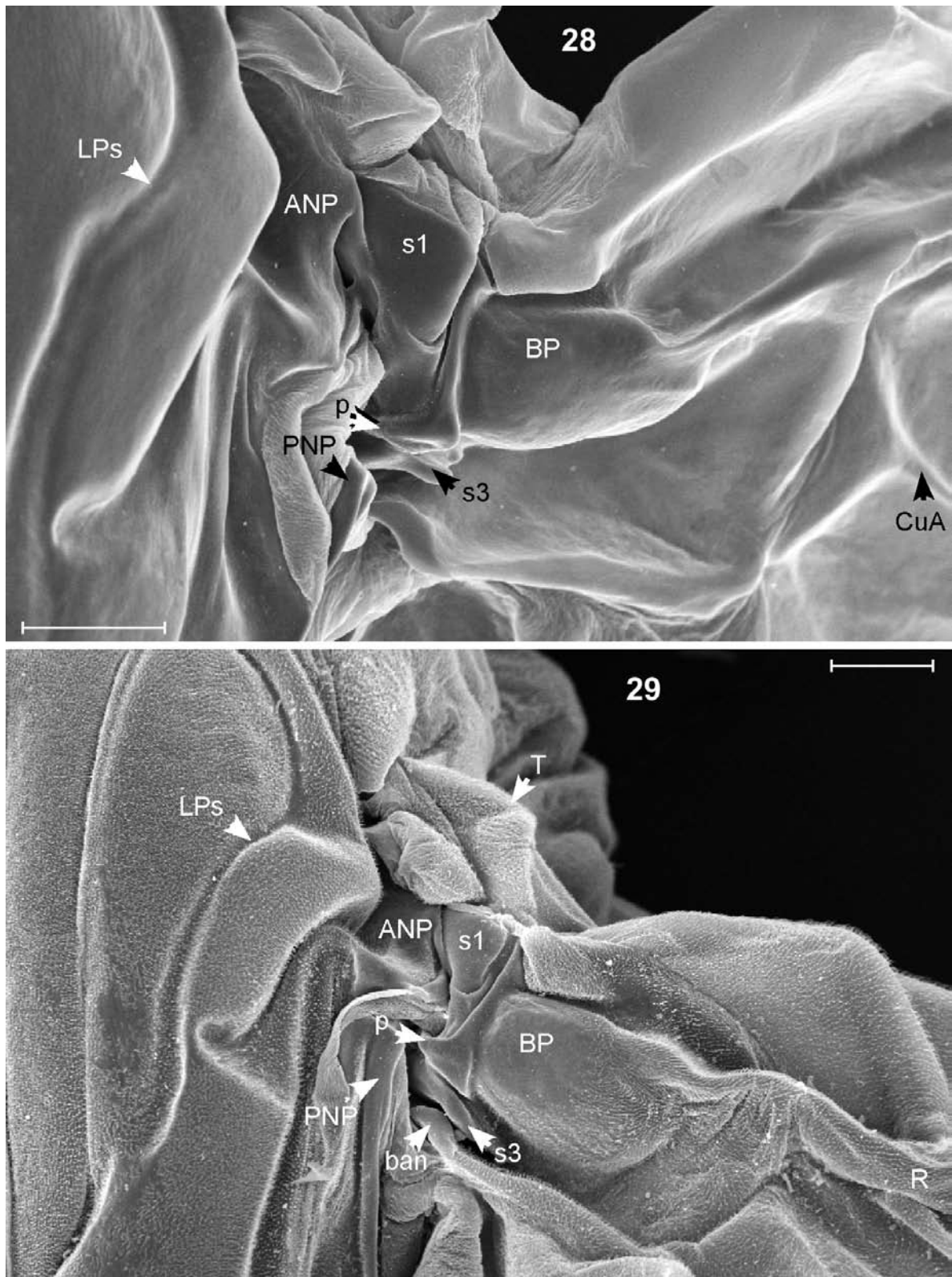
The three branches of the prealar arms are rather long. The dorsal and the ventral arc are connected to each other and the posterior arc reaches the anterior wing base at the same level as the tegula but medial to it. The spiracle lies in a large membranous area posterior to the prealar bridge.

The distinct anterior paracoxal suture (PCxsA; Fig. 32) separates the anepisternum (AES; Fig. 32) from the much broader katapisternum (KES; Fig. 32). The posterior part of the paracoxal suture (PCxsP; Fig. 32) is conspicuous in the mesothorax. It subdivides the upper anepimeron (AEM) from the lower katepimeron (KEM). Both AEM and KEM are narrow, though in several specimens the AEM is slightly broader than the KEM.

The upper part of the pleural suture (PLsS; Fig. 32) is distinct and runs obliquely forward. The pleural wing process (PWP; Figs. 32, 33) at the upper end of the pleural suture is small but clearly visible. The externally visible

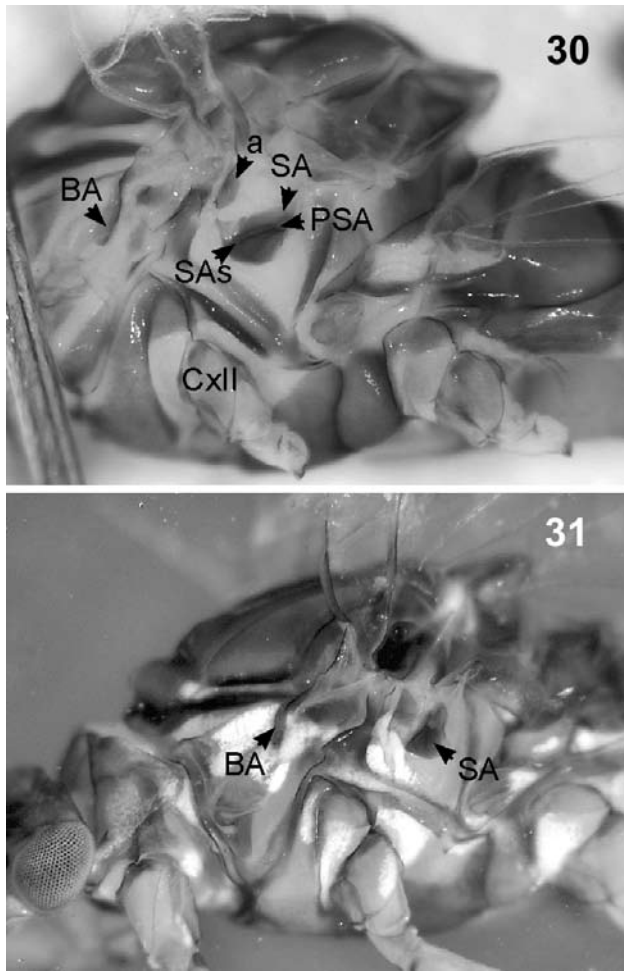


**Figs. 26–27.** *Baetis* sp. (SEM images), ♀ imago. – 26. Mesothorax, dorsal view (head to the left). 27. Base of right fore wing. – SL III = scutellum of the metathorax; p = posterior proximal process of the basal plate. – Scales: 0.1 mm.



**Figs. 28–29.** *Baetis* sp. (SEM images), detail of the right fore wing base. – 28. ♀ imago. 29 ♀ subimago. – p = posterior proximal process of the basal plate. – Scales: 0.1 mm.

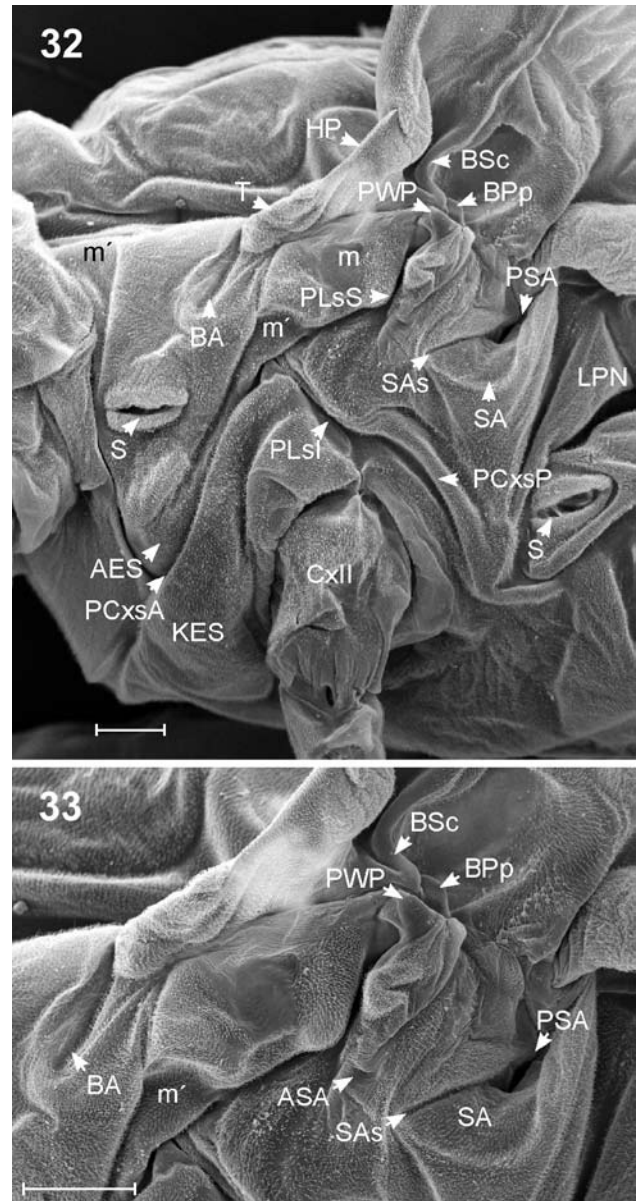




**Figs. 30–31.** *Baetis* sp., overview of the mesopleurum of *Baetis* sp. – 30. ♂ imago. 31. ♀ imago.

condylus of the PWP articulates with a ventral process of the basal plate (BPp; Figs. 32, 33) of the wing base. In some subimaginal specimens the upper part of the pleural suture is not as distinct as its lower part, i. e. the inferior pleural suture (PLsI; Fig. 32). The PLsI is conspicuous and runs obliquely towards the back (downwards) to the point where the coxa articulates with the pleurum.

Anterior to the PWP lies the basalare (BA; Figs. 30–33), which is curved slightly forwards. The subalare (SA; Figs. 31, 33) is located posterior to the PWP. The ventral part of the subalare is narrow but clearly visible sclerotised, whereas the dorsal part is rather inconspicuous in most of the examined specimens. Only the most anterior part of the SA, next to the PWP, is clearly sclerotised; it is a distinct and narrow sclerite. The subalar suture (SAs; Figs. 30, 32, 33), at the anterior rim of the posterior part of the subalare and the posterior apodeme (PSA; Figs. 30, 32, 33) are conspicuously developed. The anterior subalar



**Figs. 32–33.** *Baetis* sp. (SEM images), ♀ subimago. – 32. Mesopleurum 33. Mesopleurum, detail of upper area. – m = ventral attachment of BA.Pm; m' = attachment points of AN.Pm. – Scales: 0.1 mm.

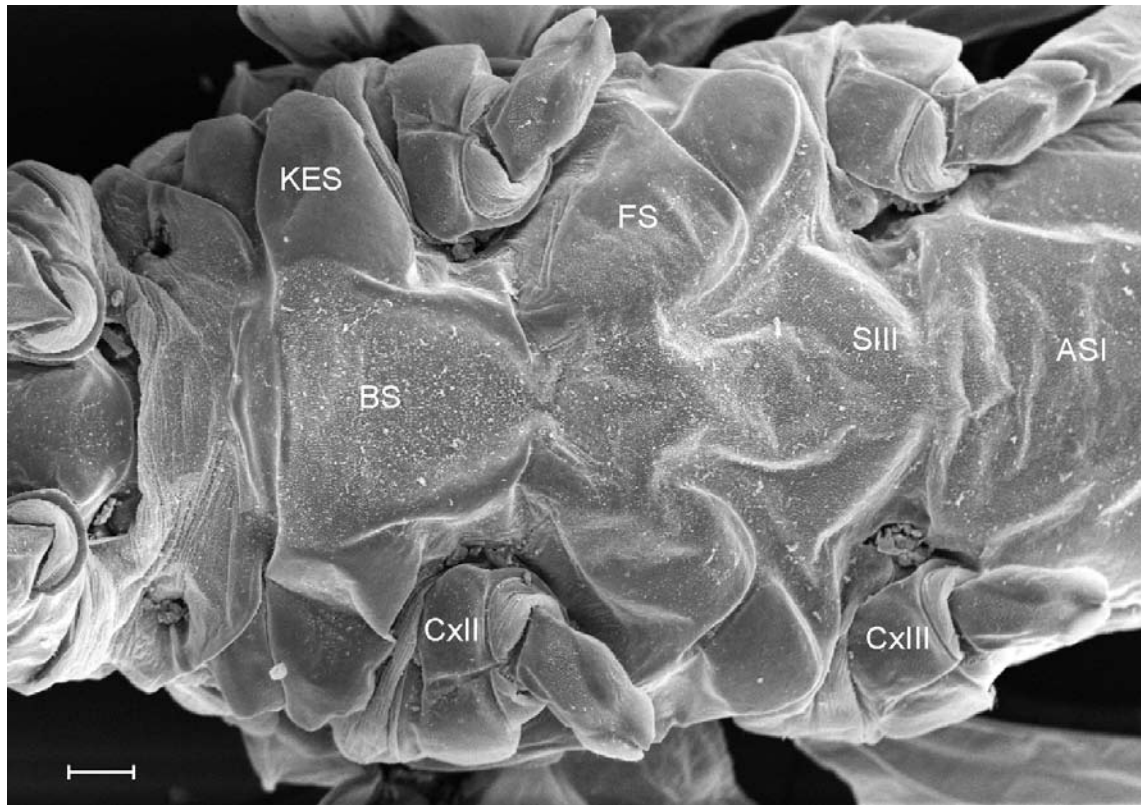
apodeme (ASA; Fig. 33) is rather inconspicuous and usually not visible from outside.

#### Muscles of the mesothorax

##### Dorsal muscles

**MTm:** The median tergal muscle (Figs. 35–37) runs from the anterior to the middle phragma. It is a large muscle, which encompasses at least one half of the height of the mesothorax.





**Fig. 34.** *Baetis* sp. (SEM image), ♀ imago, mesosternum and metasternum, ventral view (head to the left). – Scale: 0.1 mm.

**t13:** It is absent in the mesothorax.

**S.LPNm:** The scuto-lateropostnotal muscle (Fig. 37) is dorsally attached to the posterior part of the scutum (Psp). Ventrally, it is attached to the lateropostnotum (LPN). It is a relatively large muscle, which is dorsally almost as wide as ventrally.

#### Dorso-ventral muscles

**S.ESm:** The scuto-episternal muscle (Figs. 35, 36) is dorsally attached to the scutum (just posterior to the ANi up to the part just anterior to the Psp and lateral to the MPs) and runs to the episternum. The ventral attachment encompasses only about one third of the area of the dorsal attachment. The area of the dorsal attachment encompasses approximately one half of the length of the mesothorax.

**S.CmA:** The anterior scuto-coxal muscle (not pictured) runs from the scutum, lateral to the lateroparapsidal sutures (LPs) to the anterior rim of the coxa. It is a flat muscle, which is not as wide as the S.ESm.

**S.CmP:** The posterior scuto-coxal muscle (not pictured) is dorsally attached to the scutum (just anterior to the S.LPNm and lateral to the S.CmA) and runs to

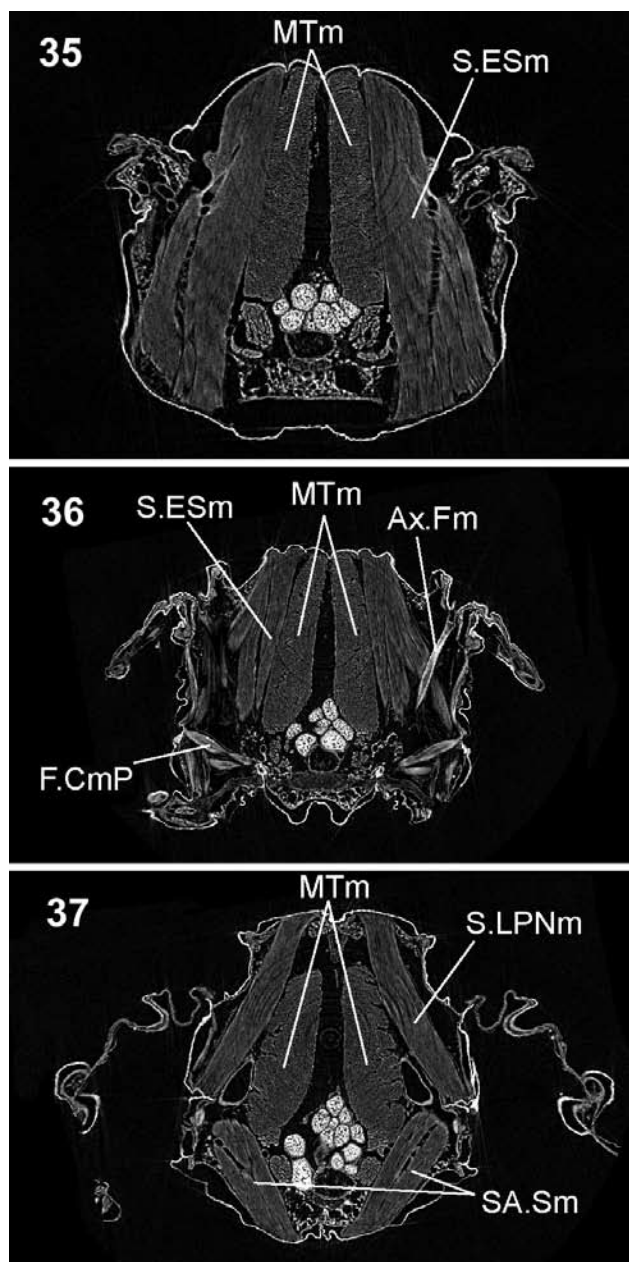
the posterior coxal rim. The S.CmP is not as large as the S.CmA, approximately half as large as the S.ESm.

**S.Trm:** The scuto-trochanteral muscle (not pictured) runs from the lateral part of the scutum to the trochanter. It is a rather slender muscle, which is smaller than S.CmA and S.ESm.

**PSL.Cm:** The parascutello-coxal muscle (not pictured) is dorsally attached to the anterior area of the parascutellum and runs to the posterior rim of the coxa. The PSL.Cm is approximately as large as in other Ephemeroptera (if not slightly larger).

**AN.Pm:** The anteronoto-pleural muscle runs from the posterior arc of the prealar bridge (anterior part) to the anterior paracoxal suture (PCxsA, directly above the P.Cm) (Figs. 32, 33). It is a slender muscle consisting only of a few fibres.

**SrA.Pm:** The suralar-pleural muscle (not pictured) is dorsally attached to the anterior area of the suralare and ventrally attached to the anterior paracoxal suture (PCxsA, where the pleural suture and the posterior paracoxal suture are approximated) next to the AN.Pm. It is a flat but distinct muscle.



**Figs. 35–37.** *Baetis* sp., ♀ subimago, mesothorax (μCT-data), cross sections from anterior (35) to posterior (37).

#### Pleural muscles

- P.Cm:** The pleuro-coxal muscle (not pictured) runs from the anterior paracoxal suture (PCxsA) to the antero-lateral rim of the coxa. It is a flat but wide muscle.
- P.Trm:** The pleuro-trochanteral muscle (not pictured) is dorsally attached to the pleural suture and runs to the trochanter. It is a flat muscle, which is a little wider dorsally than ventrally.

#### Ventral muscles

- iFm:** The intersegmental furcal muscle (not pictured) is a slender muscle, running from the anterior part of the mesofurca to the presternite.
- Fm:** The furcal muscle (not pictured) is stretched between the left mesofurca and the right mesofurca. It is a short but robust muscle, which is almost elliptical in cross section.
- F.CmP:** The posterior furco-coxal muscle (F.CmP in Fig. 36) runs from the postero-lateral part of the furca to the coxo-pleural articulation point (just medial to the BA.Cm). It is a small and flat muscle.

#### Direct flight muscles

- BA.SmS:** The superior basalar-sternal muscle (not pictured) is dorsally attached to the upper part of the basalare (BA) and runs to the prothoracic furca.
- BA.SmI:** The inferior basalar-sternal muscle (not pictured) runs from the lower part of the basalare (BA) to the presternite. Both basalar-sternal muscles are slender and rather indistinct.
- BA.Pm:** The basalar-pleural muscle (Fig. 32) is dorsally attached to the sclerite, which is connected to the crescent-shaped sclerite (just posterior to the posterior arc of the prealar bridge). BA.Pm proceeds to the pleurum.
- BA.Cm:** The basalar-coxal muscle (not pictured) is dorsally attached to the posterior branch of the dorsal sclerite, just anterior to the first free wing base sclerite, and runs to the pleurum where the coxa articulates with the pleura. It is a slender muscle.
- SA.Sm:** The subalar-sternal muscle (Fig. 37) is dorsally attached to the posterior subalar apodeme (PSA) and ventrally attached to the furcasternite (FS; Fig. 34). The SA.Sm is slightly wider ventrally than dorsally.
- SA.Fm:** The subalar-furcal muscle runs from the PSA to the postero-lateral part of the mesofurca (sometimes it is shifted slightly medial to the medio-posterior rim of the coxa). It is a slender muscle, which is almost indistinguishable from SA.Sm.
- SA.Cm:** The subalar-coxal muscle (not pictured) is attached to the anterior subalar apodeme (ASA) and runs to the posterior part of the coxo-pleural articulation (just posterior to the BA.Cm). The anterior apodeme is reduced to a sclerotised and pigmented “bulge” and the SA.Cm is a much more slender muscle in the mesothorax of *Baetis* sp. compared to SA.Cm of other taxa.
- Ax.Fm:** The axillar-furcal muscle (Fig. 36) is attached to the proximal process at the postero-dorsal part of the basal plate (p in Figs. 27–29). It is a slender but distinct muscle in the mesothorax.
- Ax.PmI:** The inferior axillar-pleural muscle is not present.
- Ax.PmS:** The superior axillar-pleural muscle (not pic-

tured) is short but robust and stretches between the third free wing base sclerite (s3) and the pleurum.

#### External morphology of the metanotum

The hind wings in Baetidae are very small and the venation is reduced. In some genera the hind wings are even absent. The notum of the metathorax is also shortened.

The scutum is very short and the following scutellum is approximately as large as the scutum. The posterior phragma is extended posteriorly and visible from dorsal. The median longitudinal suture is visible from the middle of the scutum but most of the other sutures and convexities are indistinct in the metatergum. The wing base elements of the hind wings are reduced and partially missing.

#### External morphology of the metapleurum

Most of the sutures and sclerites that are distinct in the mesothorax are partly or completely reduced in the metathorax of *Baetis*. The upper part of the pleurum is rather less sclerotised, while the lower part is well sclerotised.

The inferior part of the pleural suture (PLsI) is conspicuous and runs obliquely towards the back (dorso-ventrally). At its ventral end lies the coxo-pleural articulation. The superior part of the pleural suture (PLsS) is rather inconspicuous. The pleural wing process (PWP) at the upper point of the superior part of the pleural suture is small but distinct in the metapleurum. There is a small sclerite containing the PWP. Both the basalare, anterior to the PWP, and the subalare posterior to the PWP, are absent.

The anterior paracoxal suture (PCxsA) is partially conspicuous but the anepisternum (AES) and the katapisternum (KES) are hardly distinguishable.

#### Muscles of the metathorax

##### Dorsal muscles

**MTm:** The median tergal muscle is large and encompasses at least one half of the metathorax. It is anteriorly attached to the middle phragma and runs to the posterior phragma.

**t13:** The small dorsal muscle is not present in the metanotum.

**S.LPNm:** The scuto-lateropostnotal muscle is not present in the metathorax.

##### Dorso-ventral muscles

**S.ESm:** The scuto-episternal muscle is dorsally attached to the antero-lateral part of the scutum and runs to the episternum. It is the second largest muscle in the metathorax.

**S.CmA:** The anterior scuto-coxal muscle is dorsally attached to the antero-lateral part of the notum and proceeds to the anterior rim of the coxa. It is a flat muscle.

**S.CmP:** The posterior scuto-coxal muscle stretches from the medio-lateral part of the notum to the posterior part of the coxal rim. It is, like the S.CmA, a slender muscle.

**S.Trm:** The scuto-trochanteral muscle runs from the anterior part of the notum (just posterior to the S.CmA) to the lateral part of the trochanter. Compared to S.CmA and S.CmP it is a large muscle, almost twice as large as S.CmP.

**PSL.Cm:** The flat muscle running from the antero-lateral part of the scutellum to the postero-medial rim of the coxa is most likely the parascutello-coxal muscle.

**AN.Pm:** The anteronoto-pleural muscle is not present in the metathorax.

**SrA.Pm:** The suralar-pleural muscle is a flat muscle running from the antero-lateral part of the notum to the anterior paracoxal suture (PCxsA). It consists only of a few fibres.

#### Pleural muscles

**P.Cm:** The pleuro-coxal muscle runs from the anterior paracoxal suture (PCxsA) to the anterior rim of the coxa. It is a flat, but broad and robust muscle.

**P.Trm:** The pleuro-trochanteral muscle is dorsally attached to the anterior paracoxal suture (posterior to the P.Cm). Ventrally, it is attached to the trochanter. This slender but robust muscle is ventrally wider than dorsally.

#### Ventral muscles

**iFm:** The intersegmental furcal muscle is not present in the metathorax.

**Fm:** The furcal muscle runs from the left furca to the right furca. It is a robust muscle, of similar size as in the mesothorax.

**F.CmP:** The posterior furco-coxal muscle is attached to the furca and runs to the coxal rim next to the coxo-pleural joint. It is a robust muscle, which is distinct and about as large as the F.CmP of the mesothorax.

#### Direct flight muscles

Since the hind wings are only small, the direct flight musculature is also reduced in the metathorax.

**BA.SmS, BA.SmI, BA.Cm, BA.Pm:** The basalar muscles (superior basalar-sternal muscle [BA.SmS] as well as the inferior basalar-sternal muscle [BA.SmI], the basalar-pleural muscle [BA.Pm] and the basalar-coxal muscle [BA.Cm]) were not found in the metathorax.

**SA.Cm, SA.Sm, SA.Fm:** There is only one flat and small muscle in the postero-dorsal area of the pleurum. It is most likely the subalar-coxal muscle (SA.Cm), which attaches to the postero-lateral rim of the coxa. The subalar-sternal muscle (SA.Sm) and the subalar-furcal

muscle (SA.Fm) are most likely reduced in the metathorax.

**Ax.Fm:** The axillar-furcal muscle runs from the membrane at the wing base to the furca. It is a slender muscle, of similar size as the corresponding muscle in the mesothorax.

**Ax.PmI/Ax.PmS:** The inferior and the superior axillar-pleural muscles are not present.

### 3.2.4 *Ephoron virgo*, winged stages (Figs. 38–55) (n = 9)

Measurements (of the described ♂ specimen)

Total length: 11.5 mm. – Length of mesothorax: 2.8 mm. – Length of mesothoracic wing: 17.6 mm. – Width of mesothoracic wing: 8.2 mm. – Length of metathorax: 1.3 mm. – Length of metathoracic wing: 7.3 mm. – Width of metathoracic wing (measured at the tornus): 3.7 mm. – Height of mesothorax: 2.5 mm (1.4 mm belong to MTm). – Height of metathorax: 1.8 mm (0.66 mm belong to MTm).

#### External morphology of the mesonotum

The scutum is characteristic in *Ephoron virgo* since it is flat and its anterior part (ANp; Figs. 38, 39) relatively large, whereas the posterior part is rather short. The ANp is rather flat in specimens of *E. virgo* and its major part it is covered by the pronotum. The anterior notal impression (ANi; Fig. 38) is less distinct than in other mayflies (e.g. *Siphonurus aestivalis*, *Habroleptoides confusa*). The posterior scutal protuberances (PSP; Figs. 38, 39, 41) are relatively large and conspicuous but also rather flat. Posterior to the PSP lies the scutellum (SL; Figs. 38, 39). The dorsal part of SL is long and narrow.

The sutures of the mesothorax are rather indistinct. The median longitudinal suture (MLs; Figs. 38, 42) is visible in the area from approximately the anterior notal impression (ANi) to the scutellum. At the anterior part of the scutum it is almost indistinguishable. The medioparapsidal sutures (MPs; Figs. 41–42) are rather faint and hardly visible in the mesotergum. The MPs are convergent posteriorly and join the lateroparapsidal sutures (LPs; Figs. 38, 39, 41, 42). The LPs, located lateral to the MPs, are not as distinct as in other mayflies. The antero-lateral scutal costa (ALSC) and the LPs are rather inconspicuous. The mesonotal suture (MNs) extends backwards and is also rather inconspicuous.

The anterior and posterior notal wing processes (ANP, PNP; Figs. 41, 42) are clearly distinguishable. The ANP is long and narrow and articulates with the first free wing base sclerite (s1; Fig. 41). The PNP is connected to the third free wing base sclerite (s3; Figs. 41, 42).

The tegula (T; Fig. 42) at the anterior base of the wing is not visibly covered with setae. Distal to the tegula lies the humeral plate (HP; Fig. 41). Between the wing base and the tergum are two separate sclerites visible.

The prominent basal plate (BP; Figs. 41, 42) is sclerotised in both dorsal and ventral layer of the wing membrane. The base of the subcostal vein (BSc; Fig. 44) is located at the antero-ventral part of the basal plate. The concave posterior part of BP is narrow and the posterior edge is conspicuous. The proximal part of the basal plate is flat and thus clearly distinguishable from its other parts. The antero-proximal part of the basal plate is developed as a pointy process (p in Fig. 41). The process (BPP; Fig. 43) at the ventro-proximal side of the basal plate is present but rather inconspicuous in the mesopleurum and it articulates with the pleural wing process (PWP; Figs. 43, 44).

The first free wing base sclerite (s1; Fig. 41) is long, narrow and tapered anteriorly. It articulates proximally with the ANP and distally with the second free sclerite (s2). The long and slender second free wing base sclerite (s2; Figs. 41, 42) articulates distally with the basal plate and, in addition, it is posteriorly connected to the third free wing base sclerite (s3; Figs. 41, 42). The s1 as well as the s2 are sclerotised only in the dorsal layer of the wing membrane. The third wing base sclerite (s3) is wide and conspicuous. Anteriorly, the s3 is connected (but not fused) to the basal plate. The proximal quarter of the s3 articulates with the PNP. The antero-proximal part of s3 is arched. The s3 is ventrally connected to the pleurum by the axillar-pleural muscle (Ax.PmS; Figs. 54, 55). Another, short muscle runs from the anterior part of the s3 to the postero-proximal part of the basal plate.

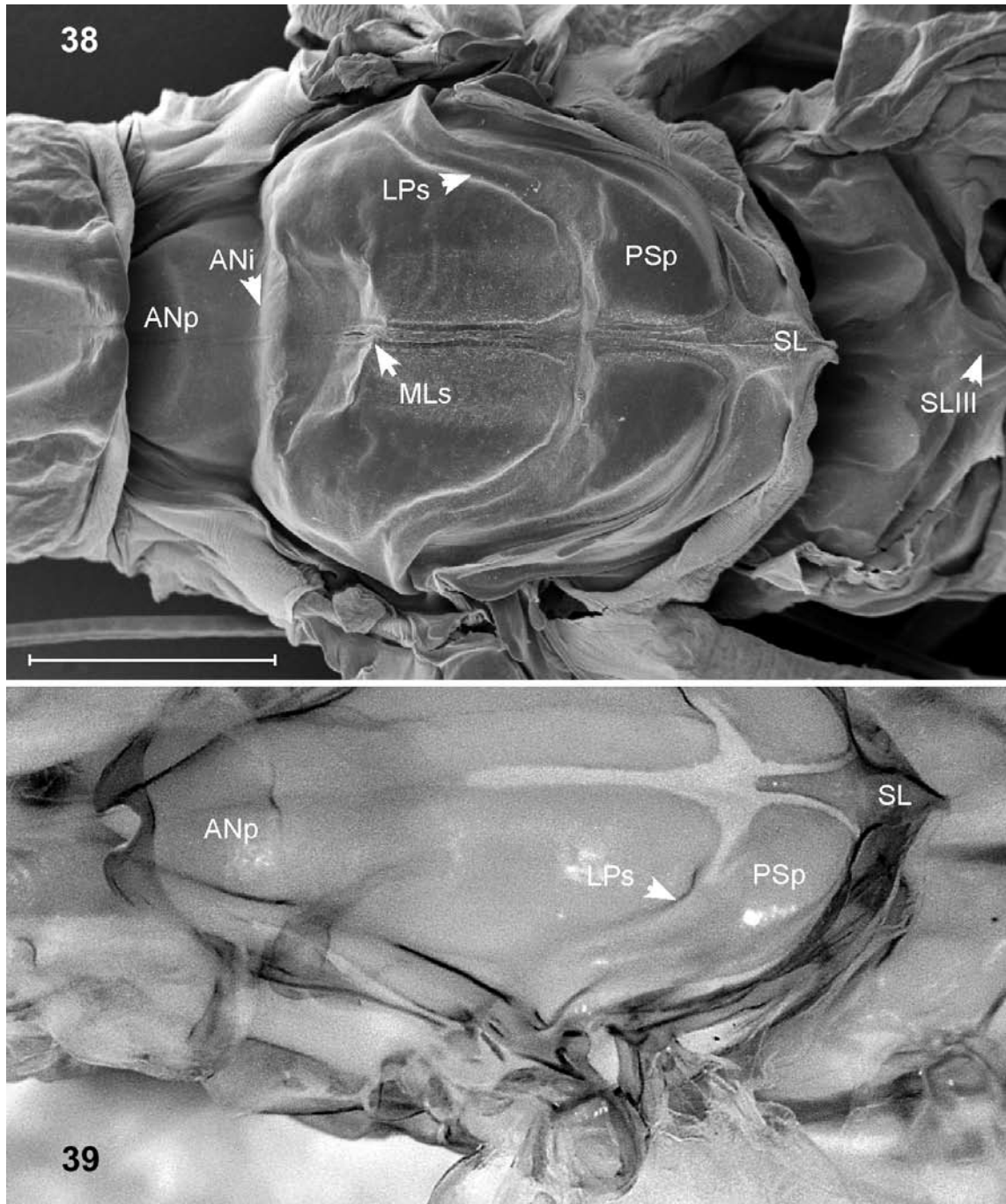
The costal brace (cb; Figs. 41, 44) and the anal brace (ab; Fig. 41) are pronounced in the wing base of *Ephoron virgo*. The costal brace connects the costal vein (C; Figs. 41, 44) with the anterior radial vein (R; Figs. 41, 42, 44). The anal brace is conspicuous and stretches between the basale (ban; Fig. 42) and the anterior radial vein. Both the proximal (or posterior) and the distal (or anterior) arch are clearly visible. The anterior anal vein arises at the anterior part of the anal brace, next to the anterior radial vein (origin more anterior than in other Ephemeroptera). The small basanale (ban) is well sclerotised.

The anterior medial vein (MA) and the sector of the radial veins (Rs) are connected at their bases. Furthermore, the sector of the media (MP) and the anterior cubital vein (CuA) are converged at their bases.

The lateropostnotum (LPN; Figs. 43, 44) is prominent and the lateropostnotal crest (LPNC) is inconspicuous.

#### External morphology of the mesopleurum

The prealar bridge is subdivided into three arcs. All three, the dorsal, ventral, and posterior arcs are long. The dorsal and the ventral arc are connected to each other. Posterior to the prealar bridge is a large membranous area with the spiracle. The spiracle is wide open in alcoholic-preserved specimens of *E. virgo* (and also in *Exeuthyplocia minima*).

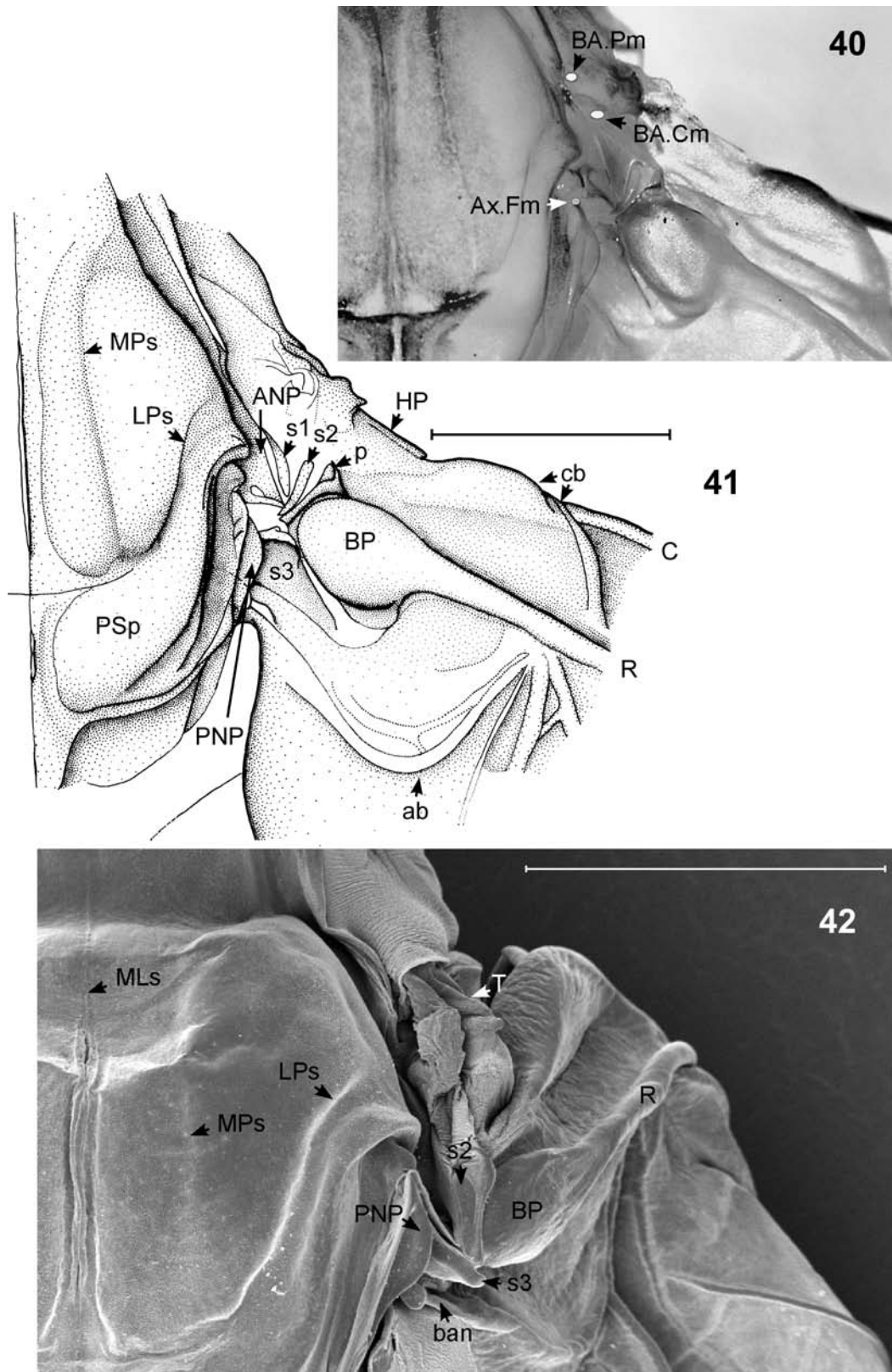


**Figs. 38–39.** *Ephoron virgo*, ♂ imago, mesothorax, dorsal view (head to the left). – 38. SEM image. 39. Mesothorax after treatment with potassium hydroxide. – Scale: 1 mm.

The most distinct suture in the pleum of *E. virgo* is the anterior paracoxal suture (PCxsA; Figs. 43, 44). The PCxsA divides the anepisternum (AES; Figs. 43, 44) from the katepisternum (KES; Figs. 43, 44). Both are narrow and similar in size. The posterior part of the paracoxal suture (PCxsP; Fig. 44) is slightly less conspicuous and carinated. The upper part of the pleural suture (PLsS;

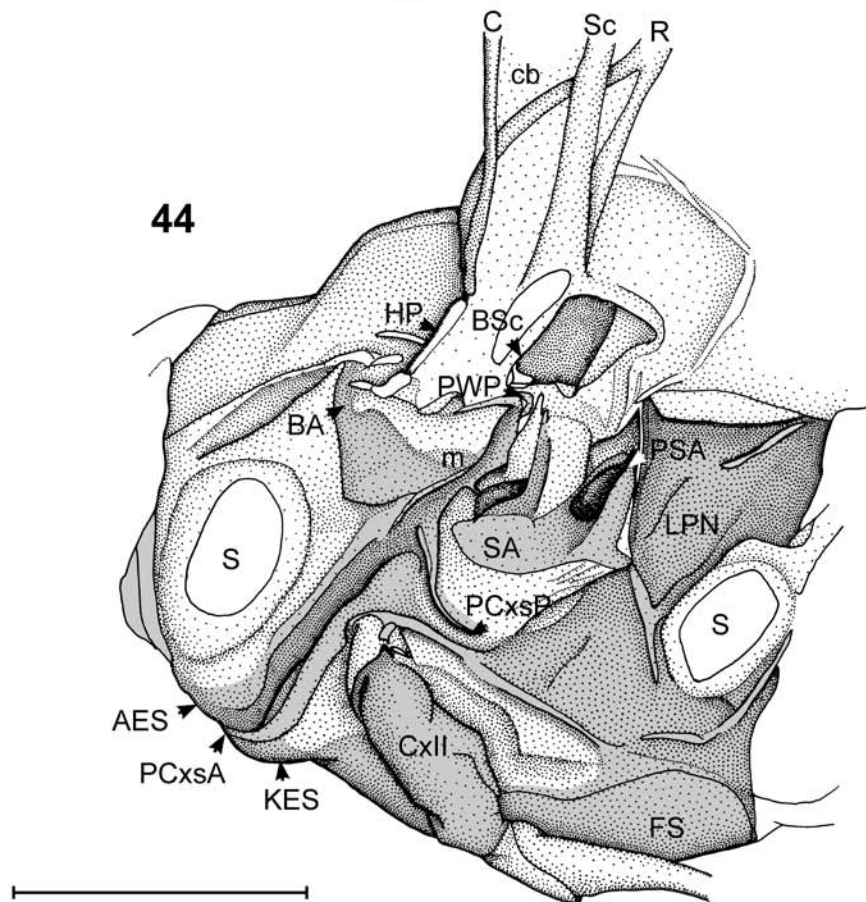
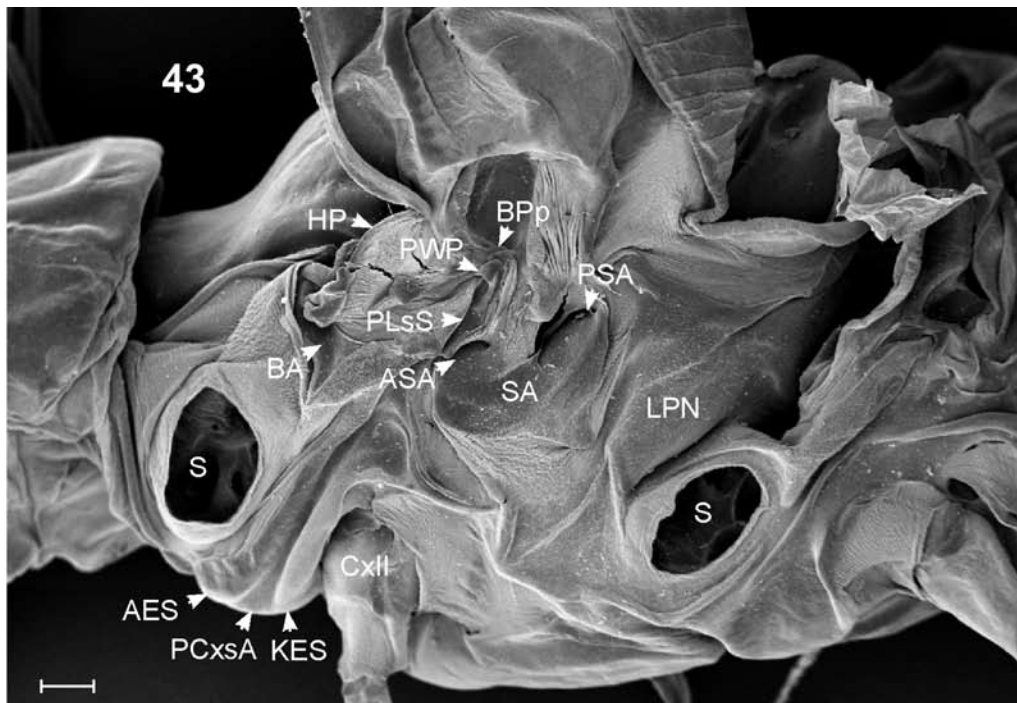
Fig. 43) is conspicuous and extends dorsally into the distinct but flat pleural wing process (PWP; Figs. 43, 44). The condylus of the PWP is directed forwards. It articulates with the ventral process of the basal plate (BPp; Fig. 43) and is rather faint. The ventral part of the pleural suture (PLsI) is indistinct.

The large basalare (BA; Figs. 43, 44) at the anterior

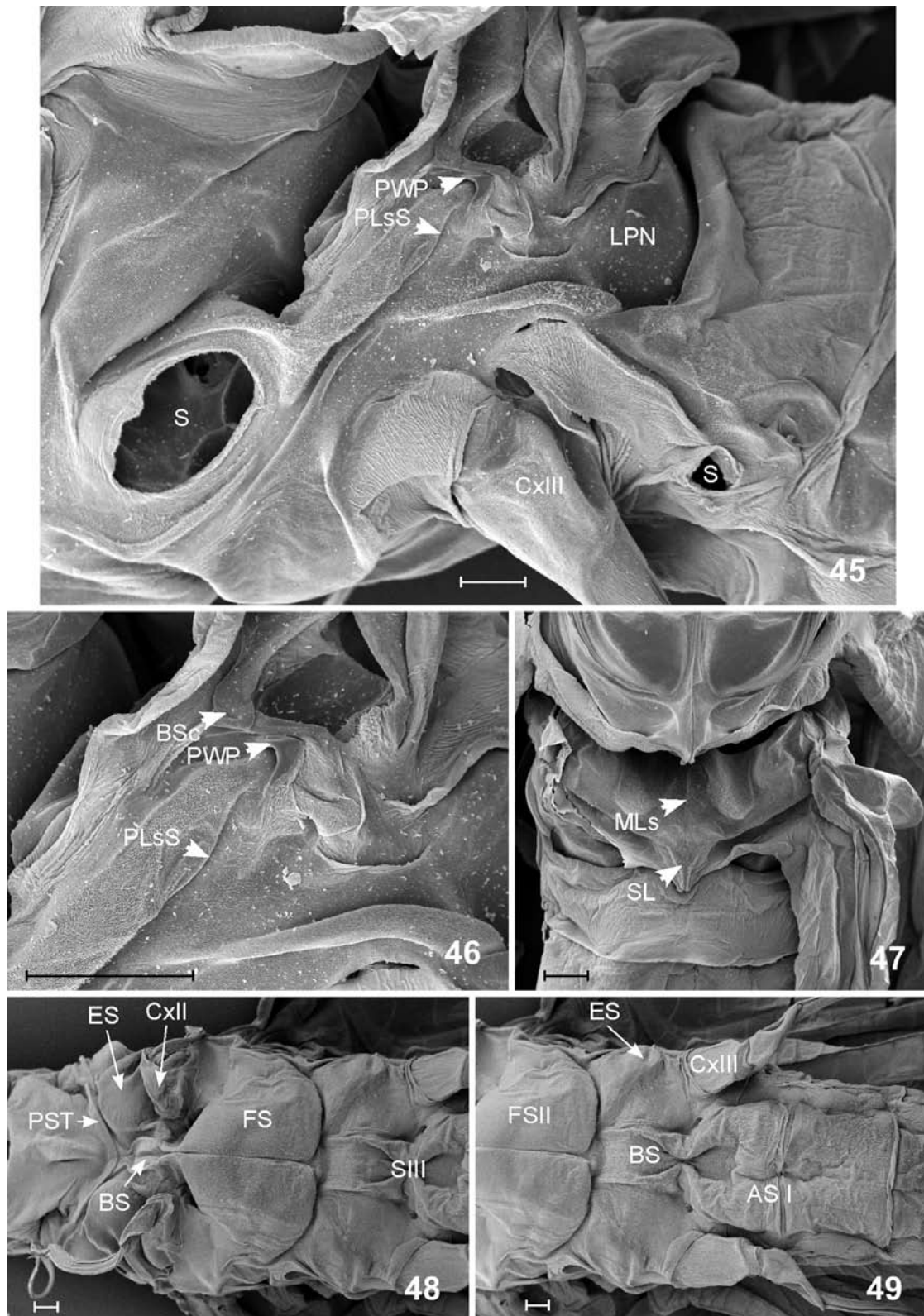


**Figs. 40–42.** *Ephoron virgo*, right fore wing base. – 40. ♀, detail with the dorsal attachments of BA.Pm, BA.Cm and Ax.Fm. 41. ♀ subimago. 42. ♂ imago (SEM image). – p = tapered process of BP. – Scales: 1 mm.



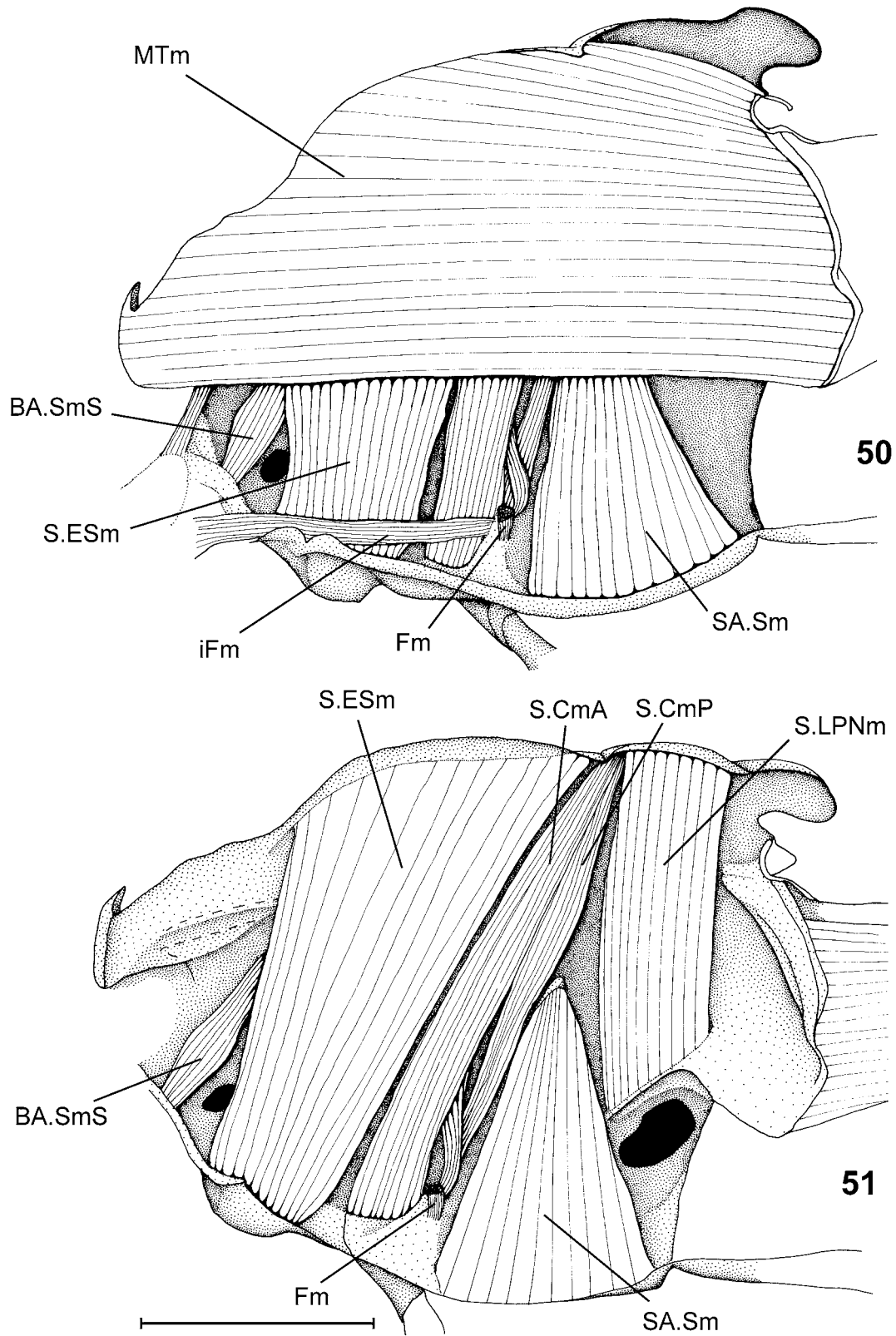


**Figs. 43–44.** *Ephoron virgo*, mesothorax, lateral view. – 43. ♂ imago (SEM image). 44. ♀ imago (grey areas sclerotised). – m = ventral attachment of BA.Pm. – Scales: 0.1 mm (43), 1 mm (44).

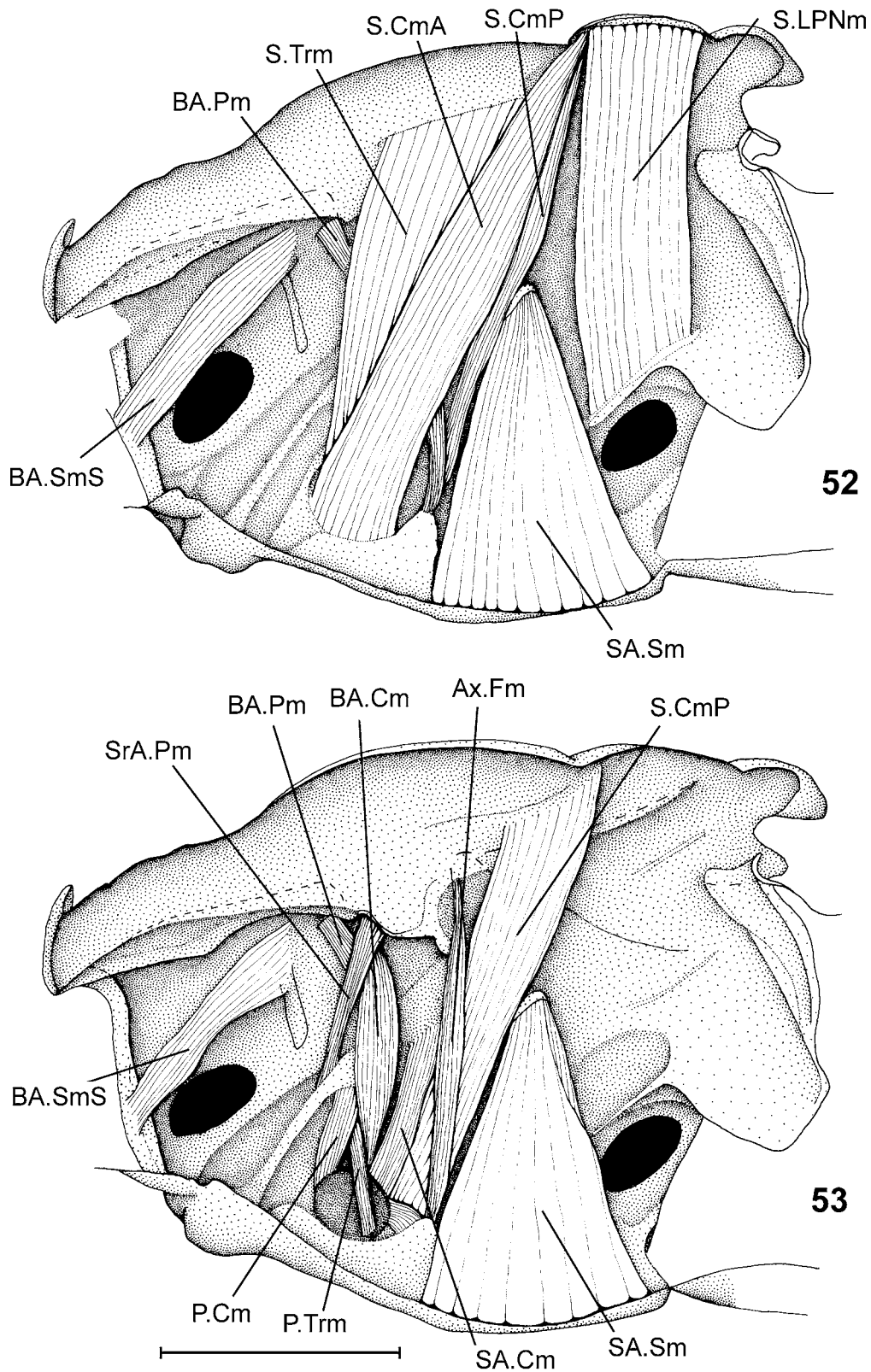


**Figs. 45–49.** *Ephoron virgo* (SEM images), ♂ imago. – 45. Metathorax, lateral view. 46. Metapleurum, upper part. 47. Metathorax, dorsal view. 48. Mesothorax, ventral view (head to the left). 49. Metathorax, ventral view (head to the left). – FSII = mesothoracic furcasternum. – Scales: 0.2 mm.

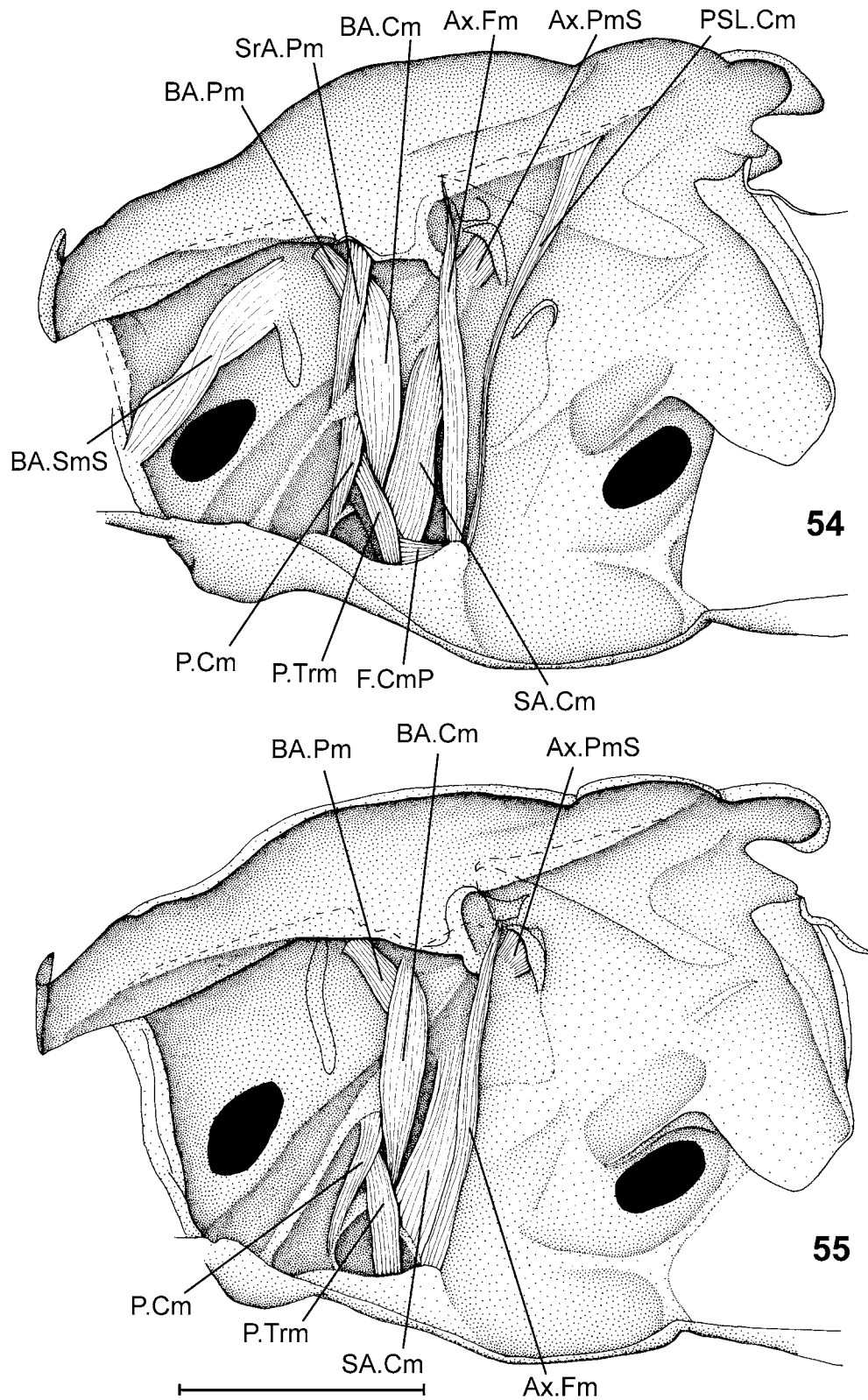




**Figs. 50–51.** *Ephoron virgo*, ♂ imago, musculature of the right half of the mesothorax at progressive stages of dissection, starting with median muscles (50) and progressively proceeding to the most lateral muscles (see Fig. 55). – Scale: 1 mm.



**Figs. 52–53.** *Ephoron virgo*, ♂ imago, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 50–51). – Scale: 1 mm.



**Figs. 54–55.** *Ephoron virgo*, ♂ imago, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 50–51). – Scale: 1 mm.

wing base is attached to the pleurum. Posterior to the PWP lies the subalare (SA; Figs. 43, 44). The ventral part of the SA is distinct and contains the large posterior subalar apodeme (PSA; Figs. 43, 44). The dorsal part of the sclerite is slender and consists of a narrow sclerite brace and a wider ventral area. This ventral area contains the conspicuous anterior subalar apodeme (ASA; Fig. 43). The subalare is surrounded by a large membranous area.

#### Muscles of the mesothorax

##### Dorsal muscles

**MTm:** The median tergal muscle (Fig. 50) is large in *E. virgo* and is attached to the anterior phragma to the point of the scuto-scutellar suture and runs to the middle phragma. MTm is located medial to all other muscles.

**t13:** The second dorsal muscle is absent in the mesothorax.

**S.LPNm:** The scuto-lateropostnotal muscle (Figs. 51, 52) is dorsally attached to the posterior part of the scutum (PSP) and runs to the lateropostnotum.

##### Dorso-ventral muscles

**S.ESm:** The scuto-episternal muscle (Figs. 50, 51) runs from the scutum to the episternum. The dorsal attachment is much wider than the ventral one and extends to the lateroparapsidal suture (LPs) (laterally). It encompasses almost one half of the length of the mesothorax. The ventral point of attachment extends over the anepisternum and the katepisternum (approximately equally on each, AES and KES). The S.ESm is a bipartite muscle.

**S.CmA:** The anterior scuto-coxal muscle (Figs. 51, 52) stretches from the posterior part of the scutum (next to PSP) to the anterior rim of the coxa. It is a compact but rather small muscle lying postero-lateral to S.ESm.

**S.CmP:** The posterior scuto-coxal muscle (Figs. 51–53) is dorsally attached to the scutum (posterior to the attachment of S.CmA and anterior to S.LPNm). This flat but broad muscle proceeds to the posterior rim of the coxa.

**S.Trm:** The scuto-trochanteral muscle (Fig. 52) is stretched between the scutum (at the lateroparapsidal suture) and the trochanter. It is a very flat but broad muscle and is almost as large as the S.CmA.

**PSL.Cm:** The parascutello-coxal muscle (Fig. 54) is dorsally attached to the antero-lateral part of the scutellum and runs to the posterior rim of the coxa. The ventral point of attachment is adjacent to the attachment point of S.CmP. The PSL.Cm of *E. virgo* is rather flat and lies more anterior than PSL.Cm in other mayflies and is not visible without dissection of S.CmP.

**AN.Pm:** The anteronoto-pleural muscle is absent.

**SrA.Pm:** The suralar-pleural muscle (Figs. 53, 54) runs

from the lateral part of the scutum (next to ANP) to the anterior paracoxal suture (where the PCxsP branches off). It is a flat and slender muscle that consists of only a few fibres.

##### Pleural muscles

**P.Cm:** The pleuro-coxal muscle (Figs. 53–55) is stretched between the paracoxal suture (where the anterior and the posterior suture branches off) and the antero-lateral rim of the coxa. It is a slender but robust muscle.

**P.Trm:** The pleuro-trochanteral muscle (Figs. 53–55) is attached to the pleural suture (above the coxo-pleural joint and near the PCxsP) and runs to the trochanter. The P.Trm lies between BA.Cm and P.Cm.

##### Ventral muscles

**iFm:** The intersegmental furcal muscle (Fig. 50) runs from the anterior part of the mesofurca to the prosternite. It is a slender muscle consisting only of a few fibres.

**Fm:** The slender furcal muscle (Figs. 50, 51) is stretched between the left and the right furca.

**F.CmP:** The flat posterior furco-coxal muscle (Fig. 54) runs from the proximal part of the mesofurca to the postero-lateral rim of the coxa.

##### Direct flight muscles

**BA.SmS:** The large superior basalar-sternal muscle (Figs. 50–54) is dorsally attached to the dorsal part of the crescent-shaped basalare and runs to the presternite.

**BA.SmI:** The inferior basalar-sternal muscle is absent.

**BA.Pm:** The basalar-pleural muscle (Figs. 40, 52–55) runs from a small sclerite of the anterior part of the wing base to the pleurum antero-ventral to the PWP.

**BA.Cm:** The basalar-coxal muscle (Figs. 40, 53–55) is dorsally attached (by a tendon) to a sclerite of the wing base anterior to sl. Ventrally, it is attached to the pleurum next to the coxo-pleural joint. It is a short but robust muscle.

**SA.Sm:** The subalar-sternal muscle (Figs. 50–53) is dorsally attached to the large posterior apodeme of the subalare (PSA) and runs to the furcasternite (Fig. 48). The muscle and its insertion area are conspicuous and large.

**SA.Fm:** The subalar-furcal muscle (not pictured) is slender and inconspicuous and stretches between the tip of the subalar apodeme (PSA) and the furca (or next to it, so that it is attached to the posterior rim of the coxa).

**SA.Cm:** The robust subalar-coxal muscle (Figs. 53–55) inserts on the anterior subalar apodeme (ASA) and runs to the postero-lateral rim of the coxa.

**Ax.Fm:** The axillar-furcal muscle (Figs. 40, 53–55) is dorsally attached to the PNP (in contrast to other

Ephemeroptera) and runs to the furca. The muscle is larger than in other Ephemeroptera.

**Ax.PmI:** The (inferior) axillar-pleural muscle is not present in *Ephoron virgo*.

**Ax.PmS:** The (superior) axillar-pleural muscle (Figs. 54, 55) is a short but robust muscle running from the third axillary sclerite to the antero-dorsal part of the subalare (and the membrane between this part of the SA and the PWP). A second and smaller part of this muscle is attached to the third axillary sclerite and runs to the postero-proximal part of the basal plate.

#### External morphology of the metanotum

The metanotum is shortened. The scutum is about three times as long as the scutellum (SL; Fig. 47). Nevertheless, the dorsal part of the scutellum is, in relation to the mesothorax, quite long. The sutures (except MLs; Fig. 47) and convexities of the metanotum are rather indistinct.

The ANP and the PNP (not pictured) are conspicuous even in the metathorax. The basal plate (BP, not pictured) of the wing base is prominent and the proximal flat part clearly distinguishable from its other parts. A short process lies at the antero-proximal margin. The posterior part of BP is connected to the third wing base sclerite (s3). The first free wing base sclerite (s1) is long and narrow and articulates with the ANP. The second wing base sclerite (s2) is not visible in the metathoracic wing base. At the posterior part of the BP lies the third wing base sclerite (s3). It is a distinct sclerite that articulates with the BP distally and with the PNP proximally. The ban is also visible in the metathoracic wing base.

#### External morphology of the metapleurum (Figs. 45, 46)

The sutures and sclerites are partly or completely reduced in the metathorax. The upper part of the pleural suture (PLsS) is conspicuous and runs obliquely towards the head (dorso-ventrally). The PLsS extends dorsally into the distinct PWP. The condylus of PWP is conspicuous and almost as large as the condylus of the mesothorax. It is also rather flat. It articulates with the proximal base of the basal plate (BP). The inferior part of the pleural suture (PLsI) is inconspicuous.

The basalare, anterior to the PWP, is not present in the metapleurum. Rudimental parts of the subalare are present posterior to the PWP.

The anterior paracoxal suture (PCxsA) is clearly visible even in the metathorax. The lateropostnotum (LPN) is conspicuous.

#### Muscles of the metathorax

##### Dorsal muscles

**MTm:** The median tergal muscle runs from the middle

phragma to the posterior phragma. It is a relatively short but robust muscle that is somewhat smaller than the metathoracic MTm of other mayflies.

**t13:** The second dorsal muscle is absent from the metathorax.

**S.LPNm:** The scuto-lateropostnotal muscle was not found.

##### Dorso-ventral muscles

**S.ESm:** The scuto-episternal muscle is dorsally attached to (about one third!) of the scutum and runs to the episternum. It is a very large muscle in the metathorax that is of similar size as the MTm of the metathorax (distinctly larger than the S.ESm of the metathorax of other mayflies, e.g. *Siphonurus aestivalis*, *Baetis* sp., *Serratella ignita*, *Habroleptoides confusa* etc.).

**S.CmA:** The anterior scuto-coxal muscle is dorsally attached to the scutum and ventrally to the anterior rim of the coxa. It is a slender muscle that is slightly stronger than the S.Trm.

**S.CmP:** The posterior scuto-coxal muscle stretches from the posterior part of the scutum to the posterior rim of the coxa. It is a slender muscle, which is slightly stronger than the S.CmA and the S.Trm ( $S.CmP > S.CmA > S.Trm$ ). S.CmP apparently consists of two parts. The second part is about half in size as the first part.

**S.Trm:** The scuto-trochanteral muscle is dorsally attached to the posterior part of the scutum and proceeds to the trochanter.

**PSL.Cm:** The parascutello-coxal muscle is either reduced in the metathorax or it is also possible that PSL.Cm is the second part of S.CmP and is shifted anteriorly.

**AN.Pm:** The anteronoto-pleural muscle runs from the antero-dorsal part of the metathorax to the pleural suture (where PCxsA, PCxsP and PLs converge). It is a flat and weak muscle.

**SrA.Pm:** The suralar-pleural muscle is a slender muscle running from the antero-lateral part of the scutum to the anterior paracoxal suture. It consists of only a few fibres.

##### Pleural muscles

**P.Cm:** The flat pleuro-coxal muscle runs from the anterior paracoxal suture (PCxsA) to the anterior rim of the coxa. It is a broad and robust muscle.

**P.Trm:** The pleuro-trochanteral muscle is attached to the anterior paracoxal suture (PCxsA) and runs to the trochanter. It is a conspicuous muscle lying posterior to P.Cm.

##### Ventral muscles

**iFm:** A slender muscle, located roughly in the same position as the intersegmental furcal muscle.

**Fm:** The furcal muscle is stretched between the left and the right metafurca. It is a conspicuous muscle, although the metafurca is small and indistinct.

**F.CmP:** The posterior furco-coxal muscle is a flat muscle running from the short furca to the lateral rim of the coxa.

#### Direct flight muscles

**BA.SmS/BA.SmI:** The superior and the inferior basalar-sternal muscles are not present in the metathorax.

**BA.Pm:** The basalar-pleural muscle runs from the scutum to the pleurum (anterior to the PWP). It is a flat and broad muscle, which is large in comparison to the mesothoracic BA.Pm.

**BA.Cm:** The basalar-coxal muscle is dorsally attached to the part of the wing base that is proximal to the sl. Ventrally, it is attached to the lateral rim of the coxa. It is a distinct muscle (stronger than S.CmP).

**SA.Sm/SA.Fm/SA.Cm:** The subalare of the metathorax is reduced to an indistinct sclerite. The subalar muscles are also reduced in the metathorax; the subalar-sternal muscle and the subalar-furcal muscle are partly or completely reduced (there is no muscle left running to the sternum or to the furca). One flat but robust muscle is dorsally attached to the pleurum (to the remains of a subalar apodeme/subalar sclerite). Ventrally, it is attached to the postero-medial rim of the coxa.

**Ax.Fm:** The axillar-furcal muscle is a slender but conspicuous muscle running from a sclerite of the wing base to the furca.

**Ax.PmS:** A muscle, possibly superior axillar-pleural one, is present running from the postero-lateral part of the scutum (at the same level as s3) to the pleurum posterior to the PWP. It is a flat muscle consisting of only a few fibres.

**Ax.PmI:** The (inferior) axillar-pleural muscle is absent.

#### 3.2.5 *Baetis* sp., late larvae (Figs. 56–57) (n = 4)

#### External morphology of the mesonotum

The notum of the mesothorax is much larger than the notum of the metathorax. The median longitudinal suture (MLs) is conspicuous over the whole length of the notum. This is the suture where the cuticula ruptures during ecdysis. The medioparapsidal sutures (MPs) and the lateroparapsidal sutures (LPs) are rather indistinct. The anterior part of the scutum (ANp, ANi) is not clearly differentiated. The middle part of the scutum and the posterior scutal protuberances (PSP), as well as the scutellum are conspicuous. The wing pads are located at the lateral parts of the tergum. No elements of the wing base are differenti-

ated in earlier larval stages. The metanotum is short and without any obvious differentiations.

#### External morphology of the mesopleurum (Fig. 56)

All three pairs of legs are well differentiated since they are important for locomotion in the larval stages. The mesothorax is not as differentiated as in the winged stages. Both the mesopleurum and the metapleurum are about equal in dimension. The pleurum consists of the simple anterior episternum and the posterior epimeron, which are separated by the pleural suture.

#### Muscles of the mesothorax (Fig. 57)

The dimensions of the pterothoracic muscles are not equivalent to the winged stages. The dorsal longitudinal muscle (MTm) is weak in earlier larval stages since the phragmata are not differentiated yet. The S.ESm is always a comparatively large muscle, at least in the mesothorax. The remaining dorso-ventral muscles are slender and almost equal in size. The S.CmP is much smaller in the metathorax than in the mesothorax in earlier larval stages. A weak muscle is present in both meso- and metathorax, which is stretched between a small sclerite in the anterior membrane of the pleurum (next to the stigma) and the presternite. Several muscles are present only in the larval stages.

#### Dorsal muscles

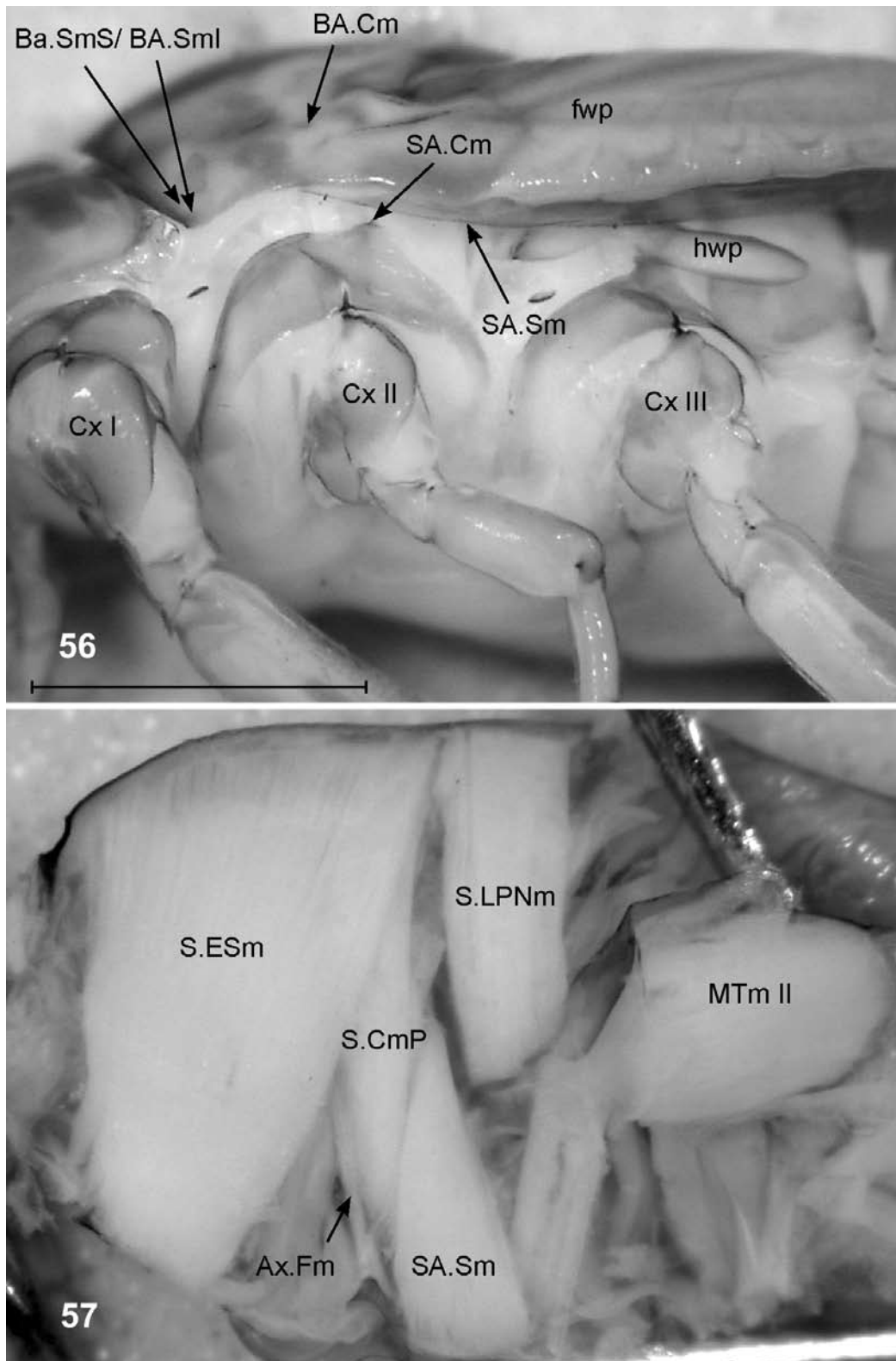
**MTm:** The median tergal muscle stretches from the middle phragma to the posterior phragma. It is a flat muscle, which is not enlarged as it is in subimaginal and imaginal Ephemeroptera. The height of MTm is less than one half of the height of the mesothorax (in a late larval stage).

**t13:** The second dorsal muscle stretches from the posterior part of the scutum to the posterior phragma. It is small and slender but distinct.

**S.LPN.m:** The scuto-lateropostnotal muscle is dorsally attached to the posterior part of the scutum (or posterior scutal protuberance, PSP) lateral to t13 and proceeds to the lateropostnotum. It is a short, flat and small muscle, which becomes much larger in winged stages.

#### Dorso-ventral muscles

**S.ESm:** The scuto-episternal muscle runs from the anterior part of the scutum to the anterior rim of the pleural sclerite, i. e. the episternum. The dorsal point of attachment of the S.ESm is the second widest attachment of the mesothoracic muscles. It encompasses almost one half of the scutum length. Ventrally, the muscle becomes more slender.



**Figs. 56–57.** *Baetis* sp., late larva, same specimen, lateral view. – **56.** Mesopleurum and metapleurum; the arrows show the attachment of the basalar and the subalar muscles. **57.** Musculature of the right half of the mesothorax, showing the large S.ESm and the small SA.Sm. – Scale: 1 mm.

**S.CmA:** The anterior scuto-coxal muscle is dorsally attached to the scutum (lateral to the lateroparapsidal suture, LPs) and runs to the anterior rim of the coxa. The dorsal attachment of this muscle lies latero-ventral to that of S.ESm. The S.CmA is a flat and slender muscle and seems to consist of two parts.

**S.CmP:** The posterior scuto-coxal muscle is dorsally attached to the posterior part of the scutum and runs to the posterior rim of the coxa. The S.CmP is slightly larger than the S.CmA.

**S.Trm:** The scuto-trochanteral muscle running from the scutum (antero-medial to the Ax.Fm) to the trochanter is a very large muscle. It is larger than the S.CmP and the S.CmA.

**PSL.Cm:** The parascutello-coxal muscle runs from the anterior part of the scutellum to the posterior rim of the coxa. It is distinct and larger than the PSL.Cm of subimagines and imagines.

**AN.Pm:** The anteronoto-pleural muscle stretches from the antero-lateral part of the notum to the anterior paracoxal suture (PCxsA, anterior rim of the pleural sclerite, which is well sclerotised). It is a clearly visible but flat muscle consisting only of a few fibres.

**SrA.Pm:** The suralar-pleural muscle runs from the lateral part of the scutum to the pleurum above the attachment of AN.Pm.

#### Pleural muscles

**P.Cm:** The pleuro-coxal muscle is dorsally attached to the anterior rim of the pleurum and ventrally to the anterior coxal rim. It is a short, flat and broad muscle, which is almost oval in cross section.

**P.Trm:** The pleuro-trochanteral muscle stretches between the pleural suture (above the coxal articulation) and the trochanter. It is a robust muscle, which is almost round in cross section and gets broader ventrally.

#### Ventral muscles

**iFm:** The intersegmental furcal muscle runs from the anterior side of the mesofurca to the posterior part of the prothoracic furca.

**Fm:** The short but robust furcal muscle stretches between the proximal side of the right furca and the proximal side of the left furca.

**F.CmP:** The posterior furco-coxal muscle, which runs from the furca to the posterior rim of the coxa, is a distinct and robust muscle.

#### Future direct flight muscles

**BA.SmS:** There is one broad muscle in a position similar to BA.SmS and BA.SmI of the thorax of adult stages. Most likely the superior basalar-sternal muscle and the inferior basalar-sternal muscle (**BA.SmI**) run parallel

in close proximity to each other in larvae of *Baetis* sp. The muscles are dorsally attached to the antero-lateral part of the scutum and ventrally to the furca of the prothorax.

**BA.Pm:** The basalar-pleural muscle is dorsally attached to the scutum (posterior to the BA.Sm and lateral to the SrA.Pm). It proceeds to the pleural membrane directly below the anterior part of the fore wing pad.

**BA.Cm:** The basalar-coxal muscle is dorsally attached to the scutum (posterior to the BA.Pm) and runs to the coxo-pleural joint.

**SA.Sm:** The subalar-sternal muscle is dorsally attached to a small sclerite in the pleural membrane (below the posterior part of the fore wing pad) and runs to the sternum. It is only a slender muscle in contrast to the SA.Sm of subimagines and imagines (Fig. 57).

**SA.Fm:** The flat and slender subalar-furcal muscle is dorsally attached to the same sclerite as the SA.Sm. Ventrally, it is attached to the furca of the mesothorax.

**SA.Cm:** The subalar-coxal muscle runs from the pleural sclerite (postero-dorsal edge of the pleural sclerite, the epimeron) to the postero-lateral rim of the coxa.

**Ax.Fm:** The axillar-furcal muscle is stretched between the scutum (slightly posterior to the BA.Cm) and the furca. It is a slender muscle and is almost as large as the mesothoracic Ax.Fm of the winged stages.

#### Muscles of the metathorax

##### Dorsal muscles

**MTm:** The median tergal muscle is anteriorly attached to the middle phragma and posteriorly to the posterior phragma. It is rather small in relation to the MTm of subimagines and imagines.

**t13:** This short and weak muscle is stretched between the posterior part of the notum and the upper part of the posterior phragma.

**S.LPN.m:** The scuto-lateropostnotal muscle is absent in the metathorax.

##### Dorso-ventral muscles

**S.ESm:** The slender scuto-episternal muscle is dorsally attached to the anterior part of the scutum and ventrally to the anepisternum (more lateral than in the mesothorax).

**S.CmA:** The anterior scuto-coxal muscle runs from the antero-lateral part of the scutum to the anterior coxal rim. It is a flat, broad muscle and smaller than both the S.CmP and the S.Trm.

**S.CmP:** The posterior scuto-coxal muscle is dorsally attached to the middle part of the scutum (posterior to the S.Trm) and runs to the posterior coxal rim.

**S.Trm:** The scuto-trochanteral muscle is dorsally attached to the middle part of the scutum (lateral to S.CmA and



S.CmP) and runs to the trochanter. S.Trm is considerably larger than S.CmA and S.CmP.

**PSL.Cm:** The parascutello-coxal muscle is a slender muscle that stretches between the posterior area of the notum and the posterior rim of the coxa.

**SrA.Pm:** The suralar-pleural muscle is a flat and relatively broad muscle running from the lateral part of the scutum to the anterior rim of the pleural sclerite next to the dorsal attachment of the SA.Cm. A weak and narrow muscle diverges from the SrA.Pm and runs to the pleural sclerite posterior to the SrA.Pm.

#### Pleural muscles

**P.Cm:** The pleuro-coxal muscle is a flat but wide muscle running from the pleurum (PCxsA, anterior rim of the pleural sclerite) to the anterior coxal rim. It is a broad but flat muscle, which consists only of a few fibres.

**P.Trm:** The pleuro-trochanteral muscle is dorsally attached to the anterior rim of the pleural sclerite (PCxsA), posterior to P.Cm, and runs to the trochanter. It is a robust muscle that is almost round in cross section.

#### Ventral muscles

**iFm:** The flat and broad intersegmental furcal muscle runs from the anterior part of the metafurca to an apodeme directly posterior to the mesofurca.

**Fm:** The furcal muscle joins the left and right metafurcal branches. It is elliptic in cross section.

**F.CmP:** The posterior furco-coxal muscle runs from the furca to the posterior rim of the coxa (medial to the ventral attachment point of SA.Cm). It is a distinct flat muscle.

#### Future direct flight muscles

The basalar muscles are most likely absent in the metathorax but the small muscle that diverges from the SrA.Pm and runs to the pleurum is probably the **BA.Pm**.

The two subalar-sternal muscles (**SA.Sm** and **SA.Fm**) are missing in the metathorax.

**SA.Cm:** The subalar-coxal muscle is flat and runs from the pleurum (process at the pleural suture) to the posterior rim of the coxa.

**Ax.Fm:** The slender axillar-furcal muscle is dorsally attached to the lateral part of the scutum and ventrally to the furca.

#### Further larval muscles

A flat muscle stretches between the anterior phragma and the posterior part of the second abdominal segment. Ventrally, there is a second muscle, which runs to the posterior part of the second abdominal segment. Both muscles are flat, broad and bipartite. Each of the second parts is

attached to the anterior part of the second abdominal segment.

Furthermore, a tendon-like, slender and flat muscle is stretched between the anterior phragma and the anterior rim of the coxa. It is a weak muscle that consists of only a few fibres. It is present in the mesothorax and the metathorax.

Two flat and broad muscles are attached to the furca of the metathorax. The first muscle runs to the anterior part and the second one to the posterior part of the first abdominal segment.

A flat muscle stretches between the posterior phragma and the first abdominal segment.

A further slender muscle is attached to the posterior phragma and to the sternum (just anterior to the metasternum).

A narrow muscle stretches between the anterior part of the first abdominal tergite and the posterior rim of the coxa.

### 3.3 Odonata

(Figs. 58–66)

#### 3.3.1 General Remarks

The pterothorax of Odonata is specialised and adapted to their hunting behaviour. The mesothorax and metathorax are large and directed obliquely forwards, relative to the small and simple prothorax. The orientation of the pterothorax together with the orientation of the legs forms a characteristic capture apparatus. Most of the flight muscles are direct acting muscles.

#### 3.3.2 *Sympetrum* cf. *striolatum*

(n = 1)

##### Measurements (♂)

Total length: 38 mm. – Length of mesothorax: 3.6 mm. – Length of mesothoracic wing: 29 mm. – Width of mesothoracic wing: 7 mm. – Length of metathorax: 3.4 mm. – Length of metathoracic wing: 28 mm. – Width of metathoracic wing: 9 mm.

#### External morphology of the mesonotum

The pterothoracic notal elements are strongly reduced in Odonata. The anterior area of the notum is the conspicuous prescutum (following ASAHINA 1954), which is demarcated from the scutum (S; Fig. 58). The lateral part of the prescutum (PRS; Fig. 58) is located between the scutum and the humeral plate (hp; Fig. 58). PRS is anteriorly tightly associated with the humeral plate. It is the dorsal attachment of the short muscle 28. A further narrow sclerite, lying in-between the lateral part of the prescutum and the humeral plate, serves as the dorsal attachment for the muscle 26. The latter two sclerites have been assumed

to be the 1Ax (Pt 1 sensu TANNERT 1958). The scutum is a large convex sclerite with the associated internal tergal apophysis, which serves as attachment of the muscle 23. The convex scutal sclerite and the tergal apophysis are larger in the metathorax than in the mesothorax.

The fore and hind wings articulate with the tergum via two large plates. The anterior humeral plate (hp) articulates proximally with the prescutum and distally with the costal vein of the wing. Two muscles, 21 and 22, are attached to the lateral margin of the humeral plate. Furthermore, hp is associated with the anterior part of the pleural wing process (PWP; Figs. 59, 60). Posterior to the humeral plate lies the axillary plate (axp; Fig. 58). The anterior radial vein (R; Fig. 58) and the anterior medial vein (MA; Fig. 58) originate from the anterior part of axp. The sector of the medial vein (MP; Fig. 58) and the cubital vein (Cu; Fig. 58) are connected to the posterior part of the axillary plate. Furthermore, the anterior part of the axp is connected to the posterior pleural wing process (PWP; Figs. 59, 60). Five muscles are associated with the axillary plate: 27, 29, 32, 33 and 34. The antero-ventral part of the axillary plate serves as the dorsal attachment of muscles 27 and 32. Both muscles, 33 and 34, are indirectly connected to the postero-ventral part of the axillary plate. The short and bipartite muscle 29 is attached to the posterior part of the axillary plate and proceeds to the pleurum.

#### External morphology of the mesopleurum

The pleurum of Odonata is specialised, since the meso- and metapleurum are fused to each other. The anterior parts of the right and the left episternites are connected to each other and separated by a dorsal carina. The episternum (ES; Fig. 59) is a large sclerite that is separated from the epimeron (EM; Fig. 59) by the pleural suture (PLs; Figs. 59, 60). The conspicuous pleural suture extends dorsally into the distinct posterior pleural wing process (PWP; Figs. 59, 60) of the mesothorax that articulates with the anterior part of the axillary plate (axp). The upper part of the mesothoracic epimeron is fused to the metathoracic episternum. The area anterior and posterior to the posterior pleural wing process is membranous. A small sclerite (s in Fig. 60) is visible in the upper third of the membrane posterior to the posterior PWP. It is the dorsal attachment of the muscles 33 and 34. The epimeron is only ventrally separated from the metathoracic episternum by the interpleural suture (following ASAHINA 1954).

#### Muscles of the mesothorax (Figs. 61–66)

The muscles of mesothoracic origin are arranged after the numbers of ASAHINA (1954); the corresponding muscles of metathoracic origin are given in parentheses.

The muscles 24 and 35 are absent in *Sympetrum* cf. *striolatum* and, according to ASAHINA (1954) and MALOEUF

(1935), also in all other adult Odonata. According to ASAHINA muscle 31 is present in *Epiophlebia*, *Davidius*, and *Mnais*; it is, however, absent in *Sympetrum* cf. *striolatum* and, according to MALOEUF, in adult Odonata. Muscle 37 is present in *S.* cf. *striolatum* and, according to ASAHINA, also in *Epiophlebia* and *Davidius*. In contrast, according to MALOEUF, muscle 37 is absent in adult Odonata.

**21 (43):** The sternopleural/sternobasalar muscle is small and short. It is dorsally attached by a long tendon to the antero-lateral part of the humeral plate. The ventral attachment lies just lateral to muscle 22. In the metathorax, it is dorsally attached to the antero-lateral part of the humeral plate via a tendon. Ventrally, it is attached to the preepisternum (near the stigma), also by a tendon. It is not as closely associated with the larger muscle (44) as the corresponding muscle of the mesothorax to muscle 22.

**22 (44):** The large sternopleural/sternobasalar muscle is dorsally attached to the antero-lateral part of the humeral plate via a tendon that is sclerotised basally. A second branch of this tendon runs to the centre part of the humeral plate. Ventrally, muscle 22 is attached to the preepisternal apodeme (sensu ASAHINA 1954). The muscle is bipartite and the dorsal apodeme has a gap in the anterior area. The ventral apodeme that serves as attachment of the metathoracic sternobasalar muscle (44) is not as mobile as in the mesothorax.

**23 (46):** The large anterior tergo-sternal muscle is dorsally attached to the tergum. Ventrally, it attaches to an apodeme that runs to the antero-medial rim of the coxa. An apodeme-like sclerite, which is tightly connected to a bullous arched part of the tergite serves as the dorsal attachment.

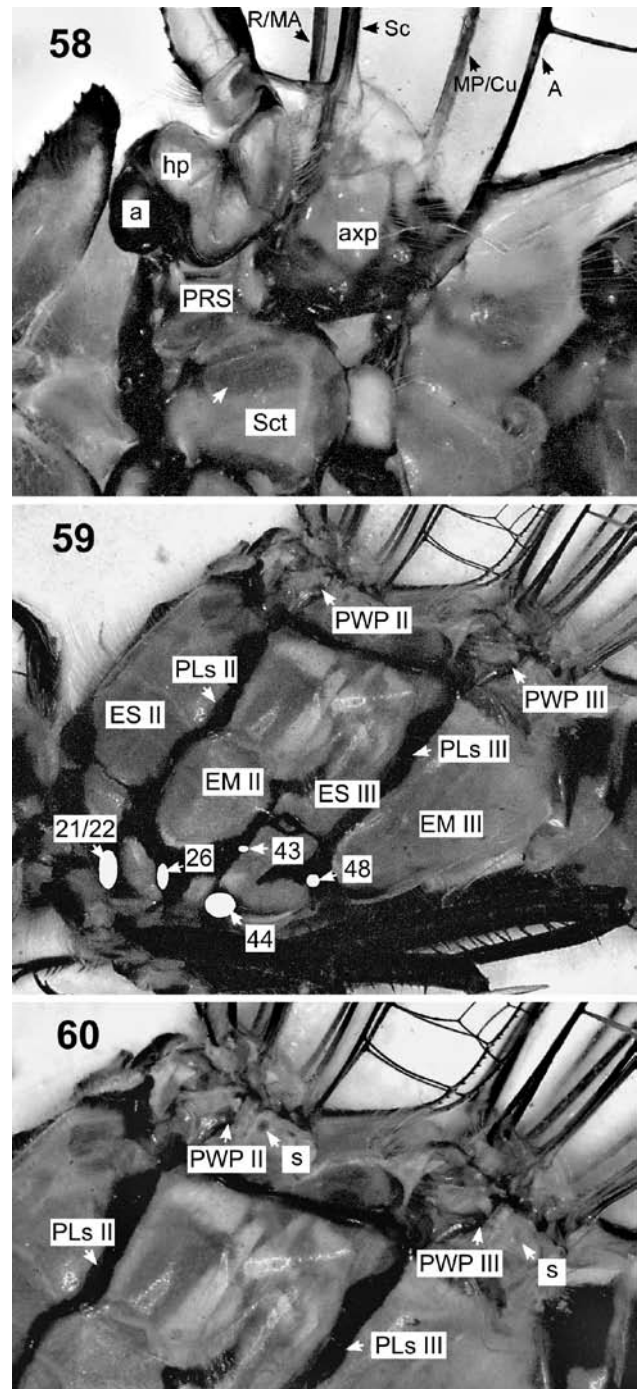
**23' (46'):** Lateral to the anterior tergo-sternal muscle 23 lies a smaller and shorter muscle (23'), which is dorsally and ventrally attached to the same points as muscle 23. It is ventrally attached by a long tendon.

**25 (45):** The dorsal longitudinal muscle is attached to the tergal apophysis (anterior phragma) and to the lateral part of the notum just between the meso- and metathorax. This rather small and weak muscle is present in the mesothorax, but absent in the metathorax.

**26 (48):** The coxobasalar muscle is dorsally attached to a tergal sclerite via a tendon, which is distally connected to the humeral plate. It runs to the pleural ridge next to the postero-lateral rim of the coxa. The muscle 26 is a rather narrow muscle and smaller than muscle 27.

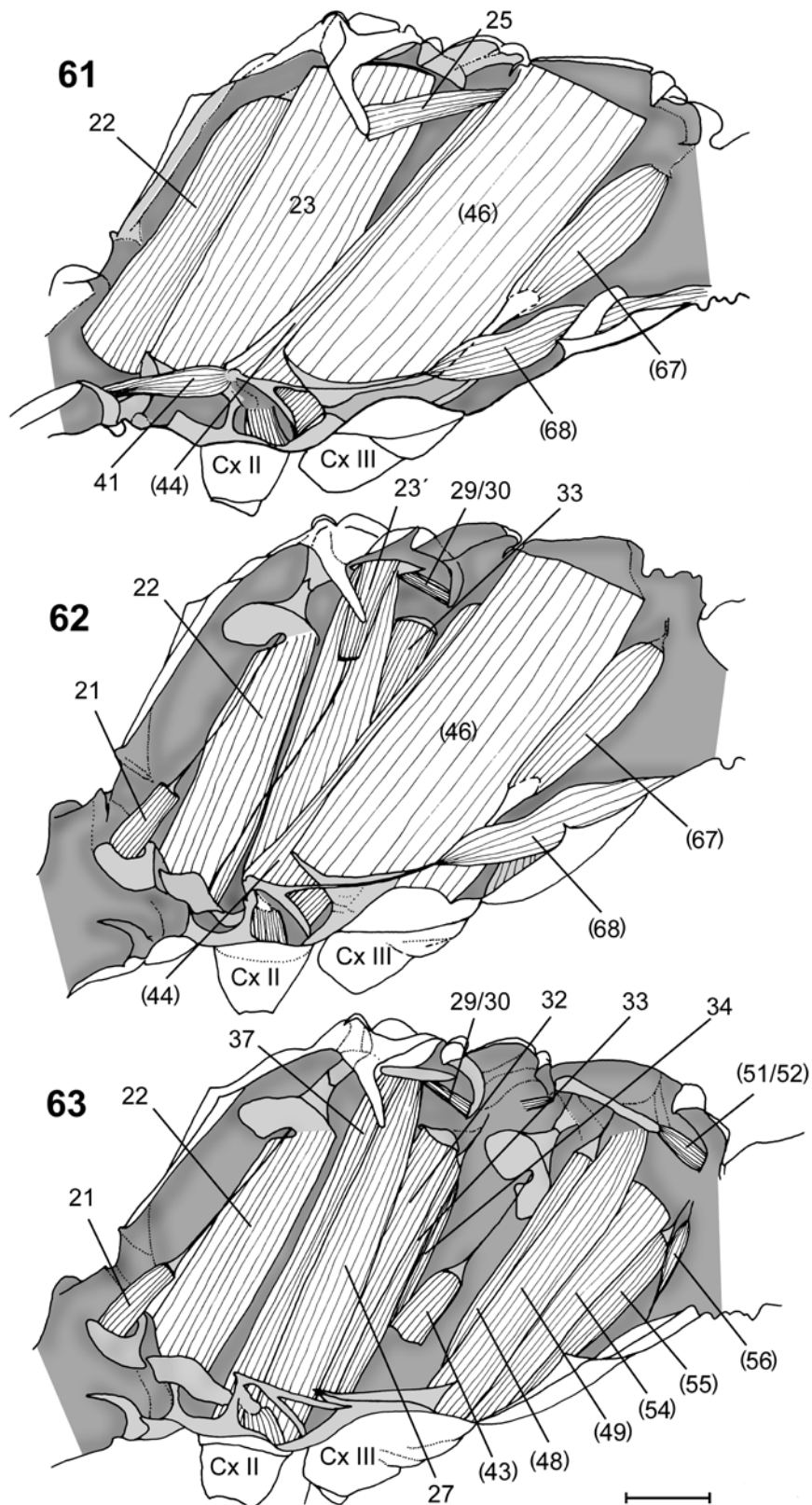
**27 (49):** The dorsal attachment of the coxosubalar muscle lies postero-medial of muscle 26. It is dorsally attached to the antero-proximal part of the axillary plate and proceeds to the pleural ridge next to the postero-lateral rim of the coxa. A second part is stretched between the same attachments of the first part, but dorsally it is attached via an apodeme.

- 28 (50):** The short but robust tergopleural muscle is dorsally attached to the prescutum (PRS; Fig. 58) and ventrally to the upper part of the pleural ridge.
- 29/30 (51/52):** Both pleuroaxillary muscles (or rather one bipartite muscle) are attached to the posterior part of the axillary plate and proceed to a narrow sclerite of the pleurum posterior to the PWP. The pleural sclerite is tightly connected to the PWP. The two parts of the muscles are better distinguishable in the metathorax. The distal part of the metathoracic muscles is attached to an indistinct pleural sclerite posterior to the PWP. It is almost round in cross section. The proximal part is wider but flat and runs to a sclerite of the pleurum that is tightly associated with the PWP similar to the mesothoracic sclerite. Nevertheless, the connection between the muscle and the sclerite is stronger in the metathorax.
- 31 (53):** This pleuroaxillary muscle is absent in *Sympetrum* (missing in adult Odonata according to MALOEUF 1935).
- 32 (54):** The conspicuous pleurosubalar muscle runs from a large dorsal apodeme to the ventral margin of the epimeron. The dorsal apodeme is connected by a tendon to the anterior part of the axillary plate. It is a broad and large muscle in the meso- and also in the metathorax. The muscles 32 and (54) are almost equal in size to the muscles 22 and (44).
- 33 (55):** The pleurosubalar muscle is rather slender and dorsally attached to a small sclerite in the pleural membrane posterior to the PWP, but also to the postero-ventral part of the axillary plate by a tendon. Ventrally, it is attached to the epimeron.
- 34 (56):** Posterior to the muscles 33 and (55) respectively lie the short and slender pleurosubalar muscles 34 and (56) respectively. Muscle 34 is dorsally attached to the small sclerite in the pleural membrane posterior to the PWP. Nevertheless, it is also connected to the postero-ventral part of the axillary plate via a tendon. The ventral attachment is on the epimeron near the spiracle. In the metathorax, it is a short muscle that is attached via a tendon dorsally as well as ventrally. The tendon of the muscle 33 and the tendon of the muscle 34 are associated and intersected so that the attachment of the muscle 34 is located anteriorly and the attachment of muscle 33 lies posteriorly. The metathoracic muscles (55, 56) proceed in the same way.
- 36 (58):** The short and flat but robust pleurocoxal muscle runs from the katapisternum (terminology following ASAHINA 1954) to the lateral rim of the coxa.
- 37 (60):** The tergoxal muscle is relatively large and dorsally attached to a tergal sclerite posterior to PRS. Ventrally, the muscle 37 is attached to the antero-lateral rim of the coxa. The metathoracic muscle (46) seems to consist of three parts; the first part is the mus-

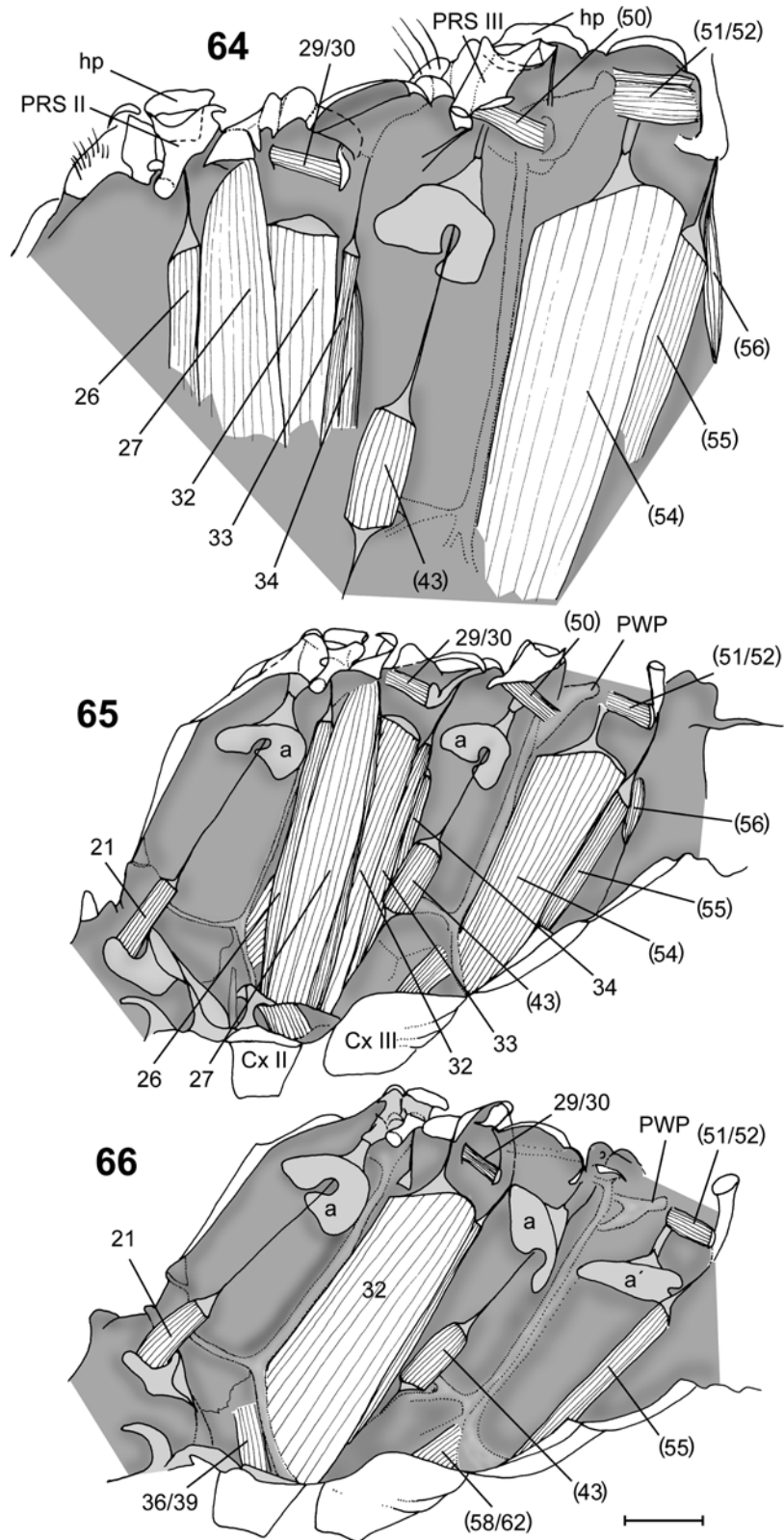


**Figs. 58–60.** *Sympetrum* cf. *striolatum*. – **58.** Mesotergum, dorsal view (head to the left); the arrow marks the apodeme shining through the arced scutal sclerite, which is the dorsal attachment of muscles 23 and 46. **59.** Pterothorax with the ventral attachment points of several muscles, lateral view. **60.** Pterothorax, upper area. – a = regio anterior of hp (following TANNERT 1958); s = dorsal attachments (sclerites) of muscles 33 (55) and 34 (56).

cle (46), the second is the small muscle (46') and the third part is the muscle 37 (see section 4.3).



**Figs. 61–63.** *Sympetrum cf. striolatum*, ♂, musculature of the right half of the pterothorax at progressive stages of dissection, starting with median muscles (61) and progressively proceeding to the most lateral muscles (see Fig. 66). – Scale: 1 mm.



**Figs. 64–66.** *Sympetrum* cf. *striolatum*, ♂, musculature of the right half of the pterothorax at progressive stages of dissection (see legend to Figs. 61–63); Fig. 64 = detail of the upper half. – a = apodeme of muscles 22 and 44; a' = apodeme of muscle 32. – Scale: 1 mm.

- 38 (61):** The small sternocoxal muscle is stretched between a ventral apodeme (furca 2 following ASAHINA 1954) and the postero-lateral rim of the coxa.
- 39 (62):** The slender pleurotrochanteral muscle 39 is attached to the katepisternum and runs to the trochanter.
- 40 (63):** The pleurotrochanteral muscle stretches between the latero-external side of the furca and the trochanter (following ASAHINA 1954). It is not pictured in Figs. 61–66 because it was hardly visible.
- 41:** The slender and robust longitudinal ventral muscle stretches between the mesofurca and the profurca.
- (68):** This ventral muscle stretches between the intersegmental sternopleural process (MALOEUF 1935; posterior end of furcal invagination following ASAHINA 1954) and the first abdominal segment. It is a distinct and robust metathoracic muscle. It might be the corresponding muscle to the mesothoracic muscle 41.

### 3.4 Plecoptera

#### 3.4.1 *Pteronarcys reticulata*

(Figs. 67–73) (n = 1)

##### Measurements (♂)

Total length: 24 mm. – Length of mesothorax: 3.8 mm. – Length of fore wing: 26.5 mm. – Length of metathorax: 4 mm. – Length of hind wing: 22.5 mm.

##### External morphology of the mesonotum

The prescutum and the prealar bridge are short but distinct (PAB; Fig. 67; metathorax: Figs. 72, 73). The scutum and the scutellum (SL; Fig. 67; metathorax: Figs. 70, 72) are conspicuous in the mesothorax. The median longitudinal suture (MLs; Fig. 67; metathorax: Figs. 70, 72) is distinct from the anterior part of the scutum to the scutellum. A distinct convex area at the lateral part of the scutum serves as a dorsal attachment point for several dorso-ventral muscles. Both the scutellum (SL) and the postnotum are conspicuous elements of the mesothoracic tergum. The tegula (T; Fig. 68; metathorax: Fig. 72) of the fore wing is distinct and densely covered with setae (more than in the metathorax; the apex of the metathoracic tegula is covered with a couple of long setae and some short ones). The indistinct humeral plate (HP, not pictured) lies at the wing base, posterior to the tegula.

The anterior notal wing process (ANP; Figs. 67, 68) is a concave and clearly demarcated but integral part of the tergum. It is slightly shorter than the ANP of the metathorax (Figs. 70, 72, 73) and approximately four times as long as wide (ANP of the metathorax is approximately six times as long as its width). The median notal wing process (MNP) is weakly developed. The distinct posterior notal wing process (PNP; Figs. 67, 69) articulates with the 3Ax

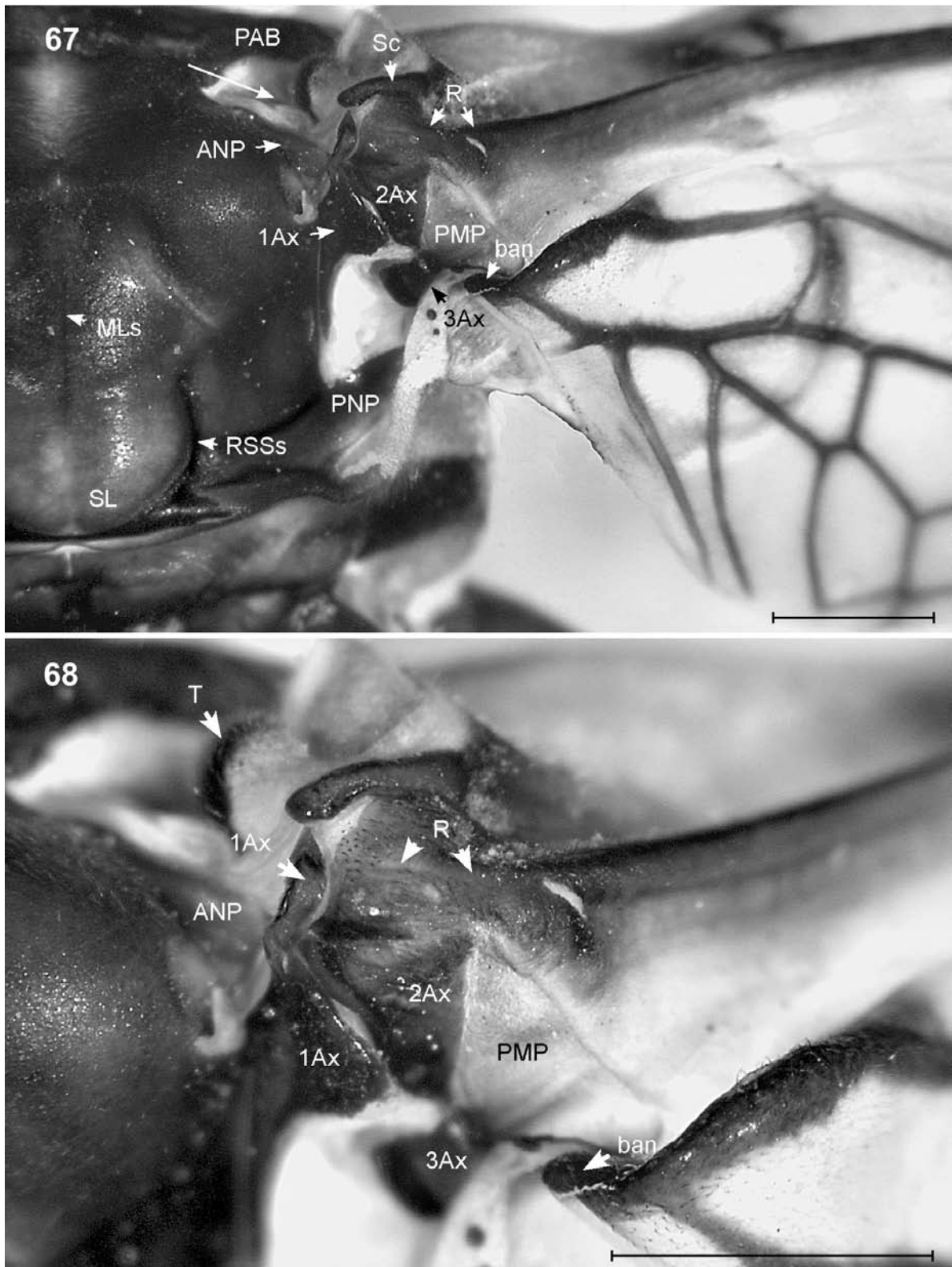
of the wing base. In the metathorax, the anterior part of the PNP (Figs. 70, 72) is detached from the tergum. The axillary cord (AxC) which is sclerotised at its base lies posterior to the PNP.

The wing base is composed of the first, second and third axillary sclerite (1Ax, 2Ax and 3Ax; Figs. 67–69). The 1Ax is subdivided into the anterior head, the middle neck and the posterior body. The entire 1Ax of the mesothorax is rather compact. The head of the 1Ax is almost three times as long as wide and tapered apically (rounded apically in the metathoracic 1Ax). The head of the 1Ax articulates with the subcostal vein (Sc; Fig. 67) but it is also connected to the base of the anterior radial vein (R; Figs. 67, 68). The neck is short and approximately as long as wide. The following body of the 1Ax is almost half as wide as long at its broadest point. It articulates distally with the triangular 2Ax. It is sclerotised only in the dorsal layer of the wing membrane. A muscle is attached to the anterior part of the body of the 1Ax, which runs to the pleurum. In addition to the articulation with the 1Ax proximally, the 2Ax articulates with the proximal median plate (PMP; Figs. 67–69) distally and with the 3Ax posteriorly. The anterior edge of the 2Ax is partly, i. e. over about one half of the edge-length, fused with the base of the anterior radial vein. The distal point of the 2Ax is also fused with the base of the anterior radial vein in the metathorax. The 2Ax is sclerotised both in the dorsal and in the ventral layer of the wing membrane. Seen from dorsally, a distinct sulcus is visible on the proximal part of the 2Ax. It possesses a process on its ventral side, which articulates with the pleural wing process (PWP, not pictured). The 3Ax is distinct and considerably more folded in the mesothorax than it is in the metathorax and is connected to the PNP posteriorly. It is a rather simple sclerite but more robust than in the metathorax and without a pronounced anterior branch. The muscle, which runs to the pleurum (tpm 48) is attached to the proximal cavity of the 3Ax. The posterior part of the 3Ax is connected to the base of the anal veins (A). This base, the basanale (ban; Fig. 68), is conspicuous and sclerotised. Only the proximal one of the two median plates (PMP) is visible.

The base of the costal vein, and also the base of the subcostal vein, is distinct. Both are also more conspicuous in the mesothorax than in the metathorax (Figs. 70–73). The anterior radial vein is the most distinct vein in the fore and the hind wing. The base of the anterior radial vein is conspicuously developed. The posterior edge of the base of the radial vein (Fig. 71, R) is partly fused with the 2Ax.

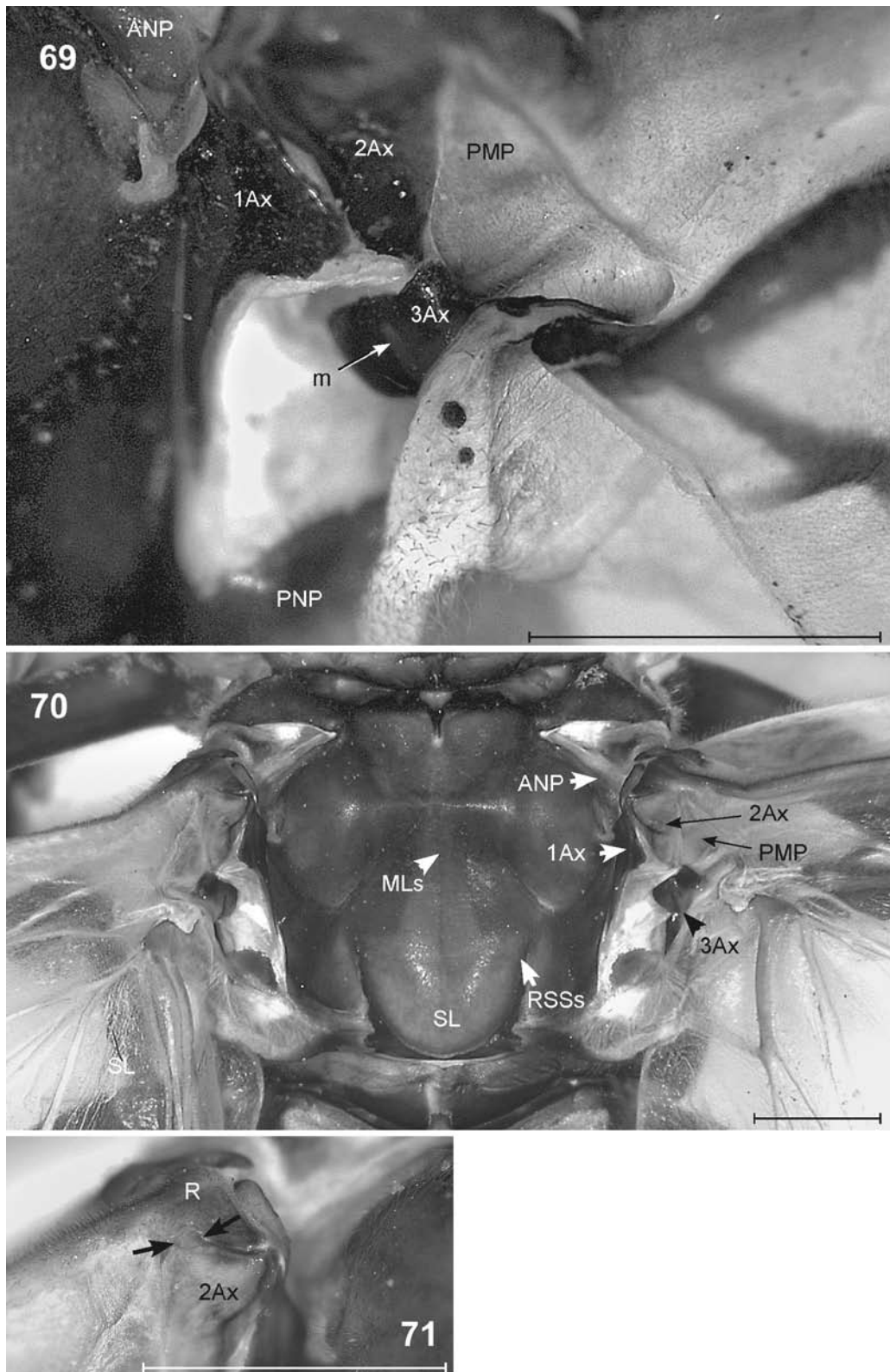
##### External morphology of the mesopleurum

The pleurum (not pictured, compare Fig. 123) is divided into the anterior episternum (ES) and the posterior epimeron (EM) by the pleural suture (PLs), which runs

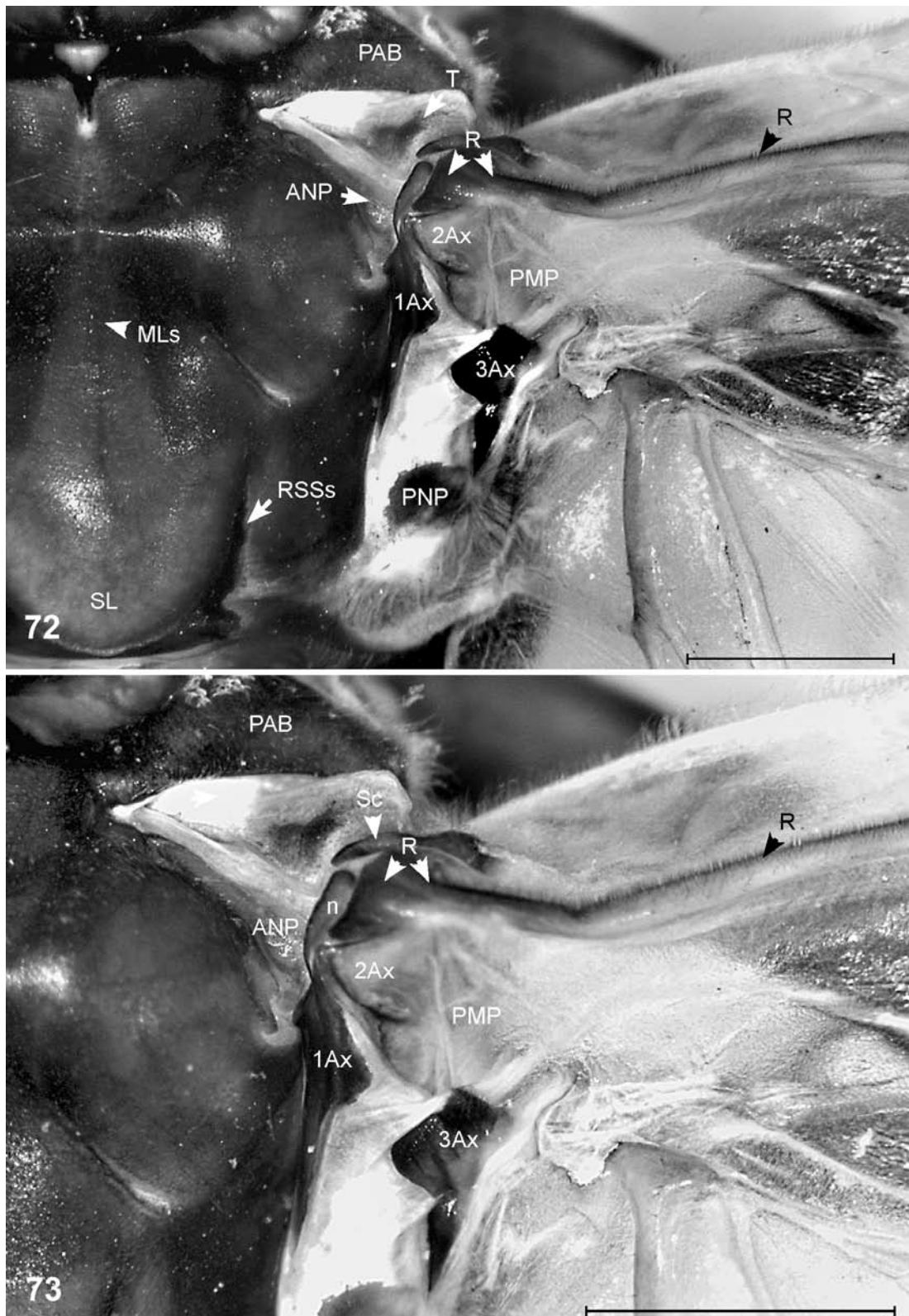


**Figs. 67–68.** *Pteronarcys reticulata*, right fore wing. – **67.** Wing base; the long arrow marks the position of the subtegula. **68.** Axillary sclerites. – Scales: 1 mm.

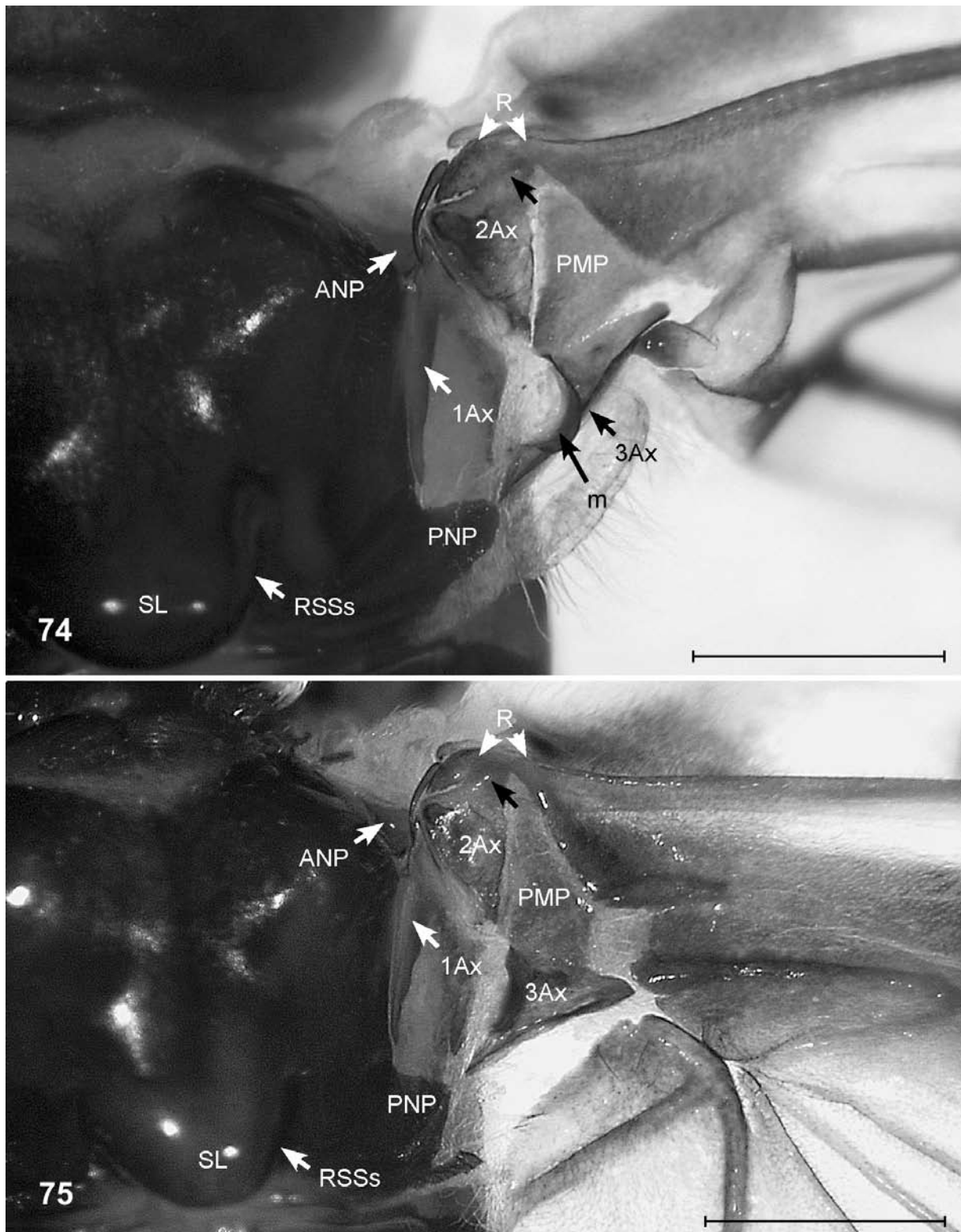




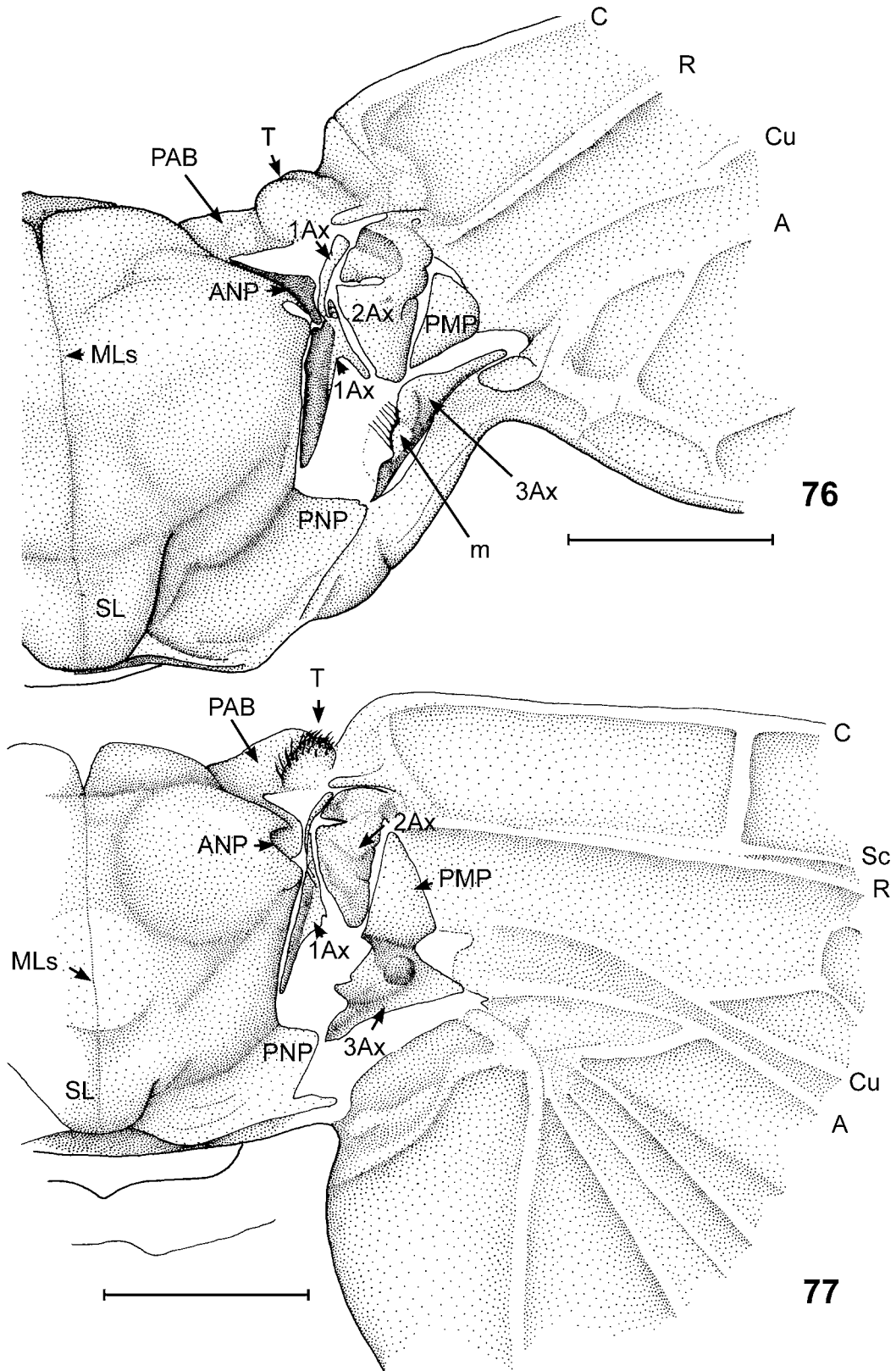
**Figs. 69–71.** *Pteronarcys reticulata*. – **69.** Detail of the right fore wing; m marks the attachment of the flexor muscle. **70.** Overview of the metanotum and the wing bases. **71.** Detail of the left hind wing base, showing the base of the anterior radial vein (R) and the 2Ax; the arrows mark the fusion of 2Ax and R. – Scales: 1 mm.



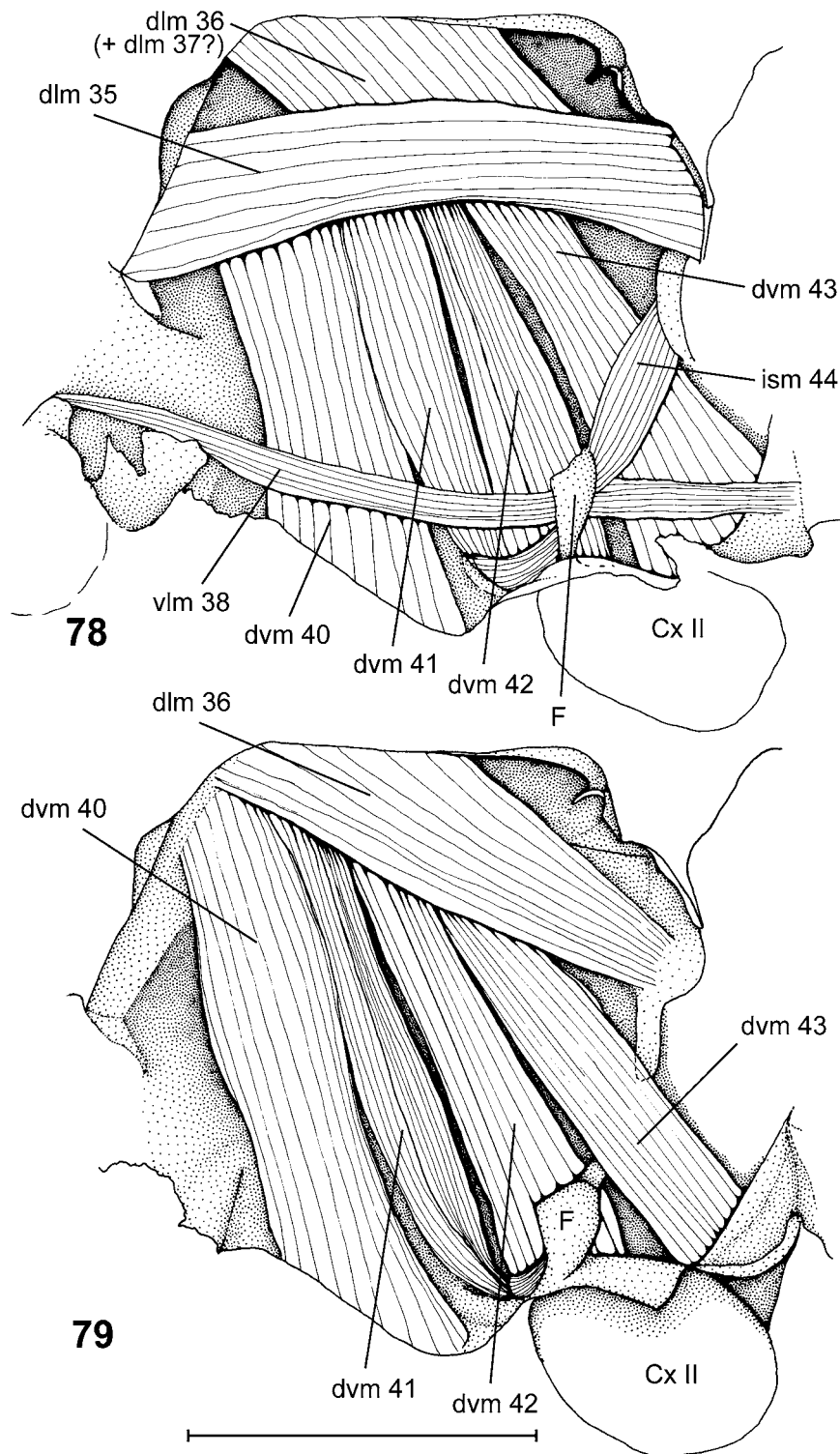
**Figs. 72–73.** *Pteronarcys reticulata*, right hind wing base; Fig. 73 = detail. – n = neck of 1Ax. – Scales: 1 mm.



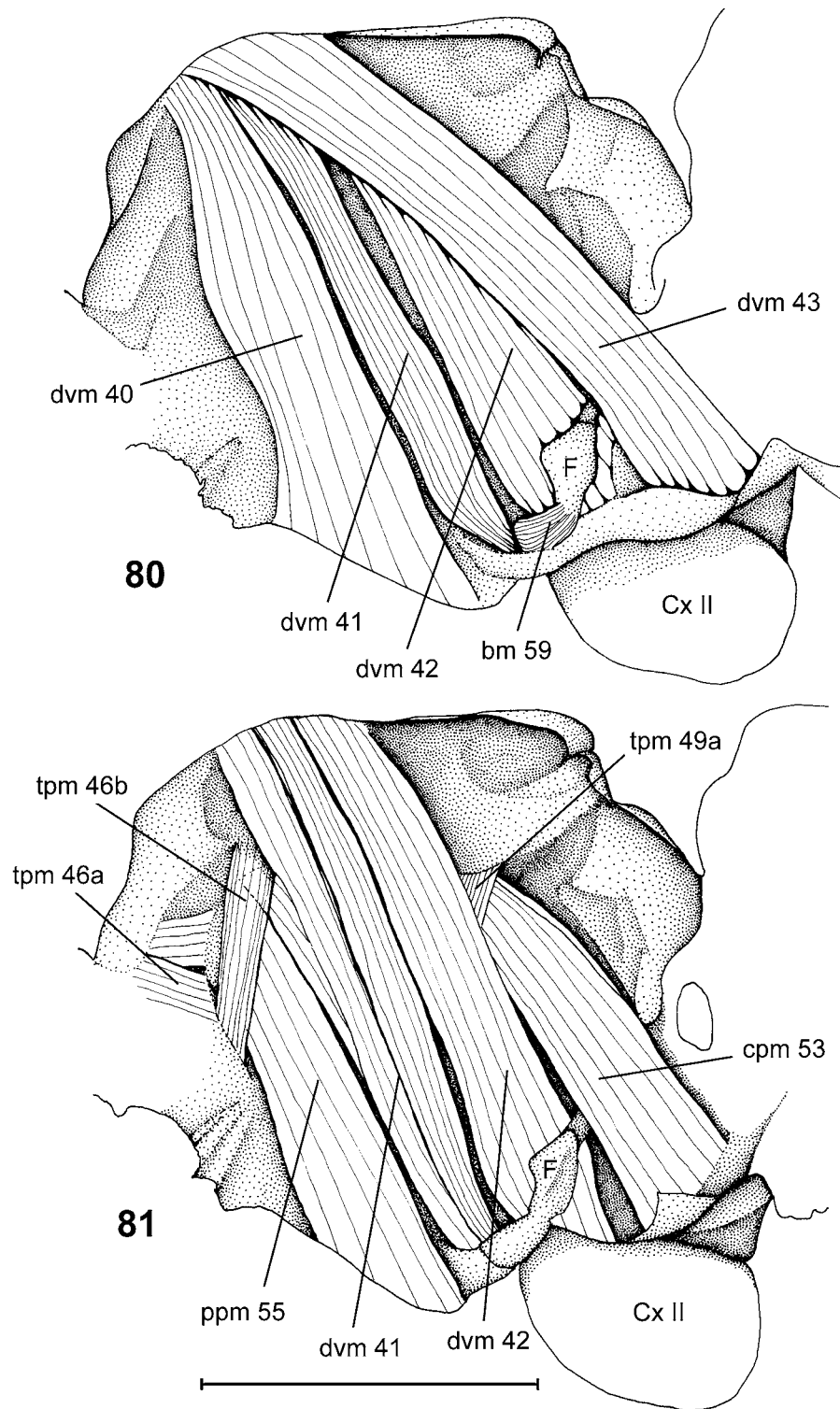
**Figs. 74–75.** *Brachyptera seticornis*. – 74. Right fore wing base; m shows the attachment of the flexor muscle of 3Ax; the upper black arrow marks the fusion of 2Ax with the base of the anterior radial vein. 75. Right hind wing base; the black arrow marks the fusion of 2Ax with the base of the anterior radial vein (R). – Scales: 0.5 mm.



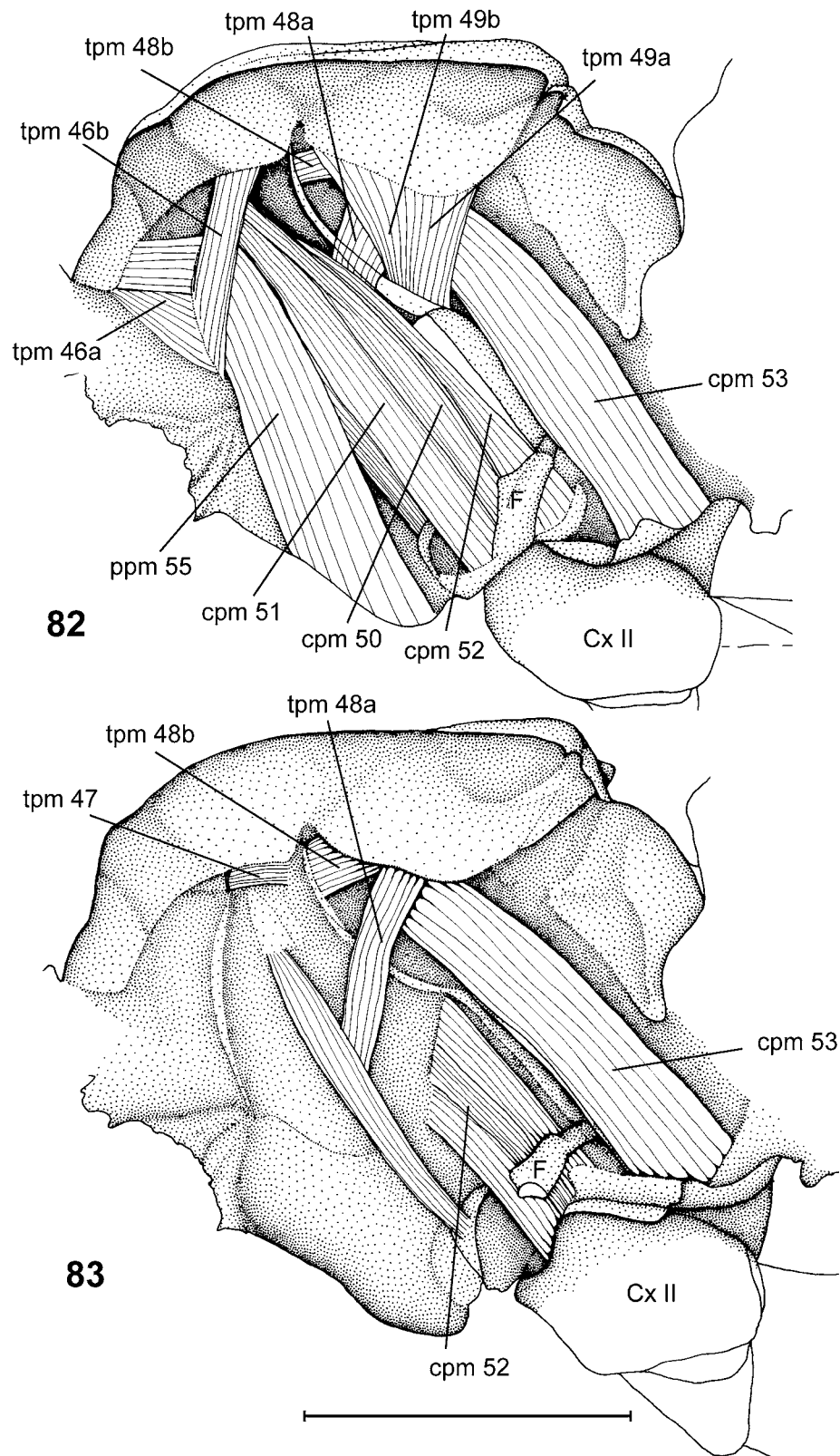
**Figs. 76–77.** *Brachyptera seticornis*. – 76. Right fore wing base. 77. Right hind wing base. – m = attachment of the flexor muscle. – Scales: 0.5 mm.



**Figs. 78–79.** *Brachyptera seticornis*, musculature of the right half of the mesothorax at progressive stages of dissection, starting with median muscles (78) and progressively proceeding to the most lateral muscles (see Fig. 83). – Abbreviations of the muscles see section 3.4. – Scales: 1 mm.



**Figs. 80–81.** *Brachyptera seticornis*, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 78–79). – Scale: 1 mm.



**Figs. 82–83.** *Brachyptera seticornis*, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 78–79). – Scale: 1 mm.



obliquely backwards. The upper part of the pleural suture is less distinct than the conspicuous lower part. The PLs extends dorsally into the pleural wing process (PWP). Anterior to the PWP lies the basalare (BA). It is a prominent part of the pleurum, which is partly detached from the episternum. The basalare is anteriorly connected to the base of the costal vein and to the PWP posteriorly. The subalare is an undifferentiated and longish but distinct sclerite. It is located in the pleural membrane below the wings. The epimeron is not as wide as the episternum.

### 3.4.2 *Brachyptera seticornis* (Figs. 74–83) (n = 3)

#### Muscles of the mesothorax (Figs. 78–83)

The musculature in adult specimens is similar in the meso- and metathorax. Therefore, in the following only the mesothorax is described, with the exception of those muscles that are different in each segment. The terminology of musculature follows WITTIG (1955) and ZWICK (1973).

#### Dorsal muscles

- d1m 35:** The *Musculus dorsalis longitudinalis* is a middle-sized muscle running from the anterior to the middle phragma.
- d1m 36:** The *M. dorsalis obliquus primus* is attached to an area stretching from the anterior scutum to the centre of the scutum dorsally and runs to the middle phragma. The d1m 36 is about as large as the d1m 35 but rather flat.
- d1m 37:** If present, the *M. dorsalis obliquus secundus* is not clearly separated from the d1m 36.

#### Dorso-ventral muscles

- dvm 40:** The *M. tergo-praecoxalis* (*M. tergo-basisternalis* sensu WITTIG 1955) is a large muscle, which is dorsally attached to the anterior part of the scutum. Ventrally, it is attached to the praecoxa (preepisternite, PES; Fig. 123).
- dvm 41:** The dorsal point of attachment of the *M. tergo-trochantinalis* lies just postero-lateral to that of dvm 40 on the scutum. Ventrally, this muscle is attached to the trochantinus. It is a large one, but not as large as the dvm 40.
- dvm 42:** The *M. tergo-endocoxalis*, running from the scutum (postero-lateral of dvm 40/41) to the trochanter, is almost as large as the dvm 41.
- dvm 43:** The dorsal point of attachment of the *M. tergo-coxalis posterior* lies postero-medial of that of dvm 40. Ventrally, this muscle is attached to the posterior rim of the coxa. The dvm 43 is larger than the dvm 41 and dvm 42.

**ism 44:** The *M. tergo-furcalis* is a robust, flat, and broad muscle, which stretches between the antecosta of the metathorax and the furca of the mesothorax.

#### Pleural muscles

- tpm 46b:** The *M. scuto-apodema episternalis* is a flat, broad muscle, which runs from the ANP to the ridge at the anterior part of the episternum. It consists of only a few fibres.
- tpm 47:** The short and robust *M. tergo-crista pleuralis anterior* is stretched between the subtegula and the upper part of the episternum next to the PWP.
- tpm 48:** Two muscles are attached to the 3Ax in *B. seticornis*. The first muscle, the *M. pterale* [ascellare]-episternalis, is attached to the 3Ax and runs to the episternum slightly ventral to the middle part of the pleural ridge (tpm 48a). It is a flat and broad muscle, which consists of only a few fibres. The second part is attached to the 3Ax (just posterior to the first part) and runs to the upper part of the pleural ridge (below the PWP; tpm 48b) (see discussion, section 4.3.6). It is not as wide as the first part and also consists of only a few fibres. The muscles, tpm 48a and tpm 48b, are wing flexor muscles.
- tpm 49:** The *M. tergo-crista pleuralis posterior* is bipartite in *B. seticornis*. The first (anterior) part (tpm 49b) is attached to the anterior part of the body of the 1Ax and to the pleural ridge ventrally. The second (posterior) part (tpm 49a) is stretched between the lateral part of the scutum and the pleural ridge.
- cpm 50:** The *M. basalare-endocoxalis* stretches between the antero-dorsal part of the basalare and the trochanter ventrally. The muscles cpm 50 and 51 are similar in dimension to cpm 53.
- cpm 51:** The *M. basalare-coxalis* is dorsally attached to the basalare and ventrally to the anterior rim of the coxa.
- cpm 52:** The *M. episterno-coxalis* stretches between the episternum and the anterior rim of the coxa. The dorsal point of attachment lies postero-ventral to cpm 50 and cpm 51.
- cpm 53:** The wide *M. subalare-coxalis* is attached to the subalare and runs to the posterior part of the coxa, the meron.
- ppm 55:** The *M. episterno-praecoxalis* is a robust muscle, which stretches between the upper part of the episternum (anterior to the BA) and the ventral part of the episternum.
- ppm 56:** The *M. pleuralis* is a flat muscle running from the posterior subalare (terminology following ZWICK 1973) to the epimeron and consists of only a few fibres.
- bm 59:** The short and flat *M. furca-coxalis anterior* stretches between the furca and the antero-lateral rim of the coxa.

**zm 61:** The short but distinct and robust *M. furca-crista pleuralis* connects the furca with the pleural arm.

## 4 Discussion

### 4.1 General Remarks

There is generally no doubt on the monophyly of Neoptera. In contrast, the sister group relationships of the three basal clades of Pterygota (Ephemeroptera, Odonata and Neoptera) remain controversial. While there is general agreement on the composition of the wing base sclerites in the ground plan of Neoptera, their homology to the wing base sclerites in Ephemeroptera and Odonata has remained unresolved. This is mainly due to the fact that the conditions in the Ephemeroptera and Odonata seem to be highly modified, since both taxa are specialised in this respect. However, it will only be possible to deduce the ground plan of the pterygote wing base when the homology of these elements is clarified.

### 4.2 The wing base elements

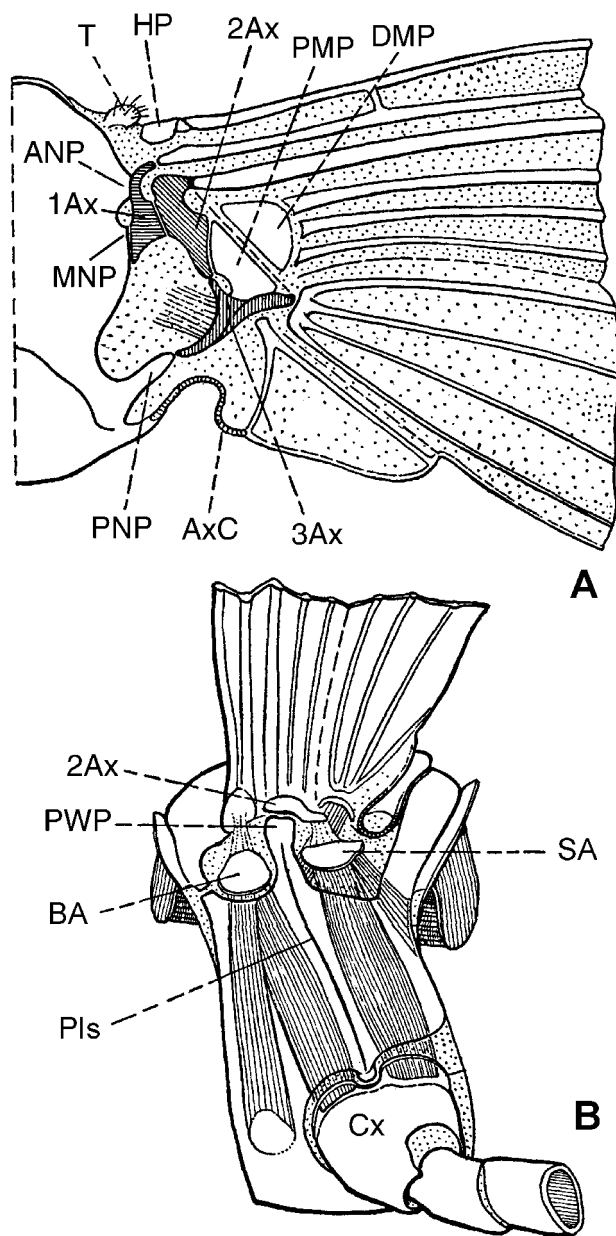
The following chapters provide a short summary of the wing base morphology of Ephemeroptera, Odonata and Neoptera and also of earlier assumptions to the homology of wing base sclerites and their musculature before the interpretation is given.

#### 4.2.1 The wing base of Neoptera (Figs. 67, 70–72, 84, 85)

In the ground plan of Neoptera the wing base is composed of the tergal anterior notal wing process (ANP), the median notal wing process (MNP), and the posterior notal wing process (PNP). Furthermore, there are three axillary sclerites (1Ax, 2Ax, 3Ax), the proximal median plate (PMP) and the distal median plate (DMP) in the wing base of Neoptera (BRODSKY 1994, SNODGRASS 1935). The PMP as well as the DMP are sclerotised in both the dorsal and ventral layer of the wing membrane, which alludes to a wing vein origin.

The first axillary sclerite (1Ax) articulates with the ANP and, if present, also with the MNP proximally and with the second axillary sclerite (2Ax) distally. The 1Ax is sclerotised only in the dorsal layer of the wing membrane, which alludes to its tergal origin. It is directed approximately parallel to the longitudinal axis of the insect body. Furthermore, it is divided into the anterior head and neck and the posterior body. The head articulates with the sub-costal vein.

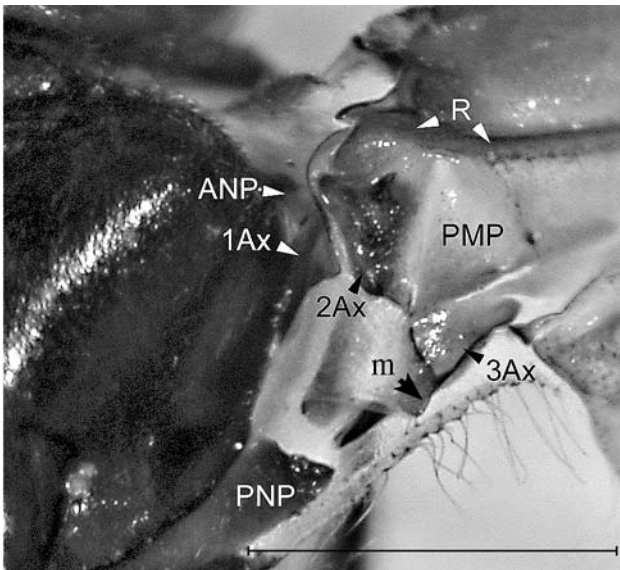
The 2Ax articulates proximally with 1Ax, distally with the proximal median plate (PMP), and posteriorly with the 3Ax. The anterior part of the 2Ax is also connected to the base of the anterior radial vein. The 2Ax is sclerotised



**Fig. 84.** Schematic representation of the neopterous wing base (modified after SNODGRASS 1935: figs. 122, 129). – **A.** Dorsal view. **B.** Lateral view.

both in the dorsal and ventral layer of the wing membrane. A proximo-ventral process of the 2Ax articulates with the pleural wing process (PWP).

The 3Ax articulates, in addition to the articulation with the 2Ax and the PMP, also with the posterior notal wing process (PNP). It is also connected to the anal veins and the jugal veins of the wing. Furthermore, it is sclerotised in both the dorsal and ventral layer of the wing membrane. The 3Ax is orientated acute-angled (about 60°) or



**Fig. 85.** *Leuctra hippopus*, right fore wing base. – m = attachment of the flexor muscle of 3Ax. – Scale: 0.5 mm.

approximately perpendicular to the longitudinal insect body axis (BRODSKY 1994, SNODGRASS 1935).

Further wing base elements in the ground plan of Neoptera are the basalar (BA) anterior to the pleural wing process (PWP) and the subalar (SA) posterior to the PWP (BRODSKY 1994, HÖRNSCHEMEYER 2002, SNODGRASS 1935).

In previous contributions it is assumed that in the ground plan of Neoptera only the 3Ax serves as dorsal attachment of a muscle running to the pleurum (e.g. SNODGRASS 1935). Both the first and third axillary sclerite are provided with such a muscle. A wide but flat muscle (Fig. 125) inserts on the proximal part of the 1Ax and proceeds to the pleural ridge in Plecoptera (WILLKOMMEN & HÖRNSCHEMEYER 2007). The proximal part of the 3Ax is the dorsal attachment of a flat muscle running to the episternum (t-p 13 sensu MATSUDA 1970). This muscle together with the wing base morphology (e.g. axillary fold- and flexion-lines, shape of axillary sclerites) enables the Neoptera to fold their wings horizontally over the abdomen. In several Neoptera a second muscle occurs, which is stretched between the 3Ax and the upper part of the pleural ridge (t-p 14). According to BRODSKY (1994) both muscles are present in insects which fold their wings over the back in a roof-like position (with exception of Psocoptera) and are also present in Diptera (which do not fold their wings in such manner), but insects, which fold their wings flat have only one of the muscles attached to the 3Ax. Nevertheless, Plecoptera have both muscles attached to the 3Ax. This suggests that the presence of two muscles attached to the 3Ax is most likely a ground plan character of Neoptera. Moreover, both the ANP and the PNP are

each provided with a muscle that proceeds to the pleurum.

In addition, there are flight muscles associated with the basalar and the subalar: at least two basalar muscles (basalar-trochanteral and basalar-coxal muscle) and one or two subalar muscles (subalar-coxal and subalar-pleural muscle) are present in the Neoptera.

#### 4.2.2 The wing base of Odonata (Fig. 58)

The morphology of pterothorax, wing base, and venation of Odonata were examined by different authors (e.g. ASAHINA 1954; BECHLY 1996; HATCH 1966; PFAU 1986, 1991; RIEK & KUKALOVÁ-PECK 1984; TANNERT 1958). The two plates in the wing base of Odonata are termed differently in these publications (Tab. 2). The anterior plate is either the humeral plate (sensu SNODGRASS 1935 and ASAHINA 1954) or costal plate (sensu TANNERT 1958). The posterior plate is termed axillary plate by SNODGRASS (1935) and ASAHINA (1954) or radio-analis plate by TANNERT (1958).

The wing base is articulated with the thoracic tergites by the anterior humeral plate and the posterior axillary plate. The humeral plate is sclerotised only dorsally and articulates with the anterior pleural process. The humeral plate of Odonata is supposed to be a product of a secondary fusion of the humeral plate of Neoptera with the base of the costal vein (TANNERT 1958). SNODGRASS (1935), however, does not assume such a secondary fusion but rather an enlargement of the humeral plate alone. Based on his morphological data ASAHINA (1954) supposed that a part of the basalar is fused with the humeral plate and that a part of the subalar is fused with the axillary plate of the wing base.

BRODSKY (1994) assumed – without arguments – that only t 14 of Odonata can be homologised to the respective muscles of other Pterygota and that the humeral plate contains at least a part of the basalar.

The radial and the anterior medial veins originate from the dorsal part of the axillary plate. The sector of the medial vein (except the anterior medial vein), the cubitus and the analis originate from the ventral part of the axillary plate (TANNERT 1958). The posterior pleural wing process of Odonata articulates with the anterior part of the axillary plate. There are two short muscles stretched between the postero-internal side of the axillary plate and the membrane just posterior to the pleural wing process (ASAHINA 1954).

**Tab. 2.** Terminology of the wing base sclerites of Odonata.

Position	SNODGRASS 1935, ASAHINA 1954	TANNERT 1958
anterior plate	humeral plate	costal plate
posterior plate	axillary plate	radio-analis plate

#### 4.2.3 The wing base of Ephemeroptera (Figs. 2, 3, 27–29, 40–42, 94, 95)

The most conspicuous element in the wing base of Ephemeroptera is the basal plate (BP). Its proximal part is flat and articulates with the pleural wing process (PWP). Furthermore, three sclerites are present lying proximal to the BP. The first free wing base sclerite (s1) articulates proximally with the anterior notal wing process (ANP) and distally with the second wing base sclerite (s2). It is sclerotised only in the dorsal layer of the wing membrane and there is no muscle attached to it. The second sclerite (s2) is proximally connected to the s1, distally to the BP and posteriorly to the s3. It is sclerotised only in the dorsal layer of the wing membrane and has a proximal process, which is bent inwards. In basal Ephemeroptera two muscles are attached to s2. The first muscle is running to the pleurum and the second one is attached to the furca. The third wing base sclerite is tightly associated with the BP and is sclerotised in both dorsal and ventral layer of the wing membrane. Posteriorly it articulates with the posterior notal wing process (PNP). The s3 is provided with a short muscle running to the pleurum next to the PWP.

#### 4.2.4 Current hypotheses on the homology of wing base sclerites (Figs. 86–88)

Hitherto several authors (BEKKER 1954; BRODSKY 1970, 1974, 1994; GRANDI 1947; KLUGE 1994, 2004; KUKALOVÁ-PECK 1974a, 1974b, 1978, 1983, 1985, 1987; KUKALOVÁ-PECK & BRAUCKMANN 1990; MATSUDA 1956, 1970; TSUI & PETERS 1972; WILLKOMMEN & HÖRNSCHEMEYER 2007) proposed different hypotheses for the homology of wing base sclerites and the associated muscles between the basal pterygote taxa.

GRANDI (1947) examined *Ephemerella* sp. (Ephemerellidae), *Ephemerella* sp. (Ephemeridae), *Ecdyonurus* sp. (Heptageniidae), *Choroterpes* sp., *Habrophlebia* sp. (Leptophlebiidae), several Baetidae, *Oligoneuriella* sp. (Oligoneuriidae) and *Caenis* sp. (Caenidae). She assumed that the wing base sclerites of Ephemeroptera are pseudopteralia without homology to the wing base sclerites of other Pterygota. The three pseudopteralia are the pseudopteralia prossimale (primo; s1), the pseudopteralia mediale (secondo; s2) and the pseudopteralia distale (terzo; proximal base of the basal plate).

KLUGE (1994: 557, 2004) suggested that there is no agreement on homologisation of these sclerites with the axillary sclerites of Neoptera. Therefore, he termed the first sclerite (s1) of the ephemeropteran wing base anterior axillary sclerite (term used by BEKKER 1954: aAx), the second sclerite (s2) was named the middle axillary sclerite, and the third sclerite (s3) was termed the posterior articulatory process.

KUKALOVÁ-PECK (1983, 1987, 1998) assumed that the

wing articulation, namely the axillary sclerites, originated from an additional part of the pleura, which articulated above the subcoxa. In her interpretation the wing base of the pterygote ground plan consists of 32 wing base sclerites, which are arranged in eight rows. The sclerites are termed the proxalaria, the axalaria, the fulcalaria and the basivenales (from proximal to distal). She assumed that the proxalaria originated from the epicoxa and the axalaria and the fulcalaria probably originated from the wing membrane.

MATSUDA (1956) examined the thorax of *Siphonurus columbianus* (Siphonuridae) and ascertained that the ordinary three axillary sclerites are clearly recognisable. Each sclerite maintains the typical topographical position compared to the other axillary sclerites and to the anterior and posterior notal wing process. He further (l.c., p. 96) mentioned that GRANDI (1947) “failed to recognize the presence of the third axillary sclerite in a series of species she examined”. The sclerite homologous to the 3Ax of Neoptera should be the additional sclerite (s5) in the wing base of several mayflies, e.g. *Siphonurus columbianus*, *S. aestivalis* (Siphonuridae) and *Rhithrogena semicolorata* (Heptageniidae) and the absence of the s5 would be secondary. Furthermore, he homologised the s1 and the s2 of the ephemeropteran wing base with the 1Ax and the 2Ax of the neopteran wing base (Fig. 86). The muscle that is attached to the posterior part of the second free sclerite (s2) and running to the pleurum is homologised by him with the muscle that inserts on the 3Ax in Neoptera. The axillar-furcal muscle (Ax.Fm sensu KLUGE 1994) as well as the loss of the relationship between the wing base sclerites and the wing veins is according to this author peculiar to the mayflies.

TSUI & PETERS (1972) examined the thorax of selected genera of the Leptophlebiidae. In five genera they found two axillary sclerites and only in *Aprionyx* three. The homology that is proposed for the sclerites s1 (1Ax) and s2 (2Ax) is the same that is suggested by MATSUDA (1956). The third axillary sclerite in *Aprionyx* (see above) is mentioned only in the text (equivalent to s5) but not in their drawings. The authors described a muscle running from the subalare to the median plate (equivalent to basal plate, BP). “The similar function of this muscle between the Ephemeroptera and other pterygotes is considered by MATSUDA (pers. comm.) as convergent evolution.” (TSUI & PETERS 1972: 340).

BEKKER (1954) assumed that the movements of the wings are regulated via five sclerites. Three of them are located between the tergum and the wing namely the anterior axillary sclerite (aAx – equivalent to s1), the first axillary sclerite (1Ax – equivalent to s2) and the fourth axillary sclerite (4Ax). There are two additional sclerites, the second axillary sclerite (2Ax – equivalent to the whole BP) and the third axillary sclerite (3Ax – equivalent to s3), that

correspond to the 2Ax and the 3Ax of Neoptera. He described a bipartite muscle with one part running from the 3Ax to the pleurum and a second part that is attached to the 2Ax (equivalent to BP).

Two publications of BRODSKY (1970, 1974) presented contradictory conclusions (Figs. 87, 88). According to BRODSKY (1970) the first wing base sclerite (s1) of Ephemeroptera is homologous with the ANP of Neoptera, s2 is assumed as homologous to the first axillary (1Ax of Neoptera) and the homologous part to the 2Ax of Neoptera is fused with the basal plate in Ephemeroptera. The third wing base sclerite (s3) should be homologous with the 3Ax of Neoptera. Given the hypothesis of BRODSKY (1974) the s1 of Ephemeroptera is homologous with the 1Ax of Neoptera, the s2 is assumed as homologous with the 2Ax and the s3 should be the homologous structure to the 3Ax of Neoptera. The additional sclerite (s5) of the ephemeropteran wing base is assumed to be a median notal wing process (MNP), which is not homologous with the MNP of Neoptera.

#### 4.2.5 Homology of the wing base sclerites and axillary muscles (Figs. 89, 91)

GRANDI (1947) assumed that the wing base elements of Ephemeroptera are not homologous with that of other Pterygota. This implies that the wings and wing base sclerites must have developed twice and independent from the other Pterygota. This assumption is, however, rather unlikely. KLUGE (1994, 2004) gives no interpretation of wing base homology.

##### First free wing base sclerite – s1

The first free wing base sclerite (s1; Figs. 3, 29, 41, 94–95, 107) in the mayfly wing base is usually characterised as follows: A narrow, triangular sclerite, sclerotised only in the dorsal layer of the wing membrane, articulates proximally with the anterior part of the notum and distally with s2; in relation to the tergum it is orientated obliquely to the longitudinal body axis. It is not directly associated with any wing vein. No muscle is attached to it, except in *H. confusa* (Leptophlebiidae) where a slender and indistinct tendon diverges from the main part of BA.Cm and is attached to the s1 (own observation). In the examined Baetidae and also in Oligoneuriidae (*Elassoneuria* sp., *Oligoneuriella rhenana*) the s1 is rather large in relation to the body size, in *Habroleptoides confusa* (Leptophlebiidae) and *Caenis rivulorum* (Caenidae) it is inconspicuous, in *H. confusa* it is not distinctly differentiated, and in *C. rivulorum* (Baetidae) it is narrow (own observations).

MATSUDA (1956) assumed that the s1 is the first axillary sclerite because a muscle is attached to this sclerite and to the coxal process ventrally. Furthermore, he wrote that the basalar-coxal muscle is absent in *Siphonurus colum-*

*bianus*, though MAKI (1938) described this muscle. The two mentioned muscles (axillary-coxal and basalar-coxal muscle) are, however, one and the same muscle in real terms. The problem of the different interpretations of this muscle is the dorsal attachment. At first sight, the muscle seems to be attached to the s1, but on closer examination one can see that it is attached to a dorsal sclerite directly anterior to the s1 (Fig. 11) (exception *Habroleptoides confusa*, see above).

The first axillary sclerite (1Ax) in Plecoptera is provided with a muscle running to the pleurum (Fig. 125). Furthermore, between the first and the second axillary sclerite runs a convex axillary flexion-line (WOOTTON 1979). Neither the first nor the second fact applies to the s1 in the ephemeropteran wing base.

BRODSKY (1970) assumed that the s1 (sclerite A in his paper) is likely to be the ANP. He examined the final instar nymph of the mayfly because it “presents a clearer picture”. According to him, the axillary apparatus is represented by five elements short before the moult to the subimago, and the structure of the axillary apparatus of the most specialised forms (Caenidae) suggests that the s1 is homologous with the anterior notal wing process. Probably, this is the right interpretation because the ANP of the Plecoptera (Figs. 67–70, 72, 73) lies in the same position as the s1 in Ephemeroptera. It is a concave and clearly demarcated but integral part of the stonefly tergum (WILLKOMMEN & HÖRNSCHEMEYER 2007). In contrast to BRODSKY (1970), BRODSKY (1974) assumes that the s1 is the first axillary sclerite. Consequently, he ascertains that the lack of a connection between the 1Ax and the subcostal vein is specific to mayflies. But the latter is irrelevant if one assumes that s2 is homologous with 1Ax of Neoptera (see below).

Thus, the orientation, sclerotisation and the (lacking) connection to the wing veins indicate that the s1 is a detached part of the ANP rather than the homologous part to the first axillary sclerite (1Ax) of Neoptera.

##### Second free wing base sclerite – s2

The 1Ax of Neoptera is characterised by the following: It is sclerotised only in the dorsal layer of the wing membrane, is connected to Sc and provided with a muscle running to the pleurum, and is characterised by a convex axillary flexion-line lying distally.

The second free wing base sclerite (s2; Figs. 3, 41, 94–95, 107) of the ephemeropteran wing base shows characteristics that are also known from the 1Ax of the Neoptera: It is orientated approximately parallel to the longitudinal body axis, it is anteriorly connected to the subcostal vein, it is distally also connected to the 2Ax and the 3Ax (see below). Furthermore, in *Siphonurus aestivalis*, a basal mayfly, the s2 is provided with two muscles (Ax.PmI, Ax.Fm), which is a plesiomorphic condition following MATSUDA (1970). The Ax.PmI is present only in

comparatively basal mayflies, besides *Siphonurus aestivalis* (own observation) also in *Parameletus chelifer*, *Ametropus eatoni*, and *Metretopus norvegicus* (according to BRODSKY 1974), and *Siphonurus columbianus* (according to MATSUDA 1956). Ax.Fm is present in most of the examined mayflies and is probably homologous with the muscle 45 of *Lepisma saccharina* (Zygentoma: Lepismatidae) (MATSUDA 1970).

A muscle running from the 1Ax to the pleural ridge is also present in Plecoptera (Fig. 125, tpm 49b). In difference to Ephemeroptera this muscle inserts nearly on the whole length of the body of the first axillary sclerite (1Ax) in Plecoptera whereas in *S. aestivalis* (Siphonuridae) it arises only from one point of the axillary sclerite.

MATSUDA (1956) assumed that the muscle Ax.PmI (sensu KLUGE 2004) shows a striking similarity to the wing flexor muscle in other pterygote insects, which usually inserts on the third axillary sclerite. However, its dorso-ventral course, its insertion not on the posterior but on the middle part of the wing base, precludes a function as a wing flexor. MATSUDA's interpretation resulted from the fact that he neither recognised the separate sclerite that is directly associated with the basal plate (BP) of the wing (lying in the same position as the 3Ax in Neoptera, see below) nor the muscle that is attached to it.

MATSUDA (1956) described a muscle running from the posterior notal process (PNP) to the base of the median plate (basal plate, BP). This muscle is present in nearly all examined Ephemeroptera but it is attached to the third wing base sclerite (s3) running to the anterior part of the subalare (or the pleurum). Sometimes this muscle is bipartite and the second part runs from the s3 to the basal plate (e.g. in *Ephoron virgo*), but not to the PNP as MATSUDA assumed.

TSUI & PETERS (1972) also described the above-mentioned muscle. According to their description the muscle is attached to the median plate running to the subalare. But presumably the right dorsal attachment is not the median (or basal) plate but rather the (not identified) third wing base sclerite (s3). Furthermore, they assumed that this muscle serves to transmit the pull exerted by the subalar muscles in depressing the wings. Nevertheless, according to a personal communication of MATSUDA, the authors did not conclude a homology between Ax.PmS and the muscle of the 3Ax of Neoptera, but regardless of a similar function and position of these muscles assumed their convergent development in Ephemeroptera and Neoptera. MATSUDA (1956) tried to homologise s5 with 3Ax and Ax.PmI with the wing flexor of Neoptera with an unlikely and not parsimonious argumentation. Thus, he did not recognise the similarity of the muscle, which is described by TSUI & PETERS (l.c.) and the muscle attaching to the 3Ax of Neoptera.

The s2 is partly the same as the sclerite B of BRODSKY

(1970), which morphologically and functionally corresponds to the 1Ax of Neoptera.

The insertion of a pleural muscle, the connection to Sc, the sclerotisation in the dorsal wing membrane, and the convex axillary flexion-line posterior to s2 are characters that point at a homology of s2 with the first axillary sclerite (1Ax) of Neoptera.

#### Proximal part of BP

The 2Ax of Neoptera is characterised by the following: It is sclerotised in both dorsal and ventral layer of the wing membrane, no muscle is attached to it (in the ground plan of Neoptera), ventrally it articulates with the PWP, it has a convex axillary flexion-line lying proximally, and is connected to the anterior radial vein, PMP and 3Ax.

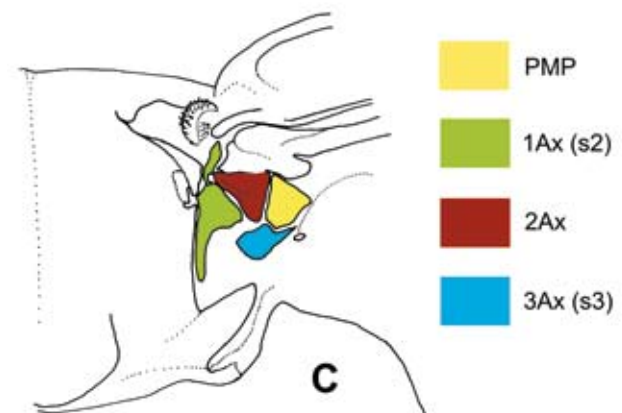
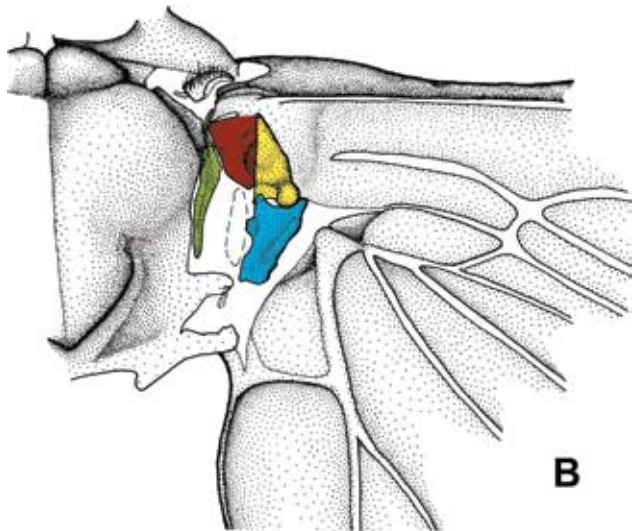
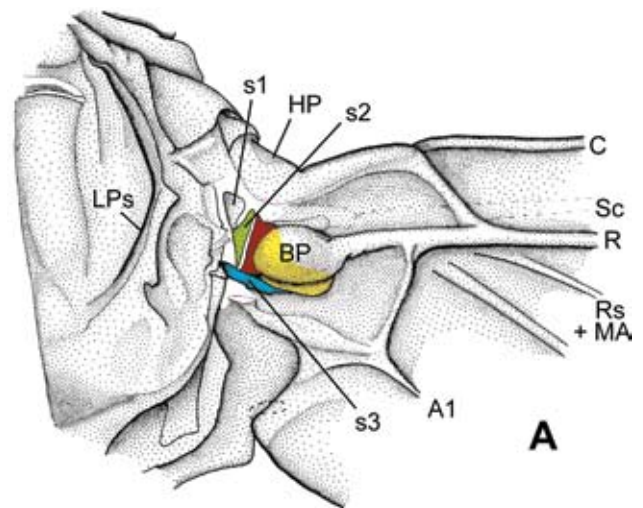
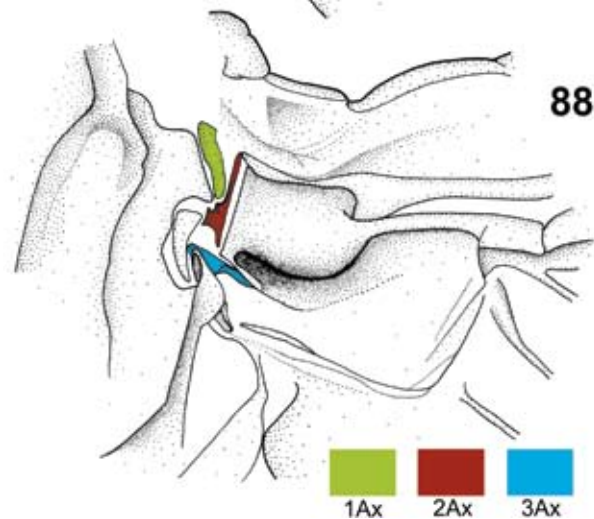
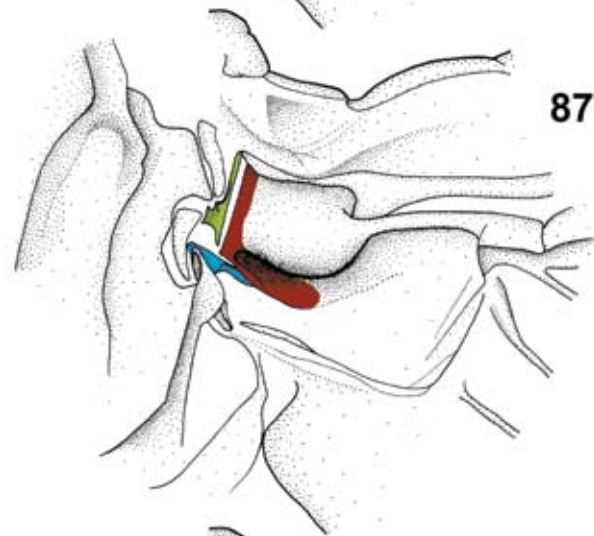
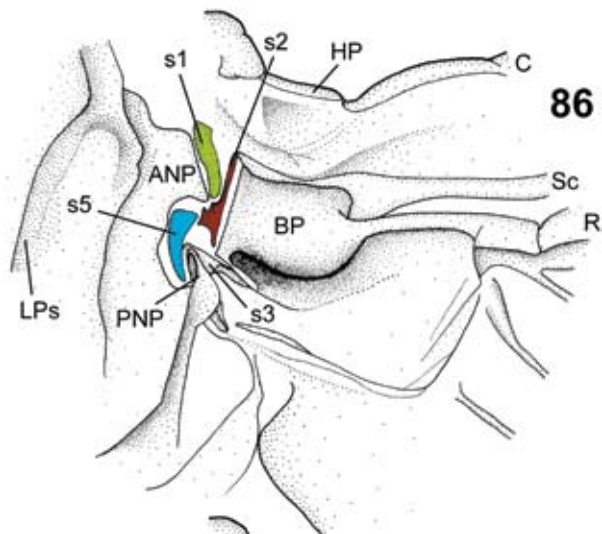
A homology of the proximal part of the basal plate (BP) of Ephemeroptera with 2Ax of Neoptera was assumed by BRODSKY (1970: 185) who wrote: "The state of the second axillary sclerite in a mayfly nymph gives an objective representation of its shape (boomerang-shaped) and its connection with the remaining sclerites. In the imago the second axillary sclerite is fused with the median plate ...", but no further morphological grounds for a homology are given. Later he (BRODSKY 1974) assumed, contradictory to his earlier view, that the loss of the connection between the 1Ax and the base of the subcostal vein is a specific character of Ephemeroptera since he suggested that the s1 (instead of s2 as proposed in his previous work) is homologous with the 1Ax of Neoptera. Furthermore, he assumed in his contribution of 1974 that the s5 in the wing base of several mayflies may be designated the median notal process that is not homologous with the median notal process of other orders, since the latter is articulated with the first axillary sclerite. But none of these two points is relevant if one postulates a homology of the s2 to the 1Ax and the proximal base of the BP to the 2Ax.

The homology of the basal plate (BP) with the second axillary sclerite is also proposed by BEKKER (1954) who, however, homologised the whole BP with the 2Ax.

Based on the morphological data presented herein a homology of the proximal part of the basal plate to the 2Ax of Neoptera is evident since the first shows characteristics of the 2Ax of Neoptera.

The proximal area of the BP is sclerotised in both the dorsal and ventral layer of the wing membrane. It possesses a process (BPp; Figs. 7–8, 32–33, 43, 93, 97) on its ventral side that articulates with the pleural wing process (PWP). The proximal flat area of the BP is connected to the anterior radial vein by the basal plate. In Plecoptera the anterior part of the 2Ax is sometimes partly or completely fused with the base of the anterior radial vein. For example, in *Pteronarcys reticulata* (Pteronarcyidae), the antero-distal part of the 2Ax is fused with the base of the radial vein over about one third of the length of the 2Ax

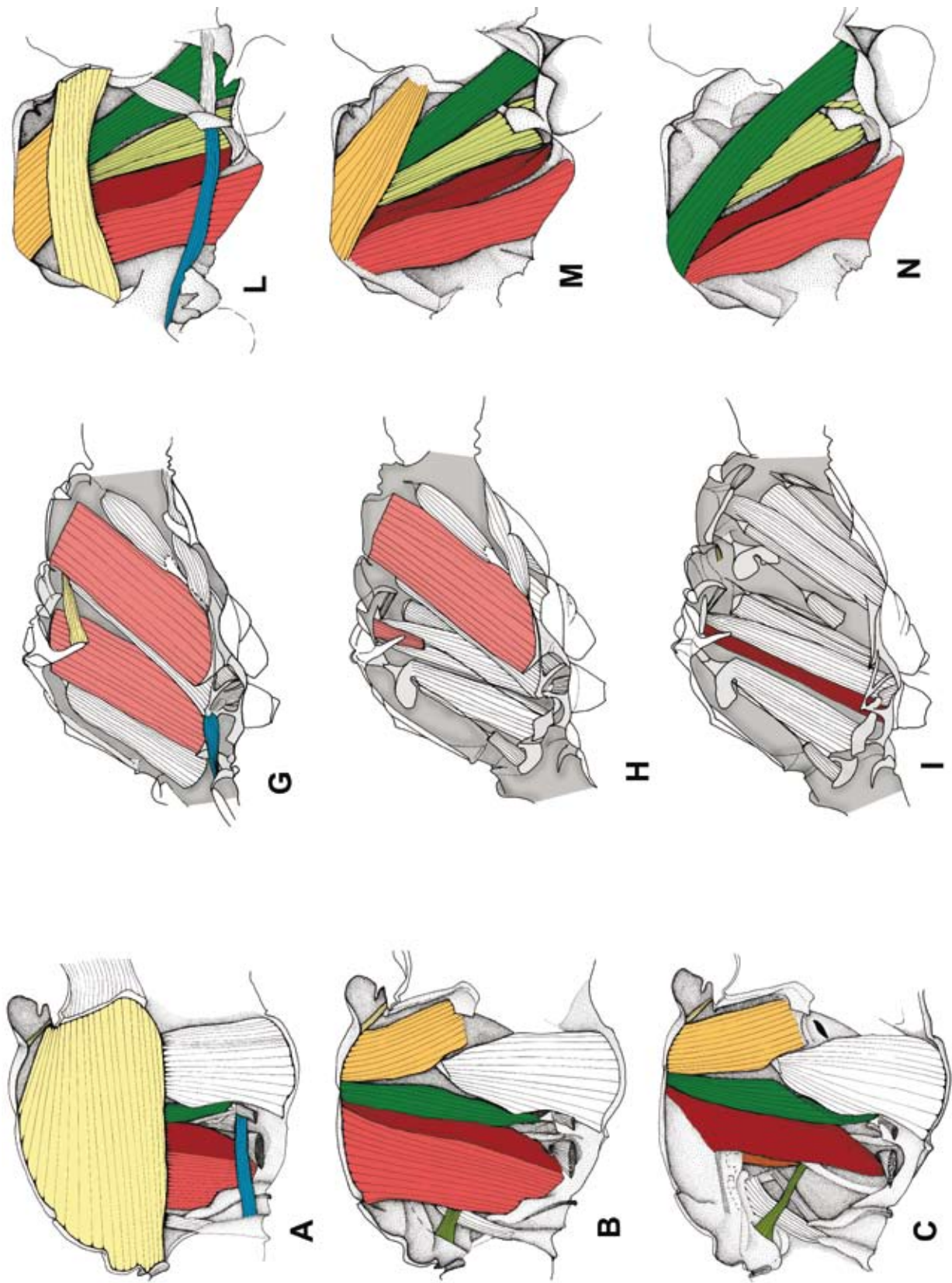


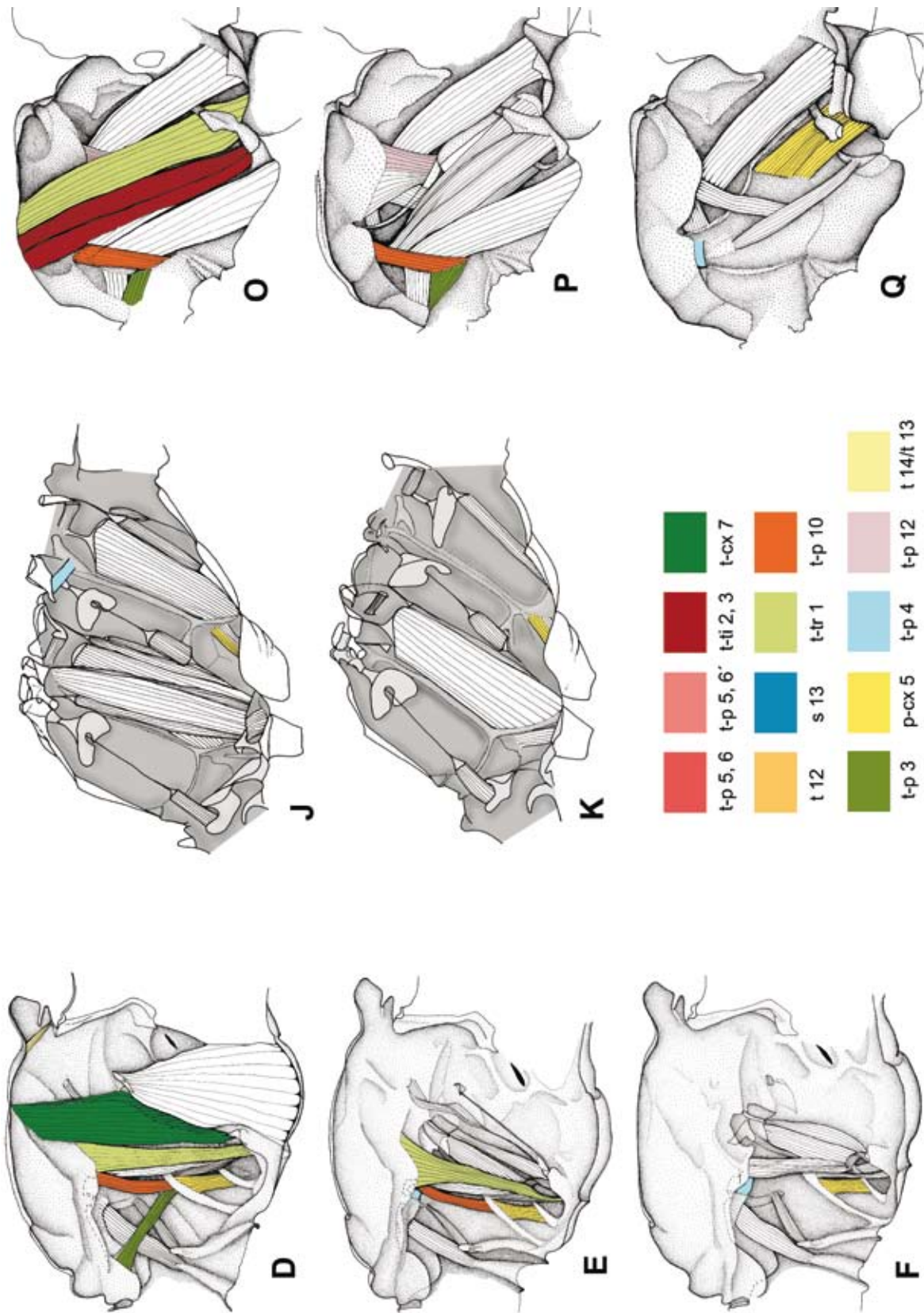


**Figs. 86–88.** Homology of the ephemeropteran wing base sclerites with the neopteran wing base sclerites (right fore wing of *Rhithrogena semicolorata*) (modified after WILLKOMMEN & HÖRNSCHEMEYER 2007: figs. 2–4). – **86.** After MATSUDA (1956). **87.** After BRODSKY (1970). **88.** After BRODSKY (1974).

**Fig. 89.** Homology of the ephemeropteran wing base sclerites with the neopteran wing base sclerites assumed in this work. – **A.** *Habroleptoides confusa* (Ephemeroptera), right fore wing. **B.** *Perlodes microcephalus* (Plecoptera), right hind wing. **C.** *Pteronarcys reticulata* (Plecoptera), right fore wing.

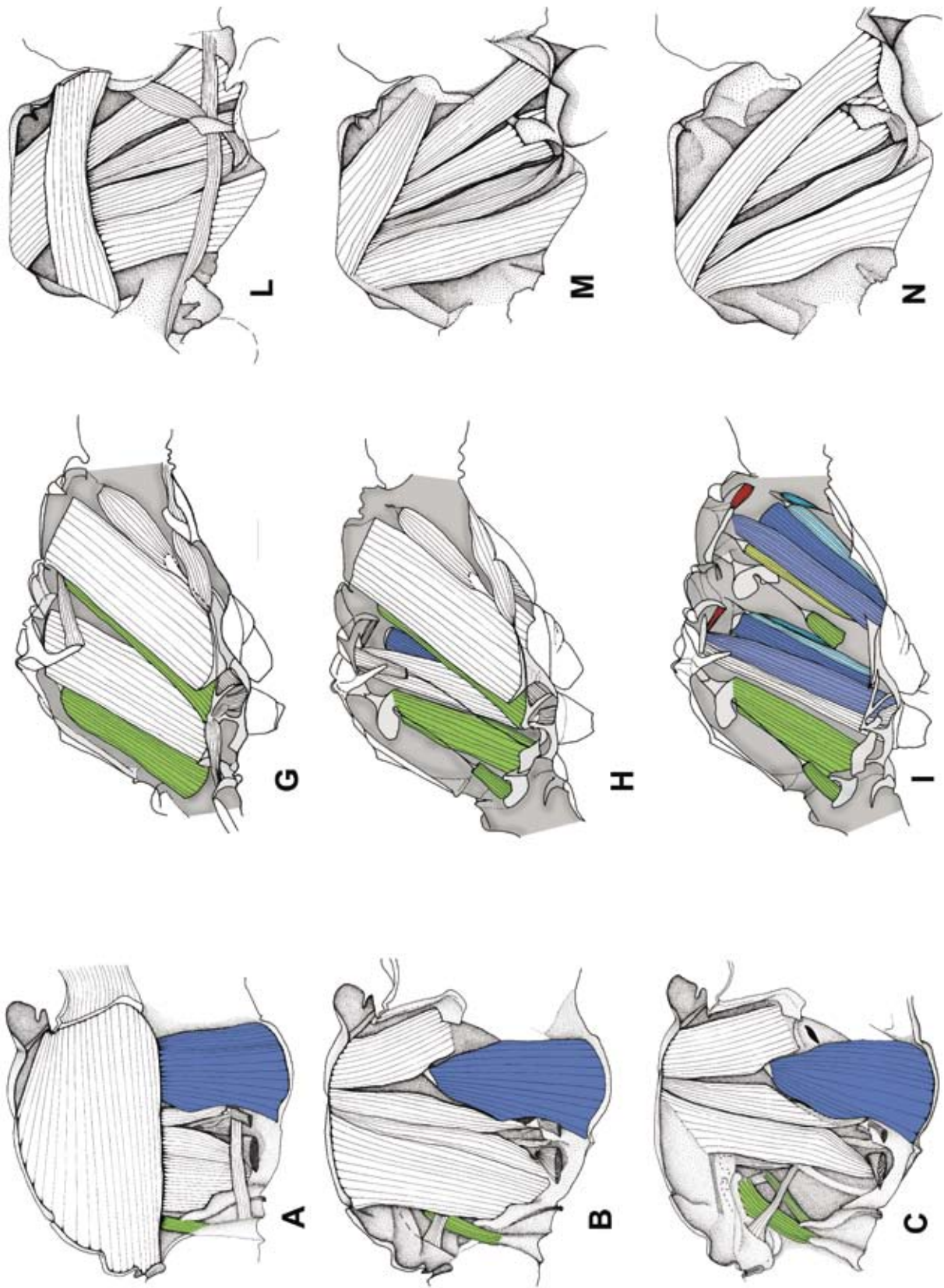


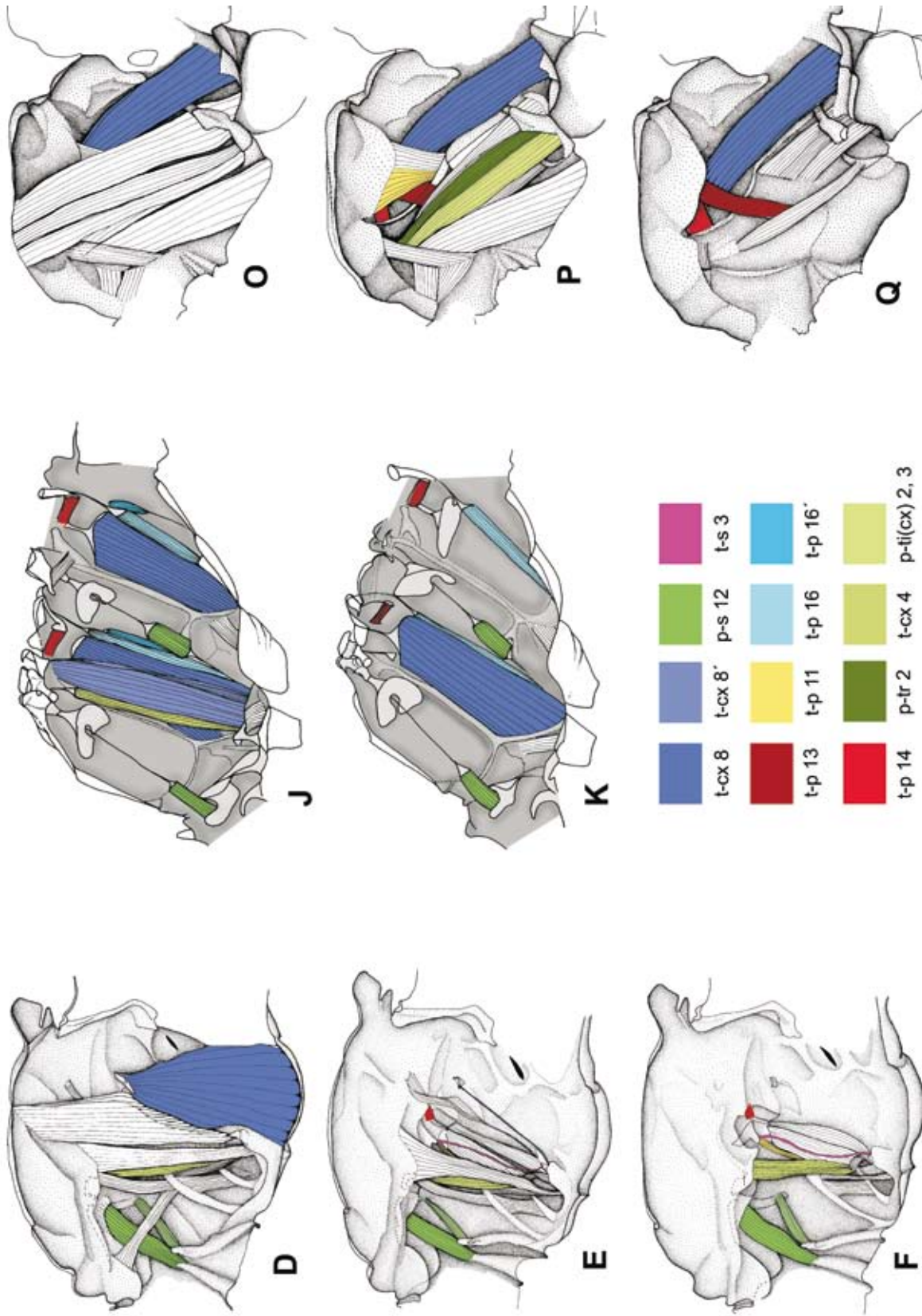




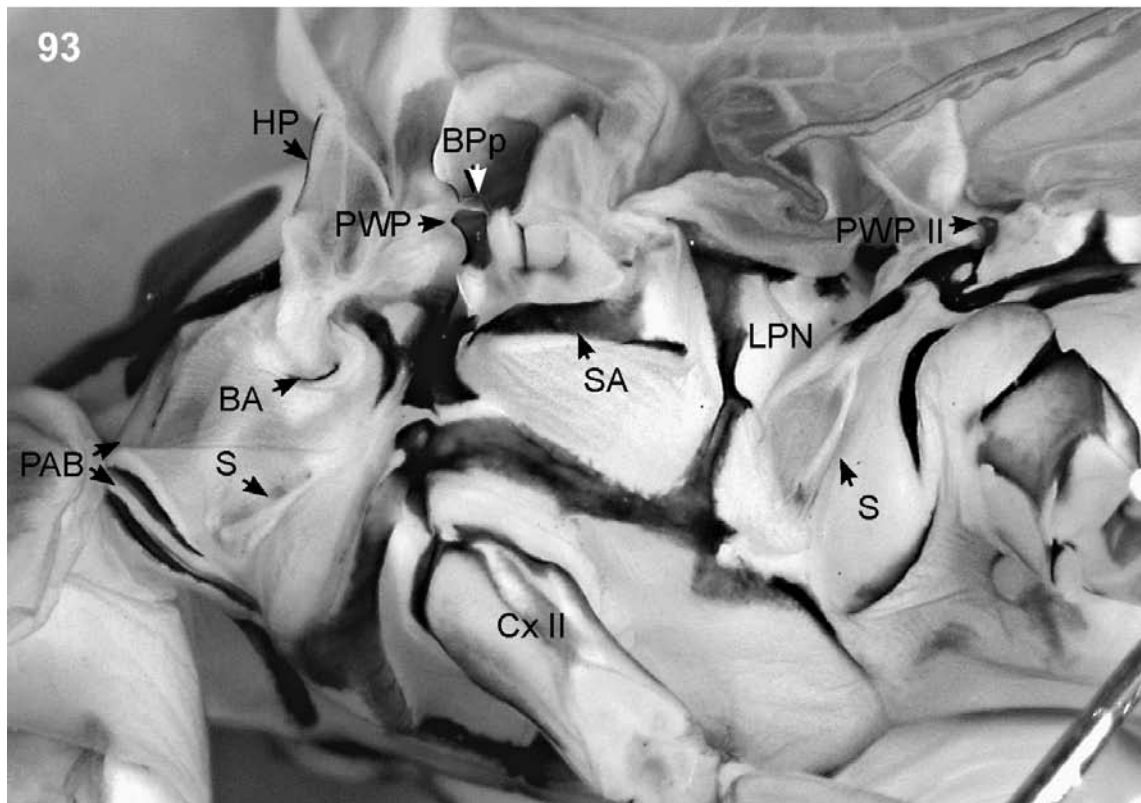
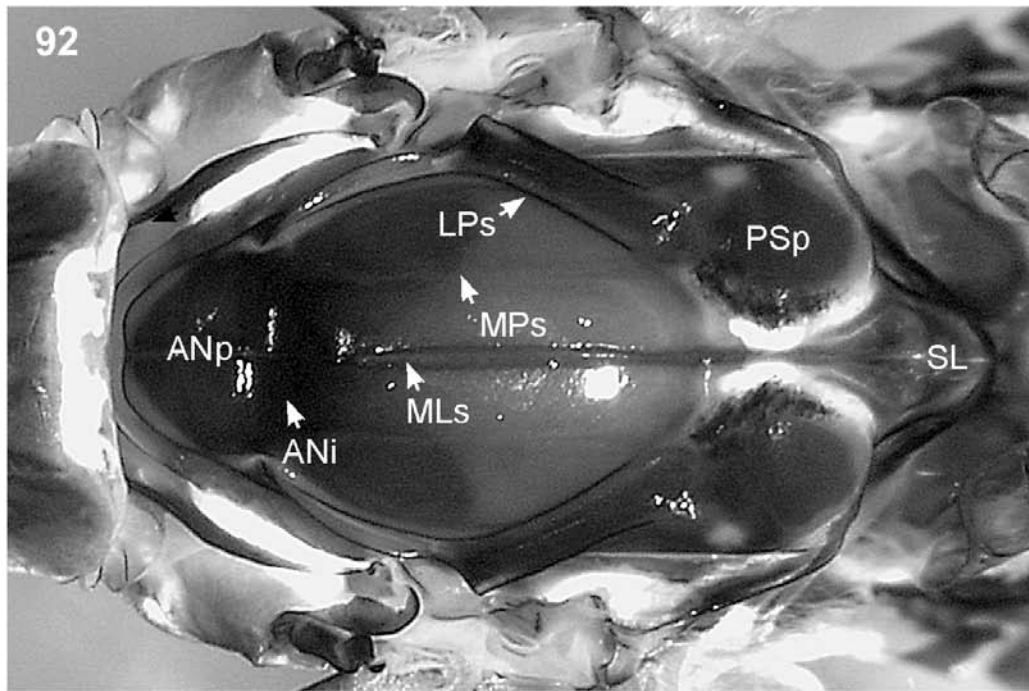
**Fig. 90.** Homology of the indirect flight muscles. – A–F. *Siphonurus aestivalis* (Ephemeroptera), mesothorax. G–K. *Symphetrum cf. striolatum* (Odonata), synthorax. L–Q. *Brachyptera seticornis* (Plecoptera), mesothorax. \* – t-p 5, 6' – homology to t-p 5, 6 assumed.





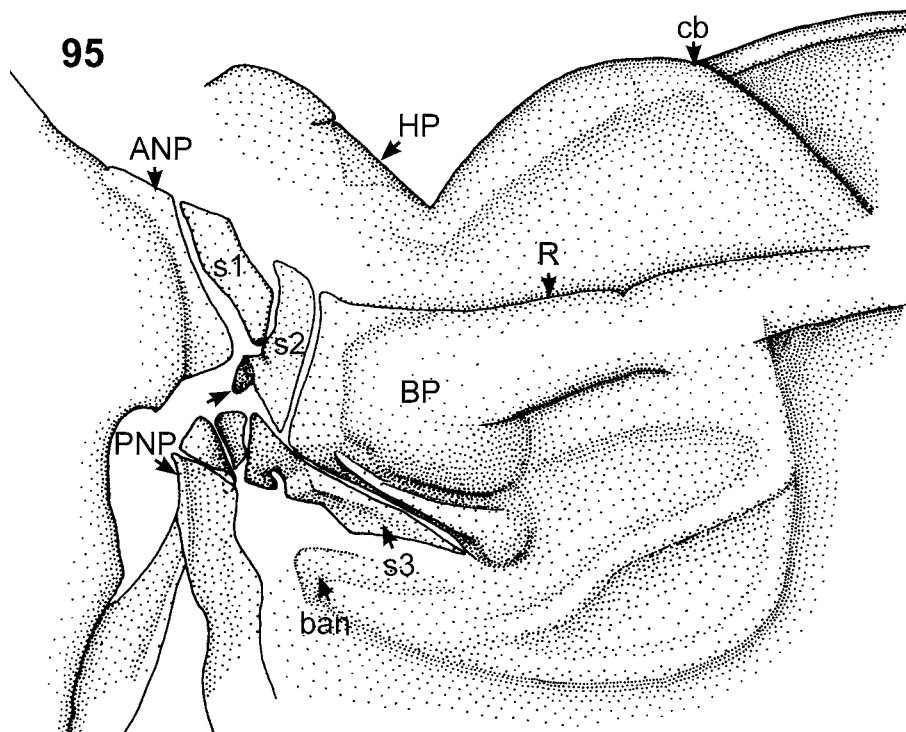
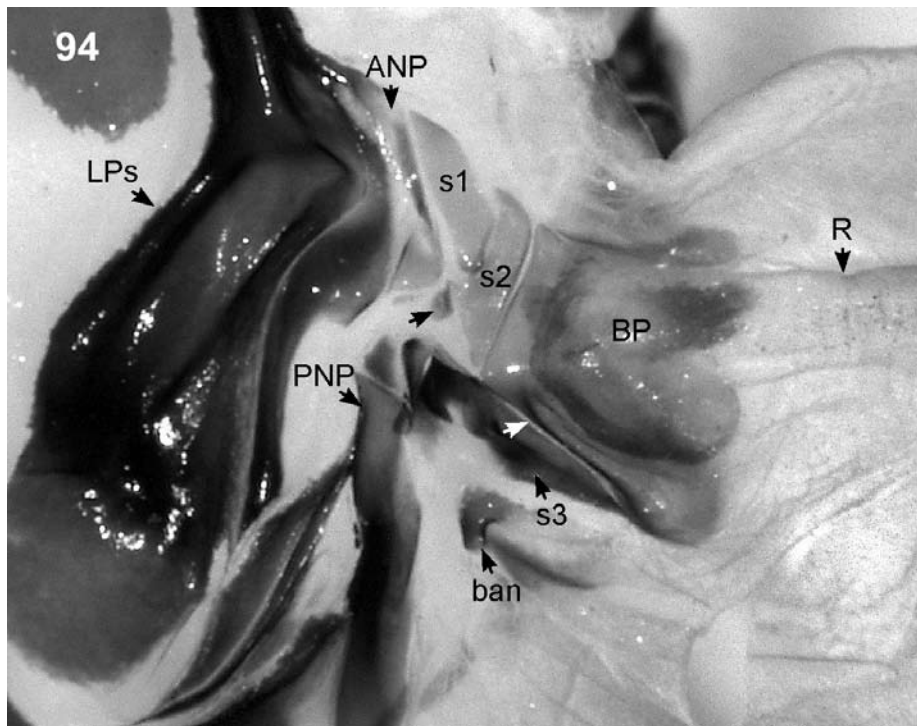


**Fig. 91.** Homology of the direct flight muscles. – **A–F.** *Siphonurus aestivalis* (Ephemeroptera), mesothorax. **G–K.** *Sympetrum* cf. *striolatum* (Odonata), synthorax. **L–Q.** *Brachyptera seticornis* (Plecoptera), mesothorax. t-cx 8' = most likely a separated part of t-cx 8; a possible homology of t-cx 4 and p-tl(cx) 2, 3 has to be further investigated; t-p 16 is also present in *B. seticornis* (compare Fig. 125, ppm 56).

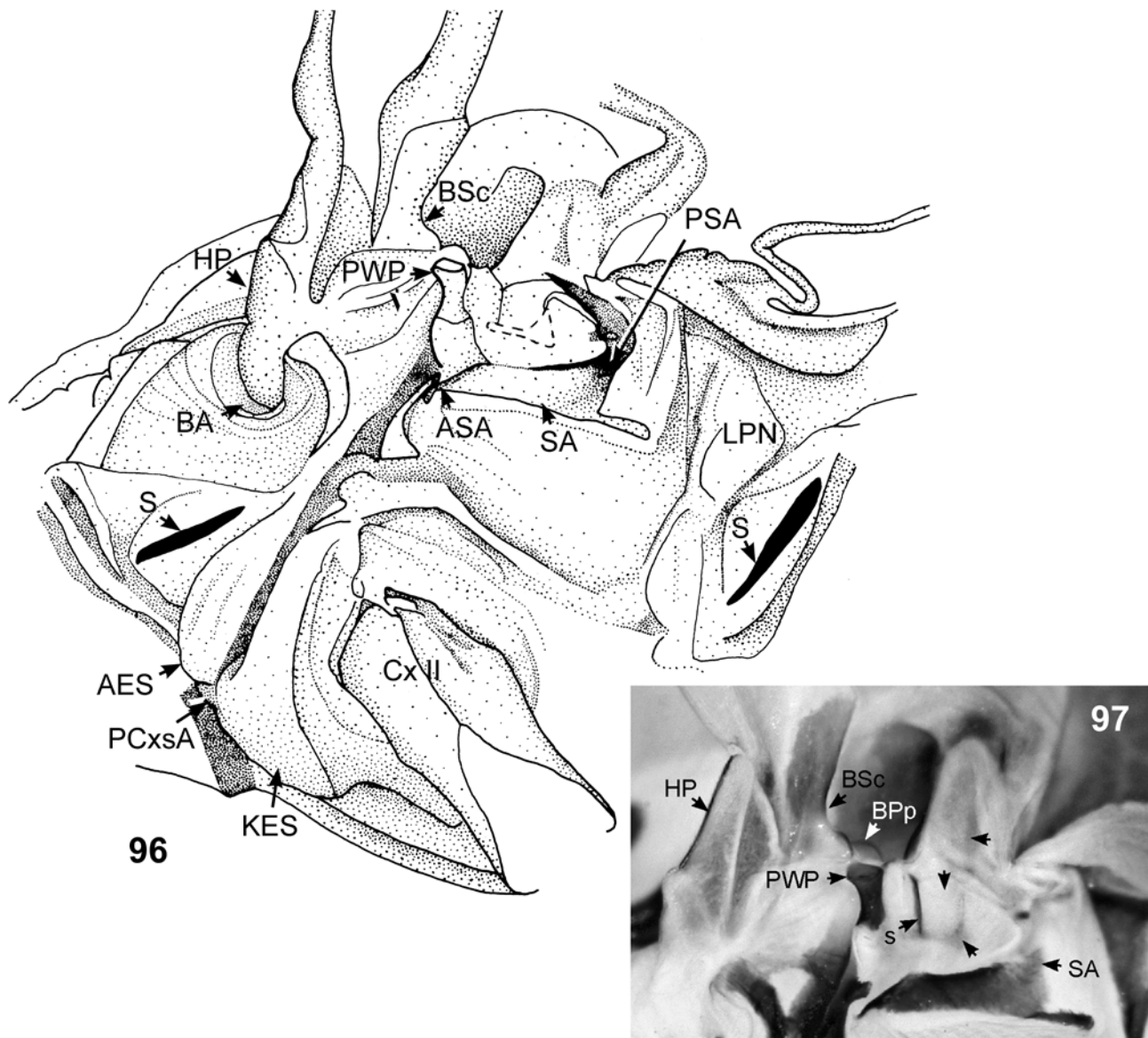


**Figs. 92–93.** *Ephemera danica*, mesothorax. – 92. ♀ imago, dorsal view (head to the left). 93. ♀ subimago, lateral view.





**Figs. 94–95.** *Ephemera danica*, ♀ subimago, wing base sclerites of fore wing. – The white arrow marks the membranous area that separates the basal plate from the third wing base sclerite (s3); the black arrow marks the proximal process of the second wing base sclerite (s2) that is bent inwards.



**Figs. 96–97.** *Ephemera danica*, ♀ subimago, mesopleurum. – **96.** Overview. **97.** Upper area. – s = anterior sclerite of the SA; the arrows, which are directed leftwards mark the s3 (3Ax) shining through the membrane; the arrow that is directed downwards marks the Ax.PmS shining through the membrane and is attached to s.

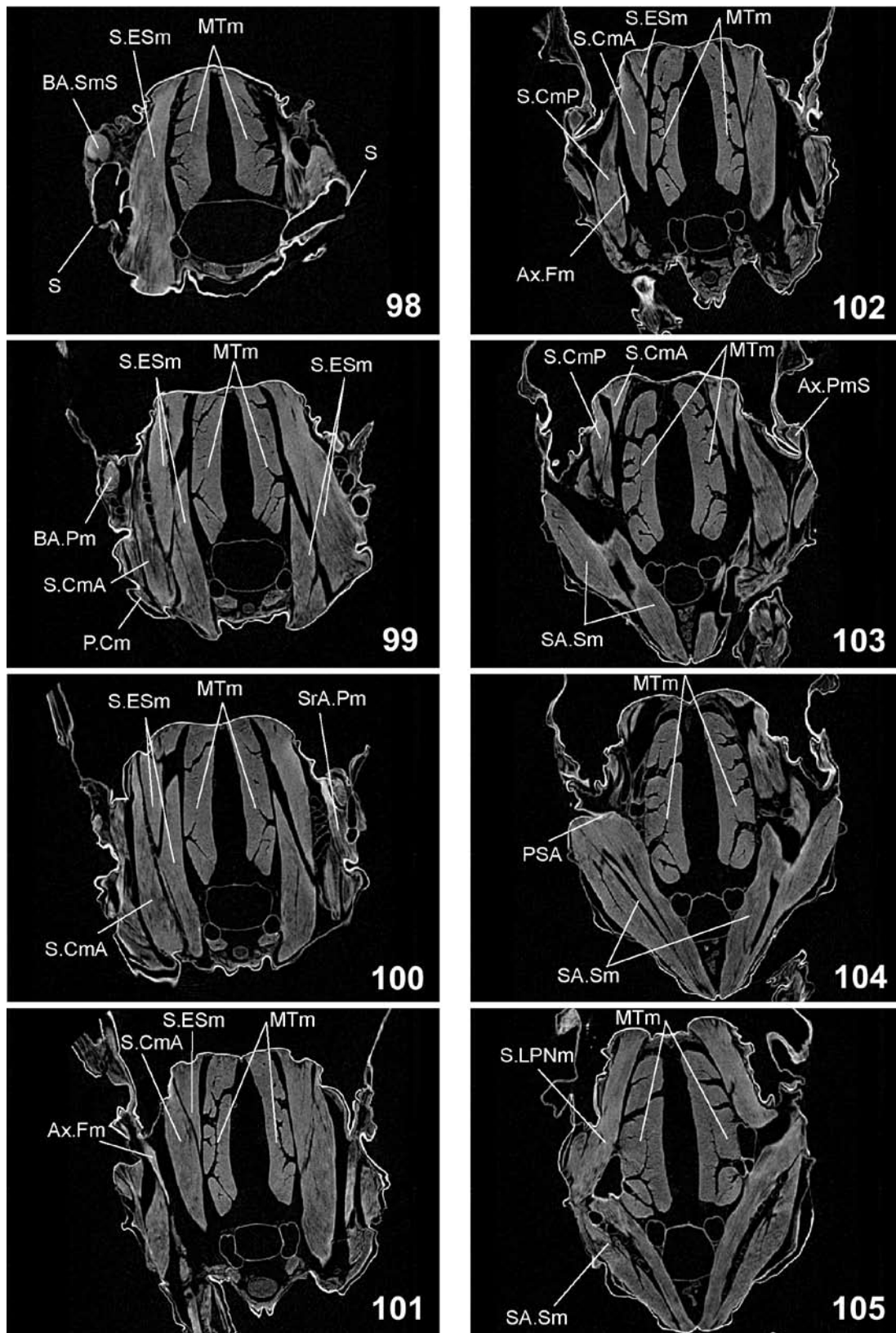
(Fig. 71). This fusion appears also in the hind wings of other Plecoptera and seems to be secondary (WILLKOMMEN & HÖRNSCHEMEYER 2007).

There is no muscle attached to the proximal part of the BP. This mirrors to the condition of the 2Ax of Neoptera. Furthermore, there is a convex flexion-line between the 1Ax and the 2Ax in Neoptera (WOOTTON 1979). This flexion-line lies between s2 and the proximal part of the basal plate in the ephemeropteran wing base. It indicates that s2 is homologous with the 1Ax and that the proximal part of the basal plate is homologous with the 2Ax of Neoptera.

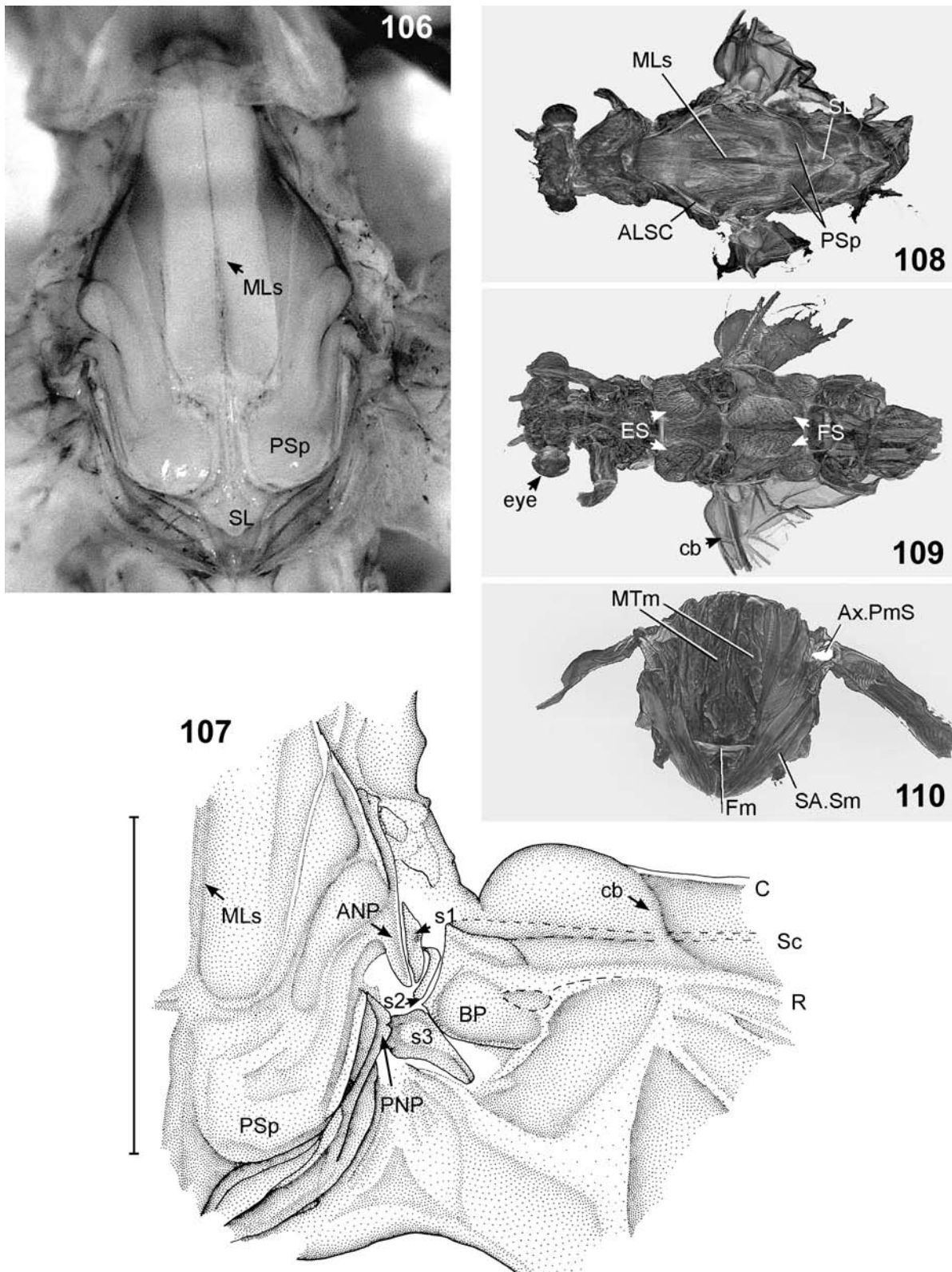
#### Third wing base sclerite – s3

The third wing base sclerite (s3; Figs. 2–3, 27–29, 41, 94–95, 107) is without a doubt the homologous part to the 3Ax of Neoptera (BEKKER 1954; BRODSKY 1970, 1974, 1994; WILLKOMMEN & HÖRNSCHEMEYER 2007). It is sclerotised in the dorsal and partly in the ventral layer of the wing membrane. In most of the examined taxa this sclerite is connected to the posterior part of the BP and it is also associated with the anal veins via the basanale (ban) and the anal brace (ab). In the examined taxa the s3 is distinctly separate in *Ephemera danica* (Ephemeridae; Figs. 94, 95). If

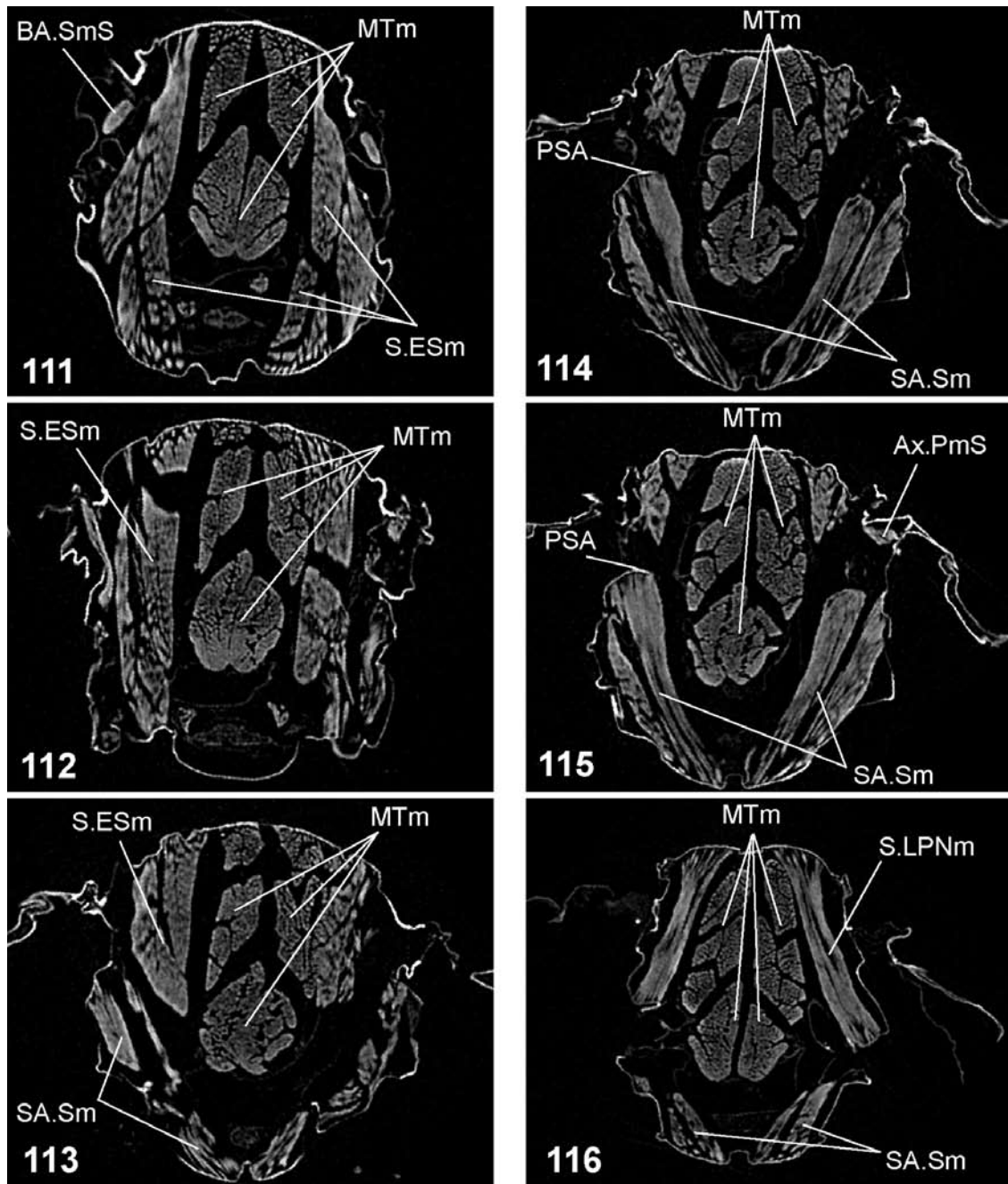




**Figs. 98–105.** *Ephemera danica*, ♀ subimago, mesothorax (μCT-data), cross sections from anterior (98) to posterior (105).



**Figs. 106–110.** *Exeuthyplocia minima*, ♂ imago. – **106.** Overview of the mesotergum. **107.** Wing base of the right fore wing. – **108–110.** Reconstruction of  $\mu$ CT-data. **108.** Thorax, dorsal view. **109.** Thorax, ventral view. **110.** Mesothorax, cross section posterior to the pleural suture, on a level with the SA and 3Ax. – Scale: 1 mm.

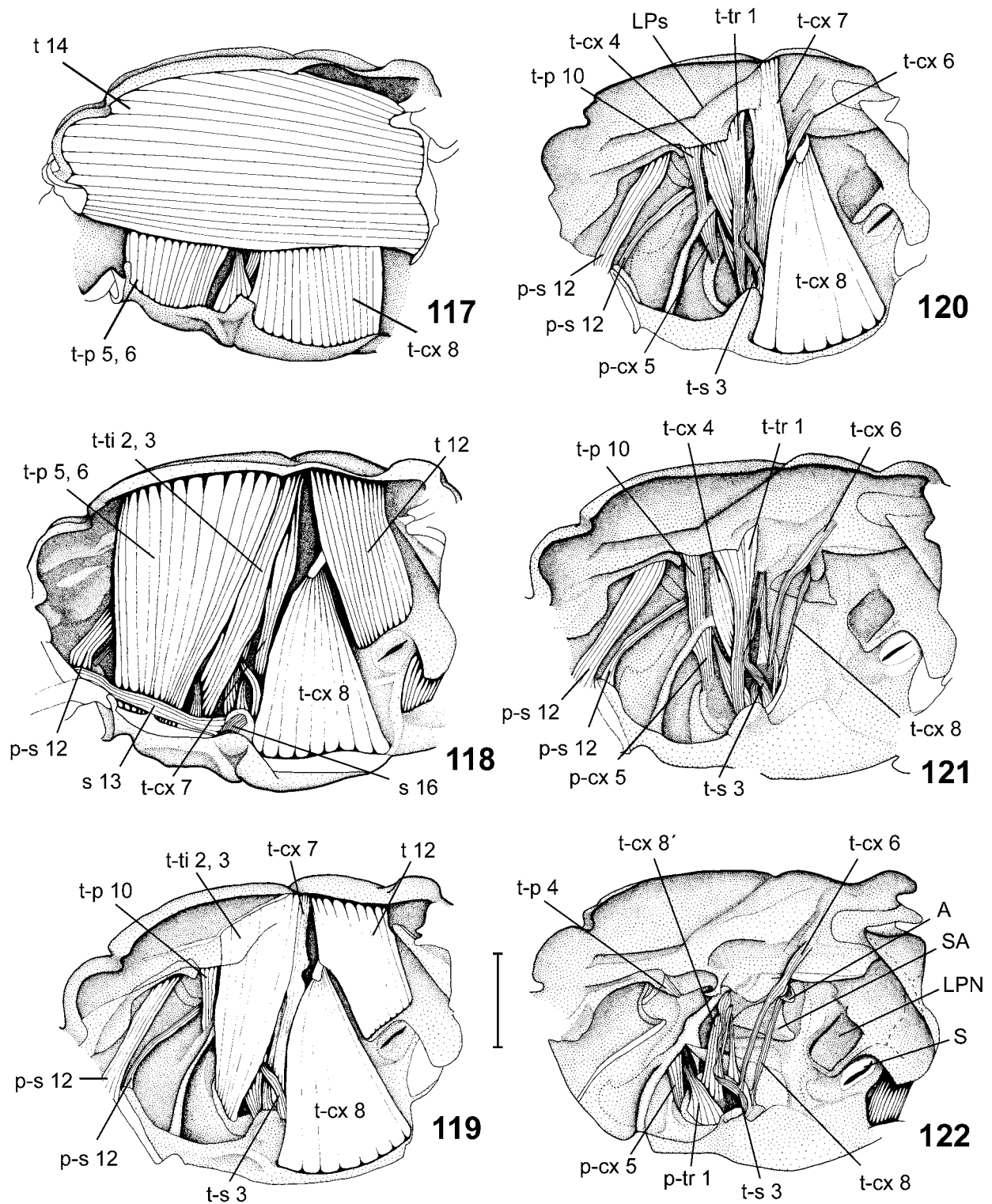


**Figs. 111–116.** *Exeuthyplocia minima*, ♂ imago, mesothorax (μCT-data), cross sections from anterior (111) to posterior (116).

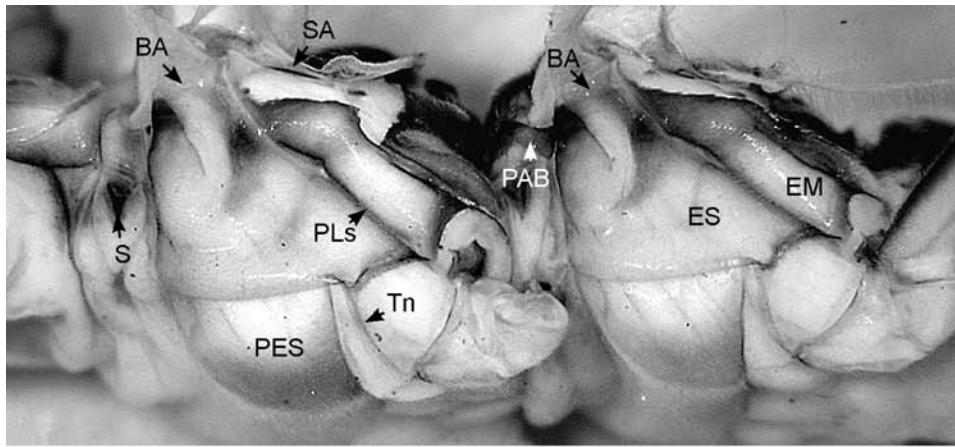
not fused, s3 is more or less tightly associated with BP e. g. in *Siphonurus aestivalis* (Siphonuridae), *Ephoron virgo* (Polymitarcyidae), *Rhithrogena semicolorata* or *Ecdyonurus submontanus* (Heptageniidae). Ventrally the s3 is associated with the subalare (SA) as it is also the case in Neoptera. The orientation of the s3 in relation to the longitudinal body axis of the insects is nearly the same in Ephemeroptera and in Neoptera. But the most important point is that a muscle (Ax.PmS; Figs. 6, 7, 10, 54–55, 103,

110, 115) inserts on the s3, running to the pleurum (posterior to the PWP; Figs. 6, 7, 10, 97, 103). The Ax.PmS was documented by GRANDI (1947), and also by BEKKER (1954), MATSUDA (1956), TSUI & PETERS (1972), KLUGE (1994) and BRODSKY (1970, 1974, 1994). The “Musculus lateralis octavus mesothoracis” (II pm8) of DÜRKEN (1907) might also be the Ax.PmS of the third axillary sclerite of Ephemeroptera.

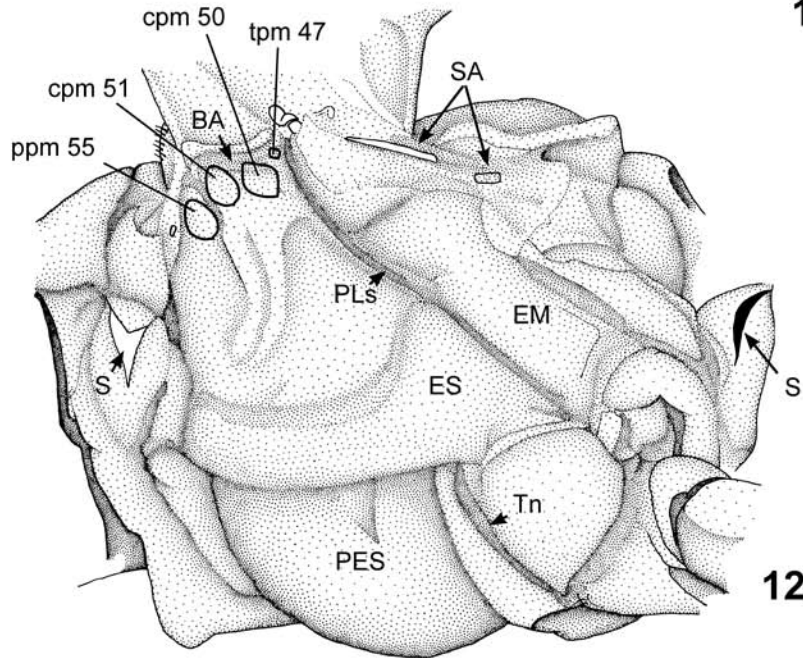
GRANDI (1947) termed the above-mentioned muscle



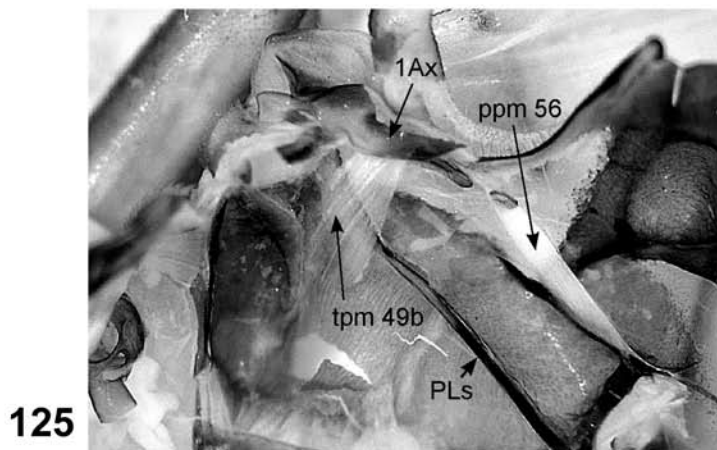
**Figs. 117–122.** *Habroleptoides confusa*, ♀ imago, musculature of the right half of the mesothorax at progressive stages of dissection, starting with median muscles (117) and progressively proceeding to the most lateral muscles (122) (modified after WILLKOMMEN & HÖRNSCHEMEYER 2007: figs. 12–17, terminology following MATSUDA 1970). – Scale: 0.5 mm.



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**Figs. 123–125.** *Isoperla* spp., ♀, thorax, lateral view. – **123.** *I. sp.*, meso- and metathorax. **124.** *I. grammatica*, mesothorax; encircled are the attachment points of several muscles that are attached to the basal area. **125.** *I. goertzi*, right mesopleurum; tpm 49b = anterior part of tpm 49.

“pleurocondilo-scutellare” and KLUGE (1994) termed it axillar-pleural muscle superior (Ax.PmS). Both authors assumed that the axillary sclerites of Ephemeroptera are not homologous with that of Neoptera. GRANDI (1947: 105, 107) pictured the muscle in her figures XVII and XIX but she did not recognise the correlation to the 3Ax and its muscle in Neoptera because she did not identify the s3 as a separate sclerite. KLUGE (1994) neither mentioned the muscle in the text (except in the abbreviation list on p. 42) nor pictured it. As well as GRANDI, KLUGE did not homologise the axillary sclerites of Ephemeroptera and Neoptera whereby he overlooked the significance of the existence of this muscle. MATSUDA (1956: 106) mentioned a muscle that “stretches between the posterior notal process and the median plate” without any further discussion (see above). But he noted a muscle that is stretched between the s2 and the pleurum (Ax.PmI equivalent to his muscle 51) that shows a striking similarity to the wing flexor muscle in other pterygote insects, which usually inserts on the third axillary sclerite (see above). Therefore, he assumed that the muscle “may be regarded as the muscle of the third axillary sclerite judging from the correlation in the occurrence between the muscle and the third axillary sclerite and the point of attachment of the muscle to the second axillary sclerite. [...] but the above example clearly indicates that the insertion also tends to shift [...]” (MATSUDA 1956: 111). He homologised the s5 with the 3Ax though this sclerite shows no characteristics of the 3Ax of Neoptera. According to own observations the 3Ax of MATSUDA is neither associated with the anal veins nor with the subalare and no muscle is attached to the s5 and it is sclerotised only in the dorsal layer of the wing membrane. Moreover, sometimes it is attached to the tergum and is orientated almost parallel or slightly acute-angled to the longitudinal body axis. Therefore, the assumption of MATSUDA is not the most parsimonious one. He overlooked the fact that the s3 shows nearly all characteristics of the 3Ax of Neoptera (including the axillar-pleural muscle) because he did not identify the sclerite posterior to the BP probably since in most cases the s3 is not distinctly separate. TSUI & PETERS (1972) described the muscle stretched between the subalare and the median plate (II-22a of these authors). They described the right function of the muscle and assumed a convergent evolution of the similar function between Ephemeroptera and other Pterygota.

BEKKER (1954) supposed a homology only of 2Ax and 3Ax in Ephemeroptera and Neoptera. According to him, the 2Ax in Ephemeroptera is the whole basal plate (BP) and the 3Ax is s3. He described a muscle, of which the first branch runs from the 3Ax (s3) to the pleural ridge and the second branch stretched between 3Ax (s3) and a cavity of 2Ax (BP).

BRODSKY (1970, 1974, 1994) assumed without a doubt a homology of the muscle, running from the s3 to the pleu-

rum, between Ephemeroptera and Neoptera (his muscle Pm14 in 1970, TPm5 in 1974 and t-p 14 in 1994) that helps to control the plane of impact (BRODSKY 1970: 187).

In Odonata there are two short muscles (29 and 30, respectively 51 and 52 in Figs. 62–66), which are attached to the postero-internal side of the axillary plate and to the membrane just behind the pleural wing process (ASAHINA 1954). These muscles are in the same position as the muscle running from the 3Ax to the pleurum (Ax.PmS) of Ephemeroptera and (t-p 14 sensu MATSUDA 1970) of Neoptera. Therefore, one can assume that a third axillary sclerite like that of Ephemeroptera and Neoptera is also present in Odonata but in the latter fused with some of the other wing base elements (for further interpretations of wing base elements in Odonata see below).

The third axillary sclerite (3Ax) in Plecoptera is rather simple in shape. The anterior arm is indistinct. In the fore and hind wings of *Pteronarcys reticulata* (Pteronarcyidae) the 3Ax is simple (Figs. 67–70, 72, 73) and likewise the 3Ax of the fore and hind wings of *Brachyptera seticornis* (Taeniopterygidae) (Figs. 74–77), *Leuctra hippopus* (Leuctridae) (Fig. 85), *Nemoura cinerea* and *Protoneura meyeri* (Nemouridae) is rather simple (own observations). The flexor muscle of the wing is stretched between a proximal concavity of the 3Ax and the pleural ridge next to the pleural wing process. In several Plecoptera the 3Ax is anteriorly partly or completely fused to the proximal median plate (PMP), for instance in the fore and hind wings of *L. hippopus*, *N. cinerea* and in the hind wings of *P. reticulata* and *B. seticornis* (own observations; Fig. 77). The fusion of the 3Ax and the PMP is most likely a secondary development in Plecoptera. Just as in Plecoptera, the close association of the s3 to the BP in the wing base of Ephemeroptera is presumably secondary, particularly since the s3 is not really fused in the examined Ephemeroptera. Actually in the basal *Siphonurus aestivalis* the s3 is not even partly fused with the BP. In Ephemeroptera it could be an adaptation for stability in flight during the nuptial dances (see section 4.4).

In summary, the characteristics of the s3 are evidence of homology of the third sclerite (s3) of Ephemeroptera with the third axillary sclerite (3Ax) of Neoptera.

#### Fifth wing base sclerite – s5

In several Ephemeroptera there is a further sclerite in the wing base (s5) lying between the s2, the s3 and the PNP (Fig. 86). Its occurrence in different taxa of the Ephemeroptera (*Siphonurus*, *Heptagenia*, and *Rhithrogena* after own observation, and also *Ametropus*, *Metretopus*, and *Parameletus* according to BRODSKY 1974) suggests that it might belong to the ground plan of Ephemeroptera. In the primordial taxon *Siphonurus aestivalis* this sclerite is not completely detached from the scutum. Also in the examined *Rhithrogena semicolorata*



and *Ecdyonurus venosus* (own observations) and in *Ecdyonurus fluminis* (GRANDI 1947) it is not completely detached from the scutum. KLUGE (1994) termed it proximal axillary sclerite since he assumed that none of the wing base sclerites in Ephemeroptera are homologous with the axillary sclerites of Neoptera. MATSUDA (1956) stated a homology of this sclerite to the 3Ax. TSUI & PETERS (1972) mentioned that a third axillary sclerite (equivalent to s5) is present only in *Aprionyx* (see above) but they have not labelled a 3Ax in their drawings. The interpretations of BRODSKY (1974, 1994) are contradictory to each other. Within his investigation of *Ephemera vulgata* (BRODSKY 1970) no discussion of this sclerite is included because in *E. vulgata* as well as in the herein examined *E. danica* (Ephemeridae) the sclerite is absent. BRODSKY (1974) wrote that the suture between the scutum and the PNP acquires particular importance in the wing base of Ephemeroptera since it makes a rotation of the posterior part relative to the anterior part of the tergite possible. More mobility is possible due to a slit in this area that is connected in its turn with the s5. Therefore this sclerite (s5) is "... the portion of the tergite remaining on the site of the previously uniformly sclerotized division" (BRODSKY 1974: 35).

On the above mentioned grounds BRODSKY (1974: 35) assumed that the s5 may be designated the median notal process. Furthermore, he annotated that this median notal process is not homologous with the MNP of other orders since the latter does not articulate with the 1Ax. However, if the homology of the wing base sclerites is as assumed herein (or by BRODSKY 1970), it is quite probable that the s5 is the homologous part of the MNP of other insect orders. Nevertheless, regarding the last-mentioned fact one can arrive at a further conclusion: The s5 could also be a detached or rather a not yet associated posterior part of the 1Ax as it is present in Neoptera. BRODSKY (1994) came to exactly this conclusion because he hypothesised, contrary to his previous work (BRODSKY 1974) that the s2 instead of the s1 is the homologous sclerite to the 1Ax of Neoptera whereas he gave no reasons for his different interpretations.

#### Wing base of Odonata

The wing base of Odonata is characterised by the presence of two plates (hp and axp in Fig. 58), of which the anterior plate is not composed of axillary sclerites (1Ax, 2Ax and 3Ax). The axillary plate of Odonata is indirectly connected to the subcostal vein (Sc). Furthermore, the anterior radial vein (R), the radial sector (Rs) and the anterior medial vein (MA) as well as the posterior medial veins (MP) and the cubital veins (Cu) are associated with the axillary plate. The anal veins (A) are connected to the posterior part of the axillary plate. The posterior pleural wing process (PWP; Figs. 59, 60), which is most likely the

homologous structure to the PWP of other orders (TANNERT 1958) is connected to the antero-ventral part of the axillary plate. A muscle is attached to the posterior part of the axillary plate running to the pleurum next to the posterior PWP (29 and 30, respectively 51 and 52 in Figs. 62–66), which is without much doubt homologous with the wing flexor (t-p 14 sensu MATSUDA 1970) of other Pterygota. On the assumption that the wing base is composed of several axillary sclerites in the ground plan of Pterygota that are arranged approximately as in the extant Plecoptera, the condition of Odonata could have been evolved as follows: As an adaptation to their manoeuvrable flight and to strengthen the wing base at least the 2Ax (connection to R and PWP), 3Ax (connection to A and "flexor" muscle), and the PMP (connection to M and Cu) are fused to the characteristic axillary plate. Whether the 1Ax is also fused to the axillary plate is unclear. The sclerite that is proposed the homologue of the 1Ax of Neoptera by TANNERT (1958) is not the 1Ax but rather the prescutum (see section 4.3). Furthermore, the basalare is enlarged in the wing base of Odonata and partly represents the humeral plate.

#### Conclusions

The assumption of a secondary strengthening of the wing base sclerites in Ephemeroptera and Odonata based on a ground plan with four wing base sclerites is more probable than their secondary fragmentation in Neoptera based on a ground plan with a mayfly-like wing base. This study agrees for the most part with the assumption of BRODSKY (1970) and partly with that of BEKKER (1954) and BRODSKY (1994). Based on morphological data presented herein a well-founded homology of the wing base sclerite is suggested as follows:

The homologous structure to the 1Ax of Neoptera is the second free wing base sclerite (s2) of Ephemeroptera (Fig. 89). The proximal part of the basal plate is proposed as homologous with the 2Ax of Neoptera. The distal and convex part of the basal plate is most likely homologous with the proximal median plate (PMP) of Neoptera. The third free wing base sclerite (s3) of Ephemeroptera is homologous with the 3Ax of Neoptera.

Ephemeroptera possess two to three axillary muscles. The first axillary sclerite (1Ax) is provided with two muscles in basal taxa (e.g. *Siphonurus aestivalis*). The first muscle runs to the furca and the second one is attached to the pleurum. The latter muscle is absent in higher ephemeropteran taxa. Nevertheless, an axillar-pleural muscle (t-p 11) running from the 1Ax to the pleurum is present in all examined Plecoptera and regarded as a ground plan character of Pterygota. MATSUDA (1970) hypothesised that the axillar-furcal muscle (Ax.Fm) is an archaic muscle that is present in Lepismatidae and seems to be reduced in Neoptera.

In Ephemeroptera no muscle is attached to the second

axillary sclerite and also the second axillary sclerite of Plecoptera and other basal Neoptera is not provided with a muscle.

A short muscle (t-p 14), running to the pleurum just posterior to the PWP, is attached to the third axillary sclerite (s3) in Ephemeroptera. This muscle is homologous with one of the wing flexor muscles of Neoptera that is also attached to the 3Ax in this taxon. Thus, the axillar-pleural muscle of the third axillary sclerite is a ground plan character of Pterygota. Furthermore, the wing base is probably composed of at least three axillary sclerites and a proximal median plate in the ground plan of Pterygota.

The strengthening of the wing base in Ephemeroptera includes the fusion of the 2Ax with the PMP and the close association of the 3Ax with both the fused 2Ax and PMP. Furthermore, both the costal brace and anal brace strengthen the wing base.

### 4.3 Homology of the flight musculature

(Figs. 90, 91, Tab. 3)

#### 4.3.1 General Remarks

The pterothorax of Ephemeroptera is specialised and adapted to their typical kind of flight. Some of the indirect mesothoracic muscles are enlarged whereas the metathorax, the hind wings and the metathoracic muscles are partly reduced in size. Ephemeroptera are distinguished from the remaining Pterygota by the presence of the subalar-sternal muscles (SA.Sm, SA.Fm) and an axillar-sternal muscle (Ax.Fm) and, furthermore, by the absence of both a posterior subalar-pleural muscle and a basalar-trochanteral muscle. Moreover, in contrast to the Neoptera, the Ephemeroptera have two basalar-sternal muscles (BA.SmS, BA.SmI). In the Plecoptera (Neoptera), SA.Sm, SA.Fm, Ax.Fm, BA.SmS and BA.SmI are absent. Generally, the presence of the subalar-sternal muscles and the axillar-furcal muscle are regarded as plesiomorphic characters of Ephemeroptera.

#### 4.3.2 Dorsal muscles

The main longitudinal muscle (MTm, t 14; Figs. 14, 35–37, 50, 98–105, 110–117) is very large in Ephemeroptera, which alludes to a good flight ability of Ephemeroptera. Usually, the anterior attachment ranges from the phragma to the posterior part of the scutum. Furthermore, the phragma between the mesothorax and the metathorax is enlarged in Ephemeroptera and provides a large posterior attachment for the MTm. This phragma is yet even extended posteriorly in *Oligoneuriella rhenana* (Oligoneuriidae) and serves as attachment to a massively enlarged MTm (own observation). The enlargement leads to a faster downstroke of the wings. Together with the also enlarged S.ESm, which leads to a faster upstroke of the wings it is

an adaptation to a flight with a high wing beat rate. Oligoneuriidae are indeed characterised by a rapid horizontal flight instead of vertical nuptial dances (see section 4.4). Nevertheless, in *Ephoron virgo* (Polymitaeridae), which is characterised by a flight behaviour resembling that of *O. rhenana*, this muscle is not exceedingly large.

The main longitudinal muscle of Plecoptera (t 14 sensu MATSUDA 1970, dlm 35 sensu WITTIG 1955; Fig. 78) is distinct but not enlarged as in Ephemeroptera. In Odonata there is only one dorsal longitudinal muscle (25 in Fig. 61), which is very weak and sometimes even absent in the metathorax (e.g. *Sympetrum* cf. *striolatum*, own observation; *Davidius nanus*, following ASAHINA 1954). The anterior attachments of the left and the right muscle are close to each other but the muscles diverge posteriorly. MATSUDA (1970) named this muscle t 19, because he assumed it to be confined to Odonata. A homology of t 19 to muscles 11 and 12 of *Lepismachilis* sp. is hypothesised by him, whereas the t 14 (MTm) is homologised with muscle 4 and 5 of *Lepismachilis* sp. Nevertheless, one can also assume that t 19 of Odonata is the homologous muscle to t 14, which is also BRODSKY's (1994: 109f) assumption. According to this author only the indirect flight muscle t 14 of recent Odonata can be reliably homologised with those of other insects.

In almost all Ephemeroptera examined the oblique dorsal muscle (S.LPNm; Figs. 15, 16, 51, 52, 105, 116; t 12 in Figs. 118, 119), dorsally attached to the posterior scutal protuberance (PSP; Figs. 1–3, 26, 38, 39, 92, 106–108) is a large muscle that extends in a nearly vertical course. Only in *Centroptilum luteolum* (Baetidae) it is rather weak and narrow, however, in contrast to the remaining examined Baetidae e.g. *Baetis* sp. and *Cloeon dipterum* where S.LPNm is about similar in size to that of other Ephemeroptera (own observation). In *Exeuthyplocia minima* (Euthyplociidae) the oblique dorsal muscle is also slightly weaker than in other mayflies, though with a rather large dorso-ventral extent since the ventral point of attachment is extended ventrally (own observation; Fig. 116). The orientation of the oblique dorsal muscle in Plecoptera (dlm 36 sensu WITTIG 1955) is rather plesiomorphic since it runs obliquely backwards and is stretched between the anterior/middle part of the scutum and the second phragma (Fig. 79). The orientation of the nearly vertically running oblique muscle in Ephemeroptera is likely a derived character state.

In a few of the examined species, there is a third weak muscle running from the notum to the postnotum (t 13; Figs. 14–17). In contrast to *Siphonurus columbianus* (MATSUDA 1956) and *Siphonurus linnaeanus* (BRODSKY 1974) where t 13 was not observed, it is present in *Siphonurus aestivalis* (Siphonuridae). It is also present in *Serratella ignita* (Ephemerellidae) and most pronounced in *Ephemera danica* (own observations). According to (BRODSKY 1994: 14), t 13 could be the detached uppermost

**Tab. 3.** Terminology of the thoracic musculature used by different authors with the underlying homology assumed in this work. – “BA” = crescent-shaped sclerite of Ephemeroptera, homology to a part of hp of Odonata assumed, homology to BA of Neoptera uncertain; \* = BA.Trm not found in examined Ephemeroptera; ? = homology to ephemeropteran muscles uncertain.

Muscle attachments	KLUGE 1994 (Ephemeroptera)	MATSUDA 1970	WITTIG 1955 (Plecoptera)
phragma I–phragma II	MT.m	t 14	d1m 35
scutum–postnotum	S.LPNm	t 12	d1m 36
scutum–postnotum		t 13	d1m 37
scutum–episternum	S.ESm	t-p 5, 6	dvm 40
scutum–trochantinus/scutum–Cx anterior	S.CmA	t-ti 2, 3	dvm 41
scutum–trochanter	S.Trm	t-tr 1	dvm 42
scutum–Cx posterior	S.CmP	t-cx 7	dvm 43
scutellum–Cx posterior	PSL.Cm	t-cx 6	–
notum–pleurum	AN.Pm	t-p 3	tpm 46a
subtegula–episternum	“BA.Pm”	t-p 4	tpm 47
ANP–episternum	SrA.Pm	t-p 10	tpm 46b
lateroscutum–pleurum	–	t-p 12	tpm 49a
episternum–Cx anterior	P.Cm	p-cx 5	cpm 52
episternum–trochanter	P.Trm	p-tr 1	–
left mesofurca–right mesofurca	Fm	s 16	–
profurca–mesofurca	iFm	s 13	v1m 38
furca–Cx anterior	F.CmA	s-cx 5	bm 59
furca–Cx posterior	F.CmP	s-cx 2	–
“BA”–sternum	BA.SmS	p-s 12	–
“BA”–sternum	BA.SmI	p-s 12	–
sclerite of scutum–coxa	BA.Cm	t-cx 4	cpm 51?
BA–trochanter*	BA.Trm	p-tr 2	cpm 50?
SA–furcasternum	SA.Sm	t-cx 8	–
SA–furca	SA.Fm	t-cx 8	–
SA–Cx posterior	–	t-cx 8	cpm 53
“SA”–Cx lateral	SA.Cm	–	–
posterior SA–pleurum	–	t-p 16	ppm 56
1Ax–furca	Ax.Fm	t-s 3	–
1Ax–pleurum	Ax.PmI	t-p 11	tpm 49b
3Ax–episternum	–	t-p 13	tpm 48a
3Ax–pleurum/epimeron	Ax.PmS	t-p 14	tpm 48b

bundle of the dorsal longitudinal muscle t14, which is indeed most likely.

#### 4.3.3 Dorso-ventral muscles

Usually, the **S.ESm** (Figs. 14, 15, 35, 36, 50, 51, 98–102, 111–113; t-p 5, 6 in Figs. 117, 118) is the largest of the dorso-ventral muscles in the mesothorax of Ephemeroptera. It is the most important antagonist to the well developed MTm. The dorsal attachment is stretched across the middle part of the scutum and the muscle becomes more slender ventrally. In *Oligoneuriella rhenana* (Oligoneuriidae) the S.ESm is conspicuous. Its ventral attachment is large since the episternum is distinctly extended ventrally in this taxon (own observation). The episternum of *Ephoron virgo* (Polymitarcyidae) bears a resemblance to that of *O. rhenana*, though the ventral attachment is not as wide in *E. virgo* (ES in Figs. 48, 49) as in *O. rhenana* (own observation). In both taxa, especially the latter, the S.ESm is enlarged together with the enlargement of MTm (see

above). The corresponding muscle (dvm 40 sensu WITTIG 1955) in Plecoptera (Figs. 78–80) is a distinct indirect flight muscle, though not as large as in Ephemeroptera.

According to MATSUDA (1970: 66), the conspicuous indirect flight muscle of Odonata (muscle 23 sensu MALOEUF 1935 and ASAHINA 1954, t-s 10 sensu MATSUDA 1970) is homologised with the muscle 64 of *Lepismachilis* sp. since it is “a genuinely tergosternal muscle from the first nymphal stage on, whereas t-p 5 (and t-p 6) is primarily a tergopleural muscle”. Neither in Ephemeroptera nor in Plecoptera does a muscle stretch between the anterior part of the tergum and the sternum. In comparison with the configuration of muscles of the Ephemeroptera and the Plecoptera, it becomes apparent that the muscle 23 of Odonata is the homologue of t-p 5, 6 (S.ESm, dvm 40). The ventral attachment of t-p 5, 6 is shifted ventrally from the larval to the adult stages of Plecoptera (WITTIG 1955). It would be conceivable that the ventral point of attachment of the muscle 23 in Odonata represents an apomorphic

condition. Furthermore, MATSUDA (1970: 66) described a muscle (t-s 7) that originates from the antero-lateral portion of the tergum and inserts on the antero-lateral corner of the sternum. It is assumed that t-s 7 occurs in *Ecdyonurus* (Heptageniidae) and may also be present in Phasmida (MATSUDA 1970), thus, a homology to the muscle 23 of Odonata is also possible. Nevertheless, in none of the examined ephemeropteran taxa such a muscle is present.

In the *Zygentoma* (*Lepisma*, *Lepismachilis*) a lot of dorso-ventral muscles occur. Therefore, it is difficult to answer the question, which muscles occurred in the last common winged ancestor and whether the condition of muscle configuration of adult and larval Odonata represents the primitive state. Nevertheless, in the proposed sister groups, there is no anterior tergo-sternal muscle.

The scuto-coxal muscles (**S.CmA**, **S.CmP**; Figs. 15–17, 51–53, 99–103; t-ti 2, 3 and t-cx 7 in Figs. 118–120) and the scuto-trochanteral muscle (**S.Trm**; Figs. 17, 18, 52; t-tr 1 in Figs. 120, 121) are not as large as the S.ESm in Ephemeroptera. In contrast to the larvae, the scuto-trochanteral muscle is the weakest of the three mentioned muscles in the winged stages of Ephemeroptera because the movement of legs becomes rather unimportant in the winged stages. Both the anterior and posterior scuto-coxal muscle are about equal in proportion in Ephemeroptera. As in Ephemeroptera, only one muscle is attached to the anterior area of the coxa in Plecoptera. This muscle, dvm 41 (M. tergo-trochantinalis sensu WITTIG 1955) is ventrally attached to the trochantinus.

In *Lepisma* sp. there are three muscles running from the middle or anterior part of the tergum to the trochantinus (muscles 71–73 sensu MATSUDA 1970). Two further muscles are attached to the anterior margin of the coxa (muscles 61–62 sensu MATSUDA 1970). Three muscles are attached to the posterior margin of the coxa (muscles 63–65 sensu MATSUDA 1970). BRODSKY (1994) assumed that three anterior tergo-coxal muscles (t-ti[cx] 1–3 including trochantinal muscles) and two posterior tergo-coxal muscles (t-cx 6–7) are present in primitive winged insects. In contrast, MATSUDA (1970) proposed that three posterior muscles must be present in primitive pterygote taxa, based on the fact that MAKI (1938) has shown that the future subalar-coxal muscle is dorsally attached to the lateral margin of the tergum in the late embryo of *Leucophaea* (Blattaria) (see section 4.3.7). This assumption is possible because the subalare is not a detached part of the pleurum but rather a new formation, which originates directly below the wing pads. Based on this assumption, the wings have to be duplications of the tergite.

MATSUDA (1970) supposed that t-ti(cx) 2 and also t-ti(cx) 3 are present in the prothorax of Ephemeroptera and in the thorax of other insects. Furthermore, he homologised t-ti(cx) 2 with dvm 41 of WITTIG (1955) and mentioned that t-ti(cx) 2 sometimes inserts on the anterior

margin of the coxa. It is assumed that the t-ti(cx) 3 is present in all thoracic segments of Ephemeroptera (MATSUDA l.c., BRODSKY 1994). If only one of those muscles is present, it is difficult to distinguish between t-ti(cx) 3 and t-ti(cx) 2 (MATSUDA l.c.). Since the trochantinus is probably reduced in Ephemeroptera, and most likely also in Odonata, it is difficult to ascertain whether the anterior tergo-coxal muscle of Ephemeroptera is rather the t-ti(cx) 2 or – more likely – the t-ti(cx) 3.

In Odonata, a muscle is distinguishable from the muscles 23 and 23', which is attached to the scutum and to the antero-lateral margin of the coxa. This third part of the large indirect flight muscle (23) is most likely the corresponding muscle to muscle 37, though MALOEUF (1935) wrote that this muscle and the metathoracic muscle 60 are absent in adult Odonata. He examined the musculature of adult and larva of *Plathemis lydia* and *Anax junius* (Anisoptera). In contrast, ASAHINA (1954) summarised that both muscles (37 and 60) are absent in Zygoptera but present in Anisoptera and also in *Epiophlebia*. The musculature of adult *Epiophlebia superstes* (Anisozygoptera), *Davidius nanus* (Anisoptera) and *Mnais strigata* (Zygoptera) provided the basis for his assumption. Nevertheless, a muscle 37 is also present in *Sympetrum* cf. *striolatum* (Anisoptera), which is closely connected to the muscle 23 in this taxon (own observation; Fig. 63). Though muscle 37 is not present in Zygoptera that are supposed to have a lot of primitive characters, it is most likely a ground plan character of Odonata since it was found in *Epiophlebia*. Furthermore, a corresponding muscle is present in Ephemeroptera and Plecoptera. MATSUDA (1970) homologised muscle 37 of Odonata with the t-cx 6 or t-cx 7, but it is probably rather t-cx 3 (or t-cx 2) since the dorsal point of attachment of muscle 26 (coxobasalar see below) lies lateral to that of muscle 37 and the ventral attachment is on the lateral rather than the posterior margin of the coxa.

Only one tergo-trochanteral muscle is described in *Lepisma* sp. (*Zygentoma*). Consequently, MATSUDA (1970) homologised it (muscle 52 of *Lepisma* sp. of this author) with the tergo-trochanteral muscle of winged insects (dvm 42 sensu WITTIG 1955, t-tr 1 sensu MATSUDA 1970, S.Trm sensu KLUGE 1994). A tergo-trochanteral muscle is missing in the pterothorax of Odonata. It is most likely reduced, as it is also present in Ephemeroptera and in Plecoptera.

The second posterior tergo-coxal muscle of Ephemeroptera is the parascutello-coxal muscle (**PSL.Cm**), which is rather weak and tapering into a tendon-like ventral part. In *Ephoron virgo* (Polymitarcyidae) it lies more anteriorly and is slightly larger than in other taxa. Furthermore, it is almost as wide dorsally as it is ventrally in this taxon. In *O. rhenana* (Oligoneuriidae) the PSL.Cm is larger than in other ephemeropteran taxa (own observation). The latter two taxa are characterised by horizontal instead of vertical

nuptial dances. The differences to other mayflies concerning the PSL.Cm in these two taxa are likely associated with their horizontal flight. MATSUDA (1970) homologised the t-cx 6 with the PSL.Cm and t-cx 7 with S.CmP of Ephemeroptera. Furthermore, he assumed that the dvm 43 sensu WITTIG (1955) consists of t-cx 6 and t-cx 7. BRODSKY (1994) stated that both, t-cx 6 and t-cx 7 are present and separated in Plecoptera. This is indeed likely because in *Isoperla grammatica* (Perlodidae) and *Brachyptera seticornis* (Taeniopterygidae) there is a muscle (own observation), which is located posterior to t-cx 7 (dvm 43 sensu WITTIG 1955). MATSUDA (1970) wrote that t-cx 6 or t-cx 7 is present in Odonata, which is actually muscle 37 sensu ASAHINA (1954).

The anteronoto-pleural muscle (**AN.Pm**; Figs. 15–17), if present, is a weak muscle that consists only of a few fibres in Ephemeroptera. It corresponds to tpm 46a (sensu WITTIG 1955) and t-p 3 (sensu MATSUDA 1970).

The suralar-pleural muscle (**SrA.Pm**; Figs. 16–18, 53, 54, 100; t-p 10 in Figs. 119–121) is absent in *O. rhenana*, but in the remaining examined taxa it is a conspicuous muscle. MATSUDA (1970) homologised t-p 8 (muscle 45 in *Siphonurus columbianus* sensu MATSUDA 1956) with SrA.Pm (sensu KLUGE 1994) but it is rather t-p 10. According to MATSUDA (1970: 63) t-p 8 connects the anterior margin of the basale or of the episternum with the lateral scutal area anterior to the anterior notal wing process. However, the SrA.Pm of Ephemeroptera is dorsally attached to the ANP rather than anterior to it and runs to the anterior paracoxal suture of the pleurum. It is not associated with the basale in Ephemeroptera. The t-p 10 (sensu MATSUDA 1970) is stretched between the pleural arm and the anterior notal wing process. Though a pleural arm is not developed in Ephemeroptera, the homologisation of the SrA.Pm with the t-p 10 is obvious.

MATSUDA (1970) assumed both t-p 8 and t-p 10 are present in Ephemeroptera, but in this area there is only one muscle (which is t-p 10, see above) in all Ephemeroptera examined. He referred to t-p 8 as muscle 45 (sensu MATSUDA 1956), however, t-p 10 is not mentioned in his publication of 1956 even though he examined a basal mayfly (*Siphonurus columbianus*). MATSUDA (1970) homologised t-p 10 with II Pm 11 sensu KNOX (1935). Nevertheless, II Pm 11 (sensu KNOX 1935) is equivalent to muscle 45 (sensu MATSUDA 1956). Both muscles are homologous with t-p 10 rather than t-p 8. Furthermore, he homologised t-p 7 with tpm 46b of *Perla abdominalis* (sensu WITTIG 1955). The muscle t-p 7 connects the antero-lateral scutal area or the prescutal area with the lower part of the basale (MATSUDA 1970: 62). According to WITTIG (1955) the tpm 46b of *Perla abdominalis* is stretched between the antero-lateral part of the scutum and the episternum. The tpm 46b of *Brachyptera seticornis* (Figs. 81, 82) is dorsally attached to the ANP and to the ridge at the anterior part of the epi-

sternum. The position of this muscle resembles SrA.Pm of Ephemeroptera and t-p 10 of Neoptera. Therefore, a homology of SrA.Pm, tpm 46b and t-p 10 is assumed. Nevertheless, t-p 7 and t-p 8 in other insects are probably the result of a splitting and can be traced back to a common origin.

#### 4.3.4 Pleural muscles

A pleuro-coxal muscle (**P.Cm**; p-cx 5 sensu MATSUDA 1970) is present in all examined Ephemeroptera (Figs. 17–19, 53–55, 99; p-cx 5 in Figs. 120–122) and also in Odonata (36 in Fig. 66; muscle 36 sensu ASAHINA 1954) as well as in Plecoptera (cpm 52 sensu WITTIG 1955; cpm 52 in Fig. 83). In most of the previous contributions on musculature of Odonata no homologisation of the muscles is given. But even MATSUDA (1970) homologised the muscle 36 of Odonata with the p-cx 5 of other winged insects since a correlation is obvious.

The pleuro-trochanteral muscle (**P.Trm**; p-tr 1 sensu MATSUDA 1970) is present in Ephemeroptera (Figs. 17–19, 53–55; p-tr 1 in Fig. 122) and also in Odonata (39 in Fig. 66; muscle 39 sensu ASAHINA 1954), but it is absent in Plecoptera. MATSUDA (1970) homologised P.Trm with muscles 53 or 54 of *Lepisma* sp. Based on this assumption, the pleuro-trochanteral muscle is secondarily reduced in the pterothorax of most Neoptera. The same author also wrote that it is often present in the prothorax of Neoptera. This muscle is also reported in the pterothorax of Coleoptera, Homoptera, and Diptera. Its presence in Ephemeroptera and Odonata is a symplesiomorphic character of these two taxa.

In basal Neoptera, the furca is usually connected to the pleural arm by a muscle. This is also the case in Plecoptera, where the conspicuous mesothoracic furca is connected with the pleural arm by a distinct muscle (zm 61 sensu WITTIG 1955, p-s 1 sensu MATSUDA 1970). In Dermaptera, Plecoptera, Neuroptera and other Neoptera the pleural arm lies approximately in the middle of the pleural ridge. The location of the pleural arm in these orders roughly corresponds to the “*processus pleural*” of CARPENTIER and BARLET” (MATSUDA 1970: 35). Furthermore, MATSUDA assumed in the same paper that p-s 1 is likely homologous with the muscle 27 of *Lepisma saccharina* (Zygentoma).

This muscle (p-s 1) is not present in Ephemeroptera at all. It is also lacking in adult Odonata. The reduction of this muscle is linked with the lack of a pleural arm in these taxa. MALOEUF (1935) mentioned a short muscle (muscle 35 sensu ASAHINA 1954) that is stretched between the furcal arm and the pleurum of larval Odonata. This muscle is absent in the adults. Most likely it is homologous to p-s 1 of other Pterygota.

As a pleural arm is well developed in Zygentoma (BARLET 1967) and basal Neoptera (MATSUDA 1970) its reduc-

tion must be assumed in Ephemeroptera and also in adult Odonata. This reduction can be supposed as a putative synapomorphic character of Palaeoptera where the muscle and the pleural arm are reduced in imagines of the stem group and in larvae of Ephemeroptera. But in all likelihood, the muscle (p-s 1) and the pleural arm are convergently reduced in Ephemeroptera and Odonata.

#### 4.3.5 Ventral muscles

The intersegmental furcal muscle (**iFm**; s 13 sensu MATSUDA 1970) is present in the mesothorax of all examined Ephemeroptera (Figs. 14, 50; s 13 in Fig. 118), Odonata (41 in Fig. 61) and also in Plecoptera (vlm 38 sensu WITTIG 1955; Fig. 78) and other Neoptera (MATSUDA 1970). Thus, the iFm (sensu KLUGE 1994) corresponds to s 13 (sensu MATSUDA 1970).

The furcal muscle (**Fm**; s 16 sensu MATSUDA 1970) running from the left to the right furcal arm is present in the pterothorax of all examined Ephemeroptera (Figs. 14–16, 50, 51, 110; s 16 in Fig. 118). It is assumed to be also present in Phasmida, Blattaria, Mecoptera, Mallophaga and Heteroptera (MATSUDA 1970). This muscle was not found by me in the mesothorax of Plecoptera and Odonata.

The posterior furco-coxal muscle (**F.CmP**; s-cx 2 sensu MATSUDA 1970) is present in both mesothorax and metathorax of all examined mayflies (Figs. 18, 19, 36, 54). It also occurs in the thorax of other pterygote insects (MATSUDA 1970). **F.CmA** was listed by KLUGE (1994) in the abbreviation list but not mentioned in the text at all. However, fig. 5 of KLUGE pictures a muscle termed F.Cm, which was not found in the examined Ephemeroptera.

The muscle which connects the lateral area of the left and the right coxal margin (**Cx.Cxm** sensu KLUGE 1994) is present only in *Siphonurus aestivalis* (Figs. 14–16) and absent in the remaining examined mayflies. It is assumed to be a derivate of s-cx 4, which is stretched between the spina and the posterior coxal margin that evolved by loss of the spina, although it may also be a modified s-cx 8 (MATSUDA 1970). This is likely although the muscle is attached to the anterior part rather than to the posterior part of the coxa in *S. aestivalis*.

A muscle that runs from the metafurca to the posterior part of the first abdominal segment or rather the anterior part of the second abdominal segment (s 20 sensu MATSUDA 1970) is present in the metathorax of *Siphonurus aestivalis*, however, it is not listed in MATSUDA's (1970: 123f) table IV. According to the same author (1970: 74) it also occurs in "Thysanoptera, Homoptera, Mecoptera, Lepidoptera etc."

#### 4.3.6 Axillary muscles

The axillary apparatus is equipped with three muscles in the examined Plecoptera, and this has most likely to be

assumed for the neopteran ground plan, too. The first muscle is stretched between the 1Ax and the pleurum (anterior part of tpm 49 sensu WITTIG 1955, tpm 49b in Fig. 82). Both second and third muscle of the neopteran axillary apparatus are dorsally attached to the 3Ax.

WITTIG (1955) could not verify the presence of a pleural muscle associated with the 1Ax in the pterothorax of *Perla abdominalis*. However, I could demonstrate its presence e.g. in *Isoperla grammatica*, *Isoperla goertzi* (Perlodidae), *Brachyptera seticornis* (Taeniopterygidae), *Leuctra hippopus* (Leuctridae) and even in *Capnia vidua* (Capniidae), a taxon with short and partly reduced wings (own observations). The muscle extends from the posterior part of the 1Ax to the pleural ridge. It might have been overlooked by WITTIG (1955) because it is obviously closely connected to tpm 49, which stretches between the lateral part of the notum and the pleural ridge.

MATSUDA (1970: 63) homologised the tpm 49 sensu WITTIG (1955) with t-p 15 of other Pterygota, which is stretched between the middle of the pleural ridge and the posterior notal wing process. The tpm 49 however, is not stretched between the PNP and the pleural ridge but rather between the lateral part of the scutum (anterior to the PNP) and the pleural ridge. In the examined Plecoptera it is a bipartite muscle, and only the first part of the muscle (tpm 49a), which is stretched between the scutum and the pleurum, is homologous to t-p 12.

The close connection between the axillary muscle (tpm 49b following this contribution) and the muscle tpm 49 (sensu WITTIG 1955) in Plecoptera suggests that the axillary muscle originated from tpm 49. In other neopteran taxa both muscles are well separated from each other, so the condition of Plecoptera could be interpreted as rather primitive.

In basal Ephemeroptera, the 1Ax is provided with two muscles (for homology of axillaries see section 4.2.5). The first muscle is ventrally attached to the pleurum (Ax.PmI) and the second one runs to the furca (Ax.Fm). According to MATSUDA (1970), the **Ax.Fm** (t-s 3 of this author) is a primitive character and homologous with the muscle 45 of *Lepisma* sp. (Zygentoma). Among adult Pterygota, it has been retained only in Ephemeroptera (Figs. 36, 53–55, 101, 102; t-s 3 in Figs. 119–122). Furthermore, MATSUDA (1970: 65) wrote that Ax.Fm (t-s 3) connects the tip of the furca and the first (s1) or second axillary sclerite (s2) in Ephemeroptera. But in none of the examined taxa Ax.Fm is attached to the sclerite that is assumed to be the 1Ax (s1) by MATSUDA. Nevertheless, the Ax.Fm is not attached to the 1Ax (s2) in several Ephemeroptera. In *Baetis* sp. and *Cloeon dipterum* (Baetidae), for example, Ax.Fm is stretched between the proximal part of the basal plate (p in Figs. 27–29) and the furca (own observation). The changes could be correlated with the miniaturisation of the body size in Baetidae. The 1Ax (s2) is not clearly distinguish-



able in the wing base of those taxa. I consider both the fusion of the 1Ax with BP or the miniaturisation of 1Ax possible. In the first case, Ax.Fm is attached to 1Ax, which is fused to BP. Given the latter possibility, the attachment of Ax.Fm has been shifted onto the BP. In *Ephoron virgo* (Polymitaeridae) the Ax.Fm is a relatively large muscle that inserts on the anterior part of the PNP (Fig. 40). In *O. rhenana* (Oligoneuriidae) Ax.Fm is absent. The latter two taxa are characterised by a swarming behaviour where the nuptial dances take place in form of a rapid horizontal flight (BRODSKY 1973). BRODSKY (1974) mentioned that Ax.Fm is reduced in Oligoneuriidae, which are characterised by the most modified flight behaviour. But the Ax.Fm is still present as a relatively large muscle in *Ephoron virgo* and according to BRODSKY (1974) it is also present in *Palingenia longicauda* (Palingeniidae). These two taxa are characterised by a flight behaviour resembling that of Oligoneuriidae.

In Ephemeroptera, there is a second muscle associated with the 1Ax, the **Ax.PmI**. It is a narrow muscle that is ventrally attached to the pleurum. The anterior part of tpm 49 (tpm 49b), which attaches to the 1Ax in Plecoptera (see above), is homologised with the Ax.PmI of Ephemeroptera in this work. The shape of the muscle, not flat and broad but slender and almost round in cross section, is most likely an apomorphic condition in Ephemeroptera. MATSUDA (1970) assumed a homology of Ax.PmI to t-p 13, which is a muscle stretching between the 3Ax and the episternum in Neoptera. This assumption is obsolete because his homology of the axillary sclerites of Ephemeroptera to that of Neoptera is not correct (see section 4.2). According to MATSUDA, the Ax.PmI is shifted from the 3Ax to the 2Ax (homology of 2Ax and 3Ax following MATSUDA 1956, 1970). Given the fact that Ax.PmI is not associated with the 3Ax but rather to the 1Ax, the Ax.PmI of Ephemeroptera is most likely the homologous muscle to t-p 11. The latter muscle stretches between the dorsal part of the pleural ridge and the 1Ax in other insects.

According to MATSUDA's (1970) description of t-p 11, the anterior part of tpm 49 (sensu WITTIG 1955) and the Ax.PmI (sensu KLUGE 1994) are homologous with t-p 11 (sensu MATSUDA 1970).

The muscle t-p 11 (pleurum–1Ax) is assumed to be a “more dorsally located t-p 10 [pleural arm–ANP]” (MATSUDA 1970: 63), the t-p 10 again is supposed to be a derivate of t-p 12 (pleural arm–lateral scutum between ANP and PNP), which reflects the close relationships of these three muscles. The condition of Plecoptera suggests, that the muscle running from the 1Ax to the pleurum originates from the tergo-pleural muscle tpm 49 (sensu WITTIG 1955, t-p 11 [or rather t-p 10] sensu MATSUDA 1970).

Furthermore, MATSUDA (1970) mentioned that t-p 15 occurs in Ephemeroptera and Plecoptera and that it is a

modified t-p 14 in Ephemeroptera. In my view it is likely that t-p 14 and t-p 15 of Ephemeroptera (sensu MATSUDA 1970) are not two different muscles but rather only one (the same) muscle. In several contributions there is only one muscle, lying in this area described. According to the same paper of MATSUDA t-p 13, t-p 14 and t-p 15 are present in Ephemeroptera. The citations (MATSUDA 1956, KNOX 1935, MAKI 1938) are inconsistent since each of the problematic muscles is cited only once (t-p 5, 6, for instance, is equivalent to muscle 43 sensu MATSUDA 1956, Dvm 1 sensu KNOX 1935 and also to muscle 25 sensu MAKI 1935). The muscle t-p 14 is equivalent to 32 sensu MAKI (1935) and not mentioned by KNOX (1935) or MATSUDA (1956), likewise the t-p 15 that is only mentioned in the work of KNOX (II Pm 6 sensu KNOX 1935) but not in the two other papers.

The t-p 13 of Ephemeroptera sensu MATSUDA (1970) is certainly not the homologous muscle to the wing flexor (t-p 13) of other insects but rather t-p 11 (see above) since it is attached to the 1Ax (see section 4.2) in Ephemeroptera. Nevertheless, a muscle that is homologous with one of the neopteran wing flexor muscles (t-p 14) is present in Ephemeroptera (see below). This muscle is probably the II Pm 6 sensu KNOX (1935; not pictured by her) and the muscle 32 sensu MAKI (1938). MATSUDA (1970), however, homologised the II Pm 6 with t-p 15, i.e. a muscle running to the PNP. This hypothesis is not correct and a muscle t-p 15 is not present in Ephemeroptera. The muscle 32 sensu MAKI (1935), t-p 14 sensu MATSUDA (1970) and II Pm 6 sensu KNOX (1935; according to MATSUDA 1970 equivalent to his t-p 15) are the same muscle namely t-p 14, which is stretched between the 3Ax and the epimeron next to the PWP.

The **3Ax** is most likely the dorsal attachment of two muscles in the ground plan of Neoptera. According to BRODSKY (1994), only one muscle is present in insects that show a flat wing folding at rest. In those groups with a roof-like wing position at rest (and also in Diptera), both muscles (t-p 13 and t-p 14) occur (BRODSKY 1994).

Only one axillary-pleural muscle is described in *Perla abdominalis* (tpm 48 sensu WITTIG 1955). It is a rather long muscle that stretches between the 3Ax and the episternum. The homologous muscle to tpm 48 (WITTIG 1955) is t-p 13 in other insects (sensu MATSUDA 1970). Nevertheless, in all of the Plecoptera, which I have dissected, there are two muscles attached to the 3Ax. The first of these two muscles is short and ventrally attached to the pleurum next to the PWP (tpm 48b in Figs. 82, 83; t-p 14 sensu MATSUDA 1970). The second muscle of the 3Ax is located adjacent to the first one and runs to the episternum next to the pleural ridge (tpm 48a in Figs. 82, 83; t-p 13 sensu MATSUDA 1970). Most likely BRODSKY (1994, e.g. in fig. 7.1 on p. 117) had mistaken t-p 14 for t-p 13 (sensu MATSUDA 1970).

The 3Ax (for homologisation of the axillaries see sec-

tion 4.2) of Ephemeroptera and Odonata is equipped with a short muscle (**Ax.PmS**, muscles 29 and 30) running to the epimeron adjacent to the PWP. At least in some Ephemeroptera (e.g. *E. virgo*) as well as in Odonata it is bipartite. The second, shorter and much weaker part of Ax.PmS of Ephemeroptera is attached to the posterior part of the basal plate instead of the pleurum. It is likely a secondary development in this taxon. In Odonata both muscles (29 and 30) are only short. They take a parallel course and are both attached to the pleurum next to the PWP. While the presence of t-p 14 is a ground plan character of Pterygota, t-p 13 is an autapomorphic character of Neoptera.

MATSUDA (1970) assumed that t-p 13 as well as t-p 14 is present in Ephemeroptera but his t-p 13 is attached to 1Ax (**Ax.PmI** sensu KLUGE 1994, see above) in Ephemeroptera. Therefore, it has to be homologised with t-p 11.

Moreover, MATSUDA (1970) confused the homologisation of the muscle that attaches to the 3Ax in Odonata. According to MATSUDA (1970: 400), muscles 29 and 30 sensu ASAHINA (1954) are possibly homologous with t-p 14. Under remark 5 (concerning his “t-p 14?”) he mentioned that these “... muscles are *M. gubernator analis* 1a, b of TANNERT 1958 ...” (MATSUDA 1970: 401). In contrast, he (MATSUDA 1970: 64) further mentioned that t-p 26 of Odonata is homologous with “*M. gubernator analis* 1a, b of TANNERT 1958” and also to muscle 31 sensu MALOEUF (1935) and ASAHINA (1954). On the same page MATSUDA wrote that this muscle arises from the posterior surface of the pleural wing process and inserts on the proximal part of the anal vein in the axillary plate. This interpretation is not correct and comprehends two different muscles. According to MALOEUF (1935) the muscle 31 is not present in adult Odonata. ASAHINA (1954), in contrast, suggests that it occurs in *Epiophlebia superstes* (Anisozygoptera), *Davidius nanus* (Anisoptera) and *Mnais strigata* (Zygoptera). In *Sympetrum* cf. *striolatum* (Anisoptera) the muscle 31 is absent according to own observations. Nevertheless, given ASAHINA's (1954: 50) description the muscle 31 is attached to the end of lateral branch of the scutellum and to the upper portion of the intrapleural ridge, which is completely different to MATSUDA's (1970) description of t-p 26. However, the description of t-p 26 (following MATSUDA 1970) is consistent with the description of muscles 29 and 30 (sensu ASAHINA 1954). Consequently, the muscles 29 and 30 (sensu ASAHINA 1954) and *M. gubernator analis* (sensu TANNERT 1958) as well as Ax.PmS (sensu KLUGE 1994) and t-p 14 (sensu MATSUDA 1970) are all the same (homologous) muscle.

#### 4.3.7 Muscles of the pleural wing sclerites

Ephemeroptera and Plecoptera show different conditions concerning the attachments of the basalar and the subalar muscles as well as the location and the appearance of the associated sclerites, the basalare and the subalare.

The basalare of Plecoptera (BA in Figs. 123, 124) is provided with two muscles, the basalar-trochanteral muscle (*M. basalar-endocoxalis*, cpm 50 sensu WITTIG 1955 and ZWICK 1973) and the basalar-coxal muscle (*M. basalar-coxalis*, cpm 51 of WITTIG 1955 and ZWICK 1973). The subalare of Plecoptera is the dorsal point of attachment of one usually large muscle running to the coxa (cpm 53, *M. subalar-coxalis* sensu WITTIG 1955 and ZWICK 1973; t-cx 8 sensu MATSUDA 1970). In some species, a second muscle is present, running from a smaller sclerite that lies posterior to the subalare of the pleurum (ppm 56 in Fig. 125). Both muscles occur in all Plecoptera examined.

In most cases the so-called basalare of Ephemeroptera is detached from the episternum situated at the anterior base of the wing margin (BA in Figs. 4–8, 32, 33, 96). This crescent-shaped sclerite is the dorsal attachment of two muscles. In *E. virgo* (Polymitarcyidae), the crescent-shaped sclerite is secondarily attached to the episternum. The subalare (SA in Figs. 4, 10, 30–33, 43, 44, 93, 96, 97) in Ephemeroptera is provided with two muscles running to the sternum and one pleural muscle running to the coxal rim (SA.Sm, SA.Fm and SA.Cm; Figs. 14–19, 37, 50–55, 103–105, 110, 113–116). Subalar-sternal muscles are not present in Plecoptera or other Neoptera (MATSUDA 1970). In Plecoptera, each of the two basalar muscles is about equal in proportion to the subalar-coxal muscle. In contrast, the subalar-sternal muscle of Ephemeroptera is considerably larger than the remaining basalar and subalar muscles.

#### Basalare and associated muscles

The basalare of Neoptera is most likely a pleural element (SNODGRASS 1935), and in basal Pterygota it is even still associated with the pleurum. In all examined Plecoptera it is still connected to the episternum. The basalare of Plecoptera articulates anteriorly with the basicostale and posteriorly with the basisubcostale.

The interpretation of the basalare and its associated muscles in Ephemeroptera is problematic. Therefore, a homologisation with the basalare of Neoptera is difficult. The crescent-shaped sclerite lying basal to the tegula in Ephemeroptera is generally considered as basalare. Its upper part is tightly connected with the tegula. The crescent-shaped sclerite is neither connected directly to the base of the subcostal vein (BRODSKY 1994) nor does it lie below the ANP (HÖRNSCHEMEYER 1998) as the basalare in Neoptera.

The two basalar-sternal muscles (BA.SmS, BA.SmI) of Ephemeroptera are attached to this crescent-shaped sclerite but the so-called basalar-coxal muscle (BA.Cm sensu KLUGE 1994, 2004) and the so-called basalar-pleural muscle (BA.Pm sensu KLUGE 1994, 2004) are not attached to it. The latter two muscles rather insert on two sclerites lying in the membrane between the notum and the anterior part of the wing base. BA.Pm usually inserts on a dorsal

sclerite that lies proximal to the crescent-shaped sclerite (Figs. 12, 40), almost at the same level as the anterior wing base (Fig. 12). Posterior to the insertion of BA.Pm and just anterior to sl (ANP following the present study) lies the sclerite, at which BA.Cm inserts (Figs. 11, 12, 40). In some mayflies (e.g. *Baetis* sp., *Rhithrogena semicolorata*, *Ecdyonurus submontanus*) these sclerites are associated with each other, and additionally also connected to the crescent-shaped sclerite and the tegula (own observations). In other taxa (e.g. *E. virgo*; Fig. 40), these sclerites lie separated from each other in the anterior part of the wing base. BA.Cm is attached to the coxo-pleural joint and runs (directly below the sl) to the sclerite lying anterior to sl.

I could not verify the basalar-trochanteral muscle (BA.Trm), which is described in *Hexagenia* (Ephemeridae) by KNOX (1935) and also in *Ephemerella* sp. (Ephemerellidae), *Ephemerella* sp. (Ephemeridae), *Ecdyonurus* sp. (Heptageniidae), *Choroterpes* sp., *Habrophlebia* sp. (Lepidopteriidae), several Baetidae, *Oligoneuriella* sp. (Oligoneuriidae) and *Caenis* sp. (Caenidae) by GRANDI (1947). On the other hand, MATSUDA (1956) states that this muscle (t-tr 2 sensu MATSUDA 1970) is not present in *Siphonurus columbianus*, whereas he later (MATSUDA 1970: 75) asserts that it is attached to the first axillary sclerite in other Ephemeroptera, very close to the point of attachment of t-cx 4 (BA.Cm sensu KLUGE 1994). MATSUDA's assumption that t-tr 2 is attached to the axillary sclerite resulted from GRANDI's (1947) interpretation who described a muscle that is dorsally attached to the 1Ax (1Ax sensu GRANDI). The dorsal point of attachment of t-tr 2 is close to that of t-cx 4 or fused with it (MATSUDA 1970). According to the same author this muscle (t-cx 4) is described only in Ephemeroptera. Another trochanteral muscle is listed for the ephemeropteran thorax by MATSUDA (p-tr 2 sensu MATSUDA 1970: 124). It is the basalar-trochanteral muscle, which also occurs in Neoptera. The two muscles t-tr 2 and p-tr 2 are one and the same muscle in Ephemeroptera. But the first mentioned muscle is described as a tergal muscle by GRANDI (1947), assuming that it inserts on the 1Ax. The second muscle is described as a pleural muscle by KNOX (1935). According to KNOX (II Pm 3 of this author) it is attached to the basalare, which is known as a pleural element in Neoptera. But if the two mentioned muscles are associated with t-cx 4, then the dorsal attachment of both t-tr 2 and p-tr 2 is the posterior sclerite lying antero-medial of sl in the ephemeropteran wing base. KLUGE (1994) mentioned a muscle BA.Trm in the list of abbreviations but he neither pictured nor mentioned the muscle in a later publication (KLUGE 2004). Furthermore, a basalar-trochanteral muscle is pictured in BRODSKY's diagram of the muscles of a generalised ephemeropteran mesothorax (BRODSKY 1974: 38, fig. 2) with the same insertion as that of TCxm5 (classified as a basalar-coxal muscle, BA.Cm). He described the function of this muscle as pronator of the wing. In spite

of this, he marked the TTrm2 as absent in the mesothorax of all Ephemeroptera examined (BRODSKY 1974: 38, tab. 1).

The scuto-trochanteral muscle (S.Trm) is attached to the lateral part of the scutum in larval Ephemeroptera (own observation). It seems to have been shifted more laterally in subimaginal and imaginal Ephemeroptera compared to its position in the larvae. Though, it is a large muscle in larvae it is diminished in the winged stages. Its lateral position and the size of S.Trm probably cause misinterpretations. Nevertheless, in none of the examined taxa a basalar-trochanteral muscle was found.

The basalar-sternal muscles (BA.SmS, BA.SmI; p-s 12 sensu MATSUDA 1970; Figs. 14–19, 50–54, 98, 111; p-s 12 in Figs. 118–121) that are present in Ephemeroptera are absent in the mesothorax as well as in the metathorax of Plecoptera and the remaining Neoptera (MATSUDA 1970). They are most likely reduced in these taxa. There are two muscles in the thorax of Lepismatidae, which lie in exactly the same position as the ephemeropteran BA.SmS and the BA.SmI (muscles 41 and 42 sensu BARLET 1953, 1954 and MATSUDA 1970). This was the reason for MATSUDA to assume a homology of the lepismatid muscles 41 and 42 with the basalar-sternal muscles in Ephemeroptera. Both muscles (41 and 42) of *Lepisma saccharina* (Zygentoma) are tergo-sternal muscles. MATSUDA (1970) interpreted them as pleuro-sternal muscles, most likely because the basalare is generally known as a pleural element in other Pterygota. However, in Ephemeroptera all of the so-called basalar muscles are of tergal origin. MATSUDA (1970: 120) also assumed – without reasoning – that the p-s 12 is shared only by Ephemeroptera and Odonata, but nevertheless omits these muscles elsewhere (MATSUDA 1970: 400, tab. XXIV). MATSUDA also wrote in this publication that a different muscle is present (t-s 2), which originates on the midlateral portion of the mesothoracic prescutum and inserts at the postero-dorsal surface of the prothoracic furca. According to (MATSUDA 1970: 65) it is probably homologous with muscle 42 of *Lepisma* sp., which in turn is homologised with p-s 12 (BA.SmS/BA.SmI sensu KLUGE 1994).

Muscle t-s 2 should also occur in larval stages of *Corydalus* sp. (Megaloptera) and in *Stagmomantis* sp. (Mantodea). Another muscle p-s 3, which is stretched between the episternum and furca of the preceding segment, occurs in Psocoptera, Hymenoptera, Coleoptera and Lepidoptera and is assumed to be a derivate of p-s 12. On the above mentioned assumptions, it is not feasible that p-s 12 is a synapomorphic character of Odonata and Ephemeroptera as assumed by MATSUDA (1970). In the examined Plecoptera, however, no homologous muscles to BA.SmS and BA.SmI of Ephemeroptera were found. In my view, BA.SmS and BA.SmI are plesiomorphic ground plan characters of Pterygota, as these muscles are already present in *Zygentoma* (BARLET 1953, 1954). Consequently these mus-

cles must be interpreted as symplesiomorphic in Ephemeroptera and Odonata. Both muscles are likely to be reduced in Neoptera.

BRODSKY (1970: 166) mentioned that the basalare of Ephemeroptera “occupies its usual place” Assuming that the basalare is, just as well as the neopteran basalare, a pleural element, he classified all basalar muscles of Ephemeroptera as pleural muscles (Pm). Four years later (with reference to MATSUDA 1970, see above) and on the grounds that the homologous muscles are associated with the tergum in *Lepisma saccharina* and not present in any other insect order, he termed the basalar-sternal muscles TSm1, tergo-sternal muscles (BRODSKY 1974). Interestingly, he also interpreted the BA.Cm (TCxm5) and the BA.Pm (TPm3) as tergal muscles in the latter publication. In larval mayflies, the two mentioned basalar-sternal muscles are indeed dorsally attached to the anterior part of the scutum (see Fig. 56).

In the pterothorax of Odonata there are two muscles present, which are connected to the lateral part of the humeral plate (hp) by a long tendon (muscles 21 and 22 sensu MALOEUF 1935 and ASAHINA 1954; Figs. 59, 61–63, 65, 66). MATSUDA (1970) suggested that both muscles are autapomorphic characters of Odonata (t-p 22 and t-p 23 sensu MATSUDA 1970). In the same contribution (on p. 120) however, he wrote that p-s 12 is shared by Ephemeroptera and Odonata without any further reasoning. In my view, p-s 12 is indeed present in Ephemeroptera (BA.SmS and BA.SmI sensu KLUGE 1994) and Odonata (muscles 21 and 22 sensu ASAHINA 1954).

The muscle 22 has a bipartite dorsal tendon that inserts in addition to the lateral attachment also to the middle part of the hp. Muscles 21 and 22 are interpreted as sternobasalar muscles by ASAHINA (1954) though they are attached to the pre-episternal sclerite sensu ASAHINA. Actually the characteristics of muscles 21 and 22 when compared to BA.SmS and BA.SmI of Ephemeroptera are nearly identical. In both taxa, these muscles are attached to a sclerite close to the anterior wing base. ASAHINA assumed in the same paper that the hp of Odonata contains a part of the basalare. Interestingly, BRODSKY (1994) homologised at least a part of the hp of Odonata with the basalare, but without any reasoning. I agree with BRODSKY's and ASAHINA's assumption since the position of the hp in Odonata is comparable with the position of the crescent-shaped sclerite in Ephemeroptera. Moreover, in Odonata two muscles are attached to the hp just in a similar position as BA.SmS and BA.SmI of the so-called basalare in Ephemeroptera. This makes it likely that BA.SmS and BA.SmI of Ephemeroptera are homologous with the muscles 21 and 22 of Odonata. The so-called basalar sclerites of Ephemeroptera and Odonata are most likely not homologous to the basalare of Neoptera. Comparing the musculature of Zygentoma (BARLET 1953), Ephemeroptera

and Odonata it becomes obvious that a reduction of the basalar-sternal muscles is an apomorphic character of Neoptera rather than a synapomorphic character of Metapterygota as assumed by WILLKOMMEN & HÖRNSCHEMEYER (2007).

In Ephemeroptera there is also a so-called basalar-pleural muscle (BA.Pm; Figs. 12, 18, 19, 40, 52–55, 99; t-p 4 in Fig. 122) present. It is dorsally attached to the sclerite lying proximal to the anterior wing base and to the crescent-shaped sclerite. From there it proceeds to the pleurum (Fig. 32). In some of the examined species (*Baetis* sp., *Rhithrogena semicolorata*, *Ecdyonurus submontanus*) this sclerite is associated with the crescent-shaped sclerite (own observation). The BA.Pm (sensu KLUGE 1994) of Ephemeroptera is similar to p5 sensu MATSUDA (1970) and m. pleurocondilo-scutale sensu GRANDI (1947). According to MATSUDA (1970) BA.Pm is only present in Ephemeroptera stretching between the BA and PWP.

Such a short but robust muscle lying in the same position is also present in Plecoptera (tpm 47 sensu WITTIG 1955; Fig. 83) and also in Odonata (own observation, see Figs. 64, 65). In *Pteronarcys reticulata* (Pteronarcyidae), *Perla abdominalis* (WITTIG 1955) and also in *Isoperla grammatica*, *Isoperla goertzi*, *Perlodes microcephalus* (Perlodidae), *Capnia vidua* (Capniidae, all Plecoptera; own observations) it inserts dorsally on a small sclerite next to the tegula (Fig. 67), i. e. the subtegula (SNODGRASS 1935, “kleine Sklerifikation hinter der Tegula” sensu WITTIG 1955, “myodiscus” sensu NELSON & HANSSON 1971). This muscle proceeds to the episternum, namely anterior to the PWP. Though tpm 47 is conspicuous in *Brachyptera seticornis* (Taeniopterygidae), this sclerite is rather indistinct.

In Odonata the short muscle 28 (ASAHINA 1954) has a similar course, as it is also dorsally attached to a tergal sclerite and running to the pleurum anterior to the PWP. MATSUDA (1970: 401) homologised muscle 28 of Odonata with t-p 11, which connects the anterior (or dorsal) part of the pleural ridge or the anterior part of the PWP with the first axillary sclerite in other insects. This assumption may result from TANNERT's interpretation of the dorsal sclerite, to which muscle 28 is attached, as 1Ax (Pt 1 sensu TANNERT 1958). The first axillary sclerite, however, is expected to be located rather posterior to this sclerite when compared to the wing base of the remaining Pterygota. It should be rather located proximal to the axillary plate since the characteristics of the axillary plate suggest homology to at least a part of the wing base sclerites (2Ax, 3Ax and PMP) of other Pterygota (see section 4.2).

The muscle 28 (metathoracic muscle 50 respectively; Fig. 65) that is attached to this sclerite in Odonata is similar to BA.Pm of Ephemeroptera and to t-p 4 of the Neoptera. The t-p 4 originates from the pleural ridge just below the pleural wing process or – if developed – from the pleural

arm (MATSUDA 1970: 62). It inserts either at the subtegula, the laterophragma, or the prealar sclerite. MATSUDA (1970: 15) also assumed that the sclerite, to which the t-p 4 is dorsally attached in Neoptera, is presumably a detached prescutal sclerite. The BA.Pm of *Siphonurus aestivalis* (Siphonuridae) is attached to a sclerite lying between the tegula and the tergum. This sclerite is also associated with the posterior arc of the prealar bridge. This is indeed an indication of the prescutal origin of the sclerite and supports ASAHINA's assumption, that the sclerite, which is located proximal to the humeral plate in Odonata (Pt 1 following TANNERT 1958), is a part of the prescutum (ASAHINA 1954).

In mayfly larvae, the muscle BA.Pm is dorsally attached to the latero-medial part of the scutum. Regarding the similar attachment of this short muscle in Ephemeroptera (BA.Pm sensu KLUGE 1994), Odonata (muscle 28 sensu MALOEUF 1935), Plecoptera, and other Neoptera (t-p 4 sensu MATSUDA 1970) it is most likely that BA.Pm, muscle 28 and muscle t-p 4 are homologous with each other.

Consequently, the BA.Pm of Ephemeroptera is not a genuine basalar muscle but rather the muscle running from the subtegula to the pleurum (t-p 4). Therefore, the sclerite to which the muscle is attached is not the basalare but rather the subtegula.

In Ephemeroptera the dorsal attachment of **BA.Cm** (Figs. 12, 40) is behind that of BA.Pm. In Plecoptera and also in other Neoptera there is a basalar-coxal muscle (basalar-coxal or M. basalar coxalis, cpm 51 sensu WITIG 1955 and ZWICK 1973), which pronates the wing. It is dorsally attached to the episternal basalare and ventrally to the anterior rim of the coxa (Fig. 82).

In contrast, the basalar-coxal muscle (BA.Cm sensu KLUGE 1994) of Ephemeroptera is often interpreted as a coxo-axillary or coxo-tergal muscle. MATSUDA (1956, 1970) assumed that the muscle is dorsally attached to the 1Ax (s1: 1Ax sensu MATSUDA 1956 and TSUI & PETERS 1972, pseudopterale prossimale sensu GRANDI 1947; s1 see also section 4.2.5). BRODSKY (1974) termed this muscle as a tergo-coxal muscle (TCxm5, see above) and KLUGE (1994) interpreted it as a basalar-coxal muscle.

In nearly all examined mayflies (in particular in *Siphonurus aestivalis*), the dorsal attachment of this so-called basalar-coxal muscle is on the dorsal sclerite next to the s1 (own observation; Fig. 11). In *S. columbianus*, examined by MATSUDA (1956), the muscle is interpreted as axillary muscle. However, in *Habroleptoides confusa* (Leptophlebiidae), *Centropilum luteolum* and *Cloeon dipterum* (Baetidae) there is a different configuration present (own observation). In addition to the usual attachment of BA.Cm in *H. confusa* there is an indistinct tendon running to s1. In *C. luteolum* the muscle is dorsally attached to an antero-proximal projection of the basal plate. In *Cloeon dipterum* the BA.Cm is attached to the con-

spicuous base of the subcostal vein. These character states in Baetidae are likely correlated with the miniaturisation of the body size and the changes in wing base sclerites.

MATSUDA (1970) assumed that the t-cx 4 (BA.Cm) is a direct flight muscle of Ephemeroptera and Odonata. Furthermore, in *Siphonurus* it is supposed to insert at the 2Ax (s2; axillary homologisation following MATSUDA 1970). However, in *Siphonurus columbianus* (muscle 50 sensu MATSUDA 1956) and in *Ecdyonurus* (Heptageniidae) it is assumed to insert at the 1Ax (s1; axillary homologisation following MATSUDA 1956, 1970). According to KNOX (1935), the BA.Cm is dorsally attached to the basalare. This is due to the fact that in several mayflies the sclerite, which is the dorsal attachment of BA.Cm, is connected to the crescent-shaped sclerite (so-called basalare, BA). The large sclerite figured in KNOX's (1935: 137) plate XX is most likely this crescent-shaped sclerite plus the tegula plus the associated dorsal sclerites (attachment of BA.Pm and BA.Cm). In several species, these elements are tightly connected to each other (see above). Nevertheless, the muscle (BA.Cm) is not associated with the 1Ax (2Ax following MATSUDA 1956, 1970) and in most cases also not with s1 (1Ax following MATSUDA 1956, 1970) in the examined Ephemeroptera.

MATSUDA (1970: 66) assumed that in Odonata there are two muscles present, which connect the disc internal to the coxal condyle with the first axillary sclerite and the axillary plate (second and third axillary sclerites). Their ventral points of attachment are confluent and their dorsal attachments lie close to each other. Therefore, MATSUDA termed the muscles t-cx 4 and t-cx 4' (assuming that t-cx 4 is homologous with BA.Cm of Ephemeroptera). These two muscles are 26 and 27 sensu MALOEUF (1935) and ASAHINA (1954).

The position of the muscle 27 of Odonata is different from the position of BA.Cm of Ephemeroptera. MAKI (1938) assumed that in addition to muscle 26 also muscle 27 is a coxo-axillary muscle, which is attached to the axillary plate of the wing base in Odonata. ASAHINA (1954: 45) assumed that it could be a coxo-subalar muscle, which is generally present in the other winged insects. The muscle 27 is dorsally attached to the axillary plate, which is likely partially fused with the subalar in Odonata (see below). As muscle 27 rather resembles a subalar muscle than a basalar-coxal muscle, this study agrees with the hypothesis of ASAHINA (1954).

Muscle 26 (Figs. 59, 65) of Odonata, however, is very similar to BA.Cm of Ephemeroptera regarding the dorsal and ventral attachment points. The dorsal attachment of muscle 26 is located proximal to the humeral plate, which is fused with the sclerite homologous with the crescent-shaped sclerite of Ephemeroptera. ASAHINA (1954: 45) wrote that it appears more reasonable to ascribe it to the coxo-basalar muscle. A homology of the muscle 26 of

Odonata with the BA.Cm of Ephemeroptera is also assumed in the present study. The so-called basalar-coxal muscle of Ephemeroptera and Odonata are possibly not homologous with the neopteran basalar-coxal muscle (see below).

The BA.Cm of Ephemeroptera is sometimes described as a basalar muscle (BA.Cm sensu KLUGE 1994, Pm3 sensu BRODSKY 1970). Nevertheless, all basalar muscles in mayfly larvae are dorsally attached to the antero-lateral or medio-lateral part of the scutum (Fig. 56). Their pleurum is rather simple and small. The pleural sclerite is separated from the tergum by a membranous area. In contrast, the pleurum of stonefly larvae is large and the upper part of the episternum is associated with the tergal parts. It lies next to the anterior wing base, whereas the epimeron is rather small. Between the posterior part of the epimeron and the ventral membrane of the wing pad there is a relatively large membranous area. So the dorsal attachment of the two basalar muscles on the episternum is next to the tergal parts in larvae of Plecoptera.

Most likely the small, isolated and simple pleurum of larval Ephemeroptera represents the plesiomorphic condition. The pleurum of larval Plecoptera is closely associated with the tergum, which probably represents a derived state. One possible interpretation is the assumption that the basalar muscles are of tergal origin in Pterygota. In Neoptera these muscles shifted ventrally onto the pleurum.

However, the BA.Cm is attached to a separate sclerite of the anterior wing base in Ephemeroptera. In subimagines, imagines and also in larvae of Ephemeroptera the attachment lies even posterior to the attachment of BA.Pm, which is not a genuine basalar muscle (see above). Therefore, it is more likely to assume that the BA.Cm of Ephemeroptera is also not a true basalar muscle. Therefore a homology of BA.Cm to the basalar-coxal muscle of Neoptera is rather unlikely, but a homology of BA.Cm of Ephemeroptera to the muscle 26 of Odonata is assumed. The sclerites, to which BA.Pm and BA.Cm are attached are separated in basal Ephemeroptera, which is likely to represent the plesiomorphic condition. Therefore, the term BAd (which includes the two sclerites) used by WILLKOMMEN & HÖRNSCHEMEYER (2007) is not correct, since the separated dorsal sclerites are not true basalar sclerites. The anterior sclerite, lying between the tegula and the tergum at the anterior wing base is homologous with the subtegula of other Pterygota (see above).

#### Subalare and associated muscles

In Plecoptera the subalare is a simple, longish sclerite without large apodemes, but conspicuous and specialised in the Ephemeroptera. In both Ephemeroptera and Plecoptera, the subalare develops from the pleural membrane below the wing pad. It is located in the upper part of the

pleurum posterior to the PWP and below the wings. The sclerite is surrounded by a membranous area in both taxa and never associated with the epimeron.

The subalar-coxal muscle (SA.Cm; Figs. 18, 19, 54, 55) of winged stages of Ephemeroptera is dorsally attached to the anterior subalar apodeme (ASA; Figs. 4–8 10, 43, 96) and ventrally to the postero-lateral rim of the coxa. Usually, it is a rather weak and sometimes bipartite muscle in imaginal Ephemeroptera. The large subalar-sternal muscle (SA.Sm; Figs. 14–17, 37, 50–53, 103–105, 110, 113–116; t-cx 8 in Figs. 117–120) is attached to the posterior subalar apodeme (PSA; Figs. 4–8, 10, 17, 18, 30, 32, 33, 43, 44, 104, 114, 115) and to the subalar suture (SAs; Figs. 8, 30, 32, 33). The SA.Sm originates from the furcasternite (FS; Figs. 4, 5, 34, 44, 48, 109).

In the larval stages of Ephemeroptera, the pleurum is rather simple and small. The SA.Cm inserts at the postero-dorsal part of the pleural sclerite next to the pleural suture (Fig. 56). It originates from the lateral rim of the coxa. In contrast, the SA.Sm is attached to a small sclerite in the upper part of the pleural membrane directly below the posterior part of the fore wing pad (Fig. 56). The subalar-furcal muscle (SA.Fm) inserts at the same sclerite and originates from the mesothoracic furca.

In Neoptera, the subalare is provided with a large muscle running to the posterior rim of the coxa (subalar-coxal muscle; t-cx 8 sensu MATSUDA 1970, cpm 53 sensu WITTIG 1955 and ZWICK 1973). In early stages of stonefly larvae (*Perla abdominalis*, WITTIG 1955), the subalar-coxal muscle is stretched between the upper part of the pleural membrane near the future ventral membrane of the wing pad and runs to the rim of the coxa. Furthermore, it is attached to a small sclerite below the wing pad in final larval stages (e.g. *Brachyptera seticornis*).

MATSUDA (1970) homologised the t-cx 8 (SA.Cm) of Ephemeroptera with the t-cx 8 of Plecoptera. However, in my opinion the SA.Cm of Ephemeroptera is most likely not homologous with the subalar-coxal muscle of Plecoptera and other Neoptera because the origin of this muscle in larval stages is different in Ephemeroptera and Plecoptera. The anterior part of the subalare, which is equipped with the anterior subalar apodeme (ASA) in Ephemeroptera is either secondarily associated with the posterior part of the subalare, or the dorsal attachment of SA.Cm has shifted onto the subalare in the winged stages. The posterior part of the SA of Ephemeroptera develops ontogenetically similar to the subalare of Plecoptera, namely below the wing pad and in the pleural membrane above the epimeron. In contrast, the anterior part of the subalare that provides the ASA may develop from the upper part of the pleurum. Later in its larval development it possibly becomes associated with the posterior sclerite of the subalare. This suggests that the anterior part of the subalare of Ephemeroptera is not homologous with the subalare of



Plecoptera and other Neoptera. A homology of the subalar-coxal muscle (SA.Cm) of Ephemeroptera to the subalar-coxal muscle (t-cx 8 sensu MATSUDA 1970) of Plecoptera and other Neoptera is rather unlikely.

MATSUDA (1970: 65) assumes that the SA.Sm of Ephemeroptera may be a derivative of the subalar-coxal muscle (t-cx 8), but does not mention any possible homologous muscle in *Lepisma saccharina* or *Lepismachilis* sp. (Zygentoma). The similar course of the SA.Sm in the larvae of Ephemeroptera compared to the SA.Cm in Plecoptera implies that MATSUDA's hypothesis concerning the origin of the SA.Sm is most probably correct.

It is difficult to decide whether the sternal attachment of the subalar muscle in Ephemeroptera could reflect a primitive or a derived condition. Nevertheless, the Ephemeroptera are characterised by a specialisation of the mesothorax that includes the enlargement of the indirect flight musculature (e.g. dorsal longitudinal muscle and some of the dorso-ventral muscles; see sections 4.2–4.4), the shortening of the metathorax and hind wings, and the coupling of fore and hind wings in flight. The above mentioned facts rather suggest that the enlarged SA.Sm of Ephemeroptera, in comparison to the conditions of the subalar-coxal muscle of Plecoptera, is a specialised homologue of the SA.Cm of Neoptera. MATSUDA (1970) assumed a homology of SA.Cm in Pterygota to a tergo-coxal muscle (62 sensu MATSUDA 1970) in *L. saccharina*.

Assuming that the SA.Sm is a specialised subalar-coxal muscle, one can also hypothesise that the subalar-furcal muscle (SA.Fm; t-s 4 sensu MATSUDA 1970) of Ephemeroptera is a split off from SA.Sm that evolved together with the specialisation of the subalare, since the SA.Fm is dorsally also attached to the PSA. Moreover, it is closely associated with the SA.Sm. A subalar-furcal muscle does not exist in the pterothorax of Plecoptera and other Neoptera. MATSUDA (1970) assumed that a subalar-furcal muscle is probably also present in certain Hymenoptera. A homology of SA.Fm to a muscle of *Lepismachilis* sp. or *Lepisma* sp. is not given by him. Assuming that SA.Fm is a specialised part of the SA.Sm it may also be homologous with muscle 62 (sensu MATSUDA 1970) of *L. saccharina*.

The homology of the subalar-sternal muscle (SA.Sm) and the subalar-furcal muscle (SA.Fm) of Ephemeroptera on the one hand to the subalar-coxal muscle (t-cx 8 sensu MATSUDA 1970) of Neoptera on the other hand is evident.

In Plecoptera there is a subalar-pleural muscle present, (ppm 56 sensu WITTIG 1955, t-p 16 sensu MATSUDA 1970), which extends between a small posterior sclerite (or the posterior part of the subalare; Fig. 125) and the ventral part of the epimeron. Such a muscle is not present in Ephemeroptera, but it occurs in lower Pterygota. Therefore, MATSUDA (1970) suggested a homology to a muscle of *Lepismachilis* (muscle 115 or 120 following MATSUDA

1970) that agrees approximately with the position of t-p 16. Consequently, the lack of a subalar-pleural muscle should be regarded as an apomorphic character of Ephemeroptera. MATSUDA (1970: 77, tab. 1) also considered the possibility of a new development in Pterygota. According to BRODSKY (1979b), the presence of the muscle t-p 16 can be attributed to the groundplan of Plecoptera. In my opinion this muscle is an apomorphic character of Metapterygota, and its absence in Ephemeroptera reflects the plesiomorphic condition.

At least three muscles are present in Odonata that could be homologised with subalar muscles. The muscles 32, 33 and 34 (sensu ASAHINA 1954) are dorsally associated with the ventral part of the axillary plate of the wing base (Figs. 62–65).

The first mentioned muscle (muscle 32) is the largest one. It is dorsally attached to the anterior part of the axillary plate by a tendon. According to MATSUDA (1970) this muscle (muscle 32; t-p 24 sensu MATSUDA 1970) is only present in Odonata. The dorsal point of attachment suggests that it is a subalar muscle since in larval Ephemeroptera, as well as in larval Plecoptera, the subalar muscles are attached to the pleural membrane immediately below the wing pad. The muscle 32 is probably the homologue of SA.Cm of Neoptera that shifted its ventral attachment as a result of a modification of the sternal and pleural elements. The ventral attachment is on the margin between katapisternum and epimeron (following ASAHINA 1954) next to the coxa.

Posterior to the muscle 32 are the dorsal points of attachment of the muscles 33 and 34. Both are rather small muscles that are attached to a small sclerite in the upper third of the membrane posterior to the pleural wing process. Each of the two muscles is also attached to the posterior part of the axillary plate, each by a tendon. According to MATSUDA (1970), both muscles (muscle 33 sensu ASAHINA 1954, t-p 25 sensu MATSUDA 1970; muscle 34 sensu ASAHINA 1954, and t-p 21 sensu MATSUDA 1970) are only present in Odonata. It would be conceivable that muscle 33 is either homologous with the subalar-coxal muscle as a separated and specialised part or rather, the homologue of the neopteran t-p 16. The latter assumption would be more parsimonious. Most likely the muscle 34 of Odonata is also the homologous part to t-p 16 (sensu MATSUDA 1970) of Neoptera. This assumption is supported by the fact that the subalare is located next to the ventral membrane of the wing pad and is fused with the axillary plate in Odonata as suggested also by ASAHINA (1954).

Furthermore, the attachment points of muscle 27 of Odonata suggest that it is most likely the homologous muscle to t-cx 8 of Neoptera. The dorsal attachment point is similar in both muscles 27 and 32. Thus, muscle 32 is probably a second, specialised part of the muscle 27.

MATSUDA (1970: 68f) hypothesised a tergal origin of

the subalar muscles (t-cx 8, t-p 16) since MAKI (1938) has shown that the future subalar-coxal muscle is dorsally attached to the lateral margin of the tergum in the late embryo of *Leucophaea* (Blattaria), or on the ventral base of the rudimentary wing in the early nymphal stages of *Locusta* (Orthoptera).

MATSUDA also wrote in the same paper that the number of prothoracic tergo-coxal muscles (where the subalare is missing) should be the same as in the pterothorax including the subalar-coxal muscle. According to him, this tendency ought to be recognisable in lower orders. He further stated (on p. 64) that in the nymph of *Perla*, according to WITTIG (1955), the subalar-pleural muscle (ppm 56, t-p 16) inserts on the posterior membrane near the area where the subalare (Flügelscheide) is later formed. WITTIG (1955), however, wrote that the muscle ppm 56 is attached to the posterior part of the pleural membrane.

The dorsal points of insertion of the subalar muscles in the examined larval mayflies and stoneflies (except the SA.Cm of Ephemeroptera) are close to the ventral membrane of the wing pads though never directly on the pterothoracic tergites. Therefore, a tergal origin of the subalar-coxal (and the respective subalar-sternal muscle of Ephemeroptera) and the subalare is conceivable but not obligatory. This assumption suggests that the wings are also of tergal origin and a duplication of the tergite.

In any case the musculature of *L. saccharina* has to be re-examined to assert the homologies of the subalar muscles and their basal precursors.

The dorsal point of attachment of SA.Cm in ephemeropteran larvae does not agree with the assumption of a tergal origin, since SA.Cm is attached to the pleural sclerite in ephemeropteran larvae (Fig. 56). It is probably even not homologous with the subalar-coxal muscle of Neoptera (see above).

In the metathorax of Ephemeroptera, the pleural sclerites and also the sternal elements are partly reduced or rather fused. Thus the subalar muscles of the metathorax are also reduced, and the furcasternum is either reduced or absent. In several Ephemeroptera both SA.Cm and SA.Sm are present and distinguishable in the metathorax. Both muscles are running close to each other, albeit the ventral attachment of the SA.Sm is on the coxa rather than on the furcasternite.

#### 4.4 Sister group relationships

(Figs. 126, 127)

##### General Remarks

There are three hypotheses on the basal splitting of Pterygota, namely the Chiasmomyaria hypothesis, the Palaeoptera hypothesis and the Metapterygota hypothesis (BECHLY et al. 2001; BÖRNER 1909; BOUDREAUX 1979; FÜRST VON LIEVEN 2000; GORB et al. 2000; HENNIG 1953, 1969;

HOVMÖLLER 2002; KRISTENSEN 1975, 1981, 1991; KUKALOVÁ-PECK 1978, 1983, 1985, 1991, 1998; LEMCHE 1940; MARTYNOV 1925; MATSUDA 1970; REHN 2003; SCHWANWITSCH 1943; SNODGRASS 1935; SOLDÁN 1997; STANICZEK 1996, 2000, 2001; WAGNER et al. 1996; WOOTTON 1979).

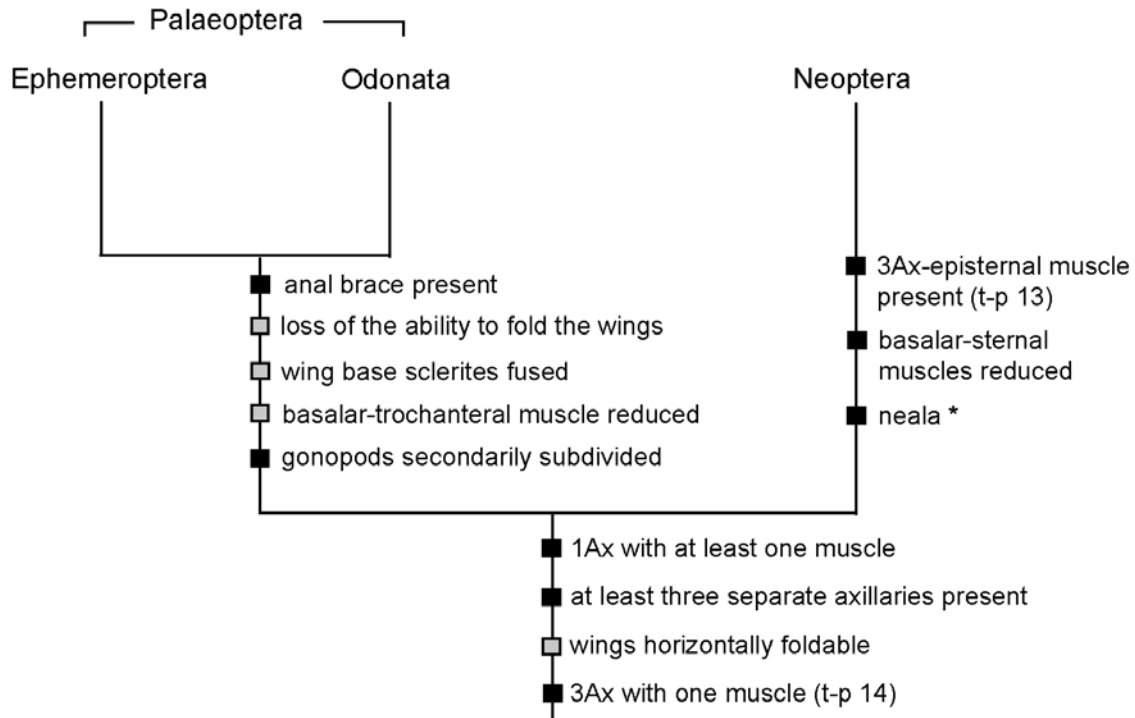
##### Chiasmomyaria hypothesis

The Chiasmomyaria hypothesis assumes a sister group relationship between Odonata and Ephemeroptera+Neoptera (LEMCHÉ 1940, SCHWANWITSCH 1943). This is based on different modes of wing pad development in both groups and also on the different development of the flight musculature. The first character is disputable because the wing pad development is inconsistent among Neoptera (HENNIG 1969, KUKALOVÁ-PECK 1978). In Odonata mainly the direct flight musculature is used, whereas in Ephemeroptera and Neoptera the indirect flight musculature is predominantly developed. A comparison with Zygentoma and Archaeognatha as outgroups implies that the direct flight musculature is an apomorphic feature of the Odonata. The indirect wing musculature is a ground plan character of Pterygota and therefore cannot be used as evidence for a sister group relationship between Ephemeroptera and Neoptera (PFAU 1986, KRISTENSEN 1981). Only the direct sperm transfer is a putative apomorphic character of Ephemeroptera and Neoptera, but also controversial because it is quite possible that the direct sperm transfer evolved convergently (BECHLY et al. 2001). In view of the large number of characters that support the Metapterygota or even the Palaeoptera hypothesis, a sister group relationship of Odonata to all other Pterygota is rather unlikely.

##### Palaeoptera hypothesis

The Palaeoptera hypothesis (MARTYNOV 1925) assumes that Ephemeroptera+Odonata is the sister group of Neoptera. The Palaeoptera are characterised by their inability to fold the wings horizontally over the abdomen (HENNIG 1969; KUKALOVÁ-PECK 1978, 1985; MARTYNOV 1925; WOOTTON 1979).

The proximate stem of the anterior and the posterior radial vein (R, Rs) are interpreted as plesiomorphic characters of the Palaeoptera. The fused medial stem is supposed to be the apomorphic condition shared by all Palaeoptera (including fossil taxa) (KUKALOVÁ-PECK & BRAUCKMANN 1990, KUKALOVÁ-PECK 1991). The common stem of the anterior cubital vein and the cubital sector as well as the intercalary veins are given as possible synapomorphic characters supporting the Palaeoptera hypothesis (KUKALOVÁ-PECK 1983, 1985, 1991, 1998; KUKALOVÁ-PECK & BRAUCKMANN 1990; RIEK & KUKALOVÁ-PECK 1984; STANICZEK 2001). Intercalary veins, however, are not present in the fossil odonatan taxon *Eugeropteron* (WILLMANN 2005). The common stem of the medial veins is probably a derived state. A basal fusion of the wing veins support rigid-



**Fig. 126.** Palaeoptera hypothesis, argumentation scheme of character evolution (modified after WILLKOMMEN & HÖRNSCHEMEYER 2007: fig. 24). – \* = character after MARTYNOV (1925); grey box = uncertain character; for further interpretation see section 4.4.

ity at the wing base and therefore, it is difficult to exclude a convergent evolution of this character. WAGNER et al. (1996) regarded the imaginal microsculpture of ephemeropteran and odonatan wings as an autapomorphy of Palaeoptera. A similar microsculpture, however, also occurs in Neuroptera (WAGNER et al. 1996).

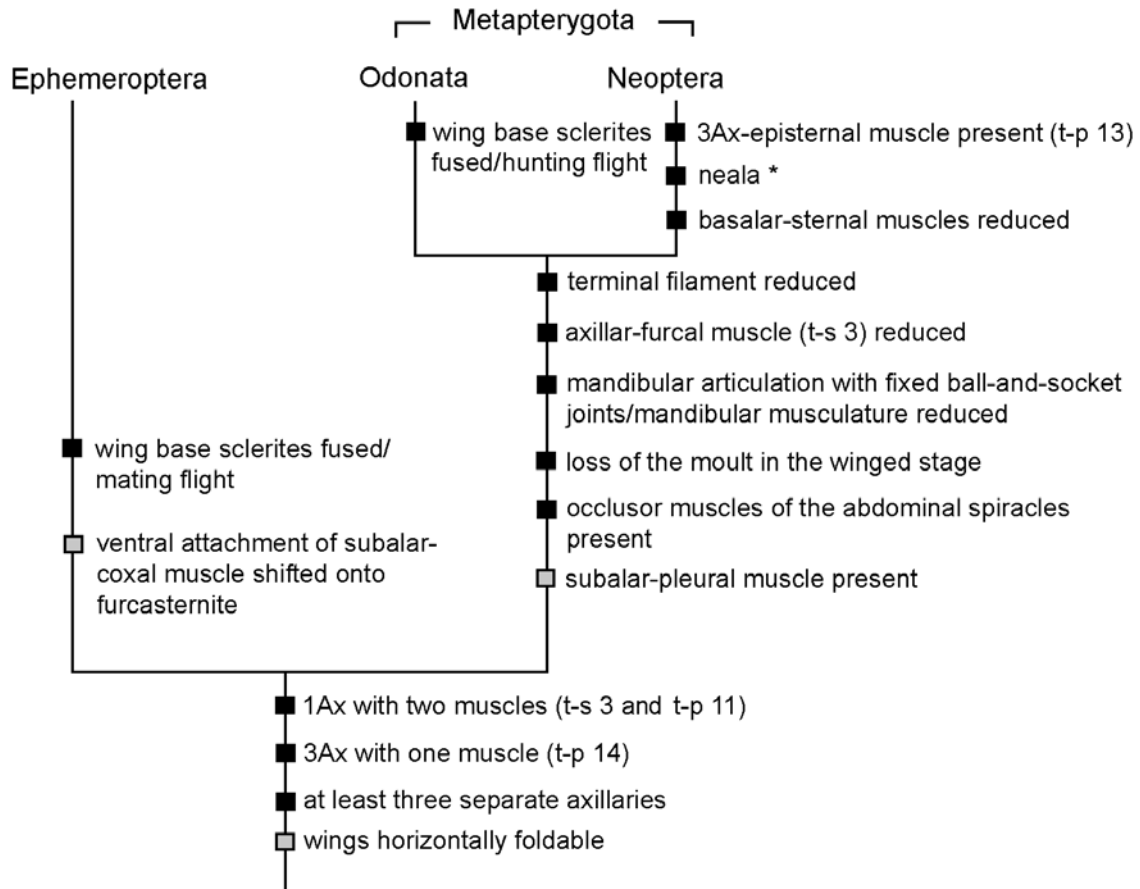
Nevertheless, it is problematic to take wing characters as apomorphies without the possibility to verify these characters in any of the basal outgroups.

The braces between the radial sector and the anterior medial vein (rp-ma), the brace between the medial vein and the cubitus (m-cu), and the brace between the posterior cubital veins and the anal vein (cup-aal) are considered as synapomorphies of Palaeoptera (KUKALOVÁ-PECK 1998). Except of the cup-aal brace, in stem group representatives of Ephemeroptera and Odonata all other braces are either present as simple cross veins (*Bojophlebia*) or even absent (*Eugeropteron*) (STANICZEK 2001). So these characters obviously evolved convergently and cannot be interpreted as synapomorphies of Palaeoptera (STANICZEK 2001). Moreover, the costal brace is possibly an autapomorphic character of Ephemeroptera (WILLMANN 1999). A further synapomorphic character of the Palaeoptera could be the paired penes (BECHLY et al. 2001) but it may be also interpreted as a plesiomorphic character of the Insecta (see STANICZEK 2001).

The short antennae in Ephemeroptera and Odonata (“Subulicornia”) evolved most likely convergently because long antennae were still present in *Namurotypus*, a stem group representative of Odonata (BECHLY et al. 2001, BRAUCKMANN & ZESSIN 1989).

The basalar-trochanteral muscle, which is present in Neoptera is absent in Ephemeroptera and Odonata. The assumption that the presence of this muscle is a ground plan character of Pterygota and the homologous structure to muscle 55 of *Lepisma* (MATSUDA 1970) suggests that it is secondarily reduced in Ephemeroptera and Odonata and supports the Palaeoptera hypothesis.

The paleopterous wing condition in Ephemeroptera and Odonata with their inability to fold the wings horizontally over the abdomen has been generally accepted as a symplesiomorphic character for a long time. Likewise, the presence of a wing flexor muscle in Neoptera is usually interpreted as derived character (MATSUDA 1970). This muscle running from the 3Ax to the pleurum allows the wing folding to a horizontal resting position over the abdomen. The arrangement and number of the wing base sclerites in Neoptera is also assumed as an apomorphy of Neoptera (MATSUDA 1970). On the other hand KUKALOVÁ-PECK (1983, 1987, 1991) assumed that the few wing base sclerites in Ephemeroptera and Odonata are the result of a secondary fusion. According to KUKALOVÁ-PECK (1983,



**Fig. 127.** Metapterygota hypothesis, argumentation scheme of character evolution (modified after WILLKOMMEN & HÖRNSCHEMEYER 2007: fig. 25). – \* = character after MARTYNOV (1925); for further interpretation see section 4.4.

1987, 1991), the wing base consists of 32 sclerites in the pterygote ground plan. As a consequence she considered the condition in the Ephemeroptera and Odonata as apomorphic. With reference to KUKALOVÁ-PECK (1974b), BOUDREAUX (1979) also suggested that the sclerites of the wing base in Ephemeroptera are probably a result of a secondary fusion correlated with their weak flight ability. Yet the paleopterous wing resting position was assumed as a primitive character of mayflies by BOUDREAUX (1979).

The fossil Diaphanopteroidea are generally classified within the otherwise paleopterous Palaeodictyoptera, although they are characterised by the ability to fold the wings horizontally over the abdomen (KUKALOVÁ-PECK 1974a, 1974b). Given the fact that all three basal extant pterygote lineages exhibit the t-p 14 (the wing flexor muscle, which is said to be responsible for the horizontal wing flexion in Neoptera), it seems to be straightforward to assume that the horizontal wing folding is a ground plan character of Pterygota. Nevertheless, due to the different wing base elements of Diaphanopteroidea and Neoptera most authors assumed that the ability to fold the wings

horizontally over the abdomen evolved convergently (KUKALOVÁ-PECK 1974a, 1974b, 1978, 1983; WOOTTON 1979; WOOTTON & KUKALOVÁ-PECK 2000). In contrast, BRODSKY (1994), KUKALOVÁ-PECK (1991), RASNITSYN (2002) and WILLMANN (1998) assumed a loss of the ability to fold the wings horizontally over the abdomen in Odonata and Ephemeroptera (see section 4.4). This assumption suggests wing folding as a ground plan character of Pterygota. The Lepidoptera, however, are an indication that this scenario could be quite possible. Within this taxon, the Papilionoidea lost the ability to fold the wings horizontally over the abdomen. The Papilionoidea are also characterised by a flight behaviour that includes short phases of gliding flights with locked wing positions. Yet the wing base elements are not fused in the Papilionoidea (IVANOV 1995, 1996, 1997; SHARPLIN 1963a, b).

Following KUKALOVÁ-PECK (1983, 1987, 1991), BRODSKY (1994) hypothesised a fusion of the wing base sclerites in Ephemeroptera and Odonata, but originating from a condition that was more similar to the neopteran wing base with only few wing base sclerites.

A synapomorphic fusion of the wing base sclerites in Ephemeroptera and Odonata cannot be excluded but is rather unlikely. Both Ephemeroptera and Odonata have a flight system that is specialised in different ways: Ephemeroptera have a reduced metathorax with small or even absent hind wings. Both hind and fore wings are coupled in flight. Furthermore, Ephemeroptera are characterised by a specialised mating flight that is usually performed along a more or less vertical axis. Odonata are adapted to a manoeuvrable hunting flight. Meso- and metathorax of Odonata are fused to an obliquely orientated synthorax. Together with the legs it forms the characteristic capture apparatus.

Thus all the characters mentioned above are autapomorphic for the Ephemeroptera and Odonata, respectively. The different adaptations to dissimilar flight behaviour are reflected by the fusion of 2Ax with PMP in the Ephemeroptera on the one hand and the fusion of at least 2Ax and 3Ax with PMP in Odonata on the other hand. This may suggest that the strengthening of the wing base in both taxa evolved independently in both lineages.

#### Metapterygota hypothesis

The Metapterygota hypothesis assumes a sister group relationship between Ephemeroptera and Metapterygota (Odonata+Neoptera). It is supported by the following apomorphic characters of the Metapterygota: Mandibular articulation with fixed ball-and-socket joints, reduction of the *Musculus mandibulo-hypopharyngealis*, reduction of several mandibular abductor and adductor muscles, and the presence of occlusor muscles of the abdominal spiracles (BÖRNER 1909; FÜRST VON LIEVEN 2000; HENNIG 1953; KRISTENSEN 1975, 1981, 1991; STANICZEK 2000, 2001). Furthermore, Odonata and Neoptera lack the ecdysis in a winged stage and the terminal filament is reduced (EDMUNDS & McCAFFERTY 1988, KRISTENSEN 1981, STANICZEK 2001). According to WILLMANN (2005) a modified terminal filament is present in the fossil odonatan taxon *Namurotypus*. Consequently this character should not be upheld as synapomorphy of the Metapterygota.

According to MATSUDA (1970) an axillar-furcal muscle is only present in Ephemeroptera but lost in Metapterygota, suggesting a closer relationship of Odonata+Neoptera.

The development of a subalar-pleural muscle is also regarded as a potential apomorphy of Metapterygota, because this muscle is present in Odonata and Plecoptera.

The pleural arm and its associated muscle p-s 1 sensu MATSUDA (1970), which is attached to the furca ventrally are probably ground plan characters of Dicondylia. Both characters are absent in Ephemeroptera and adult Odonata. The presence of this muscle in larval Odonata, however, may indicate that the reduction of the pleural arm and the associated muscle in adult Ephemeroptera and Odonata evolved independently.

The subalar-sternal muscle (SA.Sm) is generally assumed to be only present in mayflies (BRODSKY 1994). The dorsal attachment and ontogenetical development of the subalar-sternal muscle in larval Ephemeroptera is, however, identical to that of the subalar-coxal muscle of larval Plecoptera (see section 4.3.7). So I assume these muscles to be homologous. It is, however, not clear whether the ventral attachment at the furcasternum (in Ephemeroptera) or at the posterior coxal rim (in Odonata and Neoptera) represents the groundplan condition of Pterygota. According to BRODSKY (1974) the sternal attachment of this muscle represents a specialisation of the wing apparatus of Ephemeroptera. Indeed, the enlargement of the SA.Sm that obviously took place in Ephemeroptera might be correlated with an enlargement of its points of attachments. As a consequence, the subalare of Ephemeroptera got enlarged and the SA.Sm shifted ventrally to the furcasternum. In any case a putative loss of the subalar-sternal muscle as autapomorphy of Metapterygota cannot be uphold anymore, as a homologue of this muscle is present in both Odonata and Neoptera.

Ephemeroptera and Odonata have two anterior “basalar muscles” that are attached to the crescent-shaped sclerite in Ephemeroptera (BA.SmS/BA.SmI) and to the anterior part of the humeral plate in Odonata (muscles 21 and 22). These two muscles are without much doubt homologous in Ephemeroptera and Odonata. Homologous muscles are most likely not present in Neoptera but in Zygentoma. Therefore, the presence of these muscles is a sympleiomorphic character of Ephemeroptera and Odonata. The absence of these muscles is an apomorphic character of Neoptera. Thus, neither presence nor absence of the so-called basalar-sternal muscles is citable as a character supporting the Palaeoptera or the Metapterygota hypothesis.

Previous authors (e.g. HENNIG 1969, GULLAN & CRANSTON 2005) assumed that the low amount of wing base sclerites represents a primitive condition: Ephemeroptera have a free 1Ax and a partly free 3Ax, whereas in Odonata only one free wing base sclerite is present. However, as shown above, Ephemeroptera and Odonata are in all probability apomorphic concerning the wing base sclerites, i.e. the sclerites are partially fused. This does not necessarily imply a synapomorphic fusion in Ephemeroptera and Odonata. Morphological characters (absence of the subimago, mandible characters including autapomorphic characters of Metapterygota; compare STANICZEK 2001) rather support a sister group relationship of Odonata+Neoptera (Metapterygota). Based on the current knowledge it is rather unlikely to assume a homologous fusion of the wing base sclerites. Moreover, the Ephemeroptera and Odonata are adapted to different types of flight by reason of different flight behaviour. BRODSKY (1994) mentioned that the development of gliding flight was accompanied by the development of platforms in the

wing bases. He assumed an independent occurrence in Ephemeroptera and Odonata. Surely, it is not impossible to hypothesise a homologous fusion of the wing base sclerites in Ephemeroptera and Odonata, though it is rather unlikely (see above).

#### 4.5 Evolution of the wing folding mechanism

Both Ephemeroptera and Odonata are adapted to special kinds of flight. Odonata are adroit and extremely manoeuvrable flying hunters. They have a remarkably adapted morphology of the pterothoracic sclerites and flight musculature.

The flight system of Ephemeroptera is characterised by a specialised mesothorax with a large dorsal longitudinal muscle and a small metathorax with short hind wings. Shortly after their emergence the Ephemeroptera begin their impressive nuptial dances. Associated with the swarming behaviour the Ephemeroptera are adapted to a special gliding flight and parachuting and especially males are adapted to a persistent vertical mating flight BRODSKY (1973, 1994). BRODSKY (1973) distinguished between four types of swarming. In the first type of swarming the emergence of the subimago may be more or less prolonged in time (e.g. Baetidae, Ephemerellidae, Ephemeridae, Leptophlebiidae, Siphonuridae). Oligoneuriidae, Palingeniidae and Polymitarcyidae have a swarming behaviour where the nuptial dances take place in form of a rapid horizontal flight usually close to the surface of the water. FISCHER (1991) differentiated between eight types of swarming dependent on the trajectory of the mayflies. The ability to lock the wings in the gliding position correlates with the presence of SA.Fm, Ax.Fm and Ax.PmI or rather at least one of those muscles (BRODSKY 1974). Usually, only males are known to perform the vertical nuptial dances. FISCHER also noticed a vertical flight in some female specimens. Therefore, the ability to lock the wings in the gliding position as well as the presence of SA.Fm, Ax.Fm and Ax.PmI is expected to exist also in female specimens.

According to FISCHER (1991), the problems resulting from the inability to fold the wings horizontally over the abdomen (such as no longer being able to hide from hunters in crevices, being caught in cobwebs etc.) are negligible when living dependent on a substrate. Mayflies spend indeed a lot of their adult life span in the air. The inability to fold the wing does not have to be necessarily only a disadvantage. Furthermore, the steep upward flights and the perpendicular gliding flights are – according to FISCHER – only attainable with a morphological specialisation. The loss of the wing folding for example would be conceivable as such a specialisation.

The dorsal longitudinal muscles of the mesothorax of Ephemeroptera are enlarged and require at least one-half of the height of the mesothorax. The metathorax, in con-

trast, is short, bearing short hind wings not exceeding one half of the fore wing length. The hind wings are often coupled with the fore wings in flight. Compared to other pterygote insects this is an apomorphic condition. Also the Odonata show apomorphic conditions in their flight system, e.g. the fusion of both meso- and metathorax to the characteristic synthorax, correlated with the hunting flight.

Regarding the specialisations of the ephemeropteran and odonatan flight systems, concerning their flight behaviour, it can be hypothesised that the wing base is secondarily stiffened in both taxa. The wing base elements of Ephemeroptera are at least partly a result of a secondary fusion (2Ax+PMP, see above), the 3Ax is closely associated with BP (2Ax+PMP) and both the anal and costal brace support more stability at the wing base during gliding flight. This assumption is also supported by the fact that the wing veins in fossil mayflies, the Protereismatidae, are distinct even to the point of the wing base (KUKALOVÁ-PECK 1974b). Large and apparently functional mouthparts were still present in Permian mayflies. Based on this knowledge KUKALOVÁ-PECK (1974b: 420f) believed that the horizontal flight was more important in these taxa than in extant Ephemeroptera. Furthermore, she supposed that the obliteration of the adjacent stems probably occurred later in evolution.

In the present work it is assumed that the wing base in the ground plan of Pterygota consists of four separate sclerites that are arranged approximately as in the extant Plecoptera.

If one assumes that the Palaeoptera is monophyletic and the inability to fold the wings horizontally over the abdomen is a plesiomorphic character, the question remains if the secondary fusion of the wing base sclerites in Ephemeroptera and Odonata evolved convergently or as a synapomorphy of both taxa.

Currently, there are more characters supporting the Metapterygota hypothesis. Based on this assumption the evolutionary pathway of wing base development in Pterygota is assumed as follows: The wing base in the ground-plan of Pterygota is composed of four wing base sclerites (1Ax, 2Ax, 3Ax, PMP). Convergently, the wing base is strengthened and different elements are partially fused in Ephemeroptera and Odonata. In Ephemeroptera the wing base is stiffened (2Ax+PMP) as an adaptation for the vertical mating flight and for the parachuting phases in flight. In contrast the wing base elements of Odonata may be fused (at least 2Ax+PMP+3Ax) as an adaptation to their highly manoeuvrable hunting flight.

In consideration of the special kinds of flight in Ephemeroptera and Odonata together with the presence of an axillar-pleural muscle (t-p 14) in both orders, which is homologous with one of the wing flexor muscles in Neoptera, it is a legitimate question whether the inability



to fold the wings horizontally over the abdomen is a plesiomorphic or an apomorphic character. If one assumes a wing base configuration almost similar to that of the Plecoptera in the ground plan of Pterygota, horizontal wing folding may also have been possible.

Already BRODSKY (1970: 188) summarised that all the elements needed for horizontal wing folding are present on the mesothorax of *E. vulgata*: a third axillary sclerite, a pleuroalar muscle and an anal-jugal wing fold. However, the function of these formations differs from their function in insects of other orders, which fold their wings over the abdomen. According to BRODSKY (1994: 91), Ephemeroptera and Odonata have lost the ability to fold their wings; consequently, the muscle t-p 14 has changed its function.

The fossil Diaphanopteroidea combine apomorphic characters of the Palaeodictyoptera (haustellate mouthparts) with the ability to fold the wings horizontally over the abdomen (KUKALOVÁ-PECK 1974a). Therefore, this author assumed that wing folding arose at least twice in insects (KUKALOVÁ-PECK 1974a, 1974b; KUKALOVÁ-PECK & BRAUCKMANN 1990). WOOTTON (1979, 1981) and WOOTTON & KUKALOVÁ-PECK (2000) come to the same conclusion. Unlike these assumptions WILLMANN (1998: 274) suggested that the ability to fold the wings horizontally over the abdomen could be a plesiomorphic condition and that there is no need to view wing folding in the Neoptera and Diaphanopteroidea as a result of convergence. This scenario could be indeed quite possible.

A loss of the ability to fold the wings in Ephemeroptera is also assumed by BRODSKY (1994) and RASNITSYN (2002). The latter wrote that a loss of the wing flexing is supported by the fact that Ephemeroptera retain a suture that separates the posterior articulatory process of the basal plate (equivalent to s3 or 3Ax of the present study) and the rest of the basal plate, which precludes flexibility. Following this author, the posterior articulatory process, however, is clearly the 3Ax and the mentioned suture is actually not a suture but the border between the two, mostly separate, sclerites, i.e. the BP and the 3Ax. Nevertheless, the morphology of the ephemeropteran wing base enables indeed no flexibility.

If one assumes that wing folding is a plesiomorphic character and that the Metapterygota are monophyletic, the ability to fold the wings was lost at least three times during the early evolution of the Pterygota. A convergent loss of the ability to fold the wings horizontally is in any case also present in the holometabolous Papilionidae (Neoptera: Lepidoptera) (IVANOV 1996).

The hypothesis that wing folding is a plesiomorphic character of Pterygota is not supported by paleontological evidence. The fossil Palaeodictyoptera (sensu GRIMALDI & ENGEL 2005) is often treated as a monophyletic group that is characterised by its haustellate mouthparts (KUKA-

LOVÁ-PECK 1991). This taxon presumably contains the paraphyletic Palaeodictyoptera (GRIMALDI & ENGEL 2005, BECHLY pers. comm.), the Megasecoptera, the Diaphanopteroidea and the Permothemistida. That means that the ability to move the wings to a resting position over the abdomen must have been reduced several times within the paraphyletic Palaeodictyoptera, in the Ephemeroptera, and in the Odonata. Nevertheless, according to WILLMANN (2003) the Palaeodictyoptera may be a paraphyletic assemblage, as the presence of haustellate mouthparts is not confirmed in all taxa of Palaeodictyoptera. As a consequence it remains difficult to include these fossil taxa into the present argumentation until better information on their character distribution is available and the relationships among fossil taxa become better resolved.

## 5 Conclusions and future prospects

The wing base in the ground plan of Pterygota is most likely composed of four wing base sclerites. Three of these four sclerites are the first axillary (1Ax), the second axillary (2Ax) and the third axillary (3Ax). In all probability the proximal median plate (PMP) is also a ground plan character of Pterygota. The 1Ax and the 3Ax are equipped with muscles. At least one muscle running to the pleurum inserts at the 1Ax. This muscle is present in Ephemeroptera and in Plecoptera. Most likely, a second muscle running from the 1Ax to the furca is present in the pterygote ground plan. This muscle is retained only in Ephemeroptera. Furthermore, a muscle running from the upper part of the pleurum to the 3Ax is present in the pterygote ground plan (t-p 14 sensu MATSUDA 1970). This muscle is one of the wing flexor muscles of Neoptera but it is also present in the wing bases of Ephemeroptera and Odonata. In Plecoptera two muscles are attached to the 3Ax (t-p 13 and t-p 14). Muscle t-p 13 sensu MATSUDA (1970) is most likely a ground plan character of Neoptera.

The wing base of Ephemeroptera is composed of sclerites that can be homologised with the axillaries of Neoptera. The 1Ax is provided with two muscles in primordial Ephemeroptera. The 2Ax is fused to the basal plate (BP) in Ephemeroptera. The BP of Ephemeroptera is most likely a product of a fusion of the base of the anterior radial vein, the proximal median plate and the 2Ax. The 3Ax of Ephemeroptera is tightly connected to the basal plate but not completely fused to it, even in basal Ephemeroptera.

The anterior humeral plate of the wing base of Odonata is probably composed of the humeral plate (HP) and of a sclerite that is homologous to the so-called basalar sclerite of Ephemeroptera. Two muscles are attached to the lateral area of the humeral plate by a tendon. These two muscles are probably homologous to the BA.SmS and BA.SmI of Ephemeroptera. The axillary plate of the Odo-

nata is in all probability a result of a fusion of the 2Ax, the PMP and the 3Ax. The posterior area of the axillary plate (3Ax) serves as the insertion point of a short muscle that is homologous to the t-p 14 sensu MATSUDA (1970). The small sclerite that lies proximal to the humeral plate is rather a part of the prescutum than the 1Ax, as has been previously suggested (TANNERT 1958). A muscle running from the 1Ax to the pleurum was absent in the examined Odonata. Moreover, a sclerite homologous to the 1Ax of Neoptera is not obvious in the wing base of Odonata.

The basalar muscles (BA.SmS, BA.SmI and BA.Cm) of Ephemeroptera are of tergal origin. The so-called basalar-pleural muscle (BA.Pm) of Ephemeroptera is not a true basalar muscle. It is homologous with a short muscle that is attached to a tergal sclerite in Odonata (muscle 28) and to t-p 4, which is attached to the subtegula in Neoptera. A basalar-trochanteral muscle (BA.Trm), which was described in previous contributions, was not found in any of the examined Ephemeroptera.

The subalar-sternal muscle (SA.Sm) of Ephemeroptera is characterised by the same ontogenetically development in larvae as the subalar-coxal muscle of Neoptera (t-cx 8), whereas the subalar-coxal muscle (SA.Cm) of Ephemeroptera shows a different origin to t-cx 8 of Neoptera. This suggests that the subalar-coxal muscle of Ephemeroptera is not homologous to t-cx 8 of Neoptera. The SA.Sm of Ephemeroptera, however, is clearly homologous to t-cx 8 of Neoptera, rather than being a primitive muscle, which is only present in Ephemeroptera and absent in Neoptera.

The wing base structure and also the morphology of the pterothorax and the specialised flight musculature of Ephemeroptera and Odonata, together with their flight behaviour, suggest that these taxa are more advanced than previously assumed. Furthermore, the inability to fold the wings horizontally over the abdomen could be a result of a secondary strengthening and partially fusion of the wing base sclerites. The Plecoptera, usually regarded as sister-group to the remaining Neoptera or of the remaining Polyneoptera, are most likely very close to the ground plan of the Pterygota in many respects.

The innervation of the muscles associated with the basalar-complex of Ephemeroptera, Odonata and Neoptera should be further examined to verify their homology. The musculature and the innervation of the muscles in Zygentoma should be examined with particular attention paid to the muscles that are homologised with those of Pterygota. Additionally, the fate of prospective thoracic muscles in the larvae of basal pterygotes may possibly be investigated to gain more clues on their homologies in the future.

The comparison of the basalar and subalar complex of Lepidoptera and Ephemeroptera could be rewarding from a point of comparative functional morphology.

Besides a more detailed morphological comparison of Zygentoma and Pterygota, the unravelling of the relationships among the Palaeodictyoptera would be of great value to gain new arguments for a decision between the Palaeoptera or Metapterygota hypothesis.

## 6 References

- ASAHINA, S. (1954): A morphological study of a relic dragonfly *Epiophlebia superstes* Selys (Odonata, Anisozygoptera), 153 pp.; Tokyo (Japan society for the promotion of science).
- BARLET, J. (1953): Morphologie du thorax de *Lepisma saccharina* L. (Apterygote Thysanoure). II. Musculature 1. – Bulletin et Annales de la Société entomologique de Belgique **89**: 214–236.
- BARLET, J. (1954): Morphologie du thorax de *Lepisma saccharina* L. (Apterygote Thysanoure). II. Musculature 2. – Bulletin et Annales de la Société entomologique de Belgique **90**: 299–321.
- BARLET, J. (1967): Squelette et musculature thoracique de *Lepismachilis y-signata* Kratochvil (Thysanoures). – Bulletin et Annales de la Société entomologique de Belgique **103**: 110–157.
- BECHLY, G. (1996): Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer Berücksichtigung der phylogenetischen Systematik und des Grundplanes der Odonata. – Petalura (special volume) **2**: 402 pp.
- BECHLY, G. (1999): Phylogeny and systematics of fossil dragonflies (Insecta: Odonatoptera) with special reference to some Mesozoic outcrops. – Ph.D. thesis, Eberhard-Karls-Universität Tübingen, X+755 pp.
- BECHLY, G., BRAUCKMANN, C., ZESSIN, W. & GRÖNING, E. (2001): New results concerning the morphology of the most ancient dragonflies (Insecta: Odonatoptera) from the Namurian of Hagen-Vorhalle (Germany). – Journal of zoological Systematics and evolutionary Research **39**: 209–226.
- BEKKER, E. G. (1954): Concerning the origin and development of the insect wing. Part 2. Concerning the structure, mechanics and origin of the flight apparatus of mayflies (Ephemeroptera). – Vestnik Moskovskogo Universiteta, Serija fiziko-matematicheskikh i estestvennykh Nauk **3** (5): 119–130.
- BÖRNER, C. (1909): Neue Homologien zwischen Crustaceen und Hexapoden. Die Beißmandibel der Insekten und ihre phylogenetische Bedeutung. Archi- und Metapterygota. – Zoologischer Anzeiger **34**: 100–125.
- BOUDREAUX, H. B. (1979): Arthropod phylogeny, with special reference to insects, 328 pp.; New York (John Wiley & Sons).
- BRAUCKMANN, C. & ZESSIN, W. (1989): Neue Meganeuridae aus dem Namurium von Hagen-Vorhalle (BRD) und die Phylogenie der Meganisoptera. – Deutsche entomologische Zeitschrift (Neue Folge) **36**: 177–215.
- BRODSKY, A. K. (1970): Organization of the flight system of the mayfly *Ephemera vulgata* L. (Ephemeroptera). – Entomological Review **49** (2): 184–188.
- BRODSKY, A. K. (1971): An experimental study of flight in the mayfly *Ephemera vulgata* L. (Ephemeroptera). – Entomological Review **50** (1): 25–29.
- BRODSKY, A. K. (1973): The swarming behavior of mayflies (Ephemeroptera). – Entomological Review **52** (1): 33–39.
- BRODSKY, A. K. (1974): Evolution of the wing apparatus in the Ephemeroptera. – Entomological Review **53** (2): 35–43.
- BRODSKY, A. K. (1975): Kinematics of mayfly wings motion and

- analysis of the mechanism of output power regulation. – *Zoologicheskij Zhurnal* **54**: 209–220 [in Russian].
- BRODSKY, A. K. (1979a): Evolution of the flight apparatus in Plecoptera. Part I. Functional morphology of the wings. – *Entomological Review* **58** (1): 31–36.
- BRODSKY, A. K. (1979b): Evolution of the flight apparatus in Plecoptera. Part II. Functional morphology of the axillary apparatus, the skeleton, and the musculature. – *Entomological Review* **58** (4): 16–26.
- BRODSKY, A. K. (1986): Flight of the gigantic stonefly *Allonarcys sachalina* (Plecoptera, Pteronarcyidae) and the study of the wing supination mechanism in insects. – *Zoologicheskij Zhurnal* **65**: 349–360 [in Russian].
- BRODSKY, A. K. (1992): Structure, functioning and evolution of tergum in alate insects. II. Peculiarities of organization of a wing-bearing tergal plate in insects of different orders. – *Entomologicheskoe Obozrenie* **71**: 39–59 [in Russian].
- BRODSKY, A. K. (1994): The evolution of the insect flight, 248 pp.; Oxford (Oxford University Press).
- BROWNE, D. J. & SCHOLTZ, C. H. (1994): The morphology and terminology of the hind wing articulation and wing base of the Coleoptera, with specific reference to the Scarabaeoidea. – *Systematic Entomology* **19**: 133–143.
- BROWNE, D. J. & SCHOLTZ, C. H. (1995): Phylogeny of the families of Scarabaeoidea (Coleoptera) based on characters of the hindwing articulation, hind wing base and wing venation. – *Systematic Entomology* **20**: 145–173.
- BROWNE, D. J. & SCHOLTZ, C. H. (1996): The morphology of the hind wing articulation and wing base of the Scarabaeoidea (Coleoptera) with some phylogenetic implications. – *Bonner zoologische Monographien* **40**: 200 pp.
- CARPENTER, F. M. (1963): Studies on Carboniferous insects from Commeny, France. Part IV. The genus *Triplosoba*. – *Psyche* **70**: 120–128.
- CARPENTER, F. M. (1979): Lower Permian insects from Oklahoma. Part 2. Orders Ephemeroptera and Palaeodictyoptera. – *Psyche* **86**: 261–290.
- CARPENTER, F. M. (1987): Review of the extinct family Syntonopteridae (order uncertain). – *Psyche* **94**: 373–388.
- CARPENTER, F. M. (1992): Order Ephemeroptera. – In: KAESLER, R. L., BROSIUS, E., KEIM, J. & PRIESNER, J. (eds.): Treatise on invertebrate Paleontology, Part R, Arthropoda 4, Volume 3: Superclass Hexapoda, pp. 19–26; Kansas (Geological Society of America, Inc. and University of Kansas).
- CLARK, H. W. (1940): The adult musculature of the Anisopterous dragonfly thorax (Odonata, Anisoptera). – *Journal of Morphology* **67**: 523–565.
- COMSTOCK, J. H. & NEEDHAM, J. G. (1898): The wings of insects. – *American Naturalist* **1898**: 32, 43–48, 81–89, 231–257, 335–340, 413–424, 561–565, 769–777, 903–911.
- COMSTOCK, J. H. & NEEDHAM, J. G. (1899): The wings of insects. – *American Naturalist* **1899**: 33, 117–126, 573–582, 845–860.
- COMSTOCK, J. H. (1918): The wings of insects, 430 pp.; Ithaca, New York (Comstock Publishing Co.).
- CRAMPTON, G. C. (1914): The ground plan of a typical thoracic segment in winged insects. – *Zoologischer Anzeiger* **44**: 56–67.
- CRAMPTON, G. C. (1918): The thoracic sclerites of immature pterygotan insects, with notes on the relationships indicated. – *Proceedings of the entomological Society of Washington* **20**: 39–65.
- CREMER, E. (1934): Anatomische, reizphysiologische und histologische Untersuchungen an der imaginalen und larvalen Flugmuskulatur der Odonaten. – *Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere* **54**: 191–223.
- DUDLEY, R. (2002): The biomechanics of insect flight: form, function, evolution, 536 pp.; Princeton (Princeton University Press).
- DÜRKEN, B. (1907): Die Tracheenkiemen-Muskulatur der Ephemeren unter Berücksichtigung der Morphologie des Insektenflügels. – *Zeitschrift für wissenschaftliche Zoologie* **87**: 119 pp.
- EDMUNDS, G. F. & McCAFFERTY, W. P. (1988): The mayfly subimago. – *Annual Review of Entomology* **33**: 509–529.
- EDMUNDS, G. F. & TRAVER, J. R. (1954): Entomology – the flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. – *Journal of the Washington Academy of Sciences* **44**: 390–400.
- FISCHER, C. (1991): Evolution des Schwarmfluges und Flugverhalten der Ephemeropteren. – Ph.D. thesis, Universität Erlangen-Nürnberg, 171 pp.
- FORBES, W. T. M. (1943): The origin of wings and venational types in insects. – *American Midland Naturalist* **29**: 381–405.
- FÜRST VON LIEVEN, A. (2000): The transformation from moncondylous to dicondylous mandibles in the Insecta. – *Zoologischer Anzeiger* **239**: 139–146.
- GORB, S. N., KESEL, A. & BERGER, J. (2000): Microsculpture of the wing surface in Odonata: evidence for cuticular wax covering. – *Arthropod Structure & Development* **29**: 129–135.
- GRANDI, M. (1947): Contributi allo studio degli “Efemeroidi” italiani. VIII. Gli scleriti ascellari (pseudopteralia) degli Efemeroidi, loro morfologia e miologia comparate. – *Bollettino dell’Istituto di Entomologia della Università degli Studi di Bologna* **16**: 85–114.
- GRIMALDI, D. (2001): Insect evolutionary history from HANDLIRSCH to HENNIG, and beyond. – *Journal of Paleontology* **75**: 1152–1160.
- GRIMALDI, D. & ENGEL, M. S. (2005): Evolution of the Insects, 772 pp.; Cambridge (Cambridge University Press).
- GULLAN, P. J. & CRANSTON, P. S. (2005): The insects. An outline of entomology, 505 pp.; Davis, USA (Blackwell Publishing).
- HAAS, F. & KUKALOVA-PECK, J. (2001): Dermaptera hind wing structures and folding: New evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). – *European Journal of Entomology* **98**: 445–509.
- HAMILTON, K. G. A. (1971): The insect wing. Part I. Origin and development of wings from notal lobes. – *Journal of the Kansas entomological Society* **44**: 421–433.
- HAMILTON, K. G. A. (1972a): The insect wing. Part II. Vein homology and the archetypal wing. – *Journal of the Kansas entomological Society* **45**: 54–58.
- HAMILTON, K. G. A. (1972b): The insect wing. Part III. Venation of the orders. – *Journal of the Kansas entomological Society* **45**: 145–162.
- HAMILTON, K. G. A. (1972c): The insect wing. Part IV. Venational trends and the phylogeny of the winged orders. – *Journal of the Kansas entomological Society* **45**: 295–308.
- HATCH, G. (1966): Structures and mechanics of the dragonfly pterothorax. – *Annals of the entomological Society of America* **59**: 702–714.
- HENNIG, W. (1953): Kritische Bemerkungen zum phylogenetischen System der Insekten. – *Beiträge zur Entomologie* **3**: 1–85.
- HENNIG, W. (1969): Die Stammesgeschichte der Insekten, 436 pp.; Frankfurt am Main (Waldemar Kramer).
- HÖRNSCHEMEYER, T. (1998): Morphologie und Evolution des Flügelgelenks der Coleoptera und Neuropterida. – *Bonner zoologische Monographien* **43**: 126 pp.
- HÖRNSCHEMEYER, T. (2002): Phylogenetic significance of the

- wing-base of the Holometabola (Insecta). – *Zoologica Scripta* **31**: 17–29.
- HÖRNSCHEMEYER, T. (2004): Die Phylogenie der Archostemata (Insecta: Coleoptera) und die Evolution der Flügelbasis der holometabolen Insekten. – Professorial thesis, Georg-August-Universität Göttingen, 265 pp.
- HÖRNSCHEMEYER, T., BEUTEL, R. G. & PASOP, F. (2002): Head structures of *Priacma serrata* Leconte (Coleoptera, Archostemata) inferred from X-ray tomography. – *Journal of Morphology* **252**: 298–314.
- HOVMÖLLER, R., PAPE, T. & KÄLLERSJÖ, M. (2002): The Palaeoptera problem: basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. – *Cladistics* **18**: 313–323.
- HUBBARD, M. D. (1990): Mayflies of the world. A catalog of the family and genus group taxa (Insecta: Ephemeroptera), 119 pp.; Gainesville, Florida (Sandhill Crane Press).
- IVANOV, V. D. (1995): Comparative analysis of wing articulation in archaic Lepidoptera. – *Entomological Review* **74** (7): 32–53.
- IVANOV, V. D. (1996): Wing articulation in lepidopterans and status of Macrolepidoptera. – *Entomological Review* **76** (5): 592–602.
- IVANOV, V. D. (1997): Wing articulation in whites (Lepidoptera, Pieridae). – *Entomological Review* **78** (6): 667–681.
- KLUGE, N. J. (1993): New data on mayflies (Ephemeroptera) from fossil Mesozoic and Cenozoic resins. – *Palaeontological Journal* **27** (1A): 35–49.
- KLUGE, N. J. (1994): Pterothorax structure of mayflies (Ephemeroptera) and its use in systematics. – *Bulletin de la Société entomologique de France* **99**: 41–61.
- KLUGE, N. J., STUDEMANN, D., LANDOLT, P. & GONSER, T. (1995): A reclassification of Siphonuroidea (Ephemeroptera). – *Mitteilungen der schweizerischen entomologischen Gesellschaft* **68**: 103–132.
- KLUGE, N. J. (2000): *Sovremennaya sistematika nasekomyh* [Modern systematics of insects]. Part 1, 333 pp.; St. Petersburg (Lan) [in Russian].
- KLUGE, N. J. (2004): The phylogenetic system of Ephemeroptera, 456 pp.; Dordrecht (Kluwer Academic Publishers).
- KNOX, V. (1935): The body-wall and musculature of the thorax. – In: NEEDHAM, J. G., TRAYER, J. R. & HSU, Y.-C. (eds.): *The biology of mayflies*, pp. 135–178; New York (Comstock Publishing Co.).
- KRISTENSEN, N. P. (1975): The phylogeny of hexapod “orders”. A critical review of recent accounts. – *Zeitschrift für zoologische Systematik und Evolutionsforschung* **13**: 1–44.
- KRISTENSEN, N. P. (1981): Phylogeny of insect orders. – *Annual Review of Entomology* **26**: 135–157.
- KRISTENSEN, N. P. (1991): Phylogeny of extant hexapods. – In: CSIRO (eds.): *The insects of Australia*, pp. 125–140; Melbourne (Melbourne University Press).
- KUKALOVÁ-PECK, J. (1974a): Wing-folding in the Paleozoic insect order Diaphanopteroidea (Paleoptera), with a description of new representatives of the family Elmoidae. – *Psyche* **81**: 315–333.
- KUKALOVÁ-PECK, J. (1974b): Pteralia of the Paleozoic insect orders Palaeodictyoptera, Megaseoptera and Diaphanopteroidea (Paleoptera). – *Psyche* **81**: 416–430.
- KUKALOVÁ-PECK, J. (1978): Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. – *Journal of Morphology* **156**: 53–126.
- KUKALOVÁ-PECK, J. (1983): Origin of the insect wing and wing articulation from the arthropodan leg. – *Canadian Journal of Zoology* **61**: 1618–1669.
- KUKALOVÁ-PECK, J. (1985): Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera). – *Canadian Journal of Zoology* **63**: 933–955.
- KUKALOVÁ-PECK, J. (1987): New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). – *Canadian Journal of Zoology* **65**: 2327–2345.
- KUKALOVÁ-PECK, J. (1991): Fossil history and the evolution of hexapod structures. – In: CSIRO (eds.): *The insects of Australia*, pp. 141–179; Melbourne (Melbourne University Press).
- KUKALOVÁ-PECK, J. (1998): Arthropod phylogeny and “basal” morphological structures. – In: FORTEY, R. A. & THOMAS, R. H. (eds.): *Arthropod relationships (systematics association, special volume series)* **55**, pp. 249–268; London (Chapman & Hall).
- KUKALOVÁ-PECK, J. & BRAUCKMANN, C. (1990): Wing folding in pterygote insects, and the oldest Diaphanopteroidea from the early Late Carboniferous of West Germany. – *Canadian Journal of Zoology* **68**: 1104–1111.
- LEMCHÉ, H. (1940): The origin of winged insects. – *Videnskabelige Meddelelser fra dansk naturhistorisk Forening i København* **104**: 127–168.
- MAKI, T. (1938): Studies on the thoracic musculature of insects. – *Memoirs of the Faculty of Science and Agriculture, Taihoku imperial University* **24**: 1–343.
- MALOEUF, N. S. R. (1935): The postembryonic history of the somatic musculature of the dragonfly thorax. – *Journal of Morphology* **58**: 87–115.
- MARTYNOV, A. V. (1925): Über zwei Grundtypen der Flügel bei den Insekten und ihre Evolution. – *Zeitschrift für Morphologie und Ökologie der Tiere* **4**: 465–501.
- MATSUDA, R. (1956): Morphology of the thoracic exoskeleton and musculature of a mayfly *Siphonurus columbianus* McDunnough (Siphonuridae, Ephemeroptera). A contribution to the subcoxal theory of the insect thorax. – *Journal of the Kansas entomological Society* **29**: 92–113.
- MATSUDA, R. (1970): Morphology and evolution of the insect thorax. – *Memoirs of the entomological Society of Canada* **76**: 431 pp.
- MCCAFFERTY, W. P. (1990): Insects from Santana Formation Lower Cretaceous, of Brazil. Chapter 2. Ephemeroptera. – *Bulletin of the American Museum of Natural History* **195**: 20–50.
- MICKOLEIT, G. (1969): Vergleichend-anatomische Untersuchungen an der pterothorakalen Pleurotergalmuskulatur der Neuroptera (Insecta) und Mecoptera (Insecta, Holometabola). – *Zeitschrift für Morphologie der Tiere* **64**: 151–178.
- NACHTIGALL, W. (1966): Die Kinematik der Schlagflügelbewegungen von Dipteren. Methodische und analytische Grundlagen zur Biophysik des Insektenflugs. – *Zeitschrift für vergleichende Physiologie* **52**: 155–211.
- NACHTIGALL, W. (1967): Aerodynamische Messungen am Tragflügelssystem segelnder Schmetterlinge. – *Zeitschrift für vergleichende Physiologie* **54**: 210–231.
- NACHTIGALL, W. (2003): *Insektenflug: Konstruktionsmorphologie, Biomechanik, Flugverhalten*, 482 pp.; Berlin & Heidelberg (Springer).
- NACHTIGALL, W., WISSER, A. & EISINGER, D. (1998): Flight of the honey bee. VIII. Functional elements and mechanics of the “flight motor” and the wing joint – one of the most complicated gear-mechanisms in the animal kingdom. – *Journal of comparative Physiology B* **168**: 323–344.
- NELSON, C. H. & HANSON, J. F. (1968): The external anatomy of *Pteronarcys* (*Allonarcys*) *proteus* Newman and *Pteronarcys* (*Allonarcys*) *biloba* Newman (Plecoptera: Pteronarcidae). – *Transactions of the American entomological Society* **94**: 429–472.

- NELSON, C. H. & HANSON, J. F. (1971): Contribution to the anatomy and phylogeny of the family Pteronarcidae (Plecoptera). – Transactions of the American entomological Society **97**: 123–200.
- OGDEN, T. H. & WHITING, M. F. (2005): Phylogeny of Ephemeroptera (mayflies) based on molecular evidence. – Molecular Phylogenetics and Evolution **37**: 625–643.
- OGDEN, T. H. & WHITING, M. F. (2003): The problem with “the Paleoptera problem:” sense and sensitivity. – Cladistics **19**: 432–442.
- ONESTO, E. (1959a): Morfologia della regione articolare delle ali di *Anthocaris cardamines* (L.) (Lepidoptera, Pieridae). – Annuario dell'Istituto e Museo di Zoologia della Università di Napoli **11** (1): 1–40.
- ONESTO, E. (1959b): La regione articolare delle ali di *Blatta orientalis* L. (Insecta, Blattodea). – Annuario dell'Istituto e Museo di Zoologia della Università di Napoli **11** (6): 1–40.
- ONESTO, E. (1960): La regione articolare di *Ameles decolor* (Charp.) (Insecta, Mantoidea) e il suo significato morfologico per la filogenesi di Blattotteroidei. – Annuario dell'Istituto e Museo di Zoologia della Università di Napoli **12** (2): 1–27.
- ONESTO, E. (1961): Morfologia della regione articolare alari di *Forficula auricularia* L. (Insecta, Dermaptera). – Annuario dell'Istituto e Museo di Zoologia della Università di Napoli **13** (4): 1–31.
- ONESTO, E. (1963): Studio sulla morfologia comparata del dermascheletro dei Tettigonioidi. – Annuario dell'Istituto e Museo di Zoologia della Università di Napoli **15** (6): 1–38.
- ONESTO, E. (1965): Morfologia della regione articolare alare e delle pleure nei Plecotteri. – Bollettino della Società dei Naturalisti in Napoli **74**: 22–39.
- PFAU, H. K. (1977): Zur Morphologie und Funktion des Vorderflügels und Vorderflügelgelenks von *Locusta migratoria* L. – Fortschritte der Zoologie **24**: 341–345.
- PFAU, H. K. (1986): Untersuchungen zur Konstruktion, Funktion und Evolution des Flugapparates der Libellen (Insecta, Odonata). – Tijdschrift voor Entomologie **129**: 35–123.
- PFAU, H. K. (1991): Contributions of functional morphology to the phylogenetic systematics of Odonata. – Advances in Odonatology **5**: 109–141.
- RAHLE, W. (1970): Untersuchungen an Kopf und Prothorax von *Embia ramburi* Rimsky-Korsakow 1906 (Embioptera, Embiidae). – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere **87**: 248–330.
- RASNITSYN, A. P. (2002): Subclass Scarabaeona Laicharting, 1781. The winged insects (= Pterygota Lang, 1888). – In: RASNITSYN, A. P. & QUICKE, D. L. J. (eds.): History of Insects, pp. 75–82; Dordrecht (Kluwer Academic Publishers).
- REHN, A. C. (2003): Phylogenetic analysis of higher-level relationships of Odonata. – Systematic Entomology **28**: 181–239.
- RIEK, E. F. & KUKALOVÁ-PECK, J. (1984): A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. – Canadian Journal of Zoology **62**: 1150–1166.
- ROMEIS, B. (1989): Mikroskopische Technik, 697 pp.; München (Urban und Schwarzenberg).
- SCHWANWITSCH, B. N. (1943): Subdivision of Insecta Pterygota into subordinate groups. – Nature **527** (3868): 727–728.
- SHARPLIN, J. (1963a): Wing base structure in Lepidoptera I. Fore wing base. – Canadian Entomologist **95**: 1024–1050.
- SHARPLIN, J. (1963b): Wing base structure in Lepidoptera II. Hind wing base. – Canadian Entomologist **95**: 1121–1145.
- SHARPLIN, J. (1964): Wing base structure in Lepidoptera III. Taxonomic characters. – Canadian Entomologist **96**: 943–949.
- SINITSHENKOVA, N. D. (1984): The Mesozoic mayflies (Ephemeroptera) with special reference to their ecology. – In: LANDA, V., SOLDÁN, T. & TONNER, M. (eds.): Proceedings of the fourth international Conference on Ephemeroptera (Bechyne, September 4–10, 1983), pp. 61–66; České Budějovice (Institute of Entomology, Czechoslovak Academy of Sciences).
- SINITSHENKOVA, N. D. & CORAM, R. A. (2002): The first mayfly from the Lower Cretaceous of southern England (Insecta: Ephemera = Ephemeroptera). – Cretaceous Research **23**: 461–463.
- SNODGRASS, R. E. (1909): The thorax of the insects and the articulation of the wings. – Proceedings of the United States national Museum **36**: 511–595.
- SNODGRASS, R. E. (1927): Morphology and mechanism of the insect thorax. – Smithsonian miscellaneous Collections **80**: 1–108.
- SNODGRASS, R. E. (1935): Principles of insect morphology, 667 pp.; New York & London (McGraw-Hill Book Co.).
- SOLDÁN, T. (1997): The Ephemeroptera: Whose sister-group are they? – In: LANDOLT, P. & SARTORI, M. (eds.): Ephemeroptera & Plecoptera: biology-ecology-systematics, pp. 514–519; Fribourg (Mauron + Tinguely & Lachat).
- STANICZEK, A. H. (1996): The mandibular articulation of mayflies (Insecta: Ephemeroptera) and its implications for the phylogeny of the lower Pterygote lineages. – Proceedings of the 20<sup>th</sup> international Congress of Entomology, Firenze: 2.
- STANICZEK, A. H. (2000): The mandible of silverfish (Insecta: Zygentoma) and mayflies (Ephemeroptera): its morphology and phylogenetic significance. – Zoologischer Anzeiger **239**: 147–178.
- STANICZEK, A. H. (2001): Der Larvenkopf von *Oniscigaster wakefieldi* McLachlan, 1873 (Insecta: Ephemeroptera: Oniscigasteridae). – Ph.D. thesis, Universität Tübingen, 160 pp.
- TANNERT, W. (1958): Die Flügelgelenkung bei Odonaten. – Deutsche entomologische Zeitschrift (Neue Folge) **5**: 394–455.
- TSHERNOVA, O. A. (1970): On the classification of the fossil and recent Ephemeroptera. – Entomologicheskoe Obozrenie **49**: 124–145 [in Russian].
- TSUI, P. T. P. & PETERS, W. L. (1972): The comparative morphology of the thorax of selected genera of the Leptophlebiidae (Ephemeroptera). – Journal of Zoology **168**: 309–367.
- WAGNER, T., NEINHUIS, C. & BARTHLOTT, W. (1996): Wettability and contaminability of insect wings as a function of their surface sculptures. – Acta zoologica **77**: 213–225.
- WEBER, H. (1924a): Das Grundschema des Pterygotenthorax. – Zoologischer Anzeiger **60**: 17–37, 57–83.
- WEBER, H. (1924b): Das Thoraxskelett der Lepidopteren. – Zeitschrift für Anatomie und Entwicklungsgeschichte **23**: 277–331.
- WEBER, H. (1925): Der Thorax der Hornisse. Ein Beitrag zur vergleichenden Morphologie des Insektenthorax. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere **47**: 1–100.
- WHEELER, W. C., WHITING, M. F., WHEELER, Q. D. & CARPENTER, J. C. (2001): The phylogeny of the extant hexapod orders. – Cladistics **17**: 113–169.
- WHITING, M. F., CARPENTER, J. C., WHEELER, Q. D. & WHEELER, W. C. (1997): The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. – Systematic Biology **46**: 1–68.
- WILLKOMMEN, J. & HÖRNSCHEMEYER, T. (2007): The homology of wing base sclerites and flight muscles in Ephemeroptera and Neoptera and the morphology of the pterothorax of *Habro-leptoides confusa* (Insecta: Ephemeroptera: Leptophlebiidae). – Arthropod Structure & Development **36**: 253–269.

- WILLMANN, R. (1998): Advances and problems in insect phylogeny. – In: FORTEY, R. A. & THOMAS, R. H. (eds.): Arthropod relationships (systematics association, special volume series) **55**, pp. 269–279; London (Chapman & Hall).
- WILLMANN, R. (1999): The Upper Carboniferous *Lithoneura lameerei* (Insecta, Ephemeroptera?). – Paläontologische Zeitschrift **73**: 289–302.
- WILLMANN, R. (2003): Die phylogenetischen Beziehungen der Insecta: Offene Fragen und Probleme. – Verhandlungen westdeutscher Entomologentag **2001**: 1–64.
- WILLMANN, R. (2005): Phylogenese und System der Insecta. – In: DATHE, H. H. (ed.): Lehrbuch der speziellen Zoologie. Begründet von A. KAESTNER, **I** (5), pp. 1–66; Berlin (Spektrum Akademischer Verlag).
- WITTIG, G. (1955): Untersuchungen am Thorax von *Perla abdominalis* Burm. (Larve und Imago) unter besonderer Berücksichtigung des peripheren Nervensystems und der Sinnesorgane. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere **74**: 491–570.
- WOOTTON, J. R. (1979): Function, homology and terminology in insect wings. – Systematic Entomology **4**: 81–93.
- WOOTTON, R. J. (1981): Palaeozoic insects. – Annual Review of Entomology **26**: 319–344.
- WOOTTON, R. J. (1992): Functional morphology of insect wings. – Annual Review of Entomology **37**: 113–140.
- WOOTTON, J. R. & KUKALOVÁ-PECK, J. (2000): Flight adaptations in Palaeozoic Palaeoptera (Insecta). – Biological Reviews **75** (1): 129–167.
- YOSHIZAWA, K. & SAIGUSA, T. (2001): Phylogenetic analysis of Paraneopteran orders (Insecta: Neoptera) based on forewing base structure, with comments on morphology of Auchenorrhyncha (Hemiptera). – Systematic Entomology **26**: 1–13.
- ZHOU, C.-F. & PETERS, J. G. (2003): The nymph of *Siphuriscus chinensis* and additional imaginal description: A living mayfly with Jurassic origins (Siphuriscidae new family: Ephemeroptera). – Florida Entomologist **86**: 345–352.
- ZWICK, P. (1973): Insecta: Plecoptera. Phylogenetisches System und Katalog. – Das Tierreich **94**, 465 pp.; Berlin & New York (Walter de Gruyter).
- ZWICK, P. (1980): Plecoptera (Steinfliegen). – Handbuch der Zoologie **4** (2) 2/7: 1–115; Berlin (Walter de Gruyter).

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Manuscript received: 3.IX.2007, accepted: 9.XI.2007.