65 (1) 15–23
© Museum für Tierkunde Dresden, eISSN 1864-8312

The Contribution of Flight System Characters to the Reconstruction of the Phylogeny of the Pterygota

Thomas Hörnschemeyer * & Jana Willkommen

Institut für Zoologie und Anthropologie, Abteilung Morphologie & Systematik,
Berliner Str. 28, 37073 Göttingen, Germany [thoerns@gwdg.de]

* Corresponding author

Received 21.xii.2005, accepted 30.x.2006.
Published online at www.arthropod-systematics.de on 28.iii.2007

> Abstract

The ability to fly is an important factor for the evolutionary success of insects. Their flight apparatus contains numerous sclerites and muscles, which represent valuable characters for phylogenetic analysis. We present a summary of the current state of knowledge on autapomorphies of the flight system of high-level taxa of the Pterygota. To date, no formal phylogenetic analysis based on flight system characters with the exception of wing venation has been presented. Nevertheless, this review shows that the wing base and the flight muscles contain valuable characters that can help to resolve current open questions of phylogenetic relationships among the Pterygota. It also becomes apparent that there are still many taxa without comprehensive descriptions of the wing base morphology.

> Key words

Wing base, flight musculature, thorax, flight, Insecta.

1. Introduction

Study of an organism's functional morphology is essential to understand how structures evolved and to reconstruct events that took place during the evolution of taxa and structures.

An extremely interesting and important morphological system is the flight system of pterygote insects. The ability to fly is a very important feature of the Pterygota. It probably is one of the most significant factors for their evolutionary success. From a functional point of view, the insect flight system is unique. It is the only example where wings are newly evolved, additional structures and not just modified legs. Hence, we should be able to learn much about how evolution works if we study and finally understand how the insect flight system evolved. In this context, the investigation of the basal Pterygota, the Ephemeroptera, Odonata and e.g. Plecoptera, is of special importance (Willkommen & Hörnschemeyer 2007). Certainly, the elements which constitute the flight system also contain much information, i.e. many characters that can be helpful in phylogenetic reconstructions (e.g. Brown et al. 1993; Brown & Scholtz 1994; Hörnschemeyer 1998; Yoshizawa & Saigusa 2001).

1.1. Morphology of the flight system of insects

The two primary functional elements of the insect flight system are the skeleton and the muscles. The role of the membrane that forms the expanse of the wing and connects the sclerites is not considered here. The skeleton consists of a number of individual sclerites, which give stability to the thorax and form the wing base. The muscles deliver the power for active flight and adjust the wings during flight. The sclerites of the wing base, which connect the wing to the thorax, are of special importance because they mediate the power transfer from the thoracic muscles to the wing. Furthermore, their arrangement and their shapes affect the wing beat. They enable adjustments for different flight modes and allow the wings be moved into a resting position over the abdomen in the Neoptera.

1.2. Thoracic and wing base sclerites

The dorsal elements of the wing base (Fig. 1B) include three lateral processes of the notum: the anterior (ANP), the median (MNP) and the posterior notal

wing process (PNP). These processes are the points of contact between the notum and the first (1Ax) and third (3Ax) axillary sclerites. The axillaries are functionally the most important elements of the wing base. Their shapes and arrangement enable different wing movements. They are also associated with the wing veins: The 1Ax has a flexible connection to the ANP and to the 2Ax and is associated with the base of the Subcosta (Sc). The 2Ax lies next to the distal border of the 1Ax and is connected to the base of the Radius (R) and to the proximal median plate (PMP), which lies next to the distal median plate (DMP). The DMP gives rise to the Media (M) and to the Cubitus (Cu). The 3Ax bridges the gap between the PNP and the caudal tip of the 2Ax. The two points of contact with the PNP and the 2Ax also serve as a joint around which the 3Ax rotates when the wing is moved to its resting position over the abdomen. The 3Ax is also the point of origin of the Anals (A).

The anterior margin of the wing, which usually is formed by the Costa (C), is connected to the thorax via the humeral plate (H) and the Tegula (Tg), which is a very characteristic patch of sensilla. The most basal section of the posterior margin of the wing is tubular and slightly inflated due to its function as a haemolymph vessel. It is called axillary cord (AxC).

Elements of the pleural skeleton (Fig. 1A) that are related to the wings are the pleural suture (PlS), which usually extends from the dorsal coxal articulation to the dorsal process of the pleuron, the pleural wing process (PWP). The PlS is a long groove-like invagination of the pleuron. It is represented internally as the pleural ridge (PlR), which is an important stabilizing element of the pleuron. The dorsal tip of the PWP is the fulcrum (F), which together with the 2Ax forms the joint around which the wing rotates. Craniad of the PWP lies the basalar sclerite (Ba). Caudad of the PWP is the subalar sclerite (Sa). Both sclerites serve as attachment areas for muscles.

1.3. Thoracic muscles

The thoracic muscles (Fig. 1C,D) can be subdivided into three functional groups. The first group contains muscles that are not related to flight, i.e. the ventral longitudinal muscles and muscles which only move the legs or close the spiracles. The second functional group are the indirect flight muscles: the dorsal longitudinal muscles and the dorso-ventral muscles. These few but large muscles produce the force for the flapping of the wings. They make up most of the muscle mass in the pterothorax of insects capable of active flight. The third group consists of many smaller muscles that directly effect movements of the wing. These are for example the muscles of the basalar (Ba) and of the subalar (Sa) sclerites, which move the wing from the resting to the flight position and adjust the wing during various manoeuvres. Another important muscle or group of muscles inserts on the 3Ax. In Neoptera, this muscle moves the wing to its resting position over the abdomen. During flight it probably effects minor adjustments of the wing in both the neopterous and palaeopterous orders. The muscles inserted on 3Ax, basalare, subalare and on the notal wing processes are located in the lateral areas of the meso- and metathorax. These are also the muscles showing the greatest degree of variation among the different taxa of Pterygota (Snodgrass 1935; Maki 1938; Matsuda 1970). They also provide the greatest number of muscle characters for phylogenetic analysis.

2. The use of flight system characters for the phylogenetic reconstrauction

The value of flight system characters for the analysis of phylogenetic relationships varies greatly depending on the taxonomic level of the group examined.

At a low taxonomic level, i.e. between species, the musculature and the sclerites of the wing base usually do not show significant variation (Hörnschemeyer 1998). Very detailed observations in the attempt to find informative characters may reveal that certain structures of the individual sclerites, e.g. small processes on the cranial margin of the 1Ax or the shape of the caudal tip of the 3Ax, might vary between species. However, in these cases more comprehensive investigation often shows that these differences are also present between specimens of one species, thus rendering the character worthless for phylogenetic reconstructions (Hörnschemeyer 1998).

Some elements of the wing base show highly different degrees of variability in or between different taxa. The median plates (PMP, DMP), for example, are variable in most order- and family-level taxa and thus may be helpful in the analysis of lower level phylogenies. They are an important element in the investigations of the family-level phylogeny of the Scarabaeoidea (Coleoptera) by Browne et al. (1993), Browne & Scholtz (1995, 1996) and Scholtz & Browne (1996). These investigations and those of Kukalová-Peck & Lawrence (1993, 2004), Hörnschemeyer (1998) (both on the phylogeny of Coleoptera), Ivanov (1985, 1987a,b, 1995, 1996, 1998; on the phylogeny of Trichoptera and Lepidoptera) and Haas & Kukalová-Peck (2001; on Dermaptera) are among the few examples in which wing base characters were used for the analysis of sub-ordinal relationships.

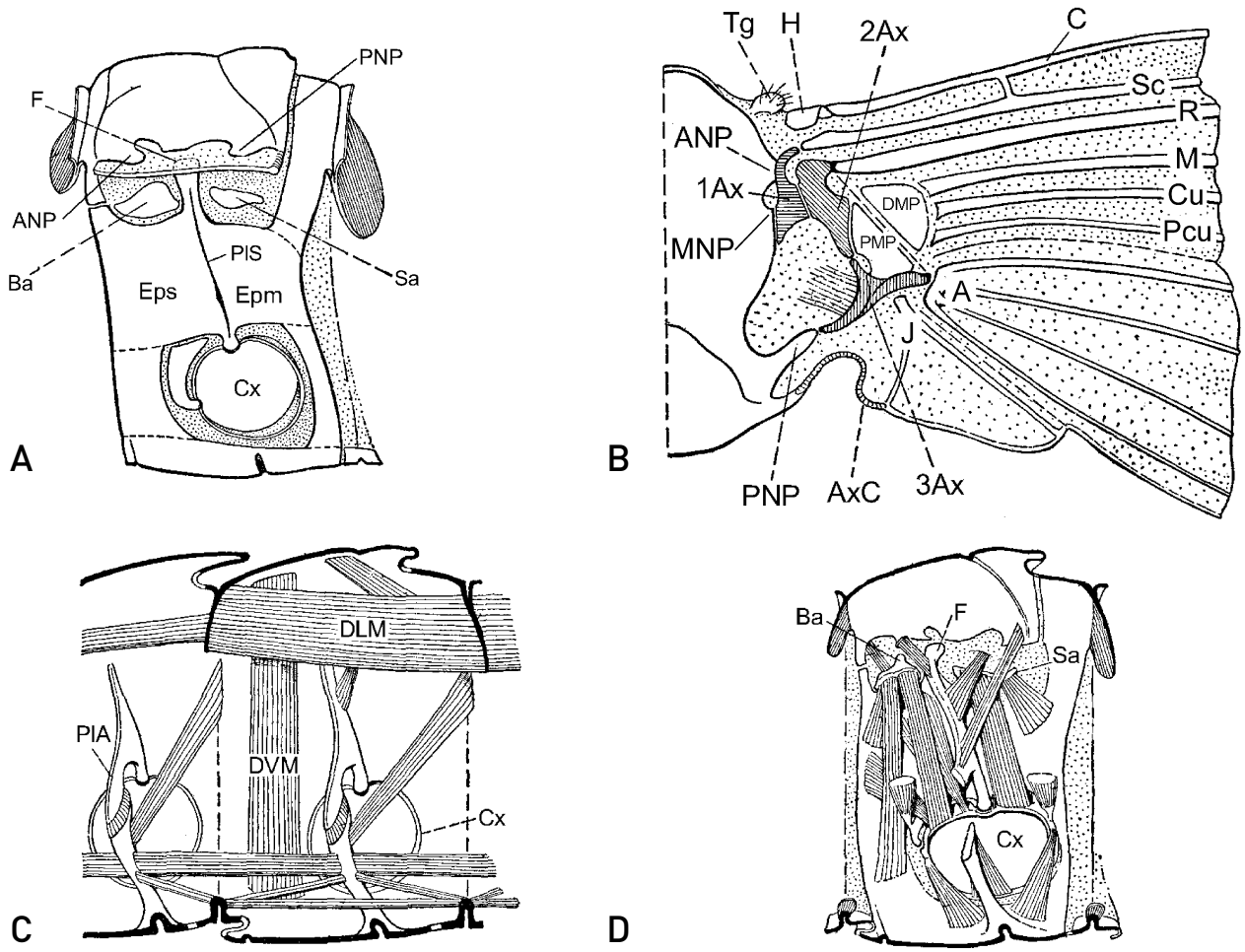


Fig. 1. Schematic representation of the morphology of a winged segment of a neopterous insect (modified from Snodgrass 1935). **A**: Lateral view of left pleuron. **B**: Dorsal view of right wing base. **C**: Musculature of right half of segment, seen from the left. **D**: Ditto, large median muscles removed to show the peripheral muscles. 1Ax, 2Ax, 3Ax – first, second and third axillary, ANP – anterior notal wing process, AxC – axillary cord, Ba – Basalare, C – Costa, Cx – Coxa, DLM – dorsal longitudinal muscle, DMP – distal median plate, DVM – dorsoventral muscle, Epm – Epimeron, Eps – Episternum, F – Fulcrum, H – humeral plate, M – Media, MNP – median notal wing process, PlA – pleural arm, PlS – pleural suture, PMP – proximal median plate, PNP – posterior notal wing process, R – Radius, Sa – Subalare, Sc – Subcosta, Tg – Tegula.

In all these studies the wing base characters turned out to be highly informative for phylogenetic reconstructions at family to suborder level. At lower taxonomic levels, the characters used (mainly of wing base sclerites) did not provide sufficient resolution, usually because they did not show enough variability.

Since most sclerites of the wing base and their related muscles evolve at a very slow rate (Hörnschemeyer 2002), they are most useful for the reconstruction of higher level phylogenies. Nevertheless, few attempts to use such characters to investigate the relationships among the Pterygota have been made. Hörnschemeyer (2002) compiled information on the state of wing base sclerites throughout the Holometabola. When mapping these characters on a cladogram (Fig. 2) it is possible to identify a number of character states as possible synapomorphies for higher taxa in the Holometabola.

In the following we present apomorphic character states for some of the pterygote monophyla. Autapomorphies are marked with braced abbreviations, e.g. {Eu1}, which are also used in the cladogram (Fig. 2).

2.1. Ephemeroptera & Odonata

The ground pattern of the flight system of the Pterygota and its subsequent evolution to the ground pattern of the Neoptera are still not fully understood. To homologise the diverse sclerites of the wing base and their associated muscles is difficult. Based on a comprehensive study of Ephemeroptera and Plecoptera, Willkommen & Hörnschemeyer (2007) developed a hypothesis to homologise the sclerites and muscles. They suggest that neither the wing base of extant Ephemeroptera nor those of extant Odonata

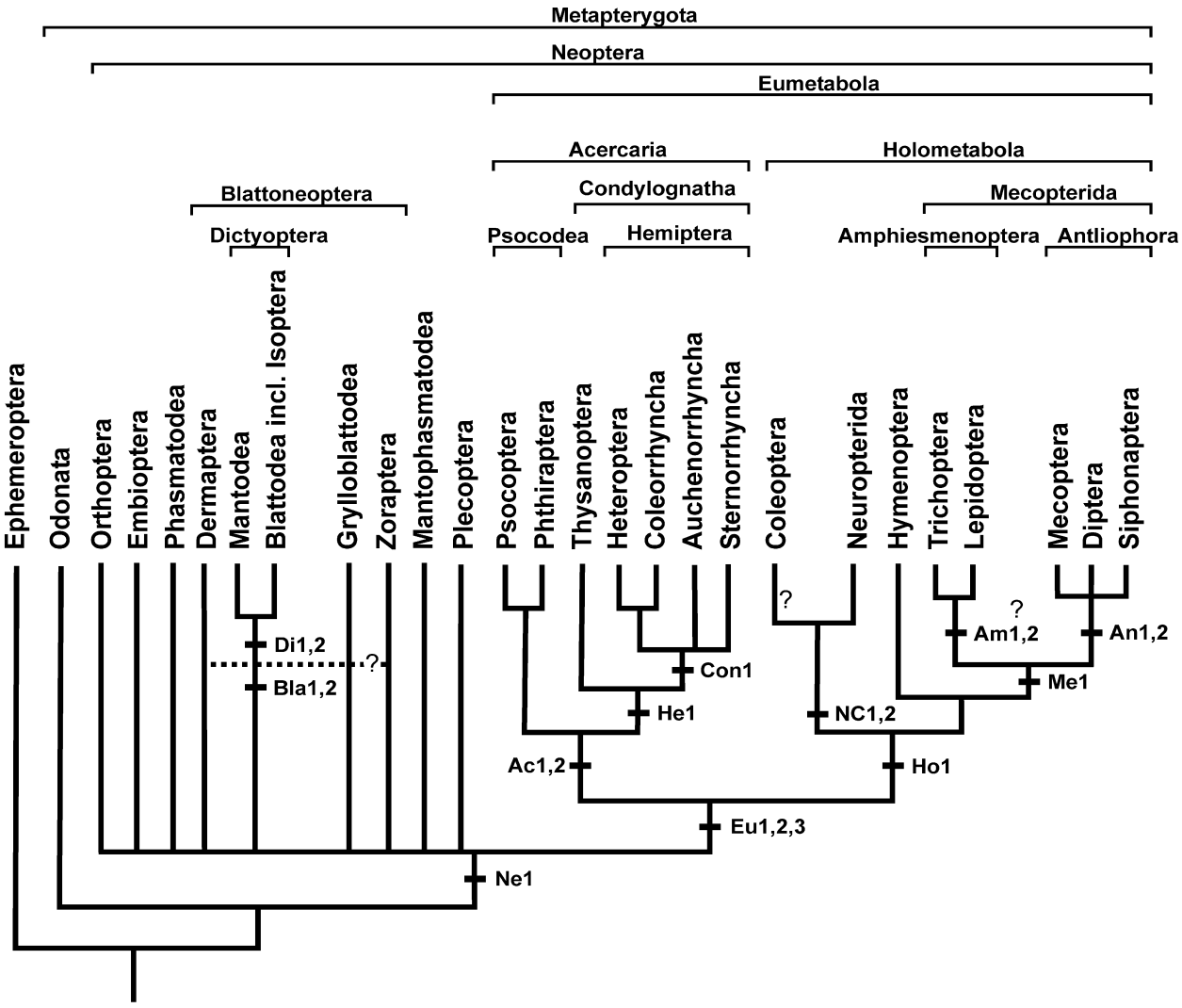


Fig. 2. Phylogenetic relationships of Pterygota modified after KRISTENSEN (1991). Abbreviations on the tree are potential apomorphies of super-ordinal taxa explained in the text.

or Neoptera exactly reflect the ground pattern of the Pterygota. According to this model, the wing base of the ancestor of the Pterygota was composed of a similar number of sclerites as can be observed in the extant Neoptera. The modifications present in the extant taxa are directly connected to specialisations in their modes of flight. In the Ephemeroptera and Odonata fusions are predominant. The wing base of the Neoptera probably is quite similar to the pterygote ground pattern and the ability to move the wings to the resting position over the abdomen may even be plesiomorphic.

The flight system of a few species of Odonata was described by HATCH (1966), TANNERT (1958) and PFAU (1986). The latter also proposed hypotheses for homologisation of some wing base sclerites of the Odonata and the Neoptera. However, the phylogenetic relationships of Ephemeroptera, Odonata and Neoptera remain unsolved. Therefore, detailed comparisons of the flight systems of Ephemeroptera, Odonata and Neoptera are still necessary.

2.2. Neoptera

A potential autapomorphy often mentioned for Neoptera is the ability to flex their wings to a resting position over the abdomen, in contrast to the horizontally or vertically extending wings of Odonata and Ephemeroptera. The presence of a muscle inserting on the 3Ax is essential for this flexing ability. Nevertheless, in Ephemeroptera and Odonata there also is a muscle that inserts on a sclerite that is probably homologous to the 3Ax of Neoptera (WILLKOMMEN & HÖRNSCHEMEYER 2007). The important innovation – if not plesiomorphic for Pterygota – in the wing base of the Neoptera is the acquisition of folding lines {Ne1} in the wing base, which enable flexing of the wing over the abdomen.

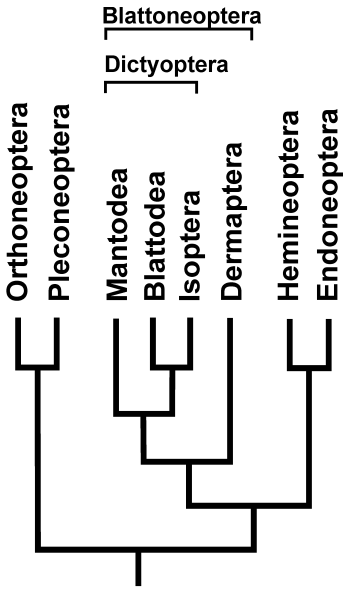


Fig. 3. Phylogenetic relationships of Pterygota as reconstructed by Haas & Kukalová-Peck (2001). Orthoneoptera = Ensifera, Caelifera, Phasmatodea; Pleconeoptera = Plecoptera, Embioptera; Hemineoptera = Acercaria; Endoneoptera = Holometabola = Endopterygota; for further description see text and Haas & Kukalová-Peck (2001).

2.3. Lower Neoptera

Haas & Kukalová-Peck (2001) investigated representatives of these taxa. Their phylogenetic hypothesis (Fig. 3), which is based on the wing characters, assumes a sistergroup relationship of Pleconeoptera (Embioptera + Plecoptera) and Orthoneoptera (Orthoptera + Phasmatodea). Together this monophylum is considered to be the sistergroup of the remaining Neoptera. This split between Pleconeoptera + Orthoneoptera and the remaining Neoptera is supported mainly by characters of the wing venation. The area covered by derivatives of the anterior branch of the Anal vein (AA) is of special importance: In Pleconeoptera + Orthoneoptera this area equals about half of the surface of the wing, whereas in the other Neoptera it is restricted to a narrow field of about an eighth of the wing surface. The latter condition is interpreted as the derived one.

2.4. Blattoneoptera

Haas & Kukalová-Peck (2001) analysed the phylogenetic relationships of the Dermaptera, based on characters of the wing venation, base and folding. They also present information on the ground patterns and on possible autapomorphies for these character systems of many high-level taxa of the Pterygota. After Haas & Kukalová-Peck (2001: 446) the taxon Blattoneoptera includes Grylloblattodea, Zoraptera(?), Dermaptera and Dictyoptera. As autapomorphies of the Blattoneoptera Haas & Kukalová-Peck (2001) identified the absence (= complete membranisation) of the PNP {Bla1} (PRAJ in their nomenclature) and a 2Ax with a curved body (= AXM of Haas & Kukalová-Peck 2001) with a thickened proximal margin and a thin, often membranous distal part {Bla2} (Fig. 4).

2.5. Dictyoptera

According to Haas & Kukalová-Peck (2001) the Dictypotera are characterised by a 2Ax with an ear-shaped body {Di1} (Fig. 4) and a short, curved base of the Radius (R) (= FR of Haas & Kukalová-Peck 2001) that is missing an anterior lobe {Di2}.

2.6. Eumetabola

There are quite a number of characters that support a sistergoup relationship of Holometabola and Acercaria. Among the possible autapomorphies of the Eumetabola are a 2Ax with a distinctly triangular body {Eu1} (= AXM, Haas & Kukalová-Peck 2001); a broad and lobate base of the Radius (R) {Eu2} (= FR, Haas & Kukalová-Peck 2001) and an elongate base of the Media (M) {Eu3} (= BM, Haas & Kukalová-Peck 2001). Furthermore, the 3Ax has 2 muscles (t-p13 and t-p14, Matsuda 1970) attached to it. Since there is only one muscle attached to the 3Ax in the other Pterygota, this probably also is a derived character of the Eumetabola (Hörnschemeyer 1998).

2.7. Acercaria

The fore wing base of the Acercaria (Fig. 5) was studied comprehensively by Yoshizawa & Saigusa (2001). They reconstructed the phylogenetic relationships of seven higher taxa, based on a data matrix with characters exclusively derived from the wing base. According to their analysis, the Acercaria are characterised by nine autapomorphies of wing base characters. The numerous fusions between elements of the wing base are very conspicuous in this taxon. Two of them involve the fusion of the humeral plate (H) and the base of the Subcosta (BSc) {Ac1} and the fusion of the base of the anal veins (BA) to the PMP {Ac2}.

2.8. Condylognatha

In the sub-taxa of the Paraneoptera more fusions occur: A probable autapomorphy of the Condylognatha (Thysanoptera + Hemiptera) is the fusion of the base

of the Subcosta (BSc) to the 2Ax {Con1} (Fig. 5) (YOSHIZAWA & SAIGUSA 2001).

2.9. Hemiptera

The fusions of sclerites in the wing base certainly have effects on the motility of the wings (BETTS 1986a,b). The membranous lines between the sclerites allow them to move against each other. As such, the fusions of sclerites also affect the fold lines. An autapomorphy of the Hemiptera is the modification of the anterior axillary fold-line (AAF), which acquires an additional fork {He1} (Fig. 5) (YOSHIZAWA & SAIGUSA 2001).

2.10. Holometabola

In all orders of the Holometabola a locking mechanism {Ho1} is present in meso- and methathorax that locks the wing in the resting position (HÖRNSCHEMEYER 1998, 2002). This mechanism is composed of a knob in the dorsal area of the Basalare (Fig. 6B: BaK) and a cavity in the anterior area of the wing base, which fits onto this knob. The cavity is formed by ventral sclerotisations of the humeral plate (H) and of the base of the Subcosta (BSc). Variations of this locking mechanism within the Holometabola involve the size and position of the knob on the Ba. In some taxa it occupies nearly the complete dorsal half of the Ba (e.g. in Coleoptera: Archostemata). In others, it is small (e.g. Hymenoptera) and may be located more craniad or more caudad on the dorsal margin of the Ba. In non-holometabolan Pterygota the locking mechanism is consistently absent.

2.11. Neuropterida & Coleoptera

Two characters of the wing base probably support a sistergroup relationship of Coleoptera and Neuropterida, although the assumption may not be stringent (HÖRNSCHEMEYER 1998): In Neuropterida and Coleoptera, the ratio of the length of the notum and the length of the 1Ax of the hind wing ranges from 3.0 to 3.8. In some cases it is even lower than 3.0. In other words: the 1Ax in fore- and hind wing is comparatively large {NC1} in these two taxa (Fig. 6A). In other Neoptera the ratio usually lies over 3.8. A second probable synapomorphy of Coleoptera and Neuropterida is a long, sclerotised caudal projection on the ventral part of the 2Ax of the hind wing {NC2}. Such a process is not known from any other Neoptera.

The interpretation of additional characters, like the position of the fulcrum in relation to the 1Ax and the 2Ax, by HÖRNSCHEMEYER (1998) was revised by HÖRNSCHEMEYER (2002), who showed that these characters are most likely homoplastic in Coleoptera and Neuropterida.

2.12. Hymenoptera & Mecopterida

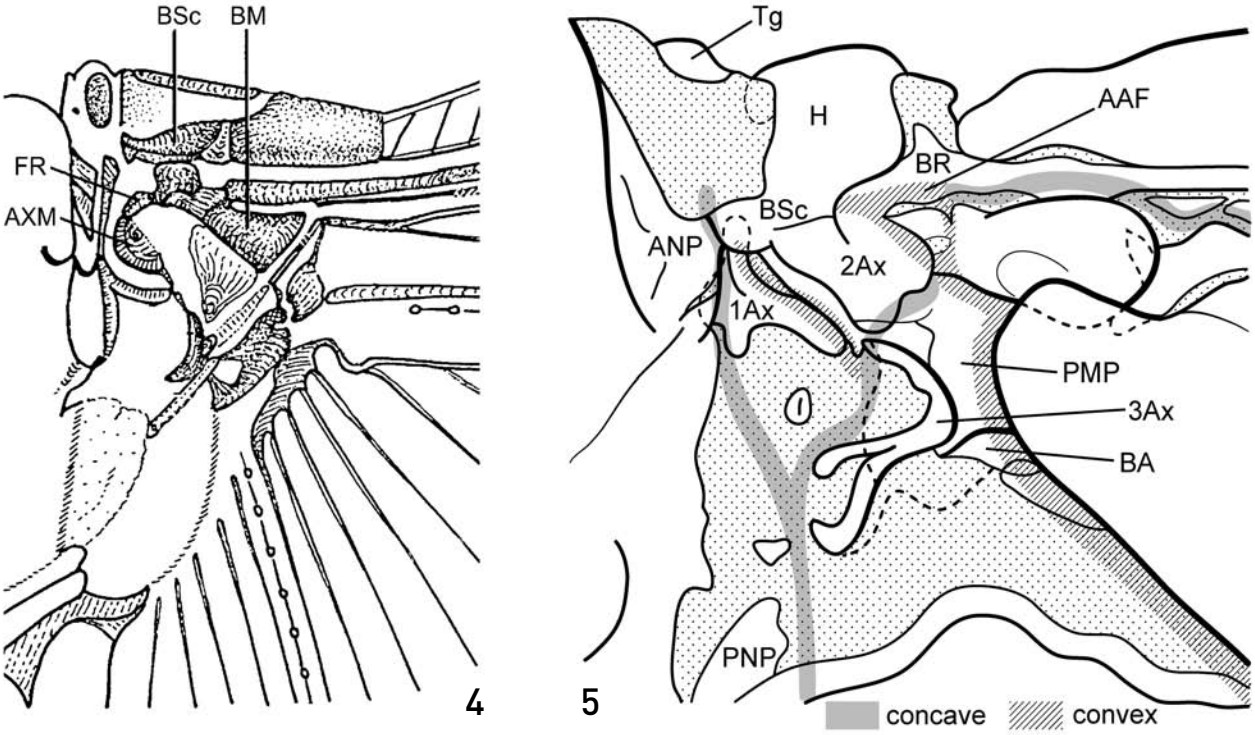
The sistergroup relationship of Hymenoptera and Mecopterida is not supported to date by autapomorphies from the flight system. Also other character systems contribute few potential autapomorphies, such as the larval silk production in labial glands and the presence of a sclerotised sitophore plate at the base of the hypopharynx. However, the support for other relationships of the Hymenoptera is even weaker (WILLMANN 2003). Analyses based on genetic data usually produce similar results: the sistergroup relationship Hymenoptera & Mecopterida is found but weakly supported (WHEELER et al. 2001; CATERINO et al. 2002).

2.13. Mecopterida (Amphiesmenoptera & Antliophora)

The Mecopterida are characterised by the presence of a fan-shaped muscle {Me1} that originates on the rim of the pleural ridge and inserts on the 1Ax (t-p10, MATSUDA 1970). In Plecoptera a similar muscle is present but in other Holometabola it is unknown (MICKOLEIT 1966). Within the Mecopterida it undergoes further modifications (see Antliophora). The muscle t-p10 is probably a modified portion of t-p12 (MATSUDA 1970), which in many taxa connects the PlR with the lateral margin of the notum between the ANP and the PNP.

2.14. Amphiesmenoptera (Trichoptera & Lepidoptera)

As with many other character systems, the Amphiesmenoptera are also well supported by probable autapomorphies of the flight system. Wing base structures of Trichoptera and Lepidoptera have been studied comprehensively by SNODGRASS (1909), MATSUDA (1970) and IVANOV (1987a,b, 1995, 1996, 1998). At least two characters unique to Amphiesmenoptera are known: There is a patch of sensilla {Am1} in the membrane of the pleuron of the metathorax that is located slightly ventrally and caudally of the subalare. This patch is usually slightly more sclerotised than the surrounding membrane (SHARPLIN 1963b; IVANOV 1987b). The second character is a ligament {Am2} that connects the 1Ax to the MNP (SHARPLIN 1963a; INVANOV 1985). Both characters are not known from other Pterygota.



Figs. 4–5. Dorsal view of base of right hind wing. **4**: *Polypsilota aeruginosa* (Goeze, 1765) (Mantodea) (modified from Haas & Kukalová-Peck 2001). AXM – medial axalare, BM – medial basivenale, BSc – subcostal basivenale, FR – radial fulcalare. **5**: *Psococerastis nubila* (Enderlein, 1906) (Psocodea) (redrawn after Yoshizawa & Saigusa 2001). 1Ax, 2Ax, 3Ax – first, second and third axillary, AAF – anterior axillary fold line, ANP – anterior notal wing process, BA – base of Anals, BR – base of Radius, BSc – base of Subcosta, H – humeral plate, PMP – proximal median plate, PNP – posterior notal wing process, Tg – Tegula.

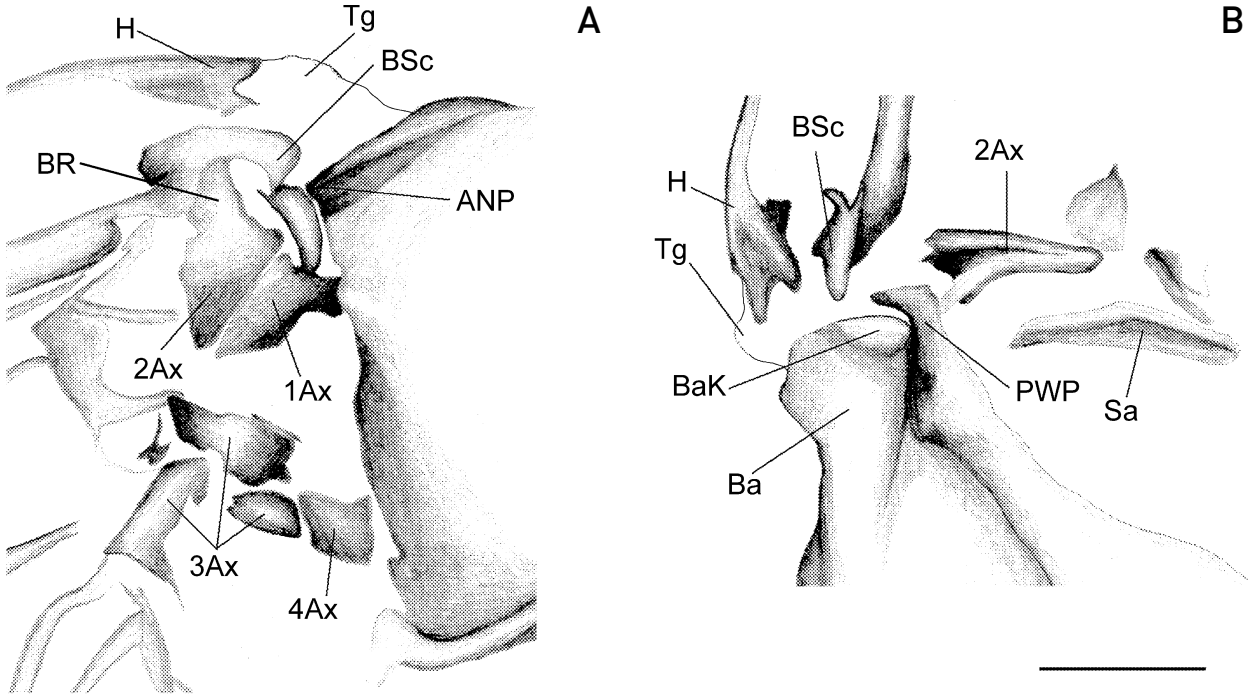


Fig. 6. Base of the left hind wing of *Sialis lutaria* (Linné, 1758) (Neuropterida). **A**: Dorsal view. **B**: Lateral view with wing pointing upward. Scale = 1mm (modified from Hörnschemeyer 1998). 1Ax, 2Ax, 3Ax, 4Ax – first, second, third and fourth axillary, ANP – anterior notal wing process, Ba – Basalare, BaK – knob on Basalare, BR – base of Radius, BSc – base of Subcosta, H – humeral plate, PWP – pleural wing process, Sa – Subalare, Tg – Tegula.

2.15. Antliophora (Mecoptera & Siphonaptera & Diptera)

An autapomorphy of the Antliophora is the modification of the muscle t-p10 {Me1}, which is larger than in other Mecopterida. Consequently, its base covers a part of the rim and part of the anterior surface of the PlR (MICKOLEIT 1966) {An1}. A second derived character of the Antliophora is the presence of a 4Ax {An2} with a muscle (t-p15, MATSUDA 1970) inserting on it. The 4Ax is present in both the fore- and hind wing. The muscle t-p15 originates on the PlR and inserts on the PNP in other taxa. This also supports the interpretation that the 4Ax is a detached PNP.

3. Conclusions

The present compilation shows that the muscles and sclerites of the flight apparatus of insects contain many valuable characters for the analysis of phylogenetic relationships. Yet, there are still many taxa in which our knowledge of the flight system is very incomplete. Comprehensive studies are still rare especially among the hemimetabolous insects. One reason for this may be that the muscles and also the sclerites of the wing base are not easily accessible. Reliable data can be collected only from fresh or well preserved specimens, since the effects of drying may especially obscure the spatial arrangement of the wing base sclerites. As such, the investigation of a representative number of species of one taxon is very time consuming.

Characters of the flight musculature and of the wing base sclerites alone will not answer all open questions in insect phylogeny. However, since this character system has been used sparsely so far, it may deliver new important and useful data. A good candidate to test the usefulness may be the phylogenetic position of the Strepsiptera, which still is not resolved satisfyingly. Furthermore, our understanding of the relationships among the Polyneoptera (if this is a monophyletic taxon), especially concerning the position of the Dermaptera, may benefit from detailed studies of the flight system.

4. Acknowledgements

We are grateful for the general support of our work by Prof. Dr. R. Willmann (Göttingen, Germany). We also wish to thank Dr. G. Tröster and Dr. S. Wedmann (both Göttingen, Germany) for valuable comments and discussions and Dr. P.S. Dingle (Lübeck, Germany), Dr. K.-D. Klass (Dresden, Germany) and Dr. F. Haas (Stuttgart, Germany) for their helpful comments on the manuscript.

5. Abbreviations

1Ax	first axillary
2Ax	second axillary
3Ax	third axillary
4Ax	fourth axillary
AAF	anterior axillary fold line
ANP	anterior notal wing process
AxC	axillary cord
AXM	medial axalare
Ba	Basalare
BA	base of Anals
BaK	knob on Basalare
BM	medial basivenale
BR	base of Radius
BSc	base of Subcosta = subcostal basivenale
C	Costa
Cx	Coxa
DLM	dorsal longitudinal muscle
DMP	distal median plate
DVM	dorsoventral muscle
Epm	Epimeron
Eps	Episternum
F	Fulcrum
FR	radial fulcalare
H	humeral plate
M	Media
PlA	pleural arm
PlR	pleural ridge
PlS	pleural suture
PMP	proximal median plate
PNP	posterior notal wing process
PWP	pleural wing process
R	Radius
Sa	Subalare
Sc	Subcosta
Tg	Tegula

6. References

BETTS, C.R. 1986a. The comparitive morphology of the wings and axillae of selected Heteroptera. – Journal of Zoology (B) **1**: 255–282.

BETTS, C.R. 1986b. The kinematics of Heteroptera in free flight. – Journal of Zoology (B) **1**: 303–315.

BRODSKIY, A.K. 1970. Organisation of the flight system of the mayfly *Ephemera vulgata* L. (Ephemeroptera). – Entomological Review, Washington **49**: 184–188.

BRODSKIY, A.K. 1974. Evolution of the wing apparatus in the Ephemeroptera. – Entomological Review, Washington **53**: 35–43.

BROWNE, D.J. & C.H. SCHOLTZ 1995. Phylogeny of the families of Scarabaeoidea (Coleoptera) based on characters of the hind wing articulation, hind wing base and wing venation. – Systematic Entomology **20**: 145–173.

BROWNE, D.J. & C.H. SCHOLTZ 1996. The morphology of the hind wing articulation and wing base of the Scarabaeoidea (Coleoptera) with some phylogenetic implications. – Bonner Zoologische Monographien **40**: 1–200.

Browne, D.J., C.H. Scholtz & J. Kukalová-Peck 1993. Phylogenetic significance of wing characters in the Trogidae (Coleoptera: Scarabaeoidea). – African Entomology **1**: 195–206.

Caterino, M.S., V.L. Shull, P.M. Hammond & A.P. Vogler 2002. Basal relationships of Coleoptera inferred from 18S rDNA sequences. – Zoologica Scripta **31**: 41–49.

Haas, F. & J. Kukalová-Peck 2001. Dermaptera hind wing structure and folding: New evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). – European Journal of Entomology **98**: 445–509.

Hatch, G. 1966. Structures and mechanics of the dragonfly pterothorax. – Annals of the Entomological Society of America **50**: 702–714.

Hörnschemeyer, T. 1998. Morphologie und Evolution des Flügelgelenks der Coleoptera und Neuropterida. – Bonner Zoologische Monographien **43**: 1–126.

Hörnschemeyer, T. 2002. Phylogenetic significance of the wing-base of the Holometabola (Insecta). – Zoologica Scripta **31**: 17–29.

Ivanov, V.D. 1985. Structure and evolution of the wing articulation of Trichoptera. 1. Original type of structure (groundplan). – Vestnik Leningradskogo Universiteta Biologija **10**: 3–12. [in Russian]

Ivanov, V.D. 1987a. Structure and evolution of the wing articulation of Trichoptera. 2. Structure of wings of Trichoptera with unsegmented palpi (Integripalpia). – Vestnik Leningradskogo Universiteta Serija 3 Biologija **1**: 11–21. [in Russian]

Ivanov, V.D. 1987b. Structure and evolution of the wing articulation of Trichoptera. 3. Articulation of wings of Trichoptera with segmented palpi (Annulipalpia). – Vestnik Leningradskogo Universiteta Serija 3 Biologija **3**: 15–25. [in Russian]

Ivanov, V.D. 1995. Comparative analysis of wing articulation in archaic Lepidoptera. – Entomological Review **74**: 32–53.

Ivanov, V.D. 1996. Wing articulation in lepidopterans and status of Macrolepidoptera. – Entomological Review **76**: 592–602.

Ivanov, V.D. 1998. Wing articulation in whites (Lepidoptera, Pieridae). – Entomological Review **78**: 667–681.

Kristensen, N.P. 1991. Phylogeny of extant hexapods. Pp. 125–140 *in*: CSIRO (ed.), The Insects of Australia. – Melbourne University Press, Melbourne, Australia.

Kukalová-Peck, J. & J.F. Lawrence 1993. Evolution of the hind wing in Coleoptera. – The Canadian Entomologist **125**: 181–258.

Kukalová-Peck, J. & J.F. Lawrence 2004. Relationships among coleopteran suborders and major endoneopteran lineages: Evidence from hind wing characters. – European Journal of Entomology **101**: 95–144.

Matsuda, R. 1970. Morphology and Evolution of the Insect Throax. – Memoirs of the Entomological Society of Canada **76**: 3–431.

Mickoleit, G. 1966. Zur Kenntnis einer neuen Spezialhomologie (Synapomorphie) der Panorpoidea. – Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere **83**: 483–496.

Pfau, H.K. 1986. Untersuchungen zur Konstruktion, Funktion und Evolution des Flugapparates der Libellen (Insecta, Odonata). – Tijdschrift voor Entomologie **129**: 35–123.

Scholtz, C.H. & D.J. Browne 1996. Polyphyly in the Geotrupidae (Coleoptera: Scarabaeoidea): a case for a new family. – Journal of Natural History **30**: 597–614.

Sharplin, J. 1963a. Wing base structure in Lepidoptera. I. Fore wing base. – The Canadian Entomologist **95**: 1024–1050.

Sharplin, J. 1963b. Wing base structure in Lepidoptera. II. Hind wing base. – The Canadian Entomologist **95**: 1121–1145.

Snodgrass, R.E. 1909. The thorax of insects and articulation of wings. – Proceedings of the United States National Museum **36**: 511–595, pls. 40–69.

Snodgrass, R.E. 1935. Principles of Insect Morphology. – McGraw-Hill Book Company Inc., New York. 667 pp.

Tannert, W. 1958. Die Flügelgelenkung bei Odonaten. – Deutsche Entomologische Zeitschrift (N.F.) **5**: 394–455.

Wheeler, W.C., M.F. Whiting, Q.D. Wheeler & J.C. Carpenter 2001. The phylogeny of the extant hexapod orders. – Cladistics **17**: 113–169.

Willkommen, J. & T. Hörnschemeyer 2007: The homology of wing base sclerites and flight muscles in Ephemeroptera an Neoptera and the morphology of the pterothorax of *Habroleptoides confusa* (Insecta: Ephemeroptera: Leptophlebiidae). – Arthropod Structure & Development doi: 10.1016/j.asd.2007.01.003.

Willmann, R. 2003. Phylogenese und System der Insecta. Pp. 1–65 *in*: H.H. Dathe (ed.), Kaestner – Lehrbuch der Speziellen Zoologie I/5: Insecta. – Spektrum Akademischer Verlag, Germany.

Yoshizawa, K. & T. Saigusa 2001. Phylogenetic analysis of paraneopteran orders (Insecta: Neoptera) based on fore wing base structure, with comments on monophyly of Auchenorrhyncha (Hemiptera). – Systematic Entomology **26**: 1–13.